

Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: support for a conservative view of thermal physiology

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Summary. The thermal sensitivity of sprint-running ability was investigated in two populations of *Sceloporus undulatus* that occupy thermally distinct habitats. Integration of field and laboratory data indicates that lizards inhabiting a cool, high-elevation habitat are frequently active at body temperatures that retard sprint-running velocity, which could affect adversely their ability to evade predators and to capture prey. These negative effects might be expected to select for local adaptation of thermal physiology. No differences in thermal physiology (optimal temperature for sprinting, critical thermal limits) were found, however, between lizards from the two habitats.

Preferred body temperature of *Sceloporus undulatus* is lower than the body temperature that maximizes sprint velocity but is still well within an 'optimal performance range' where lizards can run at better than 95% of maximum velocity. Analysis of data from other studies shows a similar concordance of preferred body temperature and temperatures that maximize sprint velocity for some, but not all lizard species studied.

Low diversity of predators and high levels of food may compensate in part for the reduced sprinting ability of high-elevation lizards active at low body temperatures. The lack of population differentiation supports the view that lizard thermal physiology is evolutionarily conservative.

Although lizards have limited physiological means of regulating body temperature, many diurnal lizard species are known to regulate body temperature effectively by using thermoregulatory behaviors (Cowles and Bogert 1944; Heath 1965; Muth 1977; Avery 1982). Behavioral shifts in basking, time of activity, postural changes, and microhabitat selection allow lizards to adjust for small-scale spatial and temporal variation in their thermal environment. Physiological acclimatization, acting more slowly, can supplement regulatory behaviors and extend the range of suitable thermal environments both seasonally and geographically.

Regulatory behaviors and acclimatization both compensate for thermal variation within a habitat. Whether lizard populations or congeneric species occupying thermally distinct environments also compensate by genetic adaptation of thermal physiology is currently unresolved and the subject of considerable discussion (Hertz et al. 1983; Hertz 1983).

Two major positions exist on the extent of lizard thermal physiology adaptation, positions seemingly shaped by the choice of taxa under investigation. Hertz et al. (1983) have labeled these positions the "static" and "labile" views of thermal physiology. The "static" view, traceable to Bogert (1949a), maintains that thermal physiology is evolutionarily conservative and resistant to directional selection. Support for the static view is derived largely from studies of temperate-desert lizards (Bogert 1949b; King 1980; Hertz et al. 1983) but support is also drawn from studies of fish (Brown and Feldmuth 1971; Calhoun et al. 1981) and other ectotherms (Usakov 1964). The labile view contends that closely related species and populations do respond to divergent thermal regimes by adaptation of thermal physiology. Support for the labile view comes from studies of tropical lizards, particularly those in the genus *Anolis* (Ruibal 1961; Ruibal and Philibosian 1970; Hertz et al. 1979).

In the iguanid lizard *Sceloporus undulatus*, populations occupying thermally distinctive habitats may exhibit different thermal-response patterns. Lizards in a high-elevation population in Colorado, for example, are active at significantly lower and more variable body temperatures than lizards in a low-elevation population from New Mexico. The labile view would predict that the Colorado population should show either a shift in thermal performance (and, possibly, preferred body temperature) toward lower temperatures or an increase in thermal performance breadth (Fig. 1A). The static view would predict no differences in thermal physiology or preference between the two populations. Thermal performance curves of the two populations would be expected to coincide (Fig. 1B).

Sprint-running performance can be used as an ecologically meaningful and direct measure of thermal physiology (see Huey and Stevenson 1979 for a discussion of measures of thermal physiological performance). Sprinting data can be obtained over a lizard's entire range of activity temperatures, allowing performance curves to be constructed that can detect possible population differences either in curve breadth or in relative curve position.

To test the alternative predictions of the static and the labile viewpoints, this study examines the thermal-sensitivity of sprint-running performance in two *Sceloporus undulatus* populations occupying thermally distinct habitats. The results of the sprinting performance trials are discussed in relationship to field thermoregulatory behaviors and the relative costs and benefits of thermoregulation in each habitat.

