

PHYLOGENETIC STUDIES OF COADAPTATION: PREFERRED TEMPERATURES VERSUS OPTIMAL PERFORMANCE TEMPERATURES OF LIZARDS

RAYMOND B. HUEY

Department of Zoology NJ-15, University of Washington, Seattle, WA 98195

AND

ALBERT F. BENNETT

School of Biological Sciences, University of California, Irvine, CA 92717

Abstract.—The view that behavior and physiological performance are tightly coadapted is a central principle of physiological ecology. Here, we test this principle using a comparative study of evolutionary patterns in thermal preferences and the thermal dependence of sprinting in some Australian skinks (Lygosominae). Thermal preferences (T_p) differ strikingly among genera (range 24° to 35°C), but critical thermal maxima (CTMax) (range 38° to 45°C) and optimal temperatures for sprinting (T_o , 32° to 35°C) vary less. Diurnal genera have relatively high T_p , T_o , and CTMax. In contrast, nocturnal genera have low T_p but have moderate to high T_o and CTMax. Both nonphylogenetic and phylogenetic (minimum-evolution) approaches suggest that coadaptation is tight only for genera with high T_p . Phylogenetic analyses suggest that low T_p and, thus, partial coadaptation are evolutionarily derived, indicating that low thermal preferences can evolve, even if this results in reduced performance. In one instance, thermal preferences and the thermal dependence of sprinting may have evolved in opposite directions, a phenomenon we call “antagonistic coadaptation.” We speculate on factors driving partial coadaptation and antagonistic coadaptation in these skinks.

Received July 28, 1986. Accepted February 13, 1987

The behavioral, physiological, and morphological traits of an organism directly and interactively influence its fitness (Wright, 1932; Arnold, 1983). Consideration of interactive effects on fitness has led to two important evolutionary principles. First, when interactions among traits have major effects on fitness, natural selection should favor the harmonious evolution of those traits (Dobzhansky, 1955)—a process often called “coadaptation” (Mayr, 1963). Second, when a major environmental shift occurs, natural selection should initially favor compensatory changes in behavior (Bogert, 1949; Mayr, 1959; Gans, 1974; Slobodkin and Rapoport, 1974; Dawson et al., 1977; Wyles et al., 1983). If behavioral changes result in reduced physiological capacity, behavioral drive should then promote selection for parallel changes in physiology and morphology, thereby increasing capacity and reestablishing coadaptation (or permitting further behavioral evolution).

Coadaptation of behavior and physiology should be conspicuous in ectotherms, animals that rely largely on behavior to buffer challenges from the physical environment (Bartholomew, 1964). For example, coad-

aptation of thermoregulatory behavior and thermal physiology should be especially tight because the body temperatures behaviorally selected by ectotherms should influence fitness via the direct and profound effects of body temperature on physiological performance (Huey and Stevenson, 1979; Huey, 1982). For example, if selection drives the thermal preference away from the thermal optima for physiological processes, then coadaptational pressures should select for a parallel shift in thermal optima for those processes (Fig. 1a). Otherwise performance will be reduced (Fig. 1b).

Lizards offer several advantages for studies of thermal coadaptation: i) many lizards live in complex thermal environments (Porter et al., 1973; Tracy, 1982), ii) their physiology is highly sensitive to body temperature (Bennett and Dawson, 1976; Huey, 1982), iii) many species control environmental influences on physiology by behaviorally regulating their body temperature at species-specific levels (Cowles and Bogert, 1944; Avery, 1982), and iv) thermal preferences vary markedly in some taxa (Huey, 1982).

Here, we examine coadaptation of ther-

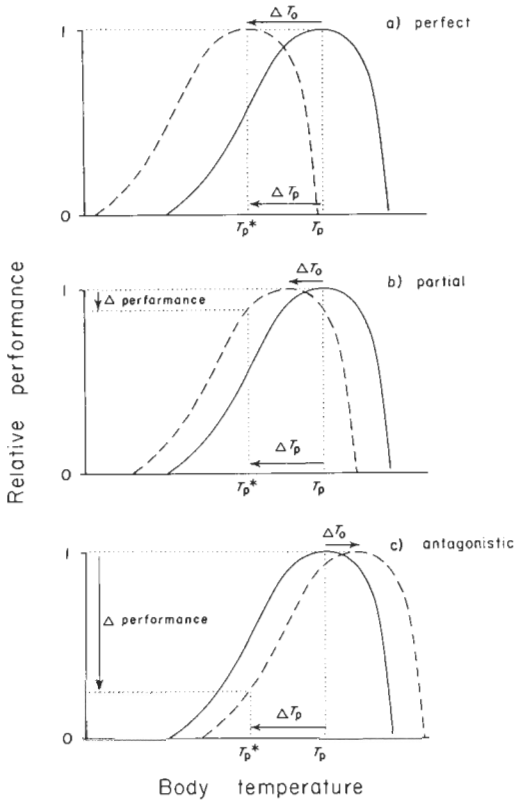


FIG. 1. a) A hypothetical case of perfect coadaptation, showing the thermal dependence of performance (solid line) and the thermal preference (T_p) of an ancestral species, as well as the performance curve (dashed line) and T_p^* of a derived species. The change in T_o equals that in T_p , such that relative performance of the derived species at T_p^* is the same as that of the ancestral species at its T_p . b) A case of partial coadaptation. The change in T_o evolves in the same direction but less rapidly than that in T_p , such that the relative performance of the derived species at T_p^* is reduced compared to that of the ancestral species. c) A hypothetical case of "antagonistic coadaptation," in which behavior and performance evolve in opposite directions (see text).

mal preference and of performance (indexed by the thermal sensitivity of sprint locomotion) in a comparative study of some scincid lizards from Australia. Australian skinks have undergone a remarkable radiation in thermal preferences, as well as in other aspects of their biology (Licht et al., 1966; Spellerberg, 1972a, 1972b, 1972c, 1972d; Greer, 1979b, 1980; Cogger, 1983; Bennett and John-Alder, 1986); their ap-

parently close evolutionary relationship (Greer, 1979b, 1985) is useful for comparative analyses (Huey and Bennett, 1986). Sprint locomotion is ecologically relevant to most reptiles (Greenwald, 1974; Bennett, 1980; Christian and Tracy, 1981), and Australian skinks often sprint to evade predators. Moreover, the thermal sensitivity of sprinting generally matches that of other performance traits in the few reptiles studied to date (Huey, 1982; Stevenson et al., 1985) and of muscle contractile properties in several of these skink genera (John-Alder and Bennett, 1987).

We first assay coadaptation from a comparative, but nonphylogenetic, perspective ("equilibrium" analysis of Lewontin [1969] and Lauder [1981]). After determining thermal preferences and optimal temperatures for a variety of taxa, we quantify the degree of coadaptation by regressing optimum temperatures for sprinting on thermal preferences. Perfect coadaptation would be indicated if a 1:1 relationship exists between these traits. In fact, coadaptation is only partial in Australian skinks (Fig. 1b): thermal optima and thermal preferences are not tightly coadapted in species with low thermal preferences.

We next assay coadaptation using a more powerful phylogenetic perspective that derives from the "transformational" approaches of Lauder (1981), Ridley (1983), and Felsenstein (1985). Here perfect coadaptation would be indicated if the evolutionary changes in behavior and in performance within lineages were congruent in magnitude and in direction. Combining a minimum-evolution approach (Edwards and Cavalli-Sforza, 1964) with Greer's (1979b) phylogeny of these skinks, we demonstrate i) that evolutionary changes in thermal preferences are of greater magnitude than those in optimal temperatures or in critical thermal maxima and ii) that the resulting partial coadaptation for genera with low thermal preferences is probably a derived condition. Accordingly, low thermal preferences appear to have evolved even though they have resulted in markedly decreased sprint capacities for some genera. Moreover, our phylogenetic analysis uncovers a possible case where behavior and performance may have evolved in opposite

directions (Fig. 1c), a phenomenon we call "antagonistic coadaptation."

Our analysis is based largely on shifts in the position of the thermal performance curves and, thus, on relative speeds (e.g., Fig. 1). However, selection works on absolute performance; and our findings (e.g., partial coadaptation) might therefore be artifactual. In fact, the absolute speeds of genera showing partial and antagonistic coadaptation are always very slow, such that an analysis based on absolute speeds would actually accentuate these patterns (see below). In any case, analysis of relative performance is required, because the lizards studied here are ecologically and morphologically very different.

Species Accounts

To interpret evolutionary changes in behavior and performance in Australian skinks, an understanding of their habits, thermal biology, geographic distributions, and phylogeny is required. Geographic associations of the Australian skinks studied here fall into two classes (Greer, 1980). Peripheral areas of southeastern Australia (often called the "Bassian region," after the Bass Straits between Australia and Tasmania) have warm dry summers and cool wet winters. In contrast, interior areas (the "Eyrean region," after Lake Eyre in central Australia) are typically much hotter and have lower and less-predictable rainfall. Our assignment of genera to these regions follows Greer (1980) and Cogger (1983). Previous research has demonstrated that skinks from peripheral areas have relatively low thermal preferences and critical thermal limits (i.e., temperatures associated with loss of righting responses) (Spellerberg, 1972a; Greer, 1980; Bennett and John-Alder, 1986). Consequently, we wished to determine whether skinks from peripheral areas also had lower optimal temperatures for sprinting.

Ctenotus regius, *C. taeniolatus*, and *C. uber* are arid-land (primarily interior), diurnal, ground-dwelling, and insectivorous lizards (Pianka, 1969, 1986). These species are relatively active foragers, reminiscent of teiid and lacertid lizards.

