

EVOLUTION OF SPRINT SPEED IN LACERTID LIZARDS: MORPHOLOGICAL, PHYSIOLOGICAL, AND BEHAVIORAL COVARIATION

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Abstract.—Organismal performance abilities occupy a central position in phenotypic evolution; they are determined by suites of interacting lower-level traits (e.g., morphology and physiology) and they are a primary focus of natural selection. The mechanisms by which higher levels of organismal performance are achieved during evolution are therefore fundamentally important for understanding correlated evolution in general and coadaptation in particular. Here we address correlated evolution of morphological, physiological, and behavioral characteristics that influence interspecific variation in sprint speed in a clade of lacertid lizards. Phylogenetic analyses using independent contrasts indicate that the evolution of high maximum sprinting abilities (measured on a photocell-timed racetrack) has occurred via the evolution of (1) longer hind limbs relative to body size, and (2) a higher physiologically optimum temperature for sprinting. For ectotherms, which experience variable body temperatures while active, sprinting abilities in nature depend on both maximum capacities and relative performance levels (i.e., percent of maximum) that can be attained. With respect to temperature effects, relative performance levels are determined by the interaction between thermal physiology and thermoregulatory behavior. Among the 13 species or subspecies of lizards in the present study, differences in the optimal temperature for sprinting (body temperature at which lizards run fastest) closely matched interspecific variation in median preferred body temperature (measured in a laboratory photothermal gradient), indicating correlated evolution of thermal physiology and thermal preferences. Variability of the preferred body temperatures maintained by each species is, across species, negatively correlated with the thermal-performance breadth (range of body temperatures over which lizards can run relatively fast). This pattern leads to interspecific differences in the levels of relative sprint speed that lizards are predicted to attain while active at their preferred temperatures. The highest levels of predicted relative performance are achieved by species that combine a narrow, precise distribution of preferred temperatures with the ability to sprint at near-maximum speeds over a wide range of body temperatures. The observed among-species differences in predicted relative speed were positively correlated with the interspecific variation in maximum sprinting capacities. Thus, species that attain the highest maximum speeds are (1) also able to run at near-maximum levels over a wide range of temperatures and (2) also maintain body temperatures within a narrow zone near the optimal temperature for sprinting. The observed pattern of correlated evolution therefore has involved traits at distinct levels of biological organization, that is, morphology, physiology, and behavior; and trade-offs are not evident. We hypothesize that this particular trait combination has evolved in response to coadaptational selection pressures. We also discuss our results in the context of possible evolutionary responses to global climatic change.

Key words.—Body size, coadaptation, comparative method, correlated evolution, lizards, locomotion, morphology, physiology, sprint speed, temperature.

Received July 9, 1993. Accepted May 10, 1994.

Natural selection is thought to act most directly on ecologically relevant performance abilities (Arnold 1983) or on behavioral variation that may sometimes act as a filter between performance capacities and selection (Garland et al. 1990; Garland and Losos 1994). The mechanisms by which higher levels of organismal performance are achieved through evolution are therefore fundamentally important for understanding the process of coadaptation. The concept of coadaptation, the evolution of particular combinations of distinct phenotypic traits in response to natural selection, is based on the notion that it is the interaction among traits that determines performance, and hence fitness (Mayr 1963; Arnold 1983; Huey and Bennett 1987; Emerson and Arnold 1989). This paradigm would be substantiated by observations

of correlated evolution of traits at distinct levels of biological organization (e.g., morphology, physiology, and behavior), with effects that jointly determine organismal performance capacities (Emerson and Arnold 1989). Such character associations are obvious in comparisons of organisms that differ profoundly in life-style (e.g., aquatic, terrestrial, and flying vertebrates). However, more critical insights would be obtained by the analysis of correlated evolution within a group of phylogenetically closely related organisms (Feder 1987; Emerson and Arnold 1989). Here we examine correlated evolution of disparate phenotypic characteristics that affect sprinting abilities in a clade of lizards.

Maximum sprint speed is an ecologically relevant index of organismal performance capacity (e.g., Huey and Stevenson 1979; Huey and Bennett 1987; Hertz et al. 1988; Bennett and Huey 1990; Garland and Losos 1994), and some evidence suggests that variation in sprinting ability can affect survival probabilities within populations of reptiles (Christian and Tracy 1981; Jayne and Bennett 1990). A variety of phenotypic

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traits can influence sprinting performance of lizards. Morphological and physiological characteristics constrain maximum burst speeds (Garland 1985; Bennett 1989; Losos 1990; Garland and Losos 1994). Behavior also can influence speed: for example, the body temperatures achieved by ectotherms during activity will alter sprint capacities via the effects of temperature on the rate of biochemical and physiological processes (e.g., Huey and Stevenson 1979; Bennett 1980; van Berkum 1986; Huey and Bennett 1987; Huey and Kingsolver 1989; Van Damme et al. 1989, 1991). The interaction between thermoregulatory behavior and thermal physiology therefore determines the levels of relative (percent of maximum) sprint speed that can be attained during routine activities. To maximize relative sprint speed, the body temperatures behaviorally selected by ectotherms should match the thermal sensitivity of sprint speed (Huey and Bennett 1987; Huey et al. 1989; Garland et al. 1991). Natural selection, however, should act on what we term "realized performance," the actual speed that can be achieved by an active lizard (Huey and Bennett 1987; Garland and Losos 1994); realized performance is the product of maximum and relative performance abilities. If realized performance is of the greatest selective importance, then one would predict the correlated evolution of all properties (morphology, physiology, and behavior) that influence maximum and/or relative performance. We tested this hypothesis through a comparative study of lacertid lizards.

We studied 13 species or subspecies of lacertid lizards. To minimize potentially confounding factors (Huey and Bennett 1986; Losos 1990; Brooks and McLennan 1991; Harvey and Pagel 1991), we chose species that are relatively closely related and that form a homogeneous group with respect to many aspects of their general biology. All species are highly similar in general body shape, active-searching foraging mode, a predominantly arthropod-based diet, and diurnal activity patterns (Arnold 1987). The lacertid lizards studied are either primarily terrestrial, or partly saxicolous and partly ground dwelling. All species thermoregulate behaviorally by restricting activity times, shuttling between sun and shade, and altering body postures, thus maintaining their body temperatures within a relatively narrow range (Avery 1982; Arnold 1987; Van Damme et al. 1987, 1989; Castilla and Bauwens 1991). The species have different, although partly overlapping, geographic distributions and habitat preferences (Arnold 1987).

Patterns of character correlation among extant species are best able to provide information on evolutionary processes if analyses incorporate phylogenetic information (Brooks and McLennan 1991). Moreover, the hierarchical nature of evolutionary descent with modification dictates that comparative analyses must employ statistical methods that incorporate estimates of phylogenetic relationships (Harvey and Pagel 1991; Martins and Garland 1991; Garland et al. 1993). We therefore analyzed our data in an explicitly phylogenetic context, using Felsenstein's (1985) method of phylogenetically independent contrasts.

We first explore evolutionary changes in lower-level morphological and physiological traits in relation to changes in maximum sprinting abilities. Specifically, we test predictions of simple biomechanical and physiological models concerning mechanistic relationships; for example, maximum sprint

speed should be positively related to leg length. Next, we investigate interspecific covariation between a physiological trait, the thermal sensitivity of sprinting, and a behavioral characteristic, preferred body temperature. In particular, we examine how the interaction between these two traits affects relative sprint speed (percent of maximum). Finally, we examine evolutionary correlation between maximum sprinting abilities and predicted levels of relative sprint speed.

Our approach consists of integrating laboratory measurements of morphological variables, maximum sprint speed at different body temperatures, and preferred body temperatures. Obviously, selection operates on levels of organismal performance that are actually exhibited in nature. Hence, we make an important assumption: the interspecific differences in sprint speed and in preferred temperatures measured in the laboratory reflect parallel variation existing in nature. No data on running speeds under field conditions are available to test this assumption with respect to sprinting performance (e.g., see Hertz et al. 1988; Garland and Losos 1994). Nevertheless, nonquantified field observations indicate that species that ran fastest in the laboratory also sprinted fastest, most often, and over the longest distances in the field (cf. Bulova 1994). Previous studies indicate that activity body temperatures recorded in the field generally match preferred temperatures measured in the laboratory in diurnal lizards (Huey 1982). Field-active body temperatures are available for a subset of the species studied (Salvador and Argüello 1987; Van Damme et al. 1987, 1989; Braña 1991; Castilla and Bauwens 1991; Gil 1992). Although these studies differ in methodology, scope, and study periods, they indicate that the distributions of field active body temperatures closely resemble those of the preferred temperatures, except in some high altitude and high latitude populations at the onset of the activity period (cf. Hertz et al. 1988).

