HOMAGE TO SANTA ANITA: THERMAL SENSITIVITY OF SPRINT SPEED IN AGAMID LIZARDS

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Ectotherms can compensate for geographical and temporal changes in the thermal environment in several ways: by behavioral regulation, by physiological acclimatization, and by genetic differentiation among populations. Most lizards (Bogert, 1949; Huey, 1982*a*) compensate by using fast-acting behavioral shifts (e.g., changes in time of activity and in basking activity), and many species also show supplementary (and slower) acclimatory responses (Corn, 1971; Spellerberg, 1972; Hertz, 1981). Whether closely related lizards living in thermally distinctive environments also show genetic adaptation in thermal physiology (Hertz et al., 1979) has frequently been debated—often in the pages of this journal. Two competing views have emerged over the last three decades.

(i) The "static" view, based largely on studies of desert lizards (Bogert, 1949; see also Ushakov, 1964; Brown and Feldmeth, 1971; Hutchison, 1976), emphasizes that thermal physiology is evolutionarily conservative and thus relatively insensitive to directional selection. This view is derived from the empirical generalization that aspects of thermal physiology of lizards typically show little differentiation within or among closely related taxa from climatically distinctive habitats. Because these taxa effectively adjust their thermoregulatory behaviors to local environmental conditions, geographic variation in body temperatures during activity—and

presumably in physiological performance—is minimal. C. M. Bogert (1949) developed this view and suggested that "thermal preferences" (his term for field activity temperatures), which are often correlated with physiologically optimal temperatures (Dawson, 1975), are ". . . fixed by heredity . . . at the species level and . . . that closely related species have similar . . . body temperature preferences" (Bogert, 1949 p. 203).

(ii) The "labile" view, based largely on recent studies of tropical iguanid lizards (Huey, 1982*a*), argues that thermal physiology does respond readily to directional selection in some taxa (see also Moore, 1939; Hutchison, 1976; Sopina, 1976; Miller and Packard, 1977; Hirshfield et al., 1980). In the tropical iguanid genus *Anolis,* mean activity temperature in nature and preferred body temperatures in laboratory thermal gradients (Ruibal, 1960; Rand, 1964*a*; Corn, 1971; Clark and Kroll, 1974; Huey and Webster, 1976), the range of activity temperatures (Ruibal and Philibosian, 1970; Huey and Webster, 1975; Lister, 1976; Hertz, 1982), and Critical Thermal Maxima (Hertz, 1979) often differ markedly among closely related species and vary in concert with environmental temperatures.

In this paper we examine evolutionary lability in the thermal physiology of two species of agamid lizards that differ in thermal biology in nature. In a background field study in Israel (Hertz and

TABLE 1. *Sample sizes (N), field active body temperatures (°C), air temperatures (°C) where lizards were, Critical Thermal Minima (CTMin, °C), and Critical Thermal Maxima (CTMax, °C) for five agamid lizard populations sampled in early summer. Data from Hertz and Nevo (1981). Superscripts identify values that were not significantly different (ANOVA, S-N-K tests for means, Bartlett's tests for variances).*

| | Field data | | | | Critical temperatures | | |
| | Body temp | | | Air temp | | CTMin | CTMax |
Population	N	$\bar{x}$	s^2	Range	$\bar{x} \pm SE$	N	$\bar{x} \pm SE$	$\bar{x} \pm SE$
A. savignyi								
330 m	57	37.9	3.2[b]	34.4–42.6	33.7 ± 0.3	8	12.0 ± 0.1[d]	47.2 ± 0.2
S. stellio								
170 m	35	36.0	3.2[b]	31.6–38.6	30.0 ± 0.6	5	11.5 ± 0.4[d]	44.6 ± 0.3[e]
530 m	54	34.4[a]	2.0[b]	30.2–37.4	28.0 ± 0.4[c]	8	12.6 ± 0.2[d]	45.0 ± 0.3[e]
920 m	37	34.1[a]	11.8	24.4–38.6	29.6 ± 0.5	15	12.5 ± 0.3[d]	45.0 ± 0.1[e]
1,500 m	35	32.9	15.4	23.4–39.2	27.2 ± 0.4[c]	10	11.9 ± 0.2[d]	44.7 ± 0.2[e]

Nevo, 1981; relevant results summarized here in Table 1), geographic and interspecific variations in thermoregulatory behaviors and body temperatures were documented for two closely related genera (Moody, 1980), *Agama* and *Stellio*. In the Middle East, species in the genus *Agama* occupy hot desert habitats, whereas *Stellio stellio* generally occurs in cooler habitats. Mean activity temperatures and Critical Thermal Maxima reflect this distributional pattern and are higher in *Agama* than in *Stellio*. Among four populations of *Stellio* distributed along an elevational transect, mean activity temperature varies inversely with altitude; moreover, the variance in body temperature is notably larger in populations from high elevations.