Eremiascincus fasciolatus, a crepuscular

and nocturnal inhabitant of sandy deserts (primarily interior), preys on other lizards (Greer, 1979a, pers. comm.). This species has reduced limbs and often waits partially buried in sand and then ambushes lizard prey moving nearby.

Hemiergis decresiensis and *H. peronii* are tiny (about 1 g), insectivorous, and cryptozoic lizards with peripheral distributions. They rarely emerge from cover (usually only in late afternoon or early evening). Their limbs are minute, and the lizards move with snake-like, lateral undulations.

Sphenomorphus kosciuskoii, *S. quoyi*, and *S. tympanum* "cool temperate" are relatively heavy bodied skinks with a peripheral distribution. These so-called "water skinks" are diurnal, insectivorous, terrestrial to semiarbooreal, range to high elevation, and are often near water. *Sphenomorphus tympanum* is thought to consist of two types ("cool temperate" and "warm temperate"), which may deserve specific status (Cogger, 1983); only the former is studied here.

Leiolopisma entrecasteauxii forms A and B are small, ground-dwelling or semiarbooreal, insectivorous, and diurnal skinks with peripheral distributions. Forms A and B may be distinct species (Jenkins and Bartell, 1980) and are treated separately here.

Skinks in the genus *Egernia* are heavy bodied, mainly insectivorous, diurnal, and geographically widespread. Some interior species are, however, nocturnal (Henzell, 1982; Cogger, 1984; Pianka, 1986).

Phylogenetic Relationships

The genera studied here are apparently closely related. All genera belong to the subfamily Lygosominae (Greer, 1979b, 1985) (but see Hutchinson [1981]). Most genera belong to the suprageneric *Sphenomorphus* group, but *Egernia* (and *Tiliqua*, see below) and *Leiolopisma* belong to the *Egernia* and *Eugongylus* groups, respectively.

Phylogenetic relationships among Australian skinks are somewhat unsettled (Hutchinson, 1981; A. E. Greer, pers. comm.; P. Baverstock, pers. comm.), such that the historical reconstructions attempted herein may ultimately require revision. Nevertheless, morphological considerations suggest that the genera *Sphenomor-*

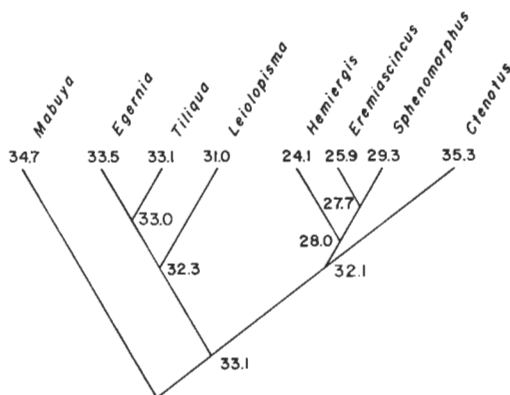


FIG. 2. A tentative tree of some Australian skink genera, based on Greer (1979b). *Mabuya* (non-Australian) is used as an outgroup (but see Hutchinson [1981]). Numbers at the tips are unweighted generic averages for thermal preferences ($^{\circ}\text{C}$). Numbers at nodes indicate presumed ancestral T_p generated by a minimum-evolution approach (see Materials and Methods). Sources: *Mabuya*, ten species, range of $T_p = 33.4^{\circ}$ to 35.6°C (Barbault, 1974; Withers, 1981; Bowker, 1984; Huey and Pianka, unpubl.); *Egernia*, four species, range of $T_p = 32.7^{\circ}$ to 34.7°C (Rawlinson, 1974; Heatwole, 1976; Johnson, 1977; Bennett and John-Alder, 1986) (see also Henzell [1982]); *Tiliqua*, three species, range of $T_p = 31.9^{\circ}$ to 34.8°C (Licht et al., 1966; Rawlinson, 1974; Bennett and John-Alder, 1986). All other data from Bennett and John-Alder (1986) and Wilhoft (1961).

phus, *Hemiergis*, and *Eremiascincus* are more closely related to each other than to *Ctenotus* (Greer, 1979a, 1979b). On this basis, we have constructed a tentative phylogeny of the lygosomine skinks studied here (Fig. 2). For completeness, we have included *Tiliqua* (an Australian skink) only in analyses of thermal preferences and critical thermal maxima: the thermal dependence of sprint speed for this lizard was not measured. We have also included *Mabuya*, a widespread but non-Australian skink, as the outgroup (Watrous and Wheeler, 1981) in our analysis of directions of evolutionary change of thermal preferences: *Mabuya* is thought to be the closest relative of the Australian lygosomine skinks (Greer, 1979b, pers. comm.) (but see Hutchinson [1981]).

MATERIALS AND METHODS

Lizards were collected between late September and late December 1983, from a variety of localities in Australia (see Bennett and John-Alder, 1986; collecting permits

Nos. 918 from South Australian National Parks and A216 from New South Wales National Parks and Wildlife). Species, sample sizes, and body sizes are listed in Table 1. We have deposited voucher specimens in the South Australian Museum, Adelaide, S.A.

Lizards were transported to the University of Adelaide and held under standardized conditions until testing, usually within two weeks of capture. All were housed in small groups in terraria containing water dishes. The lizards were provided with food (*Tenebrio* larvae and termites) and were given access to incandescent lamps for behavioral thermoregulation for 12 hr/day. At night their body temperatures dropped to ambient levels (approximately 20°C).

Thermal Data

Preferred body temperatures (T_p) in a laboratory photothermal gradient, body temperatures (T_b) in nature, and critical thermal maxima (CTMax) and minima (CTMin) are taken from Bennett and John-Alder (1986). (CTMax and CTMin are the upper and lower temperatures at which the righting response is lost).

Racing Protocols

The racing equipment and procedures follow Hertz et al. (1983). In brief, lizards were chased by hand down a 2-m track with photocell stations (vertical stacks of four photocells) positioned at 0.25-m intervals. The photocell stations were connected to an Apple II⁺ microcomputer that calculated speed (m/sec) over each 0.5-m section of the track.

Lizards were generally run at the following sequence of body temperatures ($\pm\text{SD}$): $30.9^{\circ} \pm 0.38^{\circ}$, $25.5^{\circ} \pm 0.40^{\circ}$, $20.4^{\circ} \pm 0.44^{\circ}$, $15.3^{\circ} \pm 0.45^{\circ}$, $9.7^{\circ} \pm 0.38^{\circ}$, $30.0^{\circ} \pm 0.47^{\circ}$, $34.9^{\circ} \pm 0.41^{\circ}$, $37.3^{\circ} \pm 0.27^{\circ}$, and $39.3^{\circ} \pm 0.19^{\circ}\text{C}$. Individuals of several species were unable to run at 9.7°C , and most were incapacitated at 39°C (Table 2). Most lizards were raced four times per temperature (on sand), but individuals of four small species (*Hemiergis* spp., *Leiopisma* spp.) were raced only three times per temperature and on a hard-rubber substratum. Lizards were raced at one temperature per day and were given 1-day rests between the 30° and 35°C

runs and between the 35° and 37.3°C runs. The two separate trials at 30°C (30.9° and 30.0°C) enabled us to check for changes in performance during the experiment due to illness or injury (Hertz et al., 1983). In subsequent analyses, we excluded individuals whose maximum speed in trial-2 was more than 15% slower than that in trial-1 or whose maximum speed in trial-2 was slower than at least three runs in trial-1.

Statistical Analysis

The fastest speed over 0.5 m for each lizard at each temperature was selected for analysis. We have no independent way of knowing whether these speeds actually are the maximal speeds the animals are capable of attaining. They are, however, the highest speeds attained in these circumstances. Moreover, the general correspondence of the thermal dependence of sprint speed and of muscle contractile properties (Bennett et al., 1986; John-Alder and Bennett, 1987) suggests that physiology—not just motivation—plays an important role in measured sprint speeds. Speeds of 0 m/sec were assigned to the CTMax and CTMin, using average values for each species (Bennett and John-Alder, 1986). To quantify the thermal dependence of sprinting, we used a minimum-polygon algorithm (van Berkum, 1986) to connect data points in plots of speed versus body temperature data for each individual. We selected this approach in preference to nonlinear curve fitting (Huey and Stevenson, 1979; Hertz et al., 1983), which induces systematic biases in some species (van Berkum, 1985, 1986).

We then used the polygons to calculate several statistics that quantify the thermal sensitivity of locomotor performance for each individual (see Hertz et al., 1983 fig. 1). To estimate the “thermal performance breadths” (measures of the range of T_b over which lizards run well) we estimated the ranges of temperatures over which a lizard runs at 95% (B_{95}) and at 80% (B_{80}) of V_{\max} . To estimate the “optimal” temperature (T_o) for sprinting, we calculated the midpoint of the range of temperatures over which the lizard runs at 95% of V_{\max} , following the rationale given by Hertz et al. (1983). Because of the skewed shape of performance curves (Fig. 1), T_o is usually slightly lower

than the actual temperature interval at which maximal speed was measured. We also calculated Q_{10} , a measure the thermal sensitivity of absolute performance over the range ($T_o - 10^\circ\text{C}$) to T_o and the “performance safety zone” ($\text{CTMax} - T_o$) (Heatwole, 1970). Finally, we calculated the predicted speeds of each individual (both absolute speed and speed relative to that at T_o) at certain species-specific body temperatures (e.g., at T_p or at T_b). For some species, field T_b values were unavailable or based on small samples. When the sample size for field T_b was unreliably small (<7), we calculated relative speeds (Table 4) but did not incorporate them in statistical analyses reported herein. (Inclusion of these data would not alter patterns.)