MATERIALS AND METHODS

General Procedures

We collected lizards during the summers of 1989–1991 at different sites in western and southwestern Europe. Species and sample sizes are listed in table 1. To minimize potential sexual, geographical, and seasonal variation, we used, for each species, only adult male lizards, caught within a small area (usually < 0.5 km²) and during the nonbreeding period.

Lizards were transported to the University of Salamanca (Spain) or the Field Biological Station at Kalmthout (Belgium). They were housed in small groups (three to five lizards) in terraria (0.5 × 1 m) that were filled with sand, grasses, stones, and bark. Food (mealworms, crickets, and fly larvae) and water were provided ad libitum. Lizards were tested within 2–3 wk of capture.

For each individual lizard, we recorded snout-vent length, body mass, tail length (only if intact), and hind-limb length (between the first femoral pore [which is consistently situated next to the anal scale] and the base of fourth toe with the hind limb stretched out laterally).

Data for some of the species treated here have been published elsewhere: *Lacerta vivipara* (Van Damme et al. 1991),

TABLE 1. Summary statistics (mean \pm 1 SE) of maximum sprinting speed and morphological traits for 13 species of lacertid lizards.

Species (N)	Maximum sprinting speed (cm/s)	Snout-vent length (mm)	Hindlimb length (mm)	Tail length (mm)	Mass (g)
<i>Psammodromus algirus</i> (13)	252.5 \pm 15.4	73.02 \pm 1.56	31.31 \pm 0.52	180.14 \pm 5.20	11.04 \pm 0.73
<i>Ps. hispanicus</i> (4)	149.9 \pm 34.5	40.27 \pm 1.05	15.75 \pm 0.54	64.82 \pm 2.38	1.43 \pm 0.08
<i>Lacerta monticola</i> (11)	156.6 \pm 18.9	69.38 \pm 0.83	27.81 \pm 0.26	130.90 \pm 4.12	7.65 \pm 0.29
<i>Podarcis bocagei</i> (15)	142.1 \pm 9.8	53.15 \pm 0.53	19.89 \pm 0.21	91.70 \pm 2.53	3.33 \pm 0.08
<i>P. h. hispanica</i> (9)	184.6 \pm 15.6	54.84 \pm 1.38	21.65 \pm 0.60	96.12 \pm 3.75	3.26 \pm 0.27
<i>P. h. atrata</i> (12)	152.7 \pm 12.0	68.07 \pm 0.71	24.01 \pm 0.12	135.73 \pm 1.44	7.55 \pm 0.14
<i>P. muralis</i> (15)	181.6 \pm 8.1	59.61 \pm 1.38	22.51 \pm 0.50	104.51 \pm 6.25	4.78 \pm 0.32
<i>P. lilfordi</i> (11)	233.7 \pm 11.0	67.02 \pm 0.66	27.64 \pm 0.28	103.23 \pm 2.61	7.83 \pm 0.31
<i>P. tiliguerta</i> (19)	241.1 \pm 8.4	59.89 \pm 0.37	24.84 \pm 0.16	120.48 \pm 1.51	4.75 \pm 0.08
<i>Acanthodactylus erythrurus</i> (9)	313.0 \pm 13.7	70.63 \pm 1.34	35.36 \pm 0.71	121.93 \pm 5.51	8.88 \pm 0.76
<i>Lacerta vivipara</i> (20)	90.0 \pm 4.7	50.26 \pm 0.48	16.83 \pm 0.23	86.34 \pm 1.40	2.83 \pm 0.10
<i>L. agilis</i> (9)	167.9 \pm 16.2	68.45 \pm 0.86	22.67 \pm 0.40	106.58 \pm 3.24	9.06 \pm 0.50
<i>L. schreiberi</i> (6)	178.5 \pm 14.8	92.60 \pm 2.45	32.50 \pm 1.18	177.50 \pm 6.50	21.23 \pm 1.25

Podarcis tiliguerta (Van Damme et al. 1989), *P. h. atrata* (Castilla and Bauwens 1991).

Preferred Body Temperatures

We constructed photo-thermal gradients by suspending a 150-W light bulb above one end of the lizards' home cages, thereby creating a gradient of air temperatures ranging from 20°–60°C. We recorded body temperatures of active lizards, using a thermocouple connected to a quick-reading electronic thermometer (DGT-Therma 3), with a minimum interval of 1 h between successive measurements on an individual. These readings were considered estimates of the behaviorally preferred (or "selected") body temperatures, and we assume that they index the temperatures that lizards would maintain in the absence of abiotic and biotic restrictions (Licht et al. 1966).

For each species, we pooled data from all individual lizards; the resulting distributions (fig. 1A) were slightly left skewed; thus, we used the median as an estimate of the central tendency (T_p). The preferred temperature breadth was defined as the range that includes the central 80% of all preferred temperature readings (fig. 1A). This is an estimate of the preference zone for behavioral thermoregulation. We arbitrarily chose the 80% level because it excludes outliers, for example, readings during the early morning warm-up, and yet does not lead to excessively narrow intervals, such as given by a 50% level (van Berkum 1988; Hertz et al. 1993), which we consider as biologically unrealistic for lacertid lizards.

Sprint Speed and Critical Thermal Maximum

Sprint speed was measured by chasing a lizard as fast as it would run along a 2-m racetrack, on a substrate of cork tiles that provided excellent traction. The track was equipped with photocells positioned at 25-cm intervals. Photocells were connected to a microcomputer that calculated sprint speed over each 50-cm section of the track. We ran lizards at a fixed sequence of body temperatures (35°, 30°, 25°, 37.5°, 32.5°, 40°C). Body temperature of lizards was controlled by placing them in an incubator at the appropriate test temperature for at least 1 h prior to testing. We then removed an individual lizard from the chamber, measured its body tem-

perature with a quick-reading electronic thermometer, and chased it down the track. Each run was scored as "poor," "good," or "excellent" (cf. van Berkum and Tsuji 1987; Tsuji et al. 1989). An individual lizard was raced three to five times at each body temperature, with a 1-h rest between trials. All trials at one temperature were performed on a single day. The body mass of lizards was measured every 2 d. We excluded from our analyses any lizard that lost more than 20% of its initial mass, was consistently scored as a "poor" runner, or clearly shifted its running performance during the course of the experiment. Less than 5% of the lizards were so eliminated. All lizards had intact or completely regenerated tails, and we excluded individuals that broke their tail during the course of the trials. The fastest burst speed recorded over any 50-cm interval during all trials at a given body temperature was selected as an estimate of an individual lizard's maximum sprinting ability at that temperature. Maximum sprinting speed is the fastest speed recorded for an individual lizard at any body temperature.

Subsequent to the running experiment, we assessed the critical thermal maximum (CTMax), the upper body temperature at which the righting response is lost, in a subset ($n = 5$) of individuals from each species. We heated a lizard continuously in an incubator at an approximate rate of 1°C/min, while observing its behavior. The body temperature associated with a transient loss of the righting response was used as an estimate of CTMax (Brattstrom 1971). After this experiment, all lizards were released at their site of capture.

To quantify the thermal sensitivity of sprint speed, we standardized performances among lizards by dividing an individual's speed at each temperature by its maximum sprinting speed. A speed of 0 cm/s was assigned to the CTMax, using the species' average value. For each individual, we constructed a thermal-sensitivity function by plotting standardized speed against body temperature (fig. 1B), and estimated relevant statistics by a modified minimum-polygon algorithm (van Berkum 1986). The optimal temperature for sprinting (T_o), that is, the body temperature at maximum speed (fig. 1B), was estimated by the midpoint of the body temperature range at which a lizard ran at more than 95% of its maximum speed. T_o is a convenient indicator of the position of the thermal sensitivity function on the body-temperature axis.