Based upon the results of this field study, the static and labile views lead one to make different predictions about geographic and interspecific variation in the thermal physiology of *Agama* and *Stellio*. According to the static view, "optimal" temperatures and the thermal sensitivity (i.e., the degree of thermal specialization) of physiological functions should differ minimally among populations and only slightly among species. According to the labile view, "optimal" temperatures should be higher in *Agama* than in *Stellio*; moreover, physiological responses in *Stellio* should be relatively insensitive to temperature (i.e., more eurythermal) in high altitude populations, which had high variance in field body temperatures (see Hirshfield et al., 1980).

Here we evaluate the accuracy of these sets of competing predictions. Our data include experimentally determined estimates of optimal temperatures and thermal performance breadths for sprint speed (Fig. 1). We demonstrate evolutionary conservatism in the thermal sensitivity of sprint speed in these species even though high-altitude *Stellio* are sometimes active at body temperatures that are low enough to hamper locomotor capacity.

Our study of the evolution of thermal capacity in lizards represents a conceptual and technical refinement over previous approaches that have relied upon thermal tolerance limits or behavioral data (preferred temperatures) as physiological indicators. Sprint speed is an integrated aspect of behavioral and physiological capacity that has obvious ecological importance (Elliott et al., 1977; Huey and Stevenson, 1979; Bennett, 1980; Christian and Tracy, 1981). Optimal temperatures and thermal performance breadth for sprint speed are ecologically interpretable parameters (Huey and Stevenson, 1979). In contrast, critical temperatures may have only limited ecological relevance on a daily basis because body temperatures of active reptiles rarely approach such extreme levels in nature (contrast field T_b and critical temperatures in Table 1; see also Bog-
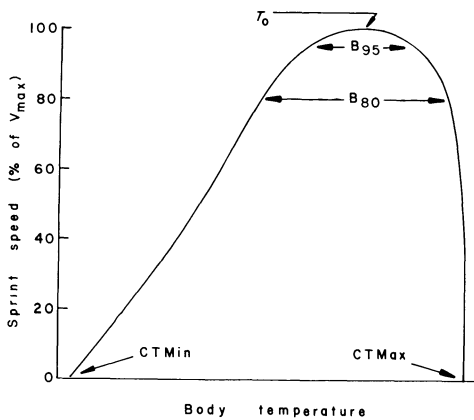
FIG. 1. Schematic diagram illustrating the variables used to analyze the thermal sensitivity of sprint speed. Optimal temperature is defined as the temperature (T_o) at which maximum speed was achieved. The optimal temperature range and the thermal performance breadth (Huey and Stevenson, 1979) are defined as the range of body temperature over which the lizard can run at 95% (B_{95}) or at 80% (B_{80}), respectively, of its V_{max} or faster. CTMin and CTMax are the Critical Thermal Minimum and Maximum, respectively.

ert, 1949; Feder, 1978; Huey and Stevenson, 1979; Huey, 1982a; for a different perspective, see Fry, 1971; Ushakov and Bugayeva, 1975; Hutchison and Maness, 1979); and preferred temperatures in laboratory gradients are at best only indirect, behavioral indices of physiological performance (Dawson, 1975; Huey, 1982a).

MATERIALS AND METHODS

We collected lizards in late June and early July 1980 at five sites in Israel where field studies had been conducted (map in Hertz and Nevo, 1981). *Agama savignyi* were captured near Wadi Sekher, 20 km S of Be'er Sheva (330 m elev.). A sample of *S. stellio brachydactyla* was obtained near Avedat in the central Negev (530 m elev.). Populations of *S. stellio* ssp. (Hoofien, 1972) were sampled at three localities separated by a maximum distance of 11 km along an altitudinal transect in the Golan of northeastern Israel (approximately 270 km N of Avedat and Wadi Sekher): Giv'at Em (170 m elev.) in the foothills east of the Hula Valley; Berekhat Ram

(920 m elev.); and near the ski lift on Mount Hermon (1,500 m elev.). Animals were shipped by air to a laboratory in Seattle where they were acclimated for 10 days at 12:12 L:D and 34 C:26 C, a cycling thermal regime that approximated average conditions (Hertz and Nevo, 1981) experienced by these lizards in nature (see Dawson, 1975; Hutchison, 1976; Huey, 1982a). Food and water were available ad libitum. *Agama savignyi* is substantially smaller than *Stellio* (Table 2; Kruskal-Wallis ANOVA, $\chi^2 = 14.128$, $P = .007$); lizards in our four samples of *Stellio* did not differ significantly in mass (Table 2; Kruskal-Wallis ANOVA, $\chi^2 = 1.869$, $P = .600$).