Standard regression analyses involving thermal statistics were not conducted, because data on thermal preference and on critical limits were available only for some of the lizards used in the present experiment. Consequently, we selected a regression model that permits multiple values of Y for a given X (Sokal and Rohlf, 1981 p. 480), generally using the mean thermal preference as the independent variable and locomotory performance measures as dependent variables.

Comparative analyses are complicated by lack of statistical independence among data from related taxa (Ridley, 1983; Clutton-Brock and Harvey, 1984; Felsenstein, 1985). Specifically, data for related species may not be statistically independent because of phylogenetic inertia. Australian skinks in fact show marked intrageneric conservatism in many thermal traits (Bennett and John-Alder, 1986; Tables 1, 3). For example, 91% of the variance in preferred body temperatures occurs at the generic level (three-level nested ANOVA [Sokal and Rohlf, 1981]). Consequently, treating values of species as independent is inappropriate. We therefore report statistical comparisons using weighted generic averages for overall heterogeneity and for a priori contrasts (interior vs. periphery) and the weighted generic averages of independent variables for regressions (Clutton-Brock and Harvey, 1984). For example, we regressed optimal temperatures for sprinting of individual lizards against the generic T_p .

Evolutionary Analyses

To speculate on past evolutionary changes in thermal behavior and performance, we developed an approach prompted by Lauder (1981), Ridley (1983), and Felsenstein (1985). First we superimposed the average thermal preference (\bar{T}_p) for each skink genus on the tips of a tentative phylogenetic tree of these skinks (Fig. 2), using *Mabuya* as an outgroup. We then reconstructed thermal preference of ancestors using parsimony as a criterion (Felsenstein, 1983) and an averaging algorithm, wherein the value for a node is computed as the iterative average of the three nearest nodes. This modification of a minimum-evolution approach (suggested to us by J. Felsenstein; based on Edwards and Cavalli-Sforza [1964]) minimizes the squared change in thermal preference for each link in the tree, summed for all branches, and it is similar but not equivalent to a maximum-likelihood estimate. This modification assumes that evolutionary change is punctuational at the generic level, such that differences in time between "speciation" events is unimportant (J. Felsenstein, pers. comm.). This assumption was made for expediency, as ages of these taxa are unknown. An alternative reconstruction using a medians-rule algorithm (Kluge and Farris, 1969), which minimizes the sum of absolute evolutionary changes, generated qualitatively similar patterns.

CTMax and T_o were similarly analyzed. We then measured the extent of coadaptation within lineages by regressing the change in CTMax (difference between the generic average and the nearest node) or the change in T_o on the change in T_p . We emphasize that the resulting regressions are based on nonindependent data, which is a consequence of using the minimum-evolution approach. If times of divergence were known, Felsenstein's (1985) "Brownian-motion" model could circumvent this problem.

RESULTS

We approach our data two ways. Initially, we present an "equilibrium" analysis (Lauder, 1981), by comparing intergeneric differences and correlations involving behavioral and performance traits. Subsequently, we incorporate phylogenetic information, which permits us to develop a "transfor-

mational" analysis of directions of evolutionary change in these lizards.

Thermal Preference

The data and statistical analyses below are summarized from Bennett and John-Alder (1986). Preferred body temperatures vary strikingly among genera (Table 1). The maximum difference among genera is 11.3°C. Crepuscular/nocturnal genera (*Hemiergus* and *Eremiascincus*) have extremely low thermal preferences. Among the diurnal lizards, peripherally distributed genera (*Sphenomorphus* and *Leiolopisma*) have lower thermal preferences than do the interior genera (*Ctenotus* and *Egernia*).

Speed Versus Body Temperature

Temperature has a profound and similar effect on the absolute running speed of skinks (Table 2). In all species (see also Fig. 1), speed increases gradually with temperature (average $Q_{10} = 1.5$; Table 3), reaches a broad plateau (average $B_{80} = 9.9^\circ\text{C}$), but then drops rapidly at temperatures above the optimum (average T_o only 7.8°C below CTMax; Table 3).

Optimal temperatures for sprint locomotion vary significantly among skink genera ($F_{[5,70]} = 5.15$, $P < 0.001$; Table 3), but the magnitude of intergeneric variation is small (maximum difference = 3.4°C). Optimal temperatures are significantly lower in genera with peripheral distributions than in genera from the warm interior (a priori ANOVA, $F_{[1,71]} = 21.0$, $P < 0.001$).

An equilibrium analysis demonstrates significant coadaptation between optimal temperatures and thermal preferences ($T_o = 26.4 + 0.25 T_p$; $F_{[1,4]} = 12.0$, $P < 0.025$; Fig. 3). Nevertheless, coadaptation is only partial (sensu Fig. 1b), for the slope of the regression of T_o on T_p is significantly less than 1.0 ($P < 0.001$; see Sokal and Rohlf, 1981 pp. 473, 485). Thus, T_o appears to have evolved less than has T_p . Partial coadaptation is primarily a consequence of the major discrepancies between T_o and T_p for genera with low T_p (Fig. 3). In contrast, coadaptation is nearly perfect for genera with high T_p .

CTMax and CTMin vary moderately among genera (maximum difference = 6.5°C for CTMax, 7.3°C for CTMin; Table 1).

TABLE 1. Characteristics of Australian skinks used for analysis of thermal dependence of sprint speed. Means \pm SE are given for mass and snout-vent length (SVL). \bar{T}_b = mean body temperature of field-active animals (range given in parentheses); \bar{T}_p = mean preferred body temperature in a laboratory thermal gradient. Data for \bar{T}_p , \bar{T}_b , CTMin, and CTMax are summarized from Bennett and John-Alder (1986).

Species (N)	Mass (g)	SVL (mm)	\bar{T}_p (°C)	\bar{T}_b (range) °C	CTMin (°C)	CTMax (°C)
Sphenomorphus group:						
<i>Ctenotus regius</i> (5)	5.5 \pm 0.32	66.0 \pm 1.58	35.6	36.4 ^c (35.7–37.1)	8.7	45.1
<i>Ctenotus taeniolatus</i> (9)	4.5 \pm 0.40	66.3 \pm 1.59	35.3	—	11.4	44.7
<i>Ctenotus uber</i> (11)	5.4 \pm 0.63	66.5 \pm 1.62	35.3	—	9.1	45.5
<i>Eremiascincus fasciolatus</i> (5)	12.5 \pm 1.48	86.5 \pm 4.48	24.4 ^b	28.1 ^c	9.0	41.2
<i>Hemiergis decresiensis</i> (10)	0.8 \pm 0.08	42.1 \pm 2.10	24.8 ^b	20.3 (17.3–23.0)	6.8	38.6
<i>Hemiergis peronii</i> (4)	1.5 \pm 0.32	58.6 \pm 4.25	23.5 ^b	23.6 (19.2–27.0)	9.6	38.8
<i>Sphenomorphus kosciuskoii</i> (12)	8.3 \pm 0.67	76.3 \pm 1.82	29.8	30.6 ^a (16.9–36.0)	2.5	40.2
<i>Sphenomorphus quoyi</i> (2)	21.1	98.0	28.8	28.6 ^a (17.4–34.2)	6.0	40.8
<i>Sphenomorphus tympanum</i> “cool temperate” (7)	14.4 \pm 2.12	88.0 \pm 5.34	29.5 ^a	30.1 ^a (16.3–34.5)	2.9	39.8
Eugongylus group:						
<i>Leiopisisma entrecasteauxii</i> form A (3)	4.7 \pm 1.30	63.7 \pm 4.70	32.5	—	2.5	42.8
<i>Leiopisisma entrecasteauxii</i> form B (4)	3.3 \pm 0.27	56.5 \pm 0.96	33.9	—	2.5	42.8
Egernia group:						
<i>Egernia whitii</i> (4)	25.1 \pm 4.32	102.8 \pm 6.95	34.1	34.0 (30.8–35.6)	4.0	42.8

^a Weighted average of values cited in Bennett and John-Alder (1986).

^b Nighttime records for crepuscular/nocturnal species.

^c $N < 7$ in these species.

CTMax and CTMin are higher for interior genera than for peripheral genera (a priori ANOVA, $P < 0.001$, see also Spellerberg, 1972a; Greer, 1980; Bennett and John-Alder, 1986).

The optimal T_b for sprinting is positively and significantly related to CTMax ($T_o = 15.9 \pm 0.43$ CTMax, $F_{[1,4]} = 89.2$, $P < 0.001$), and the slope is significantly less than 1.0 ($P < 0.001$). Thus, optimal T_b appears to have evolved less than has CTMax. The optimal T_b is positively, but not significantly, related to CTMin $F_{[1,4]} = 1.1$ ($P > 0.025$).

Thermal Performance Breadth and Q_{10}

Performance breadths (B_{95} and B_{80} values) for sprint speed of skink genera do not vary significantly (ANOVA, P 's > 0.10 ; Table 3). Moreover, neither B_{95} nor B_{80} is significantly related (ANOVA, P 's > 0.25) to optimal \bar{T}_b , \bar{T}_p , or tolerance range (CTMax – CTMin) (Table 3).

We used two measures to quantify the thermal sensitivity of sprint speed to temperatures above and below the optimum. For temperatures below the optimum, we

calculated Q_{10} values for the range ($T_o - 10$) to T_o . For temperatures above the optimum, we calculated the difference between CTMax and \bar{T}_o , a measure of the physiological “safety zone” (Heatwole, 1970).