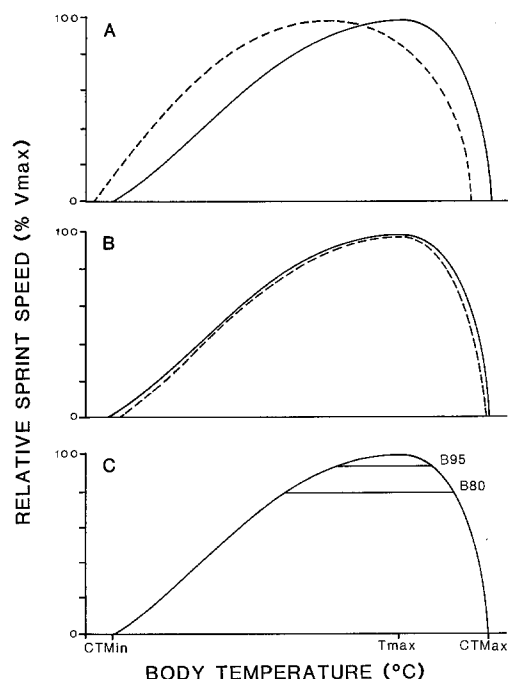


Fig. 1. **A** Pattern of thermal-performance curves predicted by the labile view of thermal physiology evolution. Dashed curve represents the performance of a species (or population) occupying a cool habitat relative to the species represented by the solid curve. **B** Pattern of thermal performance curves predicted by the static view of thermal physiology evolution. Dashed and solid curves represent the thermal performances of two species (or populations) occupying thermally distinct habitats. **C** Typical sprint-running performance curve, showing the end-points of locomotion (CT_{Min} , CT_{Max}), the body temperature at which sprint speed is maximal (T_{max}), and the selected performance intervals ($B80$, $B95$)

Sceloporus undulatus is a small iguanid lizard occupying a diverse array of habitats in the Atlantic States, the Southeast, the Midwest, and the Southwest as far as central Arizona. In the Southwest, *Sceloporus undulatus* is found in semi-arid habitats and is primarily saxicolous, favoring boulder fields and rock faces. Crevices are used as refugia and the lizards rarely venture any distance over open ground. Females tend to be slightly larger than males (maximum snout-vent length, female: 8.1 cm, males 7.4 cm; Smith 1946). The life history of this species has been extensively studied and inter-population variation demonstrated for many of its life history traits (Marion 1970; Tinkle 1972; Tinkle and Ballinger 1972). The occupancy of a diverse array of habitats over a broad geographic range

makes *S. undulatus* a suitable subject for studies of possible variation in thermal physiology.

Materials and methods

I sampled *S. undulatus* at two locations approximately 300 km apart. One site was on the eastern edge of Albuquerque, Bernalillo County, New Mexico at an elevation of 1,750 m. This site is a hillside and wash scattered with large granite boulders. The vegetation is primarily grasses interspersed with *Chrysothamnus* sp. and several species of *Opuntia*. Yearly rainfall averages 19.1 cm (NOAA 1982a). The other site consists of steep fractured basalt cliff faces and a narrow strip of shore-line along the west bank of the Rio Grande River in Conejos County, Colorado, 6 km north of the New Mexico border. This site is between 2,350 m and 2,400 m elevation with a yearly average rainfall of 20.7 cm (NOAA 1982b). Vegetation at the Colorado site is a mixture of grasses and *Juniperus* spp.

The Colorado site is consistently cooler than the New Mexico site (Table 1), being located in a cold air drainage of the Sangre de Cristo Mountains, as well as being higher in both elevation and latitude. *Sceloporus undulatus* activity begins in late February or early March and continues until late October or early November. In Colorado, lizard activity begins in late April and ends by early October.

Field methods

Each location was sampled at least once a month during the activity season at each site from 1980 to 1982. The majority of the samples cover the entire daily activity period. This allowed for the collection of body temperature data from initiation to cessation of activity and guards against summary statistics on body temperatures being biased by time of day. During months of peak activity, sites were sampled over several consecutive days.

Most lizards were captured with nooses, although a few were shot with a 0.22 pistol using "dust-shot" to allow rapid collection. Body temperatures were measured with a Schultheis quick-reading thermometer. Lizards were carefully handled so as to minimize heat exchange while body temperature was taken. Body temperatures were discarded if a lizard was chased for any distance, if there was a delay of more than 30 s between capture and measurement, or if a lizard appeared to have shifted thermal microhabitat prior to capture (e.g., from sun into shade) as a result of my presence.

With each body temperature I also recorded time of

Table 1. Air temperature (°C) at a height of 1 cm (at 1 cm) and substrate temperature (subtemp). Values are mean \pm S.E.