To determine the thermal sensitivity of sprint speed, we chased lizards down a $2.0 \times .2$ m section of a racetrack with a rough, rubberized substrate that provided excellent traction. The apparatus and methods are detailed in Huey et al. (1981) and Huey (1982b). After being trained for several days (Bennett, 1980), lizards were run every other day (one temperature per day, six trials/lizard/temperature, 1 trial/h) at the following random sequence of body temperatures (C): 30, 26, 38, 34, 18, 42, and 22. They were subsequently rerun at 30 C to determine whether captivity and the experimental regime had impaired performance; if either mass or maximum speed at 30 C had declined by more than 20%, a lizard was eliminated from the analysis. Nine of 64 animals were so eliminated. The following numbers (total = 55) of animals (adult males, adult females, juveniles) remained in the study after the application of these a priori criteria: 10 *A. savignyi* (8, 2, 0); 11 *Stellio* from 170 m (7, 4, 0); 10 *Stellio* from 530 m (4, 6, 0); 15 *Stellio* from 920 m (7, 4, 4); and nine *Stellio* from 1,500 m (2, 7, 0).

For each of the seven temperature levels, we calculated the maximum speed (m/s) of each lizard (among all six trials) over all .5 m sections of the racetrack. We also determined the Critical Thermal Minima and Maxima (loss of righting response; see Hertz and Nevo, 1981), which serve as estimators of the upper and lower temperatures for which any locomotion is pos-

sible. We then used the seven maximum speeds with the population means for Critical Thermal Minima and Maxima (each critical temperature weighted three times) to construct individual profiles of the thermal sensitivity of sprint speed for each lizard. Population means were used because critical temperatures were measured only on a subsample of lizards (Hertz and Nevo, 1981). In any case the standard deviations of critical temperatures were small (average among samples = .74 for CTMin, .69 for CTMax).

To estimate sprint speed as a function of body temperature, we fitted two curves to the data for each lizard using Marquardt's algorithm (SPSS): (1) a "double exponential" (Huey and Stevenson, 1979),

$$V = S(1 - e^{-k_1(T_b - \text{CTMin})})$$
$$\cdot (1 - e^{k_2(T_b - \text{CTMax})}) \qquad (1)$$

and (2) a "logistic-exponential" (R. D. Stevenson, pers. comm.),

$$V = S/(1 + k_1(e^{-k_2(T_b - \text{CTMin})})$$
$$\cdot (1 - e^{k_3(T_b - \text{CTMax})})). \qquad (2)$$

In both equations, V = sprint speed (m/s), S = a scaling factor, and k_1, k_2, and k_3 are fitted parameters. Sample curves illustrating fits to these models are presented in Figure 2; the two curves differ in shape only at low body temperatures. Because no underlying theoretical relationship exists for the thermal sensitivity of sprint speed, we selected the model with the smaller sum of squares (for each lizard) for analysis. Neither the proportions of lizards assigned to the models ($\chi^2 = 5.935$, $P = .204$) nor the goodness of fit of the curves (Kruskal-Wallis ANOVA, $\chi^2 = 2.596$, $P = .628$) differed among populations (Table 2).

For several lizards, speed at one body temperature was clearly inconsistent with the general profile of the thermal sensitivity of sprint speed (i.e., the speed was bounded by much higher speeds at adjacent temperatures). We eliminated a low speed before fitting a final curve if the inclusion of that point generated an initial curve for which the predicted maximum speed (V_{max}) was less than 90% of the liz-
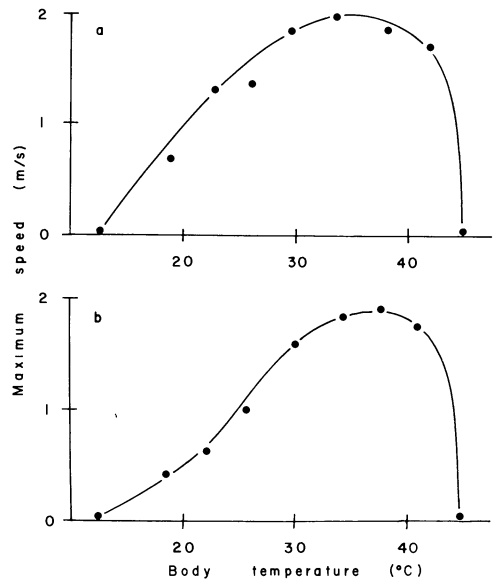

FIG. 2. Examples of the two types of curves fitted to data on sprint speed as a function of body temperature (two different lizards represented). (a) double exponential. (b) logistic-exponential. Sum of squares = .077 for double exponential, = .035 for logistic-exponential.

ard's observed maximum speed. Using this a priori criterion, we dropped one low point for each of three lizards.