Q_{10} does not vary significantly among genera (ANOVA, $P > 0.25$; Table 3) and is not significantly related to optimal temperature (ANOVA, $P > 0.10$). Thus, the lower part of the performance curve is evolutionarily conservative. In contrast, the thermal safety zone does vary significantly among genera ($F_{[5,70]} = 6.1$, $P < 0.001$; Table 3), is positively related to \bar{T}_o ($F_{[1,4]} = 24.9$, $P < 0.01$), and is relatively large for interior genera (a priori ANOVA, $P < 0.001$). Thus, species that have high optimal temperatures or live in hot regions have CTMax values that are relatively far from their optimal temperatures.

Body Temperatures and Sprint Performance

The predicted relative sprint speeds associated with the preferred body temperature or with field activity temperatures are

TABLE 2. Average absolute speeds (m/sec \pm 95% confidence limits) of Australian skinks at various body temperatures. 0 = unable to run. Sample sizes are given in Table 1.

Species	Temperature-specific racing speeds									
	9.7°C	15.3°C	20.4°C	25.5°C	30° and 30.9°C	34.9°C	37.3°C	39.3°C		
Sphenomorphus group:										
<i>Ctenotus regius</i>	0	0.18 \pm 0.051	0.44 \pm 0.133	0.50 \pm 0.221	0.89 \pm 0.206	0.99 \pm 0.341	0.68 \pm 0.315	0		
<i>Ctenotus taeniolatus</i>	0	0.29 \pm 0.044	0.59 \pm 0.082	0.79 \pm 0.142	0.96 \pm 0.185	1.05 \pm 0.152	1.04 \pm 0.225	1.18 \pm 0.230		
<i>Ctenotus uber</i>	0	0.36 \pm 0.083	0.72 \pm 0.121	1.09 \pm 0.213	1.41 \pm 0.274	1.64 \pm 0.156	1.58 \pm 0.175	1.65 \pm 0.310		
<i>Eremiascincus fasciolatus</i>	0.04 \pm 0.062	0.24 \pm 0.105	0.38 \pm 0.095	0.50 \pm 0.047	0.67 \pm 0.069	0.83 \pm 0.161	0.56 \pm 0.294	0		
<i>Hemiergis decrestiensis</i>	0.13 \pm 0.056	0.27 \pm 0.045	0.42 \pm 0.087	0.49 \pm 0.136	0.64 \pm 0.128	0.64 \pm 0.090	0.55 \pm 0.121	0		
<i>Hemiergis peronii</i>	0.11 \pm 0.144	0.27 \pm 0.196	0.39 \pm 0.186	0.37 \pm 0.230	0.49 \pm 0.304	0.37 \pm 0.412	0	0		
<i>Sphenomorphus kosciuskoi</i>	0.17 \pm 0.031	0.34 \pm 0.077	0.53 \pm 0.157	0.70 \pm 0.153	0.86 \pm 0.140	1.04 \pm 0.145	0.34 \pm 0.253	0		
<i>Sphenomorphus quoyi</i>	0	0.69	0.96	1.27	1.52	1.21	0	0		
<i>Sphenomorphus tympanum</i>	0.24 \pm 0.043	0.67 \pm 1.525	0.93 \pm 0.179	1.17 \pm 0.287	1.42 \pm 0.309	1.49 \pm 0.221	0.94 \pm 0.110	0		
Eugongylus group:										
<i>Leiopeltisma entrecasteauxii</i> form A	0.23 \pm 0.094	0.37 \pm 0.076	0.65 \pm 0.160	0.88 \pm 0.113	1.11 \pm 0.385	1.18 \pm 0.201	0.94 \pm 0.496	0		
<i>Leiopeltisma entrecasteauxii</i> form B	0.13 \pm 0.111	0.25 \pm 0.118	0.41 \pm 0.277	0.59 \pm 0.210	0.73 \pm 0.152	0.89 \pm 0.200	0.67 \pm 0.103	0		
Egernia group:										
<i>Egernia whitii</i>	0.15 \pm 0.088	0.31 \pm 0.136	0.47 \pm 0.293	0.67 \pm 0.356	0.91 \pm 0.223	0.93 \pm 0.200	1.09 \pm 0.214	—		

TABLE 3. Statistics describing thermal dependence of sprint speed and maximum speeds in some Australian skinks. Terms are defined in Materials and Methods. Values given are $\bar{x} \pm 95\%$ confidence interval. Sample sizes are given in Table 1.

Species	T_0 (°C)	B_{95} (°C)	B_{80} (°C)	Q_{10}	$CT_{Max} - T_0$	V_{max} (m/sec)
Sphenomorphus group:						
<i>Ctenotus regius</i>	33.0 ± 2.66	3.7 ± 2.80	8.5 ± 2.69	1.96 ± 0.646	12.1 ± 0.96	1.01 ± 0.284
<i>Ctenotus taeniolatus</i>	35.7 ± 2.23	5.2 ± 3.07	10.8 ± 3.22	1.51 ± 0.158	9.0 ± 0.97	1.24 ± 0.190
<i>Ctenotus uber</i>	36.5 ± 1.39	4.6 ± 1.85	10.8 ± 1.58	1.52 ± 0.186	9.0 ± 0.62	1.81 ± 0.199
<i>Eremiascincus fasciolatus</i>	34.0 ± 1.76	3.1 ± 2.84	7.9 ± 2.89	1.67 ± 0.286	7.2 ± 0.63	0.83 ± 0.156
<i>Hemiergis decresiensis</i>	33.2 ± 1.53	4.2 ± 1.53	10.7 ± 1.80	1.47 ± 0.168	5.4 ± 0.68	0.70 ± 0.110
<i>Hemiergis peronii</i>	30.8 ± 3.02	3.4 ± 2.43	11.5 ± 5.19	1.34 ± 0.207	7.8 ± 0.95	0.52 ± 0.269
<i>Sphenomorphus kosciuskoii</i>	33.6 ± 0.34	3.0 ± 1.23	8.6 ± 1.54	1.57 ± 0.171	6.6 ± 0.15	1.02 ± 0.138
<i>Sphenomorphus quoyi</i>	29.5	2.8	10.0	1.65	11.3	1.52
<i>Sphenomorphus tympanum</i>	33.1 ± 1.14	3.6 ± 1.29	10.2 ± 2.34	1.43 ± 0.131	6.7 ± 0.46	1.51 ± 0.242
"cool temperate"						
Eugongylus group:						
<i>Leiopisma entrecasteauxii</i> form A	33.4 ± 3.93	3.5 ± 4.31	10.6 ± 5.53	1.43 ± 0.226	9.42 ± 0.91	1.22 ± 0.201
<i>Leiopisma entrecasteauxii</i> form B	34.5 ± 0.56	2.7 ± 1.20	9.7 ± 3.50	1.43 ± 0.138	8.27 ± 0.18	0.89 ± 0.215
Egernia group:						
<i>Egernia whitii</i>	35.3 ± 3.38	4.2 ± 6.32	9.1 ± 6.04	1.60 ± 0.389	7.55 ± 1.06	1.10 ± 0.205

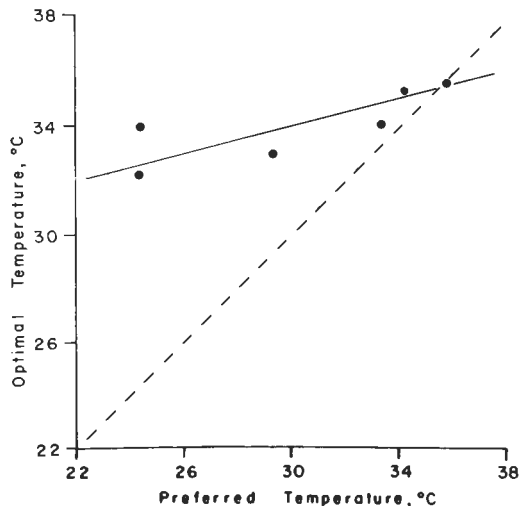


FIG. 3. Mean optimal temperature (generic average) for sprint locomotion versus preferred body temperature for Australian skinks. The dashed line represents perfect coadaptation (see Fig. 1a). For these skinks, this nonphylogenetic analysis indicates that coadaptation is only partial (Fig. 1b).

given in Table 4. Although 11 of 12 species have a mean preferred temperature that is lower than the optimal temperature for sprinting, eight of 12 species prefer temperatures that should enable them to run at speeds within 10% of their maximum possible speed. Relative sprint speed at the preferred body temperature is positively related to the preferred body temperatures ($F_{[1,4]} = 11.0, P < 0.05$), primarily because the low thermal preferences of *Eremiascincus* and *Hemiergis* are markedly suboptimal for sprinting. For example, an *Eremiascincus* at its T_p (24.4°C) is predicted to run 38% slower than if it were at 34.0°C. Of the six species for which adequate field T_b are available, four (all but the two *Hemiergis* species) are normally active at temperatures that are nearly optimal for sprinting (Table 4).

Hemiergis and *Eremiascincus* appear to be chronic underachievers with respect to relative sprint speed at their preferred temperatures (Table 4). Nevertheless, because natural selection works on absolute rather than on relative sprint speeds, the apparent locomotor disadvantage of these genera might be misleading if the absolute speeds of these lizards were higher than those of other genera. In fact, the absolute maximum

TABLE 4. Predicted relative speeds ($\pm 95\%$ confidence interval) of Australian skinks at specific body temperatures. Sample sizes are given in Table 1. \bar{T}_p = mean preferred body temperature, (see Table 1), \bar{T}_b = mean field body temperature, T_l and T_u are the lowest and highest (respectively) body temperatures recorded for each species from the field.