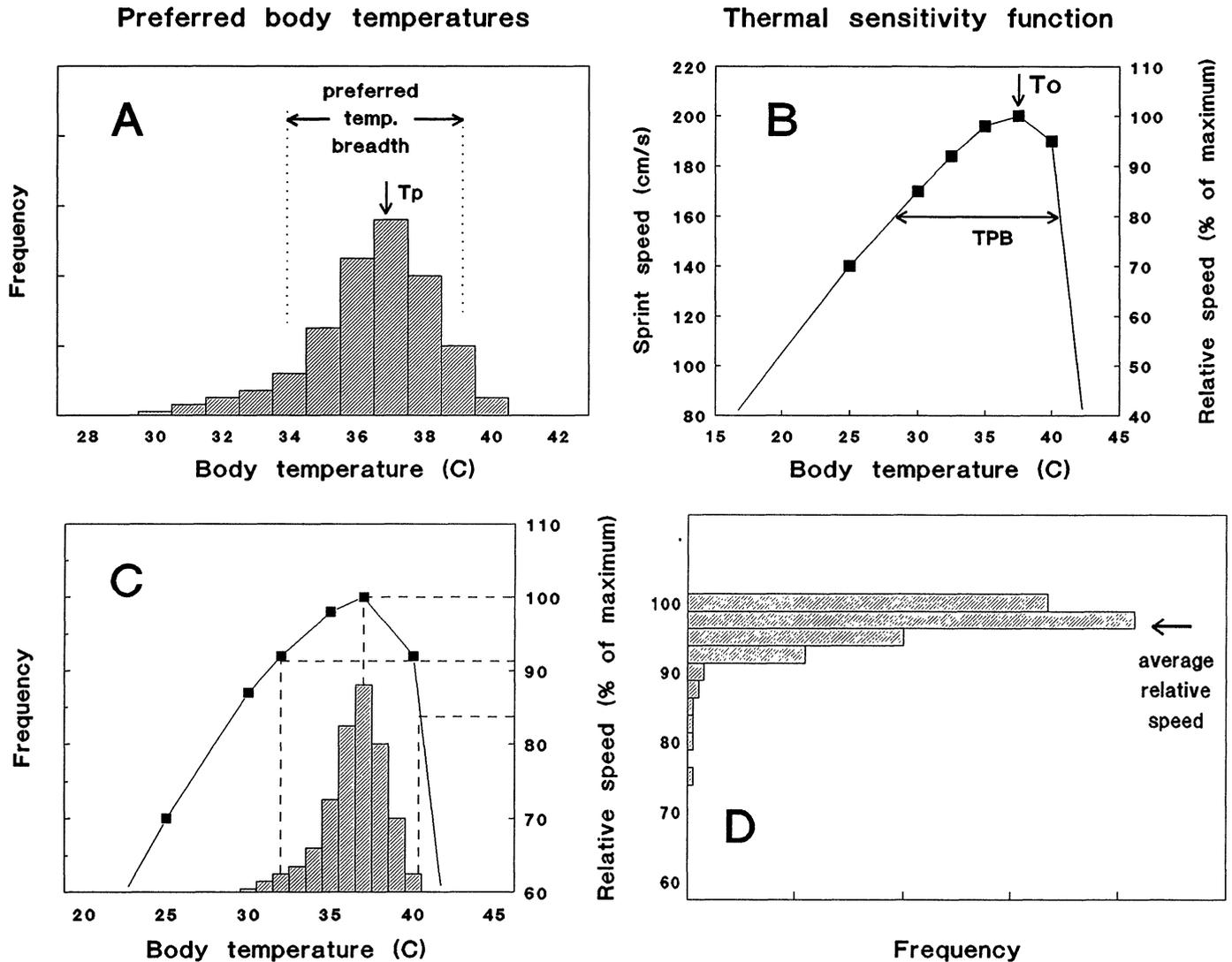


FIG. 1. Schematic diagram illustrating the variables that describe, for each species, the thermal preferences, the thermal sensitivity for sprint speed, and the predicted relative sprint speed at the preferred body temperatures. A. Distribution of preferred temperatures for a species showing the median value (T_p) and the preferred temperature breadth. B. Thermal-sensitivity function for sprint speed, indicating position of the optimal temperature (T_o) and the thermal-performance breadth (TPB). C. Superposition of the distribution of preferred temperatures on the thermal-sensitivity function. The predicted relative speed that corresponds to each preferred temperature is estimated by interpolation on the thermal-sensitivity function; the dotted lines show some examples. D. The resulting frequency distribution of predicted relative sprint-speed values (number of preferred temperature readings associated with a given level of predicted relative sprint speed). The position of the mean value from this distribution is indicated.

Thermal-performance breadth is the body temperature range over which speed is at least 80% of its maximum (fig. 1B). This statistic reflects the shape of the thermal-sensitivity function and is essentially a measure of the thermal independence of sprinting. A large thermal-performance breadth reflects a broad, flat thermal-sensitivity function, and implies that sprint speed is relatively independent of body temperature; a small thermal-performance breadth reveals a sharp, peaked thermal-sensitivity curve and indicates that speed changes rapidly with body temperature.

Predicted Relative Sprint Speed

Because of the effect of body temperature on sprinting performance, the maximum speed that can be achieved by a

lizard at a given time and place will depend on its body temperature. A lizard will be able to run at maximum speed only when its body temperature equals the optimal temperature for sprinting; any departure from this temperature will result in decreased sprinting capacities. To estimate how much sprint speed is depressed by activity at the preferred body temperatures, as compared with the optimal temperature for sprinting, we integrated the species-specific thermal sensitivity function with the distribution of preferred temperature readings. For each preferred temperature reading, we calculated the predicted relative sprint speed (percent of maximum sprint speed) by interpolation on the thermal sensitivity function (average standardized sprint speed at each experimentally set body temperature) for the corresponding species

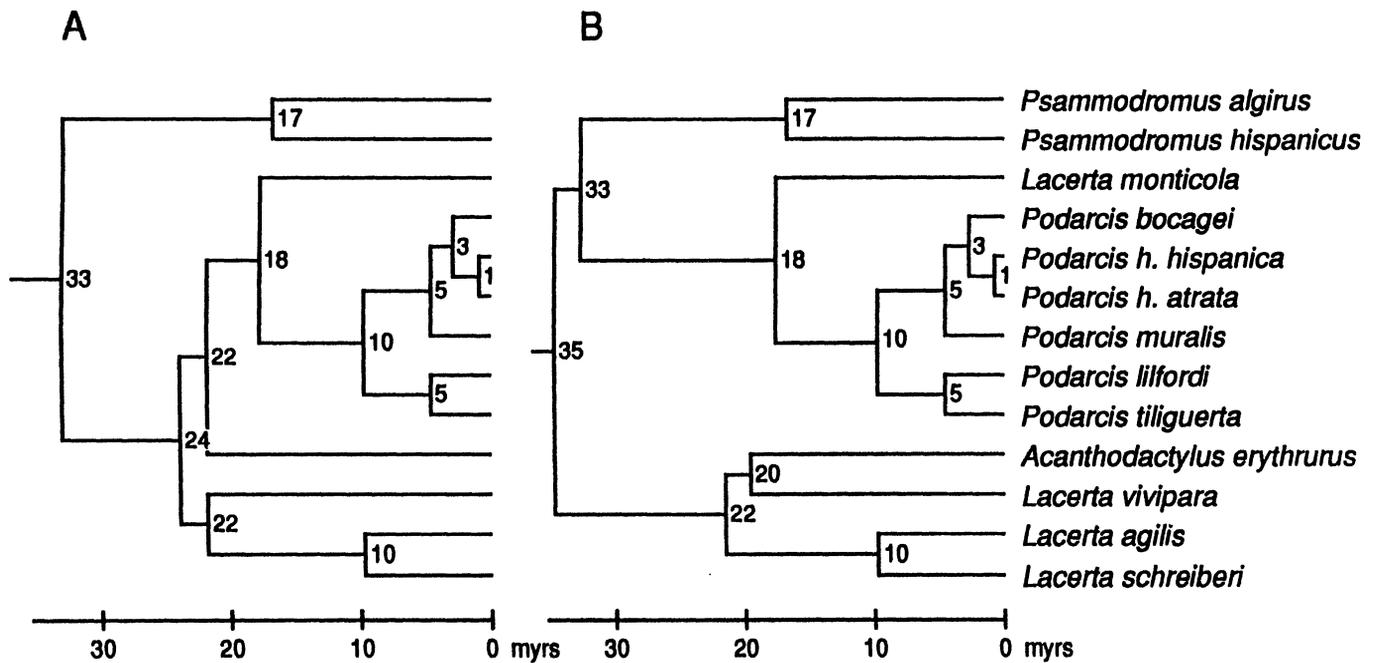


FIG. 2. Hypothesized phylogenetic relationships and estimated divergence times (numbers at nodes) for 13 species or subspecies of lacertid lizards. Branching patterns are based on (A) microcomplement-fixation of albumins and (B) external and internal morphological characteristics. Divergence times for main branching patterns are based on immunological distances and were used for both phylogenetic trees (see the Appendix).

(fig. 1C). From the resulting distribution we computed, for each species, the mean predicted relative sprint speed (fig. 1D). This is an estimate of the level (percent of maximum) of running performance at the species-specific preferred body temperature.