To characterize the thermal sensitivity of sprint speed of individuals, we derived the following statistics from the fitted curve for each lizard (see Fig. 1): predicted maximum speed (V_{max}), the body temperature at which V_{max} is achieved (T_o), the 95% performance breadth (B_{95}, the range of body temperatures over which a lizard can run at 95% of its V_{max} or faster), and, similarly, the 80% performance breadth (B_{80}). In contrast to the fitted parameters (for example, k_1, k_2) in equations (1) and (2), these derived statistics have obvious relevance to ecology (Huey and Stevenson, 1979). T_o is an estimator of the "optimal" temperature, B_{95} is an estimator of the breadth of the optimal temperature range, and B_{80} is an estimator of the thermal performance breadth for sprint speed (Fig. 1). We chose the 80% performance breadth because the lower bound of this range most closely corresponded to the lowest body

TABLE 2. *Mass (g, x̄ ± SE), number of animals fitted to logistic-exponential curve, number of animals fitted to double exponential curve, and sum of squares (x̄ ± SE) for curves fitted to data on thermal sensitivity of sprint speed in five populations of agamid lizards.*

Population		Mass	Log-expo	Expo-expo	Sum of squares
A. savignyi	330 m	22.0 ± 1.8	5	5	.191 ± .038
S. stellio	170 m	40.1 ± 5.3	6	5	.186 ± .047
S. stellio	530 m	55.1 ± 8.3	4	6	.546 ± .367
S. stellio	920 m	41.1 ± 4.6	3	12	.155 ± .029
S. stellio	1,500 m	41.9 ± 4.3	5	4	.127 ± .032

temperature recorded during the field study (Hertz and Nevo, 1981). A lower performance breadth (e.g., B_{50}) would thus be ecologically unrealistic.

RESULTS

Maximum speeds of lizards were very low at low body temperatures (Fig. 2). Speed increased with body temperature and then reached a broad plateau over which speed was essentially independent of temperature (Fig. 2, see also Bennett, 1980; Huey, 1982*b*). The mean optimal temperature range (B_{95}, Fig. 1) was large, averaging 8.4 ± .3 C among populations (Table 3). Sprint speed dropped precipitously at temperatures above this range (Fig. 2).

Selection that results in geographic and interspecific variation in thermal physiology operates only if variations in body temperature of these populations are of sufficient magnitude to hamper physiological performance (Huey, 1982*b*). We therefore combined laboratory data on the effects of temperature on sprint speed (e.g., Fig. 2) with field data on activity temperatures of these lizards (Table 1) to identify

such selective pressures, assuming that acclimatization did not confound this association.

We first calculated average relative sprint speed of lizards from each population at three temperatures: the lowest activity temperature, the average activity temperature, and the highest activity temperature observed in nature. Relative sprint speed varied significantly among populations at each of the three temperatures (Table 4); the variation is most marked at the lowest observed activity temperature. High elevation *Stellio,* which are sometimes active at low body temperatures (Table 1), apparently accept activity at lower performance levels than do their lowland counterparts (correlation between performance level at lowest observed T_b and altitude, $r_s = -1.000$, $P <$ .01). *Agama savignyi,* which are sometimes active at high body temperatures (Table 1) also apparently accept activity at suboptimal performance levels (Table 4).

Absolute speeds of *Stellio* also decline with altitude (Table 4). Average absolute speeds, both at the lowest observed body

TABLE 3. *Predicted maximum velocity (V_{max}), optimal temperature (T_o), optimal temperature range (B_{95}), and thermal performance breadth (B_{80}) for sprint speed in five populations of agamid lizards. All values are x̄ ± SE; ANOVA results in footnotes.*

Population		V_{max}[a]	T_o[b]	B_{95}[c]	B_{80}[d]
A. savignyi	330 m	2.7 ± 0.2	38.4 ± 1.6	8.9 ± 1.0	15.7 ± 1.1
S. stellio	170 m	2.7 ± 0.2	38.8 ± 1.0	8.4 ± 0.1	14.6 ± 1.0
S. stellio	530 m	2.4 ± 0.2	40.6 ± 1.3	9.0 ± 1.3	15.7 ± 0.9
S. stellio	920 m	2.5 ± 0.1	39.9 ± 0.9	7.6 ± 0.7	15.0 ± 0.7
S. stellio	1,500 m	2.3 ± 0.3	37.0 ± 1.2	8.1 ± 1.2	14.5 ± 1.0

[a] $F = .784$, $P = 541$, [b] $F = 1 259$, $P = .298$, [c] $F = .353$, $P = 841$, [d] $F = .371$, $P = 828$.