Species	Predicted relative speeds at:			
	\bar{T}_p	\bar{T}_b	T_l	T_u
Sphenomorphus group:				
<i>Ctenotus regius</i>	0.911 \pm 0.116	0.800 \pm 0.164 ^a	—	—
<i>Ctenotus taeniolatus</i>	0.925 \pm 0.046	—	—	—
<i>Ctenotus uber</i>	0.945 \pm 0.383	—	—	—
<i>Eremiascincus fasciolatus</i>	0.621 \pm 0.156	0.772 \pm 0.147 ^a	—	—
<i>Hemiergis decresiensis</i>	0.752 \pm 0.078	0.608 \pm 0.059	0.502	0.695
<i>Hemiergis peronii</i>	0.821 \pm 0.034	0.824 \pm 0.033	0.692	0.907
<i>Sphenomorphus kosciuskoi</i>	0.876 \pm 0.044	0.899 \pm 0.038	0.408	0.755
<i>Sphenomorphus quoyi</i>	0.966	0.959	0.523	0.806
<i>Sphenomorphus tympanum</i> "cool temperate"	0.906 \pm 0.051	0.924 \pm 0.050	0.444	0.973
Eugongylus group:				
<i>Leiolopisma entrecasteauxii</i> form A	0.949 \pm 0.050	—	—	—
<i>Leiolopisma entrecasteauxii</i> form B	0.968 \pm 0.009	—	—	—
Egernia group:				
<i>Egernia whitii</i>	0.930 \pm 0.059	0.927 \pm 0.062	0.839	0.966

^a Excluded from statistical analyses because of small sample sizes for T_b (see Materials and Methods).

speeds of these two genera are slow at all temperatures (Table 2). Thus the running speeds of these lizards at normal activity temperatures must be very slow, indeed, which accentuates the locomotor disadvantages associated with partial coadaptation.

Directions of Evolutionary Change

Our minimum-evolution approach (Materials and Methods) suggests that the ancestral thermal preference of the Australian skinks was approximately 33°C (Fig. 2). A thermal preference near this temperature is exhibited by *Mabuya* (the presumed outgroup for these skinks) and by lizards in the Egernia group. Lower T_p has apparently evolved in the Eugongylus group (*Leiolopisma*) and has probably evolved several times in the Sphenomorphus group (especially *Eremiascincus* and *Hemiergis*). Higher T_p may have evolved in *Ctenotus*. A sensitivity analysis, performed by iteratively fixing the ancestral T_p for the Australian skinks at values ranging from 25° to 40°C, emphasizes that the low T_p of *Eremiascincus* and *Hemiergis* are almost certainly derived (Fig. 4). Patterns for genera in the Sphenomorphus group do not depend on the validity of *Mabuya* as an outgroup. Deletion of *Mabuya* changes the nodes by a maximum of 0.4°C.

Critical thermal maxima and optimal temperatures for sprinting were similarly analyzed. The minimum-evolution analysis suggests that the ancestral CTMax was 42.5°C. In the absence of sprint data on *Mabuya*, we cannot estimate an ancestral T_o for Australian skinks, but the estimated ancestral T_o for the Sphenomorphus genera is 34.5°C.

Coadaptation between CTMax or T_o and thermal preferences is supported (Fig. 5): the directions and magnitudes of evolutionary change in mean CTMax and in T_o were significantly correlated with changes in T_p ($F_{[1,5]} = 10.9$, $P = 0.02$ and $F_{[1,4]} = 13.1$, $P < 0.001$, respectively). In both cases, however, coadaptation is only partial (i.e., the slopes are significantly less than unity).

The phylogenetically based approach of Figures 2 and 5 facilitates the discovery of an interesting exception to the overall pattern of partial coadaptation. Even though the thermal preference of *Eremiascincus* has evolved to a lower temperature (Fig. 2), its critical thermal maximum and its optimal temperature appear to have evolved to a higher temperature (Fig. 5). In part because of this shift, the optimal temperatures and the CTMax values for the two interior genera (*Eremiascincus* and *Ctenotus*) are significantly higher (a priori ANOVAs,

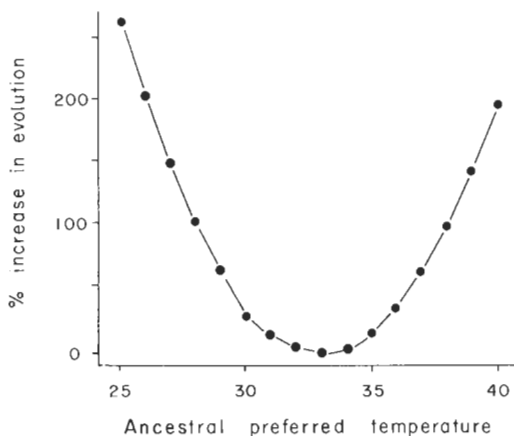


FIG. 4. A sensitivity analysis of ancestral T_p for Australian skinks. The ordinate represents, for a given ancestral T_p from 25° to 40°C, percentage increase in evolution (total squared change in °C) above that required for an ancestral skink T_p of 33.1°C, the T_p that minimizes the squared evolutionary change for the tree in Figure 2 (see Materials and Methods).

$P < 0.001$) than those of the two peripheral genera (*Hemiergis* and *Sphenomorphus*). In *Eremiascincus*, therefore, behavior and performance seem to have evolved in opposite directions, such that CTMax and T_o reflect geographic distributions better than thermal preferences.

DISCUSSION

Thermal Biology, Geography, Activity Times

Australian lygosomine skinks differ markedly in thermal preferences (maximum difference among genera = 11°C) and in activity temperatures (14°C), but they differ only moderately in critical thermal maxima (6°C) and only slightly in optimal temperatures (3°C) (Tables 1, 3). Remarkably, most of this differentiation occurs within a single generic group (*Sphenomorphus*) of Greer (1979b).

Thermal preferences and activity temperatures strongly reflect times of activity: distinctly low T_p and low T_b characterize crepuscular/nocturnal genera (Table 1). Thermal preferences also reflect zoogeography, but to a lesser extent: T_p values are slightly higher in diurnal genera from the warm interior of Australia than in those from the cooler periphery (Table 2).

Thermal sensitivity (Table 3) and CTMax (Spellerberg, 1972a; Greer, 1980; Bennett

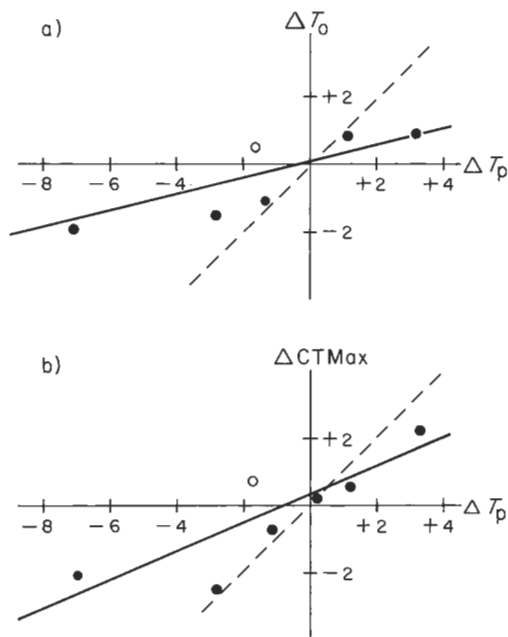


FIG. 5. a) Change in T_o versus change in T_p (generic averages) and b) change in CTMax versus change in T_p . (The open circle is *Tiliqua*.) Change is measured as the difference between values for the generic average and the nearest node (the change for *Sphenomorphus* is based on the node for the *Sphenomorphus* group). In both cases, coadaptation is partial (i.e., the slopes are less than one). The circle in the upper left quadrant of each graph represents *Eremiascincus* and demonstrates antagonistic coadaptation (Fig. 1c). The dashed line represents perfect coadaptation.

and John-Alder, 1986; Table 1) also reflect time of activity and geography, but here the ties with geography are stronger. Optimal temperatures, safety zones, and CTMax values are higher in interior genera than in peripheral genera but are not necessarily lower in nocturnal genera than in diurnal genera. Indeed, T_o and CTMax are relatively high in the nocturnal, interior genus *Eremiascincus* (Tables 1 and 3). These patterns hold even for comparisons within the *Sphenomorphus* group, indicating that the patterns are not historical artifacts.

Changes in thermal performance curves, though minor, may well be biologically significant. The ability of some *Ctenotus* to run rapidly at 39°C (Table 2), a temperature higher than the CTMax of some peripheral genera (Table 1), and to have a broad safety zone should be adaptive for a diurnal, surface-dweller in the hot interior (Heatwole,

1970, 1976; Greer, 1980; Bennett and John-Alder, 1986).

The correspondence of thermal performance with time of activity and geography is not surprising, as similar patterns have been demonstrated in other lizards (Heatwole, 1976; Avery, 1982; Huey, 1982). These correspondences may reduce thermoregulatory costs (Huey and Slatkin, 1976), maximize potential activity times (Huey and Slatkin, 1976; Huey, 1982), and even promote survival, at least for those species living in extreme environments (Cowles and Bogert, 1944; Heatwole, 1970; Spellerberg, 1972a; Greer, 1980; Hutchison and Maness, 1979; van Berkum, 1985). Nevertheless, precise matching does not always occur (Hertz et al., 1983; Crowley, 1985) (but see van Berkum [1986]).