Month	Population							
	Colorado		New Mexico					
	at 1 cm	N	subtemp	N	at 1 cm	N	subtemp	N
May	19.9 \pm 1.3	24	25.6 \pm 1.5	24	24.4 \pm 0.9	33	30.9 \pm 1.1	32
June	24.0 \pm 0.8	70	32.2 \pm 1.0	69	32.1 \pm 1.4	23	38.2 \pm 2.1	20
July	28.7 \pm 0.5	69	34.7 \pm 0.6	65	28.5 \pm 1.2	20	39.0 \pm 1.8	19
August	29.0 \pm 0.8	17	35.2 \pm 1.1	17	32.7 \pm 0.6	31	41.4 \pm 2.0	30
September	22.7 \pm 0.8	11	30.6 \pm 0.8	16	27.8 \pm 0.8	29	35.0 \pm 1.2	31
October	22.2 \pm 0.8	28	28.8 \pm 1.0	28	25.3 \pm 0.9	24	32.9 \pm 1.0	24

Table 2. Summary of logistic-exponential product curve parameters for Colorado and New Mexico *Sceloporus undulatus*. Values are mean \pm S.E. Tmax, B95, B80, CTmax, and CTmin are defined as in the text. TR is the lizards' total tolerance activity range (CTmax-CTmin)

Population	Vmax	N	Tmax	N	B95	N	B80	N	CTmax	N	CTmin	N	TR	N
Colorado	1.62 \pm 0.6	23	40.4 \pm 0.3	23	12.7 \pm 0.8	23	18.9 \pm 0.7	23	43.3 \pm 0.2	16	6.5 \pm 0.3	23	36.6 \pm 0.4	16
New Mexico	1.73 \pm 0.5	17	40.2 \pm 0.3	17	13.7 \pm 1.0	17	19.4 \pm 0.7	17	42.7 \pm 0.3	13	6.3 \pm 0.1	17	36.5 \pm 0.3	13
P-value	>0.1		>0.1		>0.1		>0.1		>0.1		>0.1		>0.1	

day, shaded air temperature 1 cm above the substrate, and substrate temperature. Ambient temperatures were measured either with a Schultheis thermometer or a model 4 Bailey Amplifying Thermometer using a copper/constantan thermocouple. The thermocouple was calibrated to the Schultheis thermometer being used. The accuracy of both the Schultheis thermometer and the thermocouple was checked in an ice-water bath. The majority of the lizards captured were marked and released as part of a related study.

Temperature-sensitivity methods

During the period 2–8 June 1981, 23 lizards were collected in Colorado and 17 in New Mexico for measurement of the temperature-sensitivity of sprint-running ability. These lizards were maintained in an environmental chamber (32° C day, 10° C night; 12L:12D) until 16 June, when they were flown to facilities at the University of Washington, Seattle.

Population samples were as evenly divided as possible as to sex (Colorado 11 males, 12 females; New Mexico 8 males, 9 females) and matched for body size (Colorado mean SVL = 6.2 cm, S.E. = 0.7; New Mexico SVL = 6.1 cm, S.E. = 0.9; $t = 0.846$, $P > 0.1$). Lizards were housed in small plastic terraria during laboratory studies. Food (consisting of crickets dusted with vitamin-mineral powder) and water were provided ad libitum.

Thermal sensitivity of sprint-running ability was determined by methods similar to those of Bennett (1980) and Hertz et al. (1983). Lizards were chased by hand down a 2.4 \times 0.2 m racetrack having a rough rubberized surface that afforded good traction. Sprint velocity was measured by 12 sets of photocells positioned along the racetrack. The photocells were connected to an Apple II computer that provided a printed record of velocity and acceleration (see Huey et al. 1981). Speed was measured to ± 0.001 m/s over 6 consecutive 0.25 m intervals. Lizards were run for several days prior to testing to control for possible training effects and to accustom the lizards to the racetrack (Bennett 1980). Following the training period, lizards were run every other day at one body temperature per day with 3 trials at each temperature, with at least 1 h between trials for each individual. The order of body temperatures used (35° C, 20° C, 25° C, 30° C, 17° C, 38° C, 41°) was randomized with the exception of the 41° C trials, which were run last, as this temperature is close to the heat tolerance limit of this species (see below). Following trials at these temperatures, lizards were rerun at 35° C to check for declines in performance over the testing period. An a priori criterion for elimination from the study was a 20% or greater decline in maximum velocity from the first trials at 35° C. No lizards exceeded this elimination value.