TABLE 4. *Predicted relative sprint speed (average percentage of* V_{max} $\pm$ *SE) and predicted absolute speed* ($\bar{x}$ $\pm$ *SE, M/S) for five agamid lizard populations at three body temperature levels: lowest, mean, and highest activity temperature observed in each population. See text for explanation.*

Population		Lowest temp	Mean temp	Highest temp
Relative speed[a]				
A. savignyi	330 m	97.2 ± 1.0	98.2 ± .5	84.1 ± 3.8
S. stellio	170 m	90.5 ± 2.5	98.4 ± .6	98.6 ± .5
S. stellio	530 m	88.4 ± 2.0	96.2 ± 1.4	98.6 ± .8
S. stellio	920 m	66.0 ± 2.5	94.1 ± .8	97.1 ± 1.3
S. stellio	1,500 m	63.2 ± 5.6	92.7 ± 2.0	96.3 ± 2.3
Absolute speed[b]				
A. savignyi	330 m	2.62 ± .15	2.64 ± .16	2.25 ± .15
S. stellio	170 m	2.45 ± .19	2.68 ± .22	2.70 ± .24
S. stellio	530 m	2.12 ± .22	2.32 ± .25	2.37 ± .25
S. stellio	920 m	1.66 ± .11	2.37 ± .14	2.46 ± .13
S. stellio	1,500 m	1.39 ± .15	2.01 ± .21	2.22 ± .28

[a] Kruskal-Wallis ANOVAs among populations: all P's < .001.
[b] One-way ANOVAs among populations: lowest temperature, P < .001; mean temperature, P > 100; highest temperature, P > .500

temperature and at the mean body temperature (r_s's = -1.000, P's < .05), are negatively correlated with altitude. Absolute speeds at the highest observed body temperature were not significantly correlated with altitude (r_s = $-.300$, P > .05).

Our analysis demonstrates that high-altitude lizards are sometimes active at low body temperatures that should hinder sprint capacity. In the absence of compensatory behaviors (Rand, 1964b), reduced sprint capacity should negatively influence the ability of high-altitude lizards to capture food or to escape predators, thereby providing a selective pressure for local adaptation of thermal physiology.

Despite this apparent selective pressure for local adaptation we were unable to demonstrate any geographic or interspecific variation in the thermal sensitivity of sprint speed. None of the four descriptive variables examined (V_{max}, T_o, B_{95}, and B_{80}) differed either among the five populations or among *Stellio* samples (Table 3). Optimal temperature for sprint speed (T_o) was not rank-correlated with mean activity temperature among populations (r_s = $-.248$, P > .05). Moreover, neither the optimal temperature range (B_{95}) nor the thermal performance breadth (B_{80}) was significantly rank-correlated with variance in field activity temperatures (Table 1) among populations, and the trends were

in the opposite direction from those predicted (r_s = $-.782$ and $-.632$, respectively, P's > .05). Our results on geographic and interspecific variation in the thermal sensitivity of sprint speed are thus consistent with the static view of the evolution of thermal physiology.

Body size did not affect the thermal sensitivity of sprint speed: size was not significantly correlated with T_o, B_{95}, or B_{80} either within populations (Spearman rank correlations, all P's > .05) or in combined samples (Fisher's combined probability tests, all P's > .05). Nevertheless, body size was positively correlated with V_{max} in two samples of *Stellio* and among all five samples (Fisher's combined probability tests, χ^2 = 22.068, P < .025; see Huey and Hertz, 1982).

DISCUSSION

Two opposing views postulate that the thermal sensitivity of physiology in lizards and other organisms is evolutionarily inert or is potentially evolutionarily labile. Our data on geographic and interspecific variation in thermal sensitivity of sprint speed in agamid lizards support the former view (Bogert, 1949). We have developed this assertion by demonstrating that the body temperatures of these agamids during activity vary geographically (despite thermoregulatory adjustments of the lizards),

that the resultant variation in body temperatures appears to be of sufficient magnitude to hinder the sprint performance of lizards living at the extremes of a natural thermal gradient, but that the thermal sensitivity of locomotor performance is invariant among populations.

Thermal environments change dramatically with altitude (McCullough and Porter, 1971). In response, many lizards (Hertz and Huey, 1981)—including the agamids presently under consideration (Hertz and Nevo, 1981)—show striking altitudinal variation in their use of thermoregulatory behaviors. For example, lizards living in cold, montane localities bask more frequently and have shorter daily activity periods than do lizards living in more moderate environments; and lizards living in very hot, lowland localities typically avoid sunlit perches and sometimes curtail activity at midday.

Altitudinal and geographical changes in thermoregulatory behaviors reduce the impact of local thermal conditions on both the body temperatures and the physiological performance of agamid lizards (Hertz and Nevo, 1981); however, the behavioral adjustments do not eliminate that impact entirely. Indeed, lizards living at the extremes of the altitudinal transect are periodically active at body temperatures (Table 1) that are suboptimal, at least with reference to sprint ability (Table 4). For example, some high-altitude *Stellio* are active at low body temperatures that may reduce sprint speeds to 65% of V_{max}, and low-altitude *A. savignyi* are sometimes active at high body temperatures that may reduce speeds to 85% of V_{max}.