Nonphylogenetic (Equilibrium) Approach to Coadaptation

Our data challenge the expectation that thermal preferences and thermal optima should be tightly coadapted in reptiles. Although optimal temperatures and CTMax values were correlated with thermal preferences (or with field activity temperatures), the coadaptation of these traits was not one-to-one. Indeed, a 4°C change in thermal preference was associated with only a 1°C change in optimal temperature (Fig. 3) or with only a 2°C change in CTMax (Bennett and John-Alder, 1986).

Available published data are generally consistent in showing limited evolution in thermal sensitivity of performance measures. Licht et al. (1969) and Bennett (1980) established positive correlations between thermal preferences and optimal temperatures of several physiological and performance functions of distantly related lizards, but they did not quantify the slope of these relationships. Hertz et al. (1983) and Crowley (1985) found no evidence of evolution in the thermal sensitivity of locomotion, in several Middle Eastern agamid lizards and in North American *Sceloporus undulatus*, respectively. Nevertheless, van Berkum's (1986) recent study of Central American *Anolis* demonstrates that differentiation in the thermal performance can occur. Thermal preferences of these *Anolis* have not been measured, but the magnitude of inter-

specific differences in optimal temperatures for sprinting (5°C) is less than that in mean field temperatures (10°C), a pattern consistent with our results. Thermal performance (but not thermoregulatory behavior) is phylogenetically conservative in most lizards (Bogert, 1949; Huey, 1982); nevertheless, it is clearly not inert (van Berkum, 1986; this study).

The existence of partial coadaptation raises two issues. First, are the low thermal preferences of *Eremiascincus* and *Hemiergis* sufficiently "sub-optimal" for sprinting to have a major, negative influence on their ecologies? Second, is the dissimilarity between thermal preference and thermal optima in these two genera ancestral or derived? An indirect answer to the first question can be extracted directly from the sprint data. The answer to the second can come only by incorporating phylogenetic information (Ridley, 1983; Huey and Bennett, 1986; Huey, 1987). We address these questions in sequence.

Predicted Ecological Consequences of Partial Coadaptation

Partial coadaptation means that some species select temperatures that are non-optimal for sprinting (Fig. 1b). Whether the resulting retardation of sprint capacity has a major effect on ecology cannot be determined directly from existing data, but the effect on relative speed at the preferred body temperature is easily predicted (Hertz et al., 1983; van Berkum, 1986).

Relative speeds of skinks at their preferred temperatures cluster into two groups (Table 4). Genera with relatively high thermal preferences (28°C and above) typically select temperatures enabling them to run within 10% of maximal speed, a trend that holds for most other lizards studied to date (Bennett, 1980; Hertz et al. 1983; Huey, 1983; Crowley, 1985; van Berkum et al., 1986). In contrast, genera with lower thermal preferences (*Hemiergis* and *Eremiascincus*) prefer temperatures markedly sub-optimal for sprinting (see also Bennett [1980] and van Berkum [1986]). For example, an *Eremiascincus* at its T_p should run only at 62% of its maximum possible speed. Given that the absolute speeds of *Eremiascincus* and of *Hemiergis* are slow at any temper-

ature (Table 2), speeds of these lizards in nature must be very slow. Such slow speeds potentially influence fitness: cold and sluggish lizards should be less successful in capturing prey or in escaping predators (Greenwald, 1974; Webb, 1976; Christian and Tracy, 1981; Huey and Hertz, 1984).

Even for genera showing tight coadaptation between thermal preferences and optimal temperatures, individual lizards are sometimes active at temperatures far from preferred levels (Table 1). As a result, their potential sprint speeds must on occasion be very slow (Table 4). For example, *Sphenomorphus kosciuskoi* is active in nature at body temperatures as low as 16.9°C (Spellerberg, 1972c), a temperature that should enable these lizards to run only 41% of maximum speed (Tables 2, 4). Clearly, reptiles in nature are not always capable of maximal speed, and the evolution of compensatory defensive behaviors attests to this fact (Rand, 1964; Hertz et al., 1982; Crowley and Pietruzka, 1983; Arnold and Bennett, 1984).

Phylogenetic Analysis of Coadaptation

If a low thermal preference was the ancestral state, then the coadaptation between behavior and performance has become closer during the evolution of other skink genera. But if derived, then coadaptation actually broke down during the evolution of *Hemiergus* and *Eremiascincus*. To address this issue, we conducted a minimum-evolution analysis on behavioral and performance traits, with Greer's (1979b) morphological phylogeny for these skinks as a foundation. Our "transformational" approach is philosophically derived from that of Lauder (1981), Ridley (1983), and Felstenstein (1985).

A thermal preference of about 33°C appears to be ancestral for Australian skinks, given the criterion of parsimony (Figs. 2, 4). Therefore, the low thermal preferences of *Eremiascincus* and of *Hemiergus* are almost certainly derived. Indeed, a low thermal preference (25°C) could be ancestral only if massive evolutionary change occurred in several lineages (Fig. 4) or if Greer's (1979b) phylogeny is found to require major revision. (Recall, however, that deletion of *Ma-*

buva as an outgroup does not influence conclusions for the *Sphenomorphus* genera).

We then repeated this analysis on optimal temperatures and on critical thermal maxima to determine whether phylogenetic trends in these traits parallel those in thermal preferences (Fig. 5), as is predicted from coadaptational considerations (Fig. 1). Actual directional changes are coincident, except for trends involving *Eremiascincus* (discussed below). The magnitude of change within lineages is, however, much greater for thermal preferences than for optimal temperatures or for CTMax (Fig. 5), indicating that thermal preference evolves relatively rapidly. Evolutionary changes within lineages in T_o or in CTMax thus do not map 1:1 on changes in thermal preference, a result reaffirming the partial coadaptation seen in the equilibrium analysis.

We are now able to answer the question of whether the partial coadaptation seen in *Eremiascincus* and *Hemiergus* (Fig. 3) is ancestral or derived. For *Hemiergus* it is clearly derived. Coadaptation is weak in this genus, because its thermal preference has seemingly evolved towards a low temperature faster than has its optimal temperature for sprinting.

For *Eremiascincus*, the pattern may be more complex. Even though this genus has also evolved a low thermal preference, its critical thermal maximum (Greer, 1980) and perhaps its optimal temperature appear to have evolved to slightly higher temperatures (Fig. 5). Our phylogenetic analysis thus uncovers something missed by the equilibrium analysis—a possible case of behavior and performance evolving in opposite directions. These patterns should, however, be further tested, using phylogenies based on molecular data.

Partial Coadaptation and Antagonistic Coadaptation

In the Introduction we applied the term "partial coadaptation" to cases where traits evolve in the same direction, but not at the same rate (Fig. 1b). *Hemiergus* exemplifies a partially coadapted lizard: both its thermal preference and its thermal performance have shifted to low temperatures, but the change in T_p is much greater than that in T_o or CTMax. In *Eremiascincus*, however,

behavior and performance curves have seemingly evolved in opposite directions. Accordingly, we call this "antagonistic coadaptation," a term that reflects the antagonism inherent in the (presumably) conflicting selective pressures forcing the thermal preferences and optimal temperatures in opposite directions.

What are evolutionary bases of partial coadaptation and of antagonistic coadaptation? The existence of partial and of antagonistic coadaptation implies that the link between performance and fitness is not a simple or even direct one (Huey and Slatkin, 1976; Arnold, 1983). The key question is: how might selection favor or perhaps ignore the evolution of reduced locomotor performance? Our project was designed to document patterns of coadaptation, not to evaluate the links between performance and fitness. Nevertheless, we can speculate on these links and suggest several hypotheses.

First, speed simply might be unimportant to these skinks, such that any decrements in locomotor performance that result from a lowered thermal preference have little or no effect on fitness. In other words, the "fitness gradient" for speed might be low (Arnold, 1983). This argument might have some justification for *Hemiergis* skinks, which are slow at any temperature (Table 2) and are rarely found away from cover, but probably not for *Eremiascincus*, which ambush other lizards (Greer, 1979a).

A subsidiary hypothesis is that other performance traits (e.g., digestive efficiency) might be more important determinants of fitness in these lizards and therefore might show perfect coadaptation even though speed does not. The thermal sensitivity of other performance traits in these lizards is presently unknown. However, optimal temperatures of several performance traits (digestion, stamina, and hearing) are similar to those for speed in the few species of reptiles studied to date (Huey, 1982; Stevenson et al., 1985), suggesting that perfect coadaptation with these traits is unlikely.

Second, the fitness gradient between performance and fitness could be positive, but the evolutionary response of thermal performance to selection could be slow relative to that of thermal preference 1) because of low heritability, negative genetic correla-

tions, or weak selection (Falconer, 1981), 2) because of insufficient time for evolutionary equilibria to be established, or 3) because burrowing and nocturnal activity reduce selection pressures favoring coadaptation (see Henzell, 1982). This hypothesis predicts that coadaptation between behavior and performance should eventually be reestablished in *Eremiascincus* and *Hemiergis*. This hypothesis is presently difficult to evaluate: the genetic parameters for the thermal dependence of sprinting have not yet been examined in any reptile, and divergence times are unknown for these genera. Ultimately, breeding experiments may be necessary to evaluate this hypothesis. Even if this explanation holds for *Hemiergis*, it is unlikely to explain patterns involving *Eremiascincus*, unless genetic correlations are temporarily confounding evolutionary patterns (see Lande, 1980).