From the three trials at each temperature, I selected the fastest performance (m/s) of each lizard from all 0.25-m racetrack intervals. These values are used as estimates of a lizard's maximum sprinting ability at each body temperature.

To establish the thermal end-points of possible locomotor activity, critical thermal maximum (CTMax) and critical thermal minimum (CTMin) were determined for each lizard. Loss of righting response was used as the indicator of having reached CTMax and CTMin (Spellerberg 1972). Critical thermal limits were determined after completion of all running trials. In each population, several lizards did not exhibit a clear loss of righting response at a single body temperature. For these lizards I used the respective population mean in subsequent calculations (Table 2).

A performance curve (speed as a function of body temperature) was constructed for each lizard using the seven sprint speed values and the critical thermal limits. Curve fitting was performed using the SAS (1982) non-linear regression procedure with the derivative-free Marquardt option. Sprinting data were fit to a "logistic-exponential product" model (Hertz et al. 1983) as below:

$$Y = A1[1/(1 + A2(e^{-A3(T_b - CTMin)})) (1 - e^{A4(T_b - CTMax)})]$$

where Y is predicted speed, T_b is body temperature and A1, A2, A3, and A4 are curve parameters.

As the choice of a curve model was based on empirical rather than theoretical criteria, the curve parameters A1, A2, A3, and A4 have no clear biological meaning and were not used in any statistical tests. The fitted performance curves, however, do allow the calculation of derived statistics of biological relevance. The fit of the data to the model was good; for the majority of the curves $R^2 > 0.90$ and for none was $R^2 < 0.74$.

Seven lizards had sprint speeds at one temperature bounded by higher speeds, showing the capability of better performance at both lower and higher body temperatures. In these cases I followed the a priori criterion of Hertz et al. (1983) in deciding to drop these points prior to curve-fitting. No more than one point was dropped for any lizard.

From each of the 40 individual curves I calculated the predicted maximum speed (Vmax), the body temperature associated with Vmax (Tmax), the range of body temperatures over which a lizard's sprint performance was at least 95% of Vmax (B95), and the range of body temperatures over which performance was at least 80% of Vmax (B80) (see Fig. 1 C). B95 was chosen as representing a temperature interval over which performance does not differ from Vmax to any biologically realistic degree. The temperature interval of B80 encompasses greater than 90% of all field body temperatures I recorded and thus is a useful index in assessing sprinting ability of active individuals under field conditions.

Table 3. Monthly field body temperatures ($^{\circ}\text{C}$) of *Sceloporus undulatus*. Body temperature means of each population were compared using a one-tailed Kolmogorov-Smirnov test; variances were compared using F-tests. Bonferroni-adjusted critical values were used in both cases to maintain the experimentwise error rate at the 0.05 level

	May	N	June	N	July	N	August	N	September	N	October	N
<i>Colorado</i>												
mean \pm S.E.	27.9 \pm 1.3	17	33.1 \pm 0.4	62	35.3 \pm 0.2	80	34.9 \pm 0.2	10	33.6 \pm 0.4	25	31.7 \pm 1.1	19
range	19.8–35.4		21.1–37.4		29.5–38.8		34.0–36.4		30.0–38.0		25.5–36.1	
<i>New Mexico</i>												
mean \pm S.E.	33.5 \pm 0.4	46	35.6 \pm 0.2	59	35.4 \pm 0.3	44	36.8 \pm 0.4	14	36.0 \pm 0.3	17	35.1 \pm 0.4	13
range	28.4–40.8		28.5–38.5		27.0–38.4		34.8–40.0		33.8–38.4		30.4–36.0	
P-value (mean)	<0.5		<0.5		>0.5		>0.5		<0.5		<0.5	
P-value (variance)	<0.5		<0.5		>0.5		>0.5		>0.5		<0.5	

Statistical analysis

Because of significant non-normality and heteroscedasticity, field body temperatures of the two populations were compared using the non-parametric Kolmogorov-Smirnov test; means and standard errors are reported for descriptive purposes (Table 3). As population body temperatures were compared on a month-by-month basis, Bonferroni-adjusted critical values were used to maintain an overall significance level of 0.05 for all comparisons (Harris 1975).