Impaired sprint ability could have important negative consequences for the ecology and behavior of these animals. Webb (1976) shows that the risk of being injured or captured by predators might increase. Christian and Tracy (1981) demonstrate that the rate of predation by hawks on juvenile land iguanas (*Conolophus pallidus*) in the Galapagos is inversely related to body temperature and to sprint speed of the iguana. Moreover, impaired sprint ability could also decrease a lizard's rate of prey capture. Greenwald (1974) demonstrates that the success and speed of captive gopher snakes (*Pituophis melanoleucus*) striking at mice are positively related to the temperature of the snake.

The apparent reduction in sprint ability experienced by some lizards (Table 4) should provide a selective pressure for compensatory shifts in the thermal sensitivity of sprint locomotion. Nevertheless, thermal profiles show remarkably little variation among populations of *Stellio* or between *Stellio* and *Agama savignyi*. We found no significant differences in estimates of optimal temperatures (T_o, Table 3) among populations, even though mean field activity temperatures vary geographically (Table 1). Similarly, we found no differences in the optimal temperature range (B_{95}, Table 3), even though variance in activity temperatures varies geographically (Table 1). Indeed, the only known physiological difference between *Stellio* and *Agama* is in Critical Thermal Maximum (Table 1).

The thermal physiology of these agamid lizards shows very limited geographic variation, thus supporting the static view of thermal physiology for these lizards. This does not necessarily imply that thermal physiology is always evolutionarily inert. We can think of several reasons why the presumed selective pressure on these agamids might be lower than we have assumed.

(*i*) In contrast to some physiological functions (Dawson, 1975), sprint capacity of all lizards examined to date (including representatives from five families) is generalized with respect to temperature (Bennett, 1980; Huey, 1982*b*; data herein). In our data on agamids, the optimal temperature range (B_{95}, Table 3) is, in fact, actually greater than the range of activity temperatures observed in three of five populations (Table 1). Thus, most of these lizards are never active at body temperatures that would reduce sprint capacity by even 5%, at least during summer. These broad optimal temperature ranges may re-

flect selection for thermal insensitivity (Soulé, 1963; Huey and Slatkin, 1976; Tracy, 1978) of this important whole-animal activity (Bennett, 1980; Huey, 1982b). In other words, the ability to run quickly (to evade predators, capture prey, or interact with conspecifics) over a wide range of temperatures (Webb, 1976; Elliott et al., 1977; Christian and Tracy, 1981; Huey, 1982a) may make a greater contribution to fitness of many ectotherms than the ability to run very quickly over a narrow range of temperatures.

The above patterns challenge the widespread belief that selection inevitably favors the evolution of local thermal specialization (but see Soulé, 1963; Huey and Slatkin, 1976; Tracy, 1978; Bennett, 1980). Given this general pattern, the lack of geographic variation in sprint capacity is perhaps not surprising.

(ii) Moreover, the probable locomotor handicaps induced by activity at extremely low or high body temperatures may not be of great ecological significance to these lizards. During early summer high-altitude Stellio are active at low body temperatures for only one-and-a-half to two hours in the morning (Fig. 2 in Hertz and Nevo, 1981). Consequently, the duration of vulnerability to predators is short, and the saxicolous habit of these agamids (Barash and Hoofien, 1956; Hertz and Nevo, 1981) provides them with ready access to refugia. Potentially, these lizards may also behaviorally compensate for impaired sprint speed by increased wariness (Rand, 1964b) or by qualitative changes in defensive behavior (Hertz et al., 1982).

(iii) Acclimatization of locomotor performance, not studied in the present experiments (or in any experiments on lizards to date), to local thermal conditions might provide some compensation for impaired sprint performance.

Resolution of the extent to which thermal physiology is evolutionarily conservative in Middle Eastern agamids—or in any other species showing limited geographic variation in thermal physiology—is presently elusive. Information on the thermal sensitivity of physiological processes in the laboratory (Table 3) will readily detect groups for which physiology is evolutionarily labile (e.g., Anolis, see Introduction). Nevertheless, for groups showing little geographic variation, such evidence alone is inadequate as a demonstration of evolutionary inertia: laboratory evidence alone does not directly address the fundamental issue of whether the animals actually experience selective pressures promoting evolutionary shifts in thermal sensitivity. Demonstration of evolutionary inertia will require additional data: that selective pressures are important and operative in nature (e.g., from data such as those of Christian and Tracy, 1981, for lizards living at different altitudes) and that acclimatization does not provide complete compensation for altitude. Moreover, some groups may show little variation in thermal physiology—not because physiology is evolutionarily inert, but because of the homogenizing effects of gene flow (Endler, 1977; Miller and Packard, 1977).