Phylogenetic Analyses

Comparative analyses of phenotypic correlations examine the extent of covariation for interspecific differences in two or more characters. In this context, traditional statistical procedures are generally invalid because hierarchical phylogenetic relationships of species imply that the phenotypes of different species cannot be considered as independent data points (Felsenstein 1985, 1988; Harvey and Pagel 1991; Garland et al. 1993). We therefore used the method of phylogenetically independent contrasts (Felsenstein 1985, 1988) to test for correlated evolutionary changes between pairs of phenotypic traits. This method uses information on the hypothesized phylogenetic relationships and separation times between sister taxa (the branch lengths of the phylogenetic tree) to transform the observed values of N extant species into $N - 1$ contrasts that are statistically independent. Of the currently available phylogenetically based statistical methods for continuous-valued characters (Miles and Dunham 1993), independent contrasts is the best understood and the best justified (see Grafen 1989; Harvey and Pagel 1991; Martins and Garland 1991; Garland 1992, 1994; Garland et al. 1992; Garland et al. 1993; Martins 1993; Pagel 1993; Martins MS). Simulations published by Gittleman and Luh (1992) suggested that the phylogenetic autocorrelation method might perform better for small numbers of species. Unfortunately,

these simulations are misleading because polytomies were not dealt with correctly when applying independent contrasts, thus reducing the number of contrasts used (see Purvis and Garland 1993). In fact, simulations by Martins (MS) show that independent contrasts actually perform far better than does the autocorrelation method when relatively few species are involved; Martins (MS) used 15 species, whereas our study involves 13 species or subspecies.

Currently, no consensus exists concerning phylogenetic relationships within the Lacertidae: phylogenies reconstructed using either immunological or morphological information yield conflicting results. We followed a conservative approach by analyzing our data using two phylogenies (fig. 2), which we consider as the currently best available hypotheses. Details of the reconstructions of both phylogenies are given in the Appendix. Estimates of divergence times are based on immunological distances and also were applied to the phylogeny based on morphological data. This implied that several arbitrary choices had to be made (see the Appendix). Because of this uncertainty in the assignment of divergence times, we conducted additional analyses on both phylogenetic trees with all branches set to unit lengths. These procedures allow us to evaluate the robustness of our results with respect to both the topology of the phylogeny and the branch lengths.

The adequacy of the branch lengths for standardization of the independent contrasts was verified by examining relations between the absolute value of standardized independent contrasts and their standard deviation (Garland et al. 1992). For the contrasts calculated with the nonunit branch lengths, no significant correlations were evident, except for thermal-performance breadth, which showed negative correlations. The

latter pattern was induced by the high value for a single contrast (*P. h. hispanica* vs. *P. h. atrata*), and bivariate scatterplots of the contrasts for thermal-performance breadth versus the contrasts of other variables did not reveal obvious patterns of nonlinearity or heteroscedasticity. Hence, untransformed branch lengths were used in all analyses (cf. Garland et al. 1991).

We performed a similar verification of the contrasts obtained with all branches set to unit length. This revealed significant negative correlations for thermal-performance breadth, and a strong tendency towards negative correlations for all morphometric traits (body length, hind-limb length, tail length, and body mass), preferred temperature breadth, and predicted relative sprint speed. Thus, this set of branch lengths does not seem to provide proper standardization of the independent contrasts, such that the results should be interpreted with caution. When the use of both sets of branch lengths yielded diverging results, we therefore favored the interpretation based on the analyses with variable branch lengths.

All reported correlation coefficients (r), path coefficients (β), and P -values refer to those obtained using phylogenetically independent contrasts. Unless otherwise noted, results reported in the text refer to those obtained using the phylogenies with nonunit branch lengths. Subscripts "A" or "B" are used to denote results pertaining to the alternative trees (those derived either from immunological or morphological information; fig. 2).

Statistical tests are one-tailed, unless otherwise noted, as they test specific, a priori, directional predictions concerning character correlations. In some cases, with one-tailed tests, estimates of correlation coefficients were not only nonsignificant but also opposite in sign to the a priori hypothesis. To indicate the strength of evidence for a relation in the direction opposite to our a priori prediction, we therefore report both the correlation coefficient and the P -value as compared with a two-tailed critical value. Inferring statistical significance in such cases must be done with caution.

To remove the effect of body length on any of the other morphometric traits (hind-limb length, tail length, and body mass), we computed residuals from the least-squares linear regression (through the origin) between the contrasts for a variable and the body-length contrasts (both variables log transformed before computing contrasts) (Garland et al. 1992). Maximum sprint-speed values also were log transformed, and estimates of predicted relative sprint speed were arcsine transformed before all analyses.

Estimates of bivariate regression slopes were based on reduced major-axis regression (using standardized independent contrasts; see Garland et al. 1992). We preferred this model over ordinary least-squares regression, because the latter will underestimate the true slope as our data do not satisfy the assumption that the independent variable has no associated error variance (LaBarbera 1989).

RESULTS

Determinants of Variation in Maximum Sprint Speed

Mean maximum sprinting speed varied among species by a factor of 3.5 (table 1). We first examine evolutionary

changes in maximum sprint speed in relation to morphological (table 1) and physiological traits (table 3) that affect stride length and/or stride frequency.

Biomechanical models predict that hind-limb length, through its effect on stride length, should be a major determinant of maximum sprinting capacities (Garland 1985; Losos 1990; Garland and Losos 1994). We therefore expect that (1) larger species, which have longer hind limbs, should run faster than smaller species and/or (2) species that have longer hind limbs relative to their body length should attain higher speeds than relatively short-legged species. Phylogenetically independent contrasts in hind-limb length were positively correlated with contrasts in body length ($r_A = 0.879$, $r_B = 0.872$, both $P < 0.001$), reflecting that larger species also tend to possess absolutely longer legs. We obtained variable statistical evidence for our first prediction. For the analyses using phylogenies with variable branch lengths, contrasts in body length did not explain a significant portion of the variation in maximum sprint-speed contrasts (fig. 3A). On the other hand, maximum sprint speed was positively related to body length for the analyses based on phylogenies with unit branch lengths (fig. 3B). However, as proper standardization of the body-length contrasts was not achieved using this set of branch lengths, we are more confident of the former results. Consistent with our second prediction, evolution of maximum speed was tightly related to the evolution of residual hind-limb length, that is, with the effect of body length removed (figs. 3A,B, 4). Other morphological traits (residual tail length and residual mass) did not explain a significant portion of the variation in maximum speed (path coefficients for residual tail length: $\beta_A = -0.026$, $\beta_B = -0.023$, both $P > 0.80$; residual mass: $\beta_A = 0.005$, $\beta_B = 0.008$, both $P > 0.90$).

Stride frequency is influenced mainly by physiological and biochemical processes affecting muscle-contraction speeds (references in Garland 1985; Gleeson and Harrison 1988; Losos 1990). Considerations of the thermodynamic properties of biochemical reactions lead to the hypothesis that the maximum performance capacities for a given physiological function should be augmented when the optimal temperature for that function increases (Hochachka and Somero 1984; Huey and Kingsolver 1989; Bennett 1990; Garland 1994). Hence, this hypothesis predicts that, across species, maximum sprint speed should be positively correlated with the optimal temperature for sprinting. In a multiple-regression analysis simultaneously accounting for the effect of body length and residual hind-limb length, maximum sprint speed was, as predicted, positively correlated with optimal temperature for sprinting. The path coefficients were marginally nonsignificant for the contrasts analyses with variable branch-length phylogenies (fig. 3A) and marginally significant for the analyses using phylogenies with unit branch lengths (fig. 3B).

Thus, morphological as well as physiological properties account for interspecific differences in maximum sprinting capacities (fig. 4). For the analyses based on phylogenies with variable branch lengths, contrasts in residual hind-limb length and optimal temperature for sprinting together explain more than 80% of the variation in maximum sprint speed contrasts (coefficients of determination of multiple regressions: $r_A^2 = 0.827$, $r_B^2 = 0.843$, both $P < 0.001$). Using the phylogenies