Third, speed might not always predict relative feeding success or predatory avoidance in comparisons between nocturnal versus diurnal species. For example, the speeds of *Hemiergis* and of *Eremiascincus* are slow relative to those of most diurnal genera (Table 2) but could actually be associated with increased feeding success and fitness if the overall capture rate of prey is relatively high at night (Huey and Pianka, 1983). Capture rates could be high either because nocturnal prey are also slow or because they are abundant. Similarly, slow speeds of nocturnal lizards need not necessarily increase risk of predation.

Fourth, perhaps the paradox of antagonistic coadaptation is associated with the evolution of nocturnal/crepuscular habits and reflects conflicting selective pressures on thermal preference versus those on the thermal sensitivity of performance. Low T_p values are common among nocturnal lizards in several lineages and appear to be ecologically advantageous for reasons outlined above (Huey and Slatkin, 1976; Huey, 1982). Although the evolution of a low T_p would be expected to drive selection for a lowered T_o for sprinting (Fig. 1a), this might sometimes be resisted by conflicting advantages of maintaining locomotor performance at high body temperatures (Fig. 1b, c).

Selection could favor maintenance of per-

formance at high T_b in two ways. First, if most predation on these nocturnal lizards takes place primarily by day rather than by night, then selection might favor maintenance of high optimal temperatures for sprinting, as this would facilitate escape from diurnal predators. However, the cryptozoic habits of these lizards makes high predation by day unlikely (but see Shine [1984]).

Alternatively, if lizards in their retreats are exposed to high and potentially dangerous temperatures during the day, then selection might favor the ability to survive such exposure (Greer, 1980), even at the expense of reduced sprint capacity at night (see Fig. 1b, c). According to this view, the evolution of performance curves reflects a balance between selection on traits that optimize performance at normal activity temperatures (Huey, 1982) and on those that ensure survival at extreme temperatures (e.g., a high CTMax; see Greer, 1980; Heinrich, 1981; van Berkum, 1985). This hypothesis assumes that it is difficult or impossible to evolve a "Panglossian" nocturnal skink—one that has a high CTMax but a low T_o .

This alternative hypothesis is subject to comparative tests: it predicts that T_o and CTMax should be higher for nocturnal lizards living in the interior than for those in the periphery, for shallow soil temperatures (where many nocturnal lizards spend the day) are often very high in Australian deserts (Heatwole, 1970). Comparisons of *Eremiascincus* and *Hemiergis* support this hypothesis: T_o and CTMax are higher in *Eremiascincus* (Tables 1, 3). Interestingly, *Lerista* is another interior genus (a derivative of the diurnal genus *Ctenotus* [Greer, 1979b]) that is nocturnal: it has lowered T_p (30°C) (Rawlinson, 1974) but nevertheless maintains a high CTMax ($\bar{x} = 43.2^\circ\text{C}$) (Greer, 1980). Alternative comparisons might involve a genus or species that occurs in both peripheral and interior areas. This would reduce potentially confounding effects of differences in habits and body shape of the skinks studied here. In any case, the assumption that interior nocturnal species are exposed to high temperatures by day requires documentation. It is probably invalid for species inhabiting spinifex (*Triodia*) clumps (Cogger, 1984).

These comparative patterns support the idea that the ability to survive high temperatures may sometimes outweigh the advantages of tight coadaptation between behavior and performance. If true, this reasoning could help explain why *Hemiergis* is not fully coadapted; it could also explain why *Eremiascincus* shows antagonistic coadaptation. Even though nocturnal activity with slow sprint capacity would seem less advantageous than nocturnal activity with higher sprint capacity, the ability to survive in deserts at all may more than compensate for this apparent disadvantage. Adequacy—not optimality—might guide the evolution of thermal performance and behavior (Bartholomew, 1986).

Importance of a Phylogenetic Approach

This study demonstrates advantages of a phylogenetic approach to comparative studies (see also Lauder, 1981; Ridley, 1983; Clutton-Brock and Harvey, 1984; Felsenstein, 1985; Cheverud et al., 1985; Huey and Bennett, 1986; Huey, 1987). The availability of phylogenetic information facilitates speculation on the directions of evolutionary change. Sometimes the direction of change might not influence the adaptive interpretations, but it clearly does here. Consider how our interpretation would have changed if *Sphenomorphus* had evolved from an *Eremiascincus*-like ancestor rather than the reverse. The relatively close correspondence of thermal preferences and optimal temperatures in *Sphenomorphus* would suggest that evolution had favored coadaptation and thus perfected the match between behavior and performance. Just the opposite appears to be true.

Another advantage of a phylogenetic approach is evident. The "equilibrium," non-phylogenetic approach exemplified in Figure 3 suggests that partial coadaptation characterizes the evolution of thermal preference and optimal temperatures for skinks. Only by considering phylogenetic information for very close relatives (*Eremiascincus* vs. *Sphenomorphus*) were we able to determine the limits of that generalization.

ACKNOWLEDGMENTS

We sincerely thank D. Bradford, C. Daniels, H. and K. John-Alder, G. J. Kenagy,

B. Martin, T. Schwaner, and M. Thompson for help in collecting the lizards used in this study. W. Osborne and I. Pulsford recommended collecting localities in the Snowy Mountains. A. E. Greer and T. Schwaner verified identifications. A. E. Greer and P. Baverstock provided critical systematic advice. S. R. Crowley, A. E. Greer, F. H. van Berkum, and two anonymous reviewers made helpful comments on the manuscript. R. Seymour generously made available his laboratory space and facilities. J. Felsenstein shared his expertise on phylogenetic methods and guided us through the analysis. G. J. Kenagy, R. S. Strathmann, and L. Van Valen asked questions that helped us to extend the analyses.

This research was funded primarily by NSF grant PCM 81-02331 to A. F. B. and secondarily by DEB-81-02124 and BSR-8415855 to R. B. H.

LITERATURE CITED

- ARNOLD, S. J. 1983. Morphology, performance and fitness. *Amer. Zool.* 23:347-361.
- ARNOLD, S. J., AND A. F. BENNETT. 1984. Behavioural variation in natural populations. III. Antipredator displays in the garter snake *Thamnophis radix*. *Anim. Behav.* 32:1108-1118.
- AVERY, R. A. 1982. Field studies of body temperatures and thermoregulation, pp. 93-166. *In* C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, Vol. 12. Academic Press, N.Y.
- BARBAULT, R. 1974. Ecologie comparée des Lézards *Mabuya blandingi* (Hallowell) et *Panaspis kitsoni* (Boulenger) dan le forêt de Lamto (Côte-d'Ivoire). *Terre Vie* 28:95-117.
- BARTHOLOMEW, G. A. 1964. The roles of physiology and behaviour in the maintenance of homeostasis in the desert environment. *Symp. Soc. Exp. Biol.* 18:7-29.
- . 1986. The role of natural history in contemporary biology. *BioScience* 36:324-329.
- BENNETT, A. F. 1980. The thermal dependence of lizard behaviour. *Anim. Behav.* 26:455-462.
- BENNETT, A. F., AND W. R. DAWSON. 1976. Metabolism, pp. 127-223. *In* C. Gans and W. R. Dawson (eds.), *Biology of the Reptilia*, Vol. 5. Academic Press, N.Y.
- BENNETT, A. F., R. B. HUEY, AND H. JOHN-ALDER. 1986. Body temperature, sprint speed, and muscle contraction kinetics in lizards. *Physiologist* 29:179.
- BENNETT, A. F., AND H. JOHN-ALDER. 1986. Thermal relations of some Australian skinks (Sauria:Scincidae). *Copeia* 1986:57-64.
- BOGERT, C. M. 1949. Thermoregulation in reptiles, a factor in evolution. *Evolution* 3:195-211.
- BOWKER, R. G. 1984. Precision of thermoregulation of some African lizards. *Physiol. Zool.* 57:401-412.
- CHEVERUD, J. M., M. M. DOW, AND W. LEUTENEGGER. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: Sexual dimorphism in body weight in primates. *Evolution* 39:1335-1351.
- CHRISTIAN, K. A., AND C. R. TRACY. 1981. The effect of the thermal environment on the ability of hatching Galápagos land iguanas to avoid predation during dispersal. *Oecologia* 49:218-223.
- CLUTTON-BROCK, T. H., AND P. H. HARVEY. 1984. Comparative approaches to investigating adaptation, pp. 7-29. *In* J. R. Krebs and N. B. Davies (ed.), *Behavioural Ecology: An Evolutionary Approach*. Sinauer, Sunderland, MA.
- COGGER, H. G. 1983. *Reptiles and Amphibians of Australia*. A. Reed, Sydney, Australia.
- . 1984. Reptiles in the Australian arid zone, pp. 235-252. *In* H. G. Cogger and E. E. Cameron (eds.), *Arid Australia*. Australian Museum, Sydney, Australia.
- COWLES, R. B., AND C. M. BOGERT. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Amer. Mus. Nat. Hist.* 83:265-296.
- CROWLEY, S. R. 1985. Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: Support for a conservative view of thermal physiology. *Oecologia* 66:219-225.
- CROWLEY, S. R., AND R. D. PIETRUSZKA. 1983. Aggressiveness and vocalization in the leopard lizard (*Gambelia wislizenii*): The influence of temperature. *Anim. Behav.* 31:1055-1060.
- DAWSON, N. R., G. A. BARTHOLOMEW, AND A. F. BENNETT. 1977. A reappraisal of the aquatic specializations of the Galapagos marine Iguana (*Amblyrhynchus cristatus*). *Evolution* 31:891-897.
- DOBZHANSKY, TH. 1955. A review of some fundamental concepts and problems of population genetics. *Cold Spr. Harb. Symp. Quant. Biol.* 20:1-15.
- EDWARDS, A. W. F., AND L. L. CAVALLI-SFORZA. 1964. Reconstruction of evolutionary trees, pp. 67-76. *In* V. H. Heywood and J. McNeill (eds.), *Phenetic and Phylogenetic Classification*. Systematics Assoc., London, U.K.
- FALCONER, D. S. 1981. *Introduction to Quantitative Genetics*, 2nd ed. Longman, London, U.K.
- FELSENSTEIN, J. 1983. Parsimony in systematics: Biological and statistical issues. *Ann. Rev. Ecol. Syst.* 14:313-333.
- . 1985. Phylogenies and the comparative method. *Amer. Natur.* 125:1-15.
- GANS, C. 1974. *Biomechanics: An Approach to Vertebrate Biology*. Lippincott, Philadelphia, PA.
- GREENWALD, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. *Copeia* 1974:141-148.
- GREER, A. E. 1979a. *Eremiascincus*, a new generic name for some Australian sand swimming skinks (Lacertilia: Scincidae). *Rec. Aust. Mus.* 32:321-338.
- . 1979b. A phylogenetic subdivision of Australian skinks. *Rec. Aust. Mus.* 32:339-371.
- . 1980. Critical thermal maximum temperatures in Australian scincid lizards: Their ecological and evolutionary significance. *Aust. J. Zool.* 28:91-102.
- . 1985. Lygosomine (Scincidae) monophyly: A third corroborating character and a reply to critics. *J. Herpetol.* 20:123-126.