SUMMARY

The evolution of thermal sensitivity of sprint speed was examined in five samples of two species of agamid lizards, Agama savignyi and Stellio stellio, from Israel.

Integration of results from field and laboratory studies indicates that Stellio at high elevations and Agama savignyi at low elevations are sometimes active at body temperatures that result in suboptimal sprint performance. Impaired sprint performance could reduce predation success and increase the risk of being captured by predators, thereby fostering selection for local adaptation of thermal physiology. Despite these expectations, we found no variation in the thermal sensitivity of sprint speed among five populations.

Experimentally determined optimal temperatures (i.e., the body temperatures at which lizards run fastest) and thermal performance breadths (i.e., the range of temperatures over which lizards perform well) for sprint speed do not differ among

samples even though field activity temperatures vary interspecifically and along an altitudinal gradient. These data suggest that thermal physiology may be evolutionarily conservative in these species.

Neither the optimal temperature nor the thermal performance breadth for sprint speed changes ontogenetically. Maximum speed, however, increases with body size in *S. stellio*.

Sprint speed is relatively independent of body temperature in all species of lizards examined to date. This result may reflect selection for thermal insensitivity of this ecologically important, whole-animal activity.

LITERATURE CITED

BARASH, A., AND J. H. HOOFIEN. 1956. Reptiles of Israel, Tel Aviv.

BENNETT, A. F. 1980. The thermal dependence of behavioral performance in small lizards. Anim. Behav. 28:752–762.

BOGERT, C. M. 1949. Thermoregulation in reptiles, a factor in evolution. Evolution 3:195–211.

BROWN, J. H., AND C. R. FELDMETH. 1971. Evolution in constant and fluctuating environments: thermal tolerances of the desert pupfish (*Cyprinodon*). Evolution 25:390–398.

CHRISTIAN, K. A., AND C. R. TRACY. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. Oecologia 49:218–223.

CLARK, D. R., AND J. C. KROLL. 1974. Thermal ecology of anoline lizards: temperate versus tropical strategies. Southwest. Natur. 19:9–19.

CORN, M. J. 1971. Upper thermal limits and thermal preferenda for three sympatric species of *Anolis*. J. Herpetol. 5:17–21.

DAWSON, W. R. 1975. On the physiological significance of the preferred temperatures of reptiles, p. 443–473. *In* D. M. Gates and R. Schmerl (eds.), Perspectives in Biophysical Ecology. Springer-Verlag, N.Y.

ELLIOTT, J. P., I. COWAN, AND C. S. HOLLING. 1977. Prey capture by the African lion. Can. J. Zool. 55:1811–1828.

ENDLER, J. A. 1977. Geographic Variation, Speciation, and Clines. Princeton Univ. Press, Princeton.

FEDER, M. E. 1978. Environmental variability and thermal acclimation in neotropical and temperate zone salamanders. Physiol. Zool. 51:7–16.

FRY, F. E. J. 1971. The effect of environmental factors on the physiology of fish, p. 79–134. *In* W. S. Hoar and D. J. Randall (eds.), Fish Physiology, Vol. 6. Environmental Relations and Behavior. Academic Press, N.Y.

GREENWALD, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. Copeia 1974:141–148.

HERTZ, P. E. 1979. Sensitivity to high temperatures in three West Indian grass anoles (Sauria, Iguanidae), with a review of heat sensitivity in the genus *Anolis*. Comp. Biochem. Physiol. 63A: 217–222.

———. 1981. Adaptation to altitude in two West Indian anoles (Reptilia: Iguanidae): field thermal biology and physiological ecology. J. Zool. (London) 195:25–37.

———. 1982. Eurythermy and niche breadth in West Indian *Anolis* lizards: a reappraisal. *In* A. Rhodin and K. Miyata (eds.), Advances in Herpetology and Evolutionary Biology, Essays in Honor of Ernest E. Williams. Special Publ. Mus. of Comp. Zool. *In press*.

HERTZ, P. E., A. ARCE-HERNANDEZ, J. RAMIREZ-VAZQUEZ, W. TIRADO-RIVERA, AND L. VAZQUEZ-VIVES. 1979. Geographical variation of heat sensitivity and water loss rates in the tropical lizard, *Anolis gundlachi*. Comp. Biochem. Physiol. 62A:947–953.

HERTZ, P. E., AND R. B. HUEY. 1981. Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. Ecology 62:515–521.

HERTZ, P. E., R. B. HUEY, AND E. NEVO. 1982. Fight versus flight: body temperature influences defensive responses of lizards. Anim. Behav. 30: 676–679.

HERTZ, P. E., AND E. NEVO. 1981. Thermal biology of four Israeli agamid lizards in early summer. Israel J. Zool. 30:190–210.