Population values of the curve-derived statistics and critical thermal limits were compared using t-tests. Comparisons of curve-derived statistics were considered as one experiment and Bonferroni adjusted critical values were used for each t-test to maintain an experiment-wide significance level of 0.05.

In the text, all measures of dispersion are one standard error unless otherwise indicated.

Results

Body temperatures of Colorado *S. undulatus* were significantly lower than those in the New Mexico population for most of the active season (Table 3). Only during the warmest months of July and August do body temperatures in Colorado equal those in New Mexico. Body temperature variance shows a similar pattern with the Colorado population having significantly more variable body temperatures in spring, early summer, and fall than lizards in the southern population (Table 3).

The sprint performance curves, however, showed no significant difference between the populations either in position (as expressed by T_{max} , CT_{Min} , or CT_{Max}) or in breadth (as expressed by B95, B80, or activity range) (Table 2). The predicted maximum speed also was not significantly different between the two populations.

All of the sprint performance curves exhibited a broad plateau over which speed remained relatively constant and independent of body temperature. The range of optimal performance, B95, averaged $13.1 \pm 0.7^{\circ}\text{C}$ for the combined populations with a midpoint of 35.0°C . B80 averaged $19.1 \pm 0.5^{\circ}\text{C}$ with a midpoint of 32.6°C .

Below the plateau interval, velocity steadily declined with decreasing body temperature, with all lizards showing marked impairment of coordinated movement at body temperatures less than 17°C .

Maximum velocities were reached at high body tempera-

Table 4. Absolute (m/s) and relative speeds predicted for the mean, lower 5th percentile, and upper 5th percentile of *Sceloporus undulatus* body temperatures of each population. Values are mean \pm S.E. The body temperature of each temperature level is given in parentheses

Population	Body temperature levels		
	lower 5th %	mean	upper 5th %
Absolute speed			
New Mexico	1.64 \pm 0.01 (29.6 $^{\circ}\text{C}$)	1.70 \pm 0.01 (34.6 $^{\circ}\text{C}$)	1.72 \pm 0.01 (39.4 $^{\circ}\text{C}$)
Colorado	1.16 \pm 0.01 (23.0 $^{\circ}\text{C}$)	1.46 \pm 0.02 (33.0 $^{\circ}\text{C}$)	1.55 \pm 0.01 (37.5 $^{\circ}\text{C}$)
Relative speed			
New Mexico	94.5 \pm 1.3	98.5 \pm 1.5	99.9 \pm 0.3
Colorado	70.2 \pm 2.4	88.6 \pm 1.6	95.9 \pm 1.8

tures, higher than virtually all field body temperatures measured. Analysis of the performance curves yielded a value of $40.3 \pm 0.3^{\circ}\text{C}$ for T_{max} (mean for both populations combined; see Table 3). At 41°C all of the lizards showed some reduction in sprint speed relative to their performance at 38°C . The degree of reduction was variable, however, with some individuals showing reductions in speed of only several per cent while others showed losses of more than 50%. While no lizards were run at body temperatures above 41°C , all showed complete immobility (CT_{Max}) before reaching body temperatures of 44°C .

As there was no significant difference in thermal sensitivity of sprint-running between the populations, despite significant differences in field body temperatures, the Colorado lizards must be active at reduced performance levels during some periods of activity. To assess the degree of this impairment, I calculated for each population absolute and relative (% of V_{max}) sprint speeds for each lizard at three body temperatures: the lower 5th percentile of body temperatures, the mean population body temperature, and the upper 5th percentile.

The Colorado lizards were significantly slower at all three temperature levels for both absolute and relative velocities (Table 4). The New Mexico lizards were within their optimal performance range (B95) at the population mean and the upper 5th percentile. Even at the lower 5th percentile, the New Mexico lizards are predicted to be only slightly

outside the optimal performance range. Colorado lizards were within their optimal performance range only at the upper 5th percentile temperature. Colorado individuals active at the lower 5th percentile level are predicted to be able to run at only 70.2% of their maximum performance.

Discussion

The results of this study are consistent with the static view of lizard thermal physiology. The two *Sceloporus undulatus* populations occupy thermally distinct habitats (Table 1) which result in significant population differences in field body temperature levels and variability (Table 2), despite the efficacy of thermoregulatory behaviors.

Body temperatures of Colorado *S. undulatus* are low enough to retard sprint velocities for much of their active season. Performance curves of several individuals predicted sprint velocities well below 70.2%, several as low as 50% of maximum velocity.