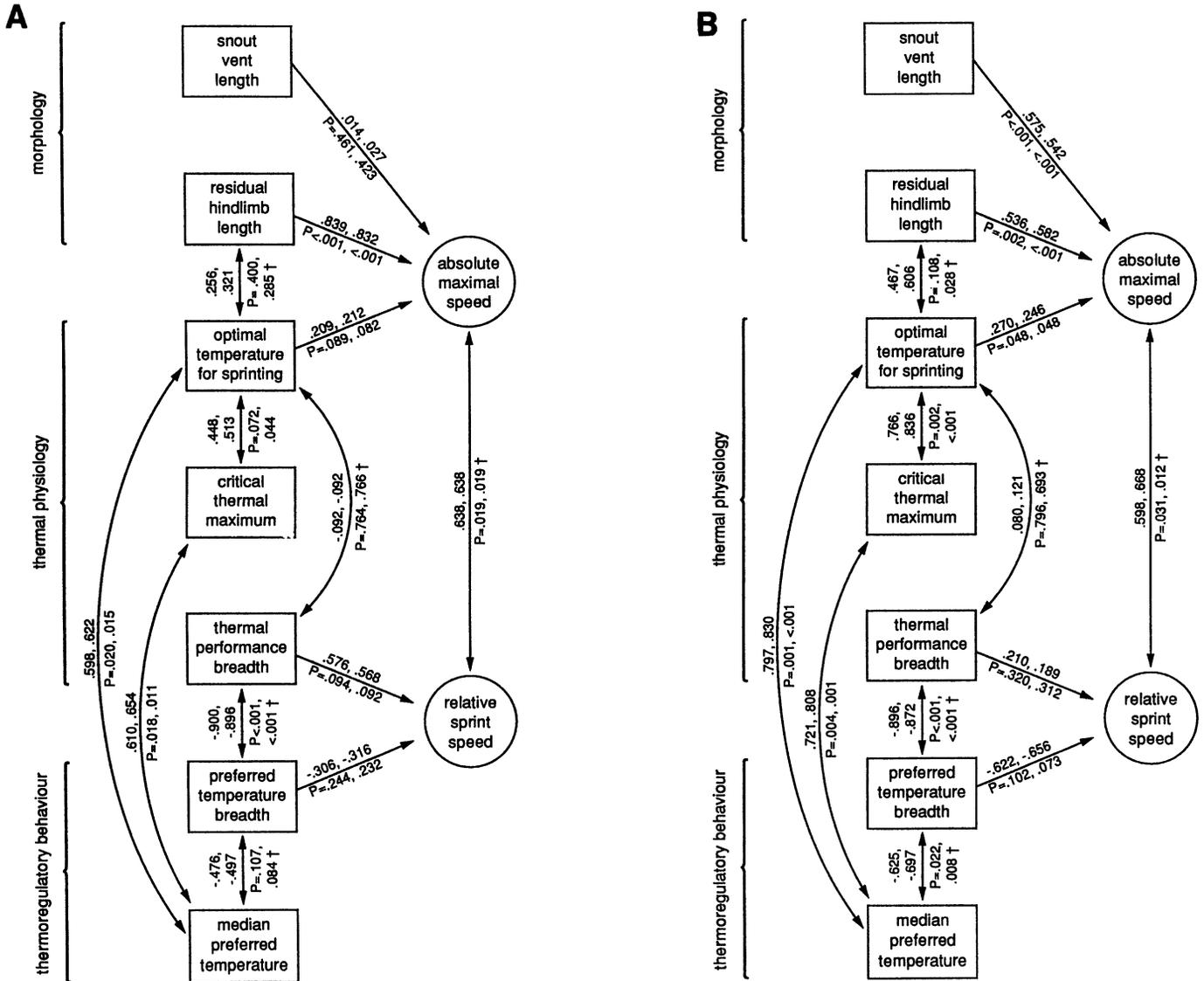


FIG. 3. Path diagram indicating evolutionary relationships of phenotypic traits, based on phylogenetically independent contrasts. Numbers above arrows are path coefficients for correlations (double-sided arrows) or hypothesized causal relationships (= standardized partial regression coefficients; single-sided arrows). First numbers are path coefficients obtained using topological relations in tree A of figure 2, second numbers are for tree B; associated probability levels (one-tailed, except †) are under the arrows. The path between snout-vent length and residual hind-limb length (from a regression on SVL) is omitted, simply because the correlation is necessarily zero. A. Results obtained for independent contrasts calculated using trees with variable branch lengths. B. Results obtained for independent contrasts calculated using trees with all branch lengths set equal to one.

with unit branch lengths, body length, residual hind-limb length, and optimal temperature for sprinting together explain more than 85% of the variation in maximum sprint speed (coefficients of determination of multiple regression: $r_A^2 = 0.853$, $r_B^2 = 0.904$, both $P < 0.001$).

Thermal Preferences and Thermal Sensitivity of Sprint Speed

The maximum among-species difference in median preferred temperature was only 4.65°C (table 3). Individuals of all species maintained their body temperature within a relatively narrow range, as evidenced by the width of the pre-

ferred temperature breadths (3.49°–5.29°C; table 3). These data indicate that these lacertid lizards constitute a fairly homogeneous group with respect to thermoregulatory preferences.

Body temperature has an important effect on sprinting abilities in all species (table 2, fig. 5). Thermal-sensitivity curves differed among species in their position along the temperature axis, as evidenced by variation in both optimal temperatures and critical thermal maxima (table 3). The observed variation in thermal-performance breadths (table 3, fig. 5) indicates among-species differences in the shape of the thermal-sensitivity functions.

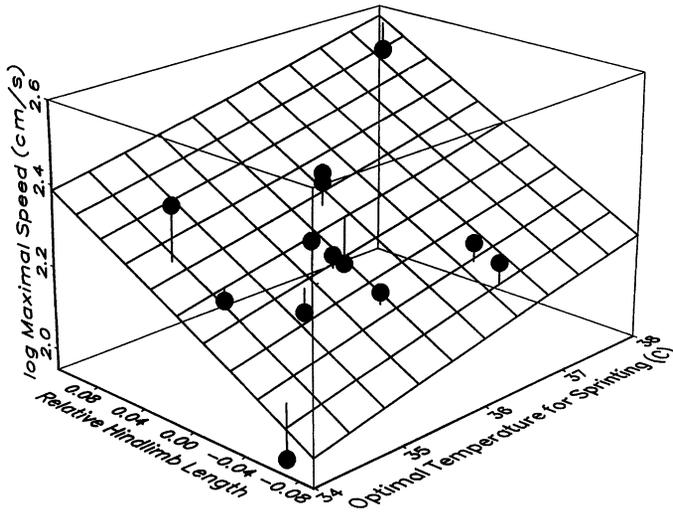


FIG. 4. Scatterplot, with multiple-regression plane, of raw species values showing positive relationships between maximum sprint speed, relative hind-limb length, and the optimal temperature for sprinting (see fig. 3 for independent contrasts path coefficients).

Because of the profound effect of body temperature on running performance, the thermal sensitivity of each species is hypothesized to match the body temperatures maintained during routine activities (Huey and Bennett 1987; Garland et al. 1991; Huey and Kingsolver 1993). In other words, lizards that are active at and prefer high body temperatures should have a high physiologically optimum temperature for sprinting. Moreover, species that prefer high temperatures should have a relatively high tolerance for high temperatures, as measured by the critical thermal maximum (CTMax). Consistent with these predictions, we found positive correlations between T_o and T_p , between CTMax and T_p , and between T_o

and CTMax (fig. 3A,B), irrespective of the phylogeny or set of branch lengths used. Slopes of these relations, estimated by reduced major-axis regression using independent contrasts (McArdle 1988; Garland et al. 1992), did not differ significantly from unity [T_o on T_p : $b_A \pm 1 \text{ SE} = 0.902 \pm 0.218$, $b_B = 0.864 \pm 0.204$; CTMax on T_p : $b_A = 1.322 \pm 0.316$, $b_B = 1.333 \pm 0.304$; T_o on CTMax: $b_A = 0.683 \pm 0.184$, $b_B = 0.648 \pm 0.168$; standards errors from least-squares regression slopes using independent contrasts (McArdle 1988)]. Thus, evolutionary changes in T_p are paralleled by approximately equivalent changes in T_o and CTMax.

Predicted Relative Sprint Speed

The predicted relative sprint speeds associated with the species-specific preferred temperatures were generally greater than 90% of maximum speed (table 3). Predicted relative sprint speed estimates the level (percent of maximum capacity) of running performance that lizards are expected to achieve while they are active at their preferred temperatures. It is essentially the product of the thermal-sensitivity curve and the distribution of preferred body temperatures (fig. 1). High levels of relative sprint speed could be achieved in one of two ways: body temperatures could be maintained in a narrow range near the optimal temperature (narrow preferred temperature breadth), or sprint performance could be largely independent of body temperature (broad thermal-performance breadth). Thus, evolution might compensate for a high variability in preferred body temperatures (i.e., a wide preferred temperature breadth) with a physiological capacity to perform well over a broad range of temperatures (i.e., a broad thermal-performance breadth). This would be manifested by a positive relation between the preferred temperature breadth and the thermal-performance breadth. In contrast to this prediction, we found a negative correlation that would have been

TABLE 2. Mean ($\pm 1 \text{ SE}$) absolute spring speeds (cm/s, first line) at different body temperatures for species of lacertid lizards. The actual body temperatures ($^{\circ}\text{C}$) recorded before running are indicated on the second line. Data for *Podarcis tiliguerta* and *Lacerta vivipara* are tabulated in Van Damme et al. (1989, 1991).