HIRSHFIELD, M. F., C. R. FELDMETH, AND D. L. SOLTZ. 1980. Genetic differences in physiological tolerances of Amargosa pupfish (*Cyprinodon*

nevadensis) populations. Science (N.Y.) 207:999–1001.

HOOFIEN, J. H. 1972. A taxonomic list of the reptiles of Israel and its administered areas according to the status on May 31, 1972. Dept. Zool. Publ., Tel Aviv Univ.

HUEY, R. B. 1982a. Temperature, physiology, and the ecology of reptiles, p. 25–91. *In* C. Gans and F. H. Pough (eds.), Biology of the Reptilia, Vol. 12. Physiological Ecology. Academic Press, N.Y.

———. 1982b. Effects of habitat, time of day, and thermoregulatory behavior on physiological performance in a lizard (*Anolis cristatellus*): a preliminary study. *In* A. Rhodin and K. Miyata (eds.), Advances in Herpetology and Evolutionary Biology, Essays in Honor of Ernest E. Williams. Special Publ. Mus. Comp. Zool. *In press*.

HUEY, R. B., AND P. E. HERTZ. 1982. Effects of body size and slope on sprint speed of a lizard (*Stellio stellio*). J. Exp. Biol. 97:401–409.

HUEY, R. B., W. SCHNEIDER, G. L. ERIE, AND R. D. STEVENSON. 1981. A field-portable racetrack for measuring acceleration and velocity of small cursorial animals. Experientia 37:1356–1357.

HUEY, R. B., AND M. SLATKIN. 1976. Costs and benefits of lizard thermoregulation. Quart. Rev. Biol. 51:363–384.

HUEY, R. B., AND R. D. STEVENSON. 1979. Integrating thermal physiology and ecology of ectotherms. Amer. Zool. 19:357–366.

HUEY, R. B., AND T. P. WEBSTER. 1975. Thermal biology of a solitary lizard: *Anolis marmoratus* of Guadeloupe, Lesser Antilles. Ecology 56:445–452.

———. 1976. Thermal biology of *Anolis* lizards in a complex fauna: the *cristatellus* group on Puerto Rico. Ecology 57:985–994.

HUTCHISON, V. H. 1976. Factors influencing thermal tolerances of individual organisms, p. 10–26. *In*. G. W. Esch and R. W. McFarlane (eds.), Thermal Ecology II. U.S. Nat. Tech. Inf. Ser., Springfield, Virginia.

HUTCHISON, V. H., AND J. D. MANESS. 1979. The role of behavior in temperature acclimation and tolerance in ectotherms. Amer. Zool. 19:367–384.

LISTER, B. C. 1976. The nature of niche expansion in West Indian *Anolis* lizards II: evolutionary components. Evolution 30:677–692.

McCULLOUGH, E. C., AND W. P. PORTER. 1971. Computing clear day solar radiation spectra for the terrestrial ecological environment. Ecology 52:1008–1015.

MILLER, K., AND G. C. PACKARD. 1977. An altitudinal cline in critical thermal maxima of chorus frogs (*Pseudachris triseriata*). Amer. Natur. 111:267–277.

MOODY, S. M. 1980. Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia). Unpubl. Ph.D. Diss., Univ. Michigan, Ann Arbor.

MOORE, J. A. 1939. Temperature tolerance and rates of development in the eggs of Amphibia. Ecology 20:459–478.

RAND, A. S. 1964a. Ecological distribution in anoline lizards of Puerto Rico. Ecology 45:745–752.

———. 1964b. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology 45:863–864.

RUIBAL, R. 1960. Thermal relations of five species of tropical lizards. Evolution 15:98–111.

RUIBAL, R., AND R. PHILIBOSIAN. 1970. Eurythermy and niche expansion in lizards. Copeia 1970:645–653.

SOPINA, V. A. 1976. The multiplication rate of amoebae related to the cultivation temperature. J. Therm. Biol. 1:199–204.

SOULÉ, M. 1963. Aspects of thermoregulation in nine species of lizards from Baja California. Copeia 1963:107–115.

SPELLERBERG, I. F. 1972. Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. I. The environment and lizard critical temperatures. Oecologia 9:371–383.

TRACY, C. R. 1978. Further thoughts on anuran thermoregulation, p. 63–67. *In* E. H. Burtt (ed.), The Behavioral Significance of Color. Garland Publishers, N.Y.

USHAKOV, B. P. 1964. Thermostability of cells and proteins of poikilotherms and its significance in speciation. Physiol. Rev. 44:518–560.

USHAKOV, B. P., AND E. A. BUGAYEVA. 1975. The environmental temperature and physiological polymorphisms of populations—I. The effect of heat acclimation on variability and survival of a population at elevated temperature. J. Therm. Biol. 1:1–6.

WEBB, P. W. 1976. The effect of size on fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator-prey interactions. J. Exp. Biol. 65:157–177.