Although infrequent, activity at very low body temperatures with consequent severe locomotor impairment has been observed in the field. On 19 June 1982, lizards at the Colorado site maintained activity during and subsequent to an afternoon thunderstorm, continuing to feed even while addressed to wet rock surfaces. I caught several lizards by hand, recording body temperatures as low as 21.5° C. These lizards showed a loss of limb coordination, undulating clumsily from side-to-side while attempting to evade capture.

Impairment of locomotor performance might be expected to contribute to strong directional selection in *S. undulatus* populations. Greenwald (1974) showed a positive dependence of gopher snake (*Pituophis melanoleucus*) prey capture success upon the snake's body temperature and strike velocity. Avery et al. (1982) demonstrated that low body temperatures reduce *Lacerta vivipara* foraging speed and ability to capture and consume prey, particularly large prey items. Low body temperatures could also have serious consequences for avoiding predation. Christian and Tracy (1981) found that hawks were more successful in preying upon land iguanas (*Conolophus pallidus*) when the iguanas' sprinting ability was reduced by low body temperatures. Low body temperatures also have been suggested to affect predator evasion in fish (Webb 1976) and frogs (Hirano and Rome 1984) adversely.

Despite the impairment of sprint capacity of Colorado *S. undulatus* at low body temperatures and the presumed adverse consequences, I found no differences between the sprint performance curves of Colorado and New Mexico lizards. High-elevation Colorado lizards accept and are active at body temperatures that reduce their sprinting ability.

Several factors may mitigate the presumed negative consequences of locomotor impairment. Due to the proximity of the Rio Grande River, food (in the form of flying insects) is in great abundance at the Colorado site. Through the lizards' activity season, insect densities are 3–10 times higher at the Colorado site than at the New Mexico site (Crowley, unpublished data). High levels of prey availability may allow for successful foraging despite low body temperatures. Predator evasion may also be less of a problem than the reduced running ability alone might suggest. High-elevation and high-latitude lizard populations often have higher survivorship than populations at lower elevations or latitudes (Tinkle 1969; Tinkle and Ballinger 1972; Turner

1977; Ferguson et al. 1980). This enhanced survivorship has been attributed in part to reduced predator pressure and diversity at high elevations and latitudes (Pianka 1970; Ballinger 1979; Schall and Pianka 1980). The observed number of potential predators upon *Sceloporus undulatus* is larger in New Mexico (*Crotalus molossus*, *Crotalus viridis*, *Crotaphytus collaris*, *Falco sparverius*, *Geococcyx californianus*, *Lanius ludovicianus*, *Masticophis flagellum*, *Masticophis taeniatus*) than in Colorado (*Crotalus viridis*, *Falco sparverius*, *Thamnophis elegans*).

In particular, roadrunners (*Geococcyx californianus*) and racers (*Masticophis flagellum*, *Masticophis taeniatus*), species well known for lizard predation, are present on the New Mexico site. I have frequently observed roadrunners stalking and consuming *S. undulatus* on the New Mexico plot. Although highly inferential, population differences in lizard wariness also suggest differential predation pressure. Even when cold, Colorado individuals tolerate humans approaching closely and can be noosed repeatedly with only slightly increased wariness. On the New Mexico site, lizards flee at greater approach distances and become extremely wary after having been noosed once (pers. obs.). Low predation pressure may reduce the selection pressure against impaired sprinting capacity of Colorado lizards.

The results of this study, while supporting the static position on thermal physiology, do not resolve the general question of how closely natural selection can shape thermal physiology to fit local thermal regimes. To date, studies of lizard sprinting capacity, on representatives of five families (Bennett 1980; Hertz et al. 1983; Crowley and Pietruszka 1983) have all demonstrated body temperature intervals over which sprinting is relatively independent of body temperature. Hertz et al. (1983) suggest that an ability to run quickly over a broad range of body temperature may contribute more to an ectotherm's fitness than an ability to run very quickly over a narrower range of body temperatures (but see also Huey and Hertz 1983). If selection does favor thermal insensitivity rather than specialization, then sprint capacity may not be the most suitable thermal performance model for detecting thermal physiology variation. Moreover, the ecological relevance of maintaining a high sprinting capacity may vary in importance for different species. Maintenance of body temperatures compatible with rapid sprinting may be constrained either by other physiological systems with conflicting thermal optima or by excessive ecological costs associated with thermoregulation (Huey and Slatkin 1976).