Species	25	30	32.5	35	37.5	40
<i>Psammodromus algirus</i>	153.6 \pm 16.8 (24.5 \pm 0.2)	216.9 \pm 13.2 (30.8 \pm 0.1)	231.6 \pm 13.8 (32.8 \pm 0.2)	238.9 \pm 14.7 (34.7 \pm 0.2)	223.0 \pm 18.0 (37.4 \pm 0.2)	201.1 \pm 16.4 (39.8 \pm 0.2)
<i>Ps. hispanicus</i>	79.1 \pm 20.3 (25.8 \pm 0.1)	89.1 \pm 18.3 (29.9 \pm 0.3)	111.7 \pm 23.3 (32.9 \pm 0.4)	135.9 \pm 27.5 (34.5 \pm 0.3)	133.6 \pm 34.4 (37.0 \pm 0.5)	109.2 \pm 24.6 (39.5 \pm 0.2)
<i>Lacerta monticola</i>	99.4 \pm 12.5 (26.6 \pm 0.6)	128.8 \pm 17.3 (30.3 \pm 0.2)	126.5 \pm 16.2 (32.6 \pm 0.1)	140.3 \pm 13.9 (34.9 \pm 0.1)	137.5 \pm 17.7 (37.3 \pm 0.2)	100.8 \pm 13.1 (40.0 \pm 0.2)
<i>Podarcis bocagei</i>	83.7 \pm 5.8 (26.2 \pm 0.1)	109.3 \pm 9.5 (30.8 \pm 0.1)	120.0 \pm 8.9 (32.7 \pm 0.2)	133.0 \pm 9.9 (35.0 \pm 0.2)	118.6 \pm 9.7 (37.6 \pm 0.2)	105.7 \pm 9.9 (39.7 \pm 0.2)
<i>P. h. hispanica</i>	98.7 \pm 8.0 (26.1 \pm 0.3)	141.7 \pm 9.7 (30.6 \pm 0.2)	162.9 \pm 12.5 (32.9 \pm 0.2)	164.7 \pm 16.6 (34.6 \pm 0.2)	168.9 \pm 18.8 (37.5 \pm 0.2)	141.4 \pm 12.4 (40.2 \pm 0.2)
<i>P. h. atrata</i>	65.4 \pm 7.9 (26.0 \pm 0.1)	81.8 \pm 6.2 (30.9 \pm 0.1)	107.4 \pm 14.3 (32.9 \pm 0.2)	119.1 \pm 7.0 (35.2 \pm 0.2)	119.8 \pm 15.2 (37.3 \pm 0.3)	111.2 \pm 15.7 (39.5 \pm 0.1)
<i>P. muralis</i>	116.7 \pm 5.8 (25.1 \pm 0.2)	143.9 \pm 6.5 (30.4 \pm 0.2)	151.0 \pm 7.9 (33.0 \pm 0.1)	173.7 \pm 7.3 (35.2 \pm 0.2)	168.5 \pm 10.0 (37.1 \pm 0.2)	142.0 \pm 9.1 (39.6 \pm 0.2)
<i>P. lilfordi</i>	135.3 \pm 8.9 (26.1 \pm 0.7)	176.7 \pm 12.0 (30.4 \pm 0.2)	195.2 \pm 13.2 (32.8 \pm 0.3)	203.9 \pm 10.1 (35.6 \pm 0.1)	212.8 \pm 11.6 (37.3 \pm 0.2)	194.9 \pm 12.6 (39.9 \pm 0.2)
<i>Acanthodactylus erythrurus</i>	197.1 \pm 12.3 (25.4 \pm 0.2)	250.9 \pm 13.4 (30.7 \pm 0.2)	269.3 \pm 14.4 (32.7 \pm 0.2)	279.2 \pm 15.9 (35.1 \pm 0.2)	283.5 \pm 17.9 (37.4 \pm 0.3)	296.3 \pm 12.8 (40.4 \pm 0.2)
<i>Lacerta agilis</i>	92.0 \pm 7.8 (25.9 \pm 0.1)	120.7 \pm 10.1 (30.7 \pm 0.1)	131.6 \pm 10.4 (33.3 \pm 0.2)	153.6 \pm 15.1 (35.5 \pm 0.1)	158.7 \pm 18.3 (37.7 \pm 0.2)	136.9 \pm 12.6 (39.5 \pm 0.2)
<i>L. schreiberi</i>	111.1 \pm 11.3 (24.8 \pm 0.3)	144.9 \pm 10.4 (30.4 \pm 0.2)	152.4 \pm 10.1 (32.1 \pm 0.3)	169.1 \pm 13.0 (35.9 \pm 0.1)	168.4 \pm 19.6 (37.4 \pm 0.3)	149.1 \pm 15.9 (40.4 \pm 0.4)

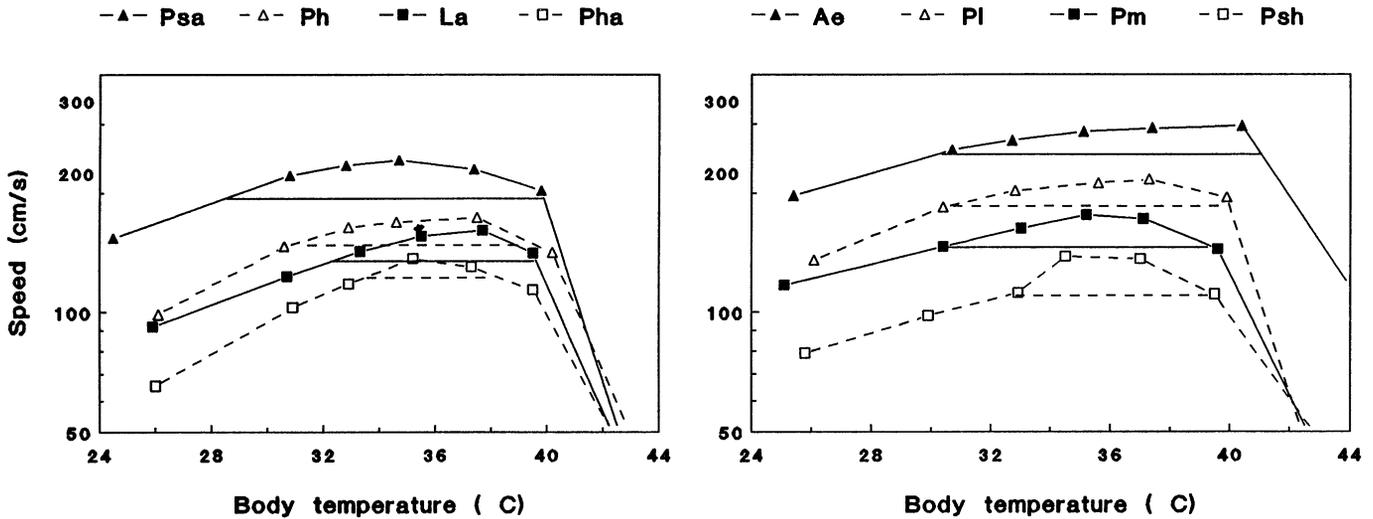


FIG. 5. Thermal-sensitivity functions for sprint speed in some of the species studied. Horizontal lines indicate the thermal-performance breadth. Species names: Psa, *Psammodromus algirus*; Ph, *Podarcis hispanica*; La, *Lacerta agilis*; Pha, *Podarcis h. atrata*; Ae, *Acanthodactylus erythrurus*; Pl, *Podarcis lilfordi*; Pm, *Podarcis muralis*; and Psh, *Psammodromus hispanicus*.

considered highly significant as compared with the critical value for a two-tailed test, irrespective of the phylogeny or set of branch lengths used (fig. 3A, B). Hence, species of lacertid lizards that exhibit high variability in preferred temperatures (broad preferred temperature breadth), were able to perform at 80% or more of maximum speed over only a relatively narrow range of body temperatures (narrow thermal-performance breadth). This result was robust to changes in the arbitrary level (i.e., 80%) used for estimating the preferred temperature breadth: the use of other levels (95%, 66%, or 50%) did not qualitatively change the relation between thermal-performance breadth and preferred temperature breadth (95%: $r_A = -0.806$, $r_B = -0.805$, both $P < 0.001$; 66%: $r_A = -0.941$, $r_B = -0.938$, both $P < 0.001$; 50%: $r_A = -0.537$, $r_B = -0.535$, both $P = 0.056$; all two-tailed tests).

We analyzed variation in predicted relative sprint speed as a function of thermal-performance breadth, preferred temperature breadth, and the absolute value of the difference

between T_0 and T_p (fig. 3A, B). The overall multiple regression is highly significant (variable branch lengths analyses: $r_A^2 = 0.730$, $P = 0.006$; $r_B^2 = 0.732$, $P = 0.006$; unit branch lengths analyses: $r_A^2 = 0.678$, $P = 0.014$; $r_B^2 = 0.715$, $P = 0.008$). The lack of statistical significance for the individual path coefficients for relations of thermal-performance breadth and preferred temperature breadth with relative sprint speed (fig. 3A,B) is probably a statistical artifact, attributable to the high correlation between the former two variables (multicollinearity, Slinker and Glantz 1985). Bivariate correlations with relative sprint speed were highly significant: thermal-performance breadth, $r_A = 0.845$, $r_B = 0.845$, $P < 0.001$ (variable branch-lengths analyses), $r_A = 0.773$, $r_B = 0.775$, $P < 0.01$ (unit branch lengths analyses); preferred temperature breadth, $r_A = -0.815$, $r_B = -0.816$, $P = 0.001$ (variable branch-lengths analyses), $r_A = -0.818$, $r_B = -0.841$, $P < 0.001$ (unit branch lengths analyses) (all two-tailed tests). Changes in the absolute value of the difference between T_0

TABLE 3. Summary statistics (mean \pm 1 SE) of the thermal dependence of sprint speed, preferred body temperatures, and predicted relative spring speed for 13 species of lacertid lizards.