- HEATWOLE, H. 1970. Thermal ecology of the desert dragon *Amphibolurus inermis*. Ecol. Monogr. 40: 425-457.
- . 1976. Reptile Ecology. Univ. Queensland Press, St. Lucia, Australia.
- HEINRICH, B. 1981. Ecological and evolutionary perspectives, pp. 235-302. In B. Heinrich (ed.), Insect Thermoregulation. Wiley, N.Y.
- HENZELL, R. P. 1982. Adaptation to aridity in lizards of the *Egernia whitei*: Species-group, pp. 229-233. In W. R. Barker and P. J. M. Greenslade (eds.), Evolution of the Flora and Fauna of Arid Australia. Peacock, Adelaide, Australia.
- HERTZ, P. E., R. B. HUEY, AND E. NEVO. 1982. Flight versus flight: Body temperature influences defensive responses of lizards. Anim. Behav. 30:676-679.
- . 1983. Homage to Santa Anita: Thermal sensitivity of sprint speed in agamid lizards. Evolution 37:1075-1084.
- HUEY, R. B. 1982. Temperature, physiology, and the ecology of reptiles, pp. 25-91. In C. Gans and F. H. Pough (eds.), Biology of the Reptilia, Vol. 12. Academic Press, N.Y.
- . 1983. Natural variation in body temperature and physiological performance in a lizard (*Anolis cristatellus*), pp. 484-490. In A. G. J. Rhodin and K. Miyata (eds.), Advances in Herpetology and Evolutionary Biology—Essays in Honor of Ernest E. Williams. Harvard Univ. Press, Cambridge, MA.
- . 1987. Phylogeny, history, and the comparative method. In M. E. Feder, A. F. Bennett, W. Burggren, and R. B. Huey (eds.), New Directions in Ecological Physiology. Cambridge University Press, Cambridge, U.K. In press.
- HUEY, R. B., AND A. F. BENNETT. 1986. A comparative approach to field and laboratory studies in evolutionary biology, pp. 82-98. In M. E. Feder and G. V. Lauder (eds.), Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates. Univ. Chicago Press, Chicago, IL.
- HUEY, R. B., AND P. E. HERTZ. 1984. Effects of body size and slope on acceleration of a lizard (*Stellio (Agama) stellio*). J. Exp. Biol. 110:113-123.
- HUEY, R. B., AND E. R. PIANKA. 1983. Temporal separation of activity and interspecific dietary overlap, pp. 281-290. In R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), Lizard Ecology: Studies of a Model Organism. Harvard Univ. Press, Cambridge, MA.
- 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: A discussion of approaches. Amer. Zool. 19:357-366.
- HUTCHINSON, M. N. 1981. The systematic relationships of the genera *Egernia* and *Tiliqua* (Lacertilia: Scincidae). A review and immunological reassessment, pp. 176-193. In C. B. Banks and A. A. Martin (eds.), Proceedings of the Melbourne Herpetological Symposium. Zoological Board of Victoria, Melbourne, Australia.
- HUTCHISON, V. H., AND J. D. MANESS. 1979. The role of behavior in temperature acclimation and tolerance in ectotherms. Amer. Zool. 19:367-384.
- JENKINS, R., AND R. BARTELL. 1980. A Field Guide to Reptiles of the Australian High Country. Inkata, Melbourne, Australia.
- JOHN-ALDER, H. B., AND A. F. BENNETT. 1987. Thermal adaptation in lizard muscle function. J. Comp. Physiol. B 157:241-252.
- JOHNSON, C. R. 1977. Thermoregulation in four Australian lizards of the genus *Egernia* (Sauria: Scincidae). Zool. J. Linn. Soc. 60:381-390.
- KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 24:244-256.
- LANDE, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 33:292-305.
- LAUDER, G. V. 1981. Form and function: Structural analysis in evolutionary morphology. Paleobiology 7:430-442.
- LEWONTIN, R. C. 1969. The bases of conflict in biological explanation. J. Hist. Biol. 2:35-45.
- LICHT, P., W. R. DAWSON, AND V. H. SHOEMAKER. 1969. Thermal adjustments in cardiac and skeletal muscles of lizards. Z. vergl. Physiol. 65:1-14.
- LICHT, P., W. R. DAWSON, V. H. SHOEMAKER, AND A. R. MAIN. 1966. Observations on the thermal relations of western Australian lizards. Copeia 1966: 97-110.
- MAYR, E. 1959. The emergence of evolutionary novelties, pp. 349-380. In S. Tax (ed.), Evolution after Darwin, Vol. 1. Univ. Chicago Press, Chicago, IL.
- . 1963. Animal Species and Evolution. Belknap, Cambridge, MA.
- PIANKA, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in Western Australia. Ecology 50:1012-1030.
- . 1986. Ecology and Natural History of Desert Lizards. Princeton Univ. Press, Princeton, NJ.
- PORTER, W. P., J. W. MITCHELL, W. A. BECKMAN, AND C. B. DEWITT. 1973. Behavioral implications of mechanistic ecology. Oecologia 13:1-54.
- RAND, A. S. 1964. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology 45:863-864.
- RAWLINSON, P. A. 1974. Biogeography and ecology of the reptiles of Tasmania and the Bass Strait area, pp. 291-309. In W. D. Williams (ed.), Biogeography and Ecology in Tasmania. Junk, The Hague, Neth.
- RIDLEY, M. 1983. The Explanation of Organic Diversity. The Comparative Method and Adaptations for Mating. Clarendon, Oxford, U.K.
- SHINE, R. 1984. Ecology of small fossorial Australian snakes of the genera *Neelaps* and *Simoselaps* (Serpentes, Elapidae), pp. 173-183. In R. A. Siegel, L. E. Hunt, J. L. Knight, L. Malaret, and N. L. Zuschlag (eds.), Vertebrate Ecology and Systematics: Tribute to Henry S. Fitch. Mus. Nat. Hist. Univ. Kansas, Lawrence.
- SLOBODKIN, L. B., AND A. RAPOPORT. 1974. An optimal strategy of evolution. Quart. Rev. Biol. 49: 181-200.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd Ed. Freeman, San Francisco, CA.
- SPELLERBERG, I. F. 1972a. Temperature tolerances of southeast Australian reptiles examined in relation

- to reptile thermoregulatory behaviour and distribution. *Oecologia* 9:23-46.
- . 1972b. Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. I. The environment and lizard critical temperatures. *Oecologia* 9:371-383.
- . 1972c. Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. II. Physiological aspects of thermoregulation. *Oecologia* 9: 358-398.
- . 1972d. Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. III. Behavioural aspects of thermoregulation. *Oecologia* 11:1-16.
- STEVENSON, R. D., C. R. PETERSON, AND J. S. TSUJI. 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiol. Zool.* 58: 46-57.
- TRACY, C. R. 1982. Biophysical modelling of reptilian physiology and ecology, pp. 275-321. In C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, Vol. 12. Academic Press, N.Y.
- VAN BERKUM, F. H. 1985. The thermal sensitivity of sprint speeds in lizards: The effects of latitude and altitude. Ph.D. Diss. Univ. Washington, Seattle.
- . 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution* 40:594-604.
- VAN BERKUM, F. H., R. B. HUEY, AND B. A. ADAMS. 1986. Physiological consequences of thermoregulation in a tropical lizard (*Ameiva festiva*). *Physiol. Zool.* 59:464-472.
- WATROUS, L. E., AND Q. D. WHEELER. 1981. The out-group comparison method of character analysis. *Syst. Zool.* 30:1-11.
- WEBB, P. W. 1976. The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator-prey interactions. *J. Exp. Biol.* 65:157-177.
- WILHOFT, D. C. 1961. Temperature responses in two tropical Australian skinks. *Herpetologica* 17:109-113.
- WITHERS, P. C. 1981. Physiological correlates of limblessness and fossoriality in scincid lizards. *Copeia* 1981:197-204.
- WRIGHT, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proc. XI Internat. Congr. Genet.* 1:356-366.
- WYLES, J. S., J. G. KUNKEL, AND A. C. WILSON. 1983. Birds, behavior, and anatomical evolution. *Proc. Nat. Acad. Sci. USA* 80:4394-4397.