If rapid running ability is a major factor in determining a species thermoregulatory behavior, a concordance of preferred body temperature (PBT) and the body temperature at which sprint velocity is maximal (Tmax) might be expected. The PBT of *Sceloporus undulatus* (35.2° C, S.E. = 0.14, $N=192$; Crowley, unpublished data) is about 5° C lower than its Tmax (mean = 40.3° C, S.E. = 0.3° C, $N=40$). At 35° C, however, the average reduction in sprint velocity from maximum velocity would be only 3%, leaving sprint capacity well within the 95% optimal performance interval (B95).

When sprinting data from Bennett (1980) are fitted to a logistic-exponential product curve, a similar concordance of PBT (data from Brattstrom 1965; Bennett 1980; Crowley, unpublished data) and Tmax exists for the thermophilic species *Dipsosaurus dorsalis*, *Uma inornata*, *Cnemidophorus murinus* (average field active temperature was used for this

Table 5. Sprint running statistics for 7 lizard species. Values are mean and (when available) standard error. See text for details

Species	N	Tmax (°C)	95% performance range (°C)	PBT (°C)	PBT source
<i>Dipsosaurus dorsalis</i> ^a	20	45.8	38.5–47.0	38.8	Licht 1964a, cited in Dawson 1967
<i>Uma inornata</i> ^a	11	43.0	33.5–43.5	37.0	Brattstrom 1965
<i>Cnemidophorus murinus</i> ^a	14	43.0	31.0–45.0	40.4 ^d	Bennett and Gorman 1979
<i>Sceloporus occidentalis</i> ^a	14	41.4	30.6–42.4	35.0	Brattstrom 1965
<i>Elgaria multicarinatus</i> ^a	12	38.8	32.1–39.7	26.2	Bennett 1980
<i>Anolis cristatellus</i> ^b	6	29.5 ± 0.85	25.5–32.0	29.6 ± 0.59	Huey 1983
<i>Sceloporus undulatus</i> ^c	40	40.3 ± 0.3	28.3 ± 0.7–41.5 ± 0.2	35.2 ± 0.14	Crowley, unpublished data

^a Tmax and 95% performance range calculated from average sprint speeds from Bennett (1980)

^b Tmax (Huey's "optimal T_b ") given in Huey (1983). Performance range estimated from Fig. 2 of Huey (1983)

^c Data from this study

^d Average of active field body temperatures

species since PBT data were unavailable), and *Sceloporus occidentalis* (July animals). Tmax was higher than PBT for all of these species but, as with *S. undulatus*, at PBT each species would still be within its 95% performance level (Table 5). For thermophilic species, maintaining a body temperature several degrees below Tmax could be beneficial in reducing water loss rates and metabolic costs with only minor sprint capacity impairment.

In *Anolis cristatellus*, a species with a relatively low thermal preference, PBT and Tmax are virtually identical (Huey 1983, see Table 5). This is not the case, however, with *Elgaria* (= *Gerrhonotus*) *multicarinatus*, which also has a low thermal preference. In a thermal gradient *E. multicarinatus* select a body temperature of 26.2° C (Bennett 1980), a value somewhat higher than the average reported for field active individuals (24.3° C, Brattstrom 1965). Sprint performance data (Bennett 1980) indicate that maximum velocity is reached at 38.8° C, a body temperature far higher than any voluntary temperature reported for this species. At 26.2° C, *E. multicarinatus* is predicted to run at only 79% of maximum velocity; at the lowest reported field active temperature (11° C, Brattstrom 1965) it is predicted to run at only 19% of maximum velocity. A number of Australian skinks show a similar pattern of activity at body temperatures well below those at which sprint velocity is maximized (R.B. Huey, personal communication).

An interpretation of this variation in the degree of concordance between PBT and Tmax is difficult given the small number of species for which data are available. The lack of PBT and Tmax concordance for some species does suggest caution in using sprint performance data in isolation from field temperature data, particularly when comparing species that differ greatly in ecology or in precision of thermoregulation.

Resolution of the general question of whether lizard thermal physiology is static or labile will require accumulation of data on species with diverse ecologies and habitat associations, using an array of relevant physiological performance measures. In all cases, a coupling of laboratory experiments with field studies will be required to understand how thermal physiology responds to environmental variation.

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