Species	Optimal temperature (°C)	80% thermal performance breadth (°C)	Lower limit 80% TPB (°C)	Critical thermal maximum (°C)	Median preferred temp. (°C)	Preferred temperature breadth (°C)	Lower limit PTB (°C)	Relative spring speed (%)
<i>Psammodromus algirus</i>	34.35 \pm 0.56	10.76 \pm 1.07	28.30 \pm 0.87	43.50 \pm 0.23	35.40	4.12	33.09	97.12
<i>Ps. hispanicus</i>	35.94 \pm 0.42	6.41 \pm 1.08	32.64 \pm 0.79	45.50 \pm 0.18	35.10	5.29	32.21	93.06
<i>Lacerta monticola</i>	34.53 \pm 0.50	8.37 \pm 1.04	29.88 \pm 0.71	43.63 \pm 0.24	33.70	4.30	31.40	95.97
<i>Podarcis bocagei</i>	35.08 \pm 0.51	7.94 \pm 0.86	30.72 \pm 0.57	45.44 \pm 0.12	35.15	4.47	32.43	94.63
<i>P. h. hispanica</i>	35.51 \pm 0.68	8.40 \pm 0.89	31.12 \pm 0.97	44.54 \pm 0.09	34.40	4.37	31.93	95.77
<i>P. h. atrata</i>	35.72 \pm 0.58	5.22 \pm 0.51	33.06 \pm 0.55	44.62 \pm 0.20	34.50	4.86	31.86	91.09
<i>Podarcis muralis</i>	35.45 \pm 0.31	9.15 \pm 0.65	30.03 \pm 0.59	44.21 \pm 0.13	34.15	4.63	31.88	94.75
<i>P. lilfordi</i>	35.87 \pm 0.90	8.79 \pm 0.85	30.66 \pm 0.86	43.26 \pm 0.36	35.00	4.09	33.10	96.56
<i>P. tiliguerta</i>	35.94 \pm 0.62	12.62 \pm 0.74	27.83 \pm 0.75	42.70 \pm 0.26	35.45	3.49	33.67	95.83
<i>Acanthodactylus erythrurus</i>	37.96 \pm 0.70	11.27 \pm 0.91	30.01 \pm 0.92	46.34 \pm 0.65	37.15	3.60	35.70	98.24
<i>Lacerta vivipara</i>	34.17 \pm 0.30	8.66 \pm 0.53	29.06 \pm 0.50	40.55 \pm 0.31	32.50	5.03	29.47	94.47
<i>L. agilis</i>	36.52 \pm 0.60	7.63 \pm 0.70	32.04 \pm 0.63	43.87 \pm 0.20	34.70	4.94	32.00	91.63
<i>L. schreiberi</i>	36.53 \pm 0.51	10.59 \pm 0.64	29.71 \pm 0.44	43.02 \pm 0.24	35.30	4.24	33.39	97.01

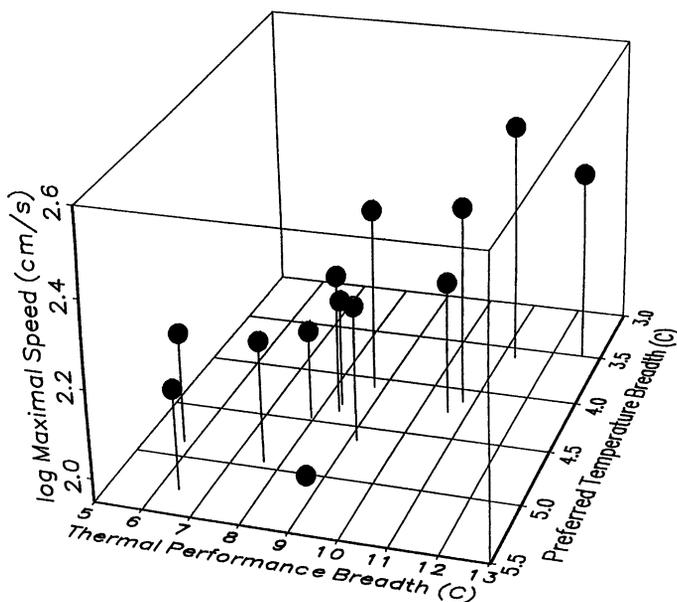


FIG. 6. Scatterplots of raw species values showing relationships between maximum sprint speed, thermal-performance breadth, and the preferred temperature breadth (see text for independent contrast correlation coefficients).

and T_p did not affect changes in predicted relative sprint speed, as evidenced by the nonsignificant path coefficients (variable branch-lengths analyses: $\beta_A = 0.022$, $\beta_B = 0.020$, both $P > 0.50$; unit branch-lengths analyses: $\beta_A = -0.020$, $\beta_B = -0.036$, both $P > 0.50$; not shown in fig. 3A,B) and bivariate correlation coefficients (variable branch-lengths analyses: $r_A = -0.287$, $r_B = -0.304$, both $P > 0.10$; unit branch lengths analyses: $r_A = -0.333$, $P > 0.10$, $r_B = -0.458$, $P > 0.05$). This is not unexpected, given that evolutionary changes in T_p and T_o were closely linked in this clade of lizards. Thus, differences in predicted relative sprint speed at the preferred body temperatures were induced mainly by the inverse relation between the preferred-temperature breadth and the thermal-performance breadth. Predicted relative speed was low in species that combine a high variability of preferred temperature (wide preferred temperature breadth) with a sharp, peaked thermal sensitivity function (narrow thermal-performance breadth). Species that are usually able to sprint near maximum capacities couple a low variability of preferred temperatures (narrow preferred temperature breadth) with a broad, flat thermal-sensitivity curve (broad thermal-performance breadth).

Maximum and Predicted Relative Sprint Speeds

Phylogenetically independent contrasts in maximum sprint speed were positively correlated with contrasts in relative sprint speed (fig. 3A, B). This positive relationship reflects the correlated evolution of maximum sprint speed, thermal-performance breadth, and preferred-temperature breadth (fig. 6). Evolutionary changes in maximum sprinting abilities were positively correlated with changes in thermal-performance breadth (variable branch-lengths analyses: $r_A = 0.632$, $r_B = 0.624$, both two-tailed $P < 0.03$; unit branch-lengths anal-

yses: $r_A = 0.601$, $r_B = 0.607$, both two-tailed $P < 0.03$; fig. 6), and negatively correlated with changes in thermal preference breadth (variable branch-lengths analyses: $r_A = -0.754$, $r_B = -0.761$, both two-tailed $P < 0.005$; unit branch-lengths analyses: $r_A = -0.777$, $r_B = -0.823$, both two-tailed $P < 0.002$; fig. 6). Hence, species with the highest maximum sprinting capacities also are able to run at near-maximum levels over the widest range of body temperatures; that is, their running abilities are least sensitive to body temperature. In addition, they maintain their preferred body temperatures within a relatively narrow zone around the thermal optimum, that is, they thermoregulate more precisely.

DISCUSSION

Our study provides a rare attempt (Emerson and Arnold 1989) to quantitatively estimate relations among measurements of an ecologically relevant performance capability and different morphological, physiological, and behavioral traits within a group of closely related organisms. We address several issues of general interest. (1) We quantify the interspecific relationship between morphology and maximum sprinting speed. The existence of a tight relation is an important assumption of various ecomorphological hypotheses (Losos 1990; Garland and Losos 1994). (2) We describe parallel evolution of the thermal sensitivity of sprinting, a physiological property, and the preferred temperatures, a behavioral trait. Correlated evolution of physiology and behavior is a paradigm of physiological ecology (e.g., Huey 1982; Bartholomew 1987; Huey and Bennett 1987; Van Damme et al. 1989; Garland 1993; Garland and Carter 1994). (3) We found no evolutionary trade-offs among maximum sprinting abilities, the thermal sensitivity of sprinting, and preferred body temperatures. A central tenet of evolutionary biology is that specialization for one task curtails the ability to perform a variety of tasks (e.g., "a jack-of-all-trades is a master-of-none"; Huey and Hertz 1984).

Evolution of Maximum Sprint Speed

Our phylogenetic analyses identified residual hind-limb length, that is, relative to body length, as an important morphological predictor of interspecific variation in maximum sprint speed. This result supports biomechanical models predicting that long hind limbs increase length of stride and thereby maximum sprinting speed (references in Garland 1985; Losos 1990). A positive relation between relative hind-limb length and running speed often has been postulated as the mechanistic link relating differences in limb proportions to differences in behavior and/or ecology (e.g., Kramer 1951; Pianka 1969; review in Garland and Losos 1994). However, only Losos (1990) has previously provided evidence supporting this assumption, by showing that sprint speed correlates positively with both body length and residual hind-limb length in a clade of *Anolis* lizards.

Our results are less conclusive with respect to the importance of body size as a factor mediating the evolution of sprinting ability. Body size was identified as an important variable in the analyses using phylogenetic trees with unit branch lengths but not when we used phylogenies with variable branch lengths (i.e., those depicted in fig. 2) to calculate

independent contrasts. As the use of phylogenies with unit branch lengths did not result in adequate standardization of the independent contrasts, we favor the latter interpretation, that is, that body size per se is not a significant factor inducing variation in maximal sprinting speed in this clade. Although several previous empirical studies have shown independent contrasts analyses of correlations to be relatively insensitive to variations in the branch lengths used for computations (e.g., Garland et al. 1991; Garland et al. 1992; Walton 1993; and see simulations in Martins and Garland 1991), our results demonstrate that such will not always be the case (see also Martins 1993).

Other empirical studies on lizards also have provided conflicting evidence for a relation between body size and sprinting abilities. Losos (1990) concluded that body size accounted for 52% of the variation in sprint speed in *Anolis* lizards. However, the apparent relation between body size and speed in *Anolis* might emerge as a consequence of the relation of both with hind-limb length (Garland and Losos 1994; see also Snell et al. 1988). In fact, a reanalysis of Losos' (1990) data (using phylogenetically independent contrasts) indicates that hind-limb length and sprint speed correlate positively when body length is partialled out by computing residuals, but speed and body length are not correlated when the effect of hind-limb length is removed by computing residuals (Garland and Losos 1994).

The optimal temperature for sprinting, considered concurrently with body length and residual hind-limb length, was positively correlated with maximum running speed across the 13 species studied herein. Garland (1994) also has reported a significant positive correlation between treadmill endurance capacities and body temperature among species of lizards. These relations are predicted by the "hotter-is-better" hypothesis (Huey and Kingsolver 1989). This hypothesis forecasts that maximum performance abilities for a physiological function, such as muscle-contraction speed, should increase with its physiological optimum temperature, unless the evolution of perfect thermal compensation has occurred (Hochachka and Somero 1984; Huey and Kingsolver 1989; Bennett 1990). Higher muscle contractile speed should increase stride frequency and hence sprint speed. In the absence of direct information on lower-level physiological traits (e.g., muscle-contraction times) and stride frequency in these species, we cannot directly examine this tentative mechanistic explanation for the increase of maximum sprint speed with the optimal temperature for sprinting. Moreover, our result does not falsify an alternative hypothesis that lizards living in warm, open habitats have been subject to independent selection pressures favoring the evolution of higher physiologically optimum temperatures and elaboration of high sprinting abilities via other mechanisms (e.g., muscle architecture or fiber types).

Correlated Evolution of Thermal Preferences and Thermal Sensitivity

The species of lacertid lizards studied herein differ only moderately in median preferred temperatures (maximum difference among species = 4.65°C), optimal temperatures for sprinting (3.79°C), and CTMax (5.79°C). This homogeneity

is not surprising, given the uniformity in activity rhythms and thermoregulatory behaviors in this clade (Avery 1982; Arnold 1987; Van Damme et al. 1990). Nevertheless, measurable differences were detected in thermal preferences and in both position and form of the thermal-sensitivity function. Evolutionary divergence of thermal physiology has therefore occurred within this clade. Moreover, evolutionary changes in T_o and in critical thermal maximum (CTMax) closely match changes in T_p , both in direction and in magnitude. Hence, during the evolutionary history of this clade, thermal-sensitivity curves have shifted their position in concert with changes in median preferred temperature. Previous studies have provided variable evidence for correlated evolution of thermal sensitivity and body temperatures. In Australian skinks, a significant positive correlation was found between CTMax and T_p , whereas the correlation between T_o and T_p was positive but insignificant (Garland et al. 1991). In a larger-scale study of iguanid lizards, Huey and Kingsolver (1993) reported a strong positive correlation between T_o and average field body temperature.

A match between T_o and T_p is considered as strong evidence for coadaptation of thermal sensitivity and thermal preferences (Huey and Bennett 1987). Selection should favor perfect thermal coadaptation because it induces similar and near-maximum levels of predicted relative sprint speed in all species (van Berkum 1986; Huey and Bennett 1987). However, predicted relative sprint speed depends not only on the mutual positions, but also on the shapes of the thermal-sensitivity functions and the distributions of preferred temperatures. We therefore expected that a high variability of the preferred body temperatures would be compensated by the ability to run well over a wide range of body temperatures. Instead, we found the opposite: species that exhibit relatively variable preferred body temperatures attained high speed over only a narrow range of body temperatures; lizards that maintained preferred temperatures in a narrow zone ran reasonably fast over a wide range of body temperatures. This inverse relation between the preferred temperature breadth and the thermal-performance breadth induced among-species variation in predicted relative sprint speed; the highest levels were attained by species that combine a narrow, precise distribution of preferred temperatures with a broad, flat thermal sensitivity curve for sprinting.

No Trade-Off between Maximum and Relative Sprint Speed

Maximum sprint speed indexes a lizard's sprinting abilities when forced to perform at its morphological and physiological limits, assuming sufficient motivation. Maximum sprinting abilities may not, however, be realized in nature (Hertz et al. 1988). Sprinting performance realized in nature depends on both maximum sprint abilities and on the relative sprint-speed levels (i.e., percent of maximum) (Huey and Bennett 1987; Garland and Losos 1994). Relative sprint speed is set by the interaction between the body temperatures maintained by behavioral thermoregulation and the thermal sensitivity of sprinting.

Natural selection can be highly context dependent. For example, with respect to locomotor abilities, its effects will depend on both maximum abilities and the extent to which

these abilities are realized in nature. Evolutionary solutions to selective problems are often sufficient, rather than optimal (Jacob 1977; Bartholomew 1987; Garland and Huey 1987; Gans 1991; Garland and Carter 1994). One might predict that a sufficient solution to selection on sprint performance in nature could have involved enhancing either maximum speed or relative speed (e.g., through maintaining body temperatures within a narrow range near the optimal temperature or by reducing the thermal sensitivity for sprinting). If so, then the evolutionary correlation between maximum and relative sprint speed could be negative. A negative correlation also would be expected if a necessary physiological or biochemical trade-off exists between the ability to function very well at one temperature (i.e., a high maximum sprinting speed at the optimal temperature) and the ability to function reasonably well across a broad temperature range (i.e., a reduced thermal sensitivity that would lead to high levels of relative sprint speed) (Huey and Hertz 1984; Huey and Kingsolver 1989). However, maximum and relative sprint speed are positively correlated in these lacertid lizards, indicating that both traits have evolved together without the trade-offs required by the scenarios described above. This positive relationship emerges because species that achieve high maximum speeds also evolved a trait combination that tends to uncouple the effect of body temperature on relative sprint speed: they have acquired the capacity to run at near-maximum levels over a wide range of temperatures, *and* they maintain their body temperatures within a narrow range, close to the optimum for sprinting.

*Correlated Evolution of Morphology,
Physiology, and Behavior*

Our phylogenetic analysis of 13 species from a relatively homogeneous clade of lizards indicates that the evolution of high maximum sprinting abilities is mechanistically related to the evolution of longer hind-limbs (relative to body length) and of a higher physiologically optimal temperature for sprinting. Thus, both morphological and physiological traits seem to have evolved as the mechanistic bases of variation in a whole-organism performance ability.

More importantly, our analyses indicate that the evolution of high maximum sprinting abilities is correlated with the evolution of both a reduced physiological sensitivity to temperature and a high precision of the behaviorally maintained preferred body temperatures. Thus, the morphological and physiological properties that determine maximum sprint speed, and the behavioral and physiological properties that set relative performance levels, have experienced correlated evolution such that they reinforce each other to induce interspecific variation in predicted realized performance (i.e., the product of absolute maximum and predicted relative sprint speed). We hypothesize that the observed trait combination has evolved in response to correlated selection pressures, and therefore consider the foregoing set of jointly evolved features as a phenotypic analogy to a coadapted gene complex (Mayr 1963; cf. Huey and Bennett 1987). Coadaptation seems to have involved multiple levels of biological organization (morphology, physiology, and behavior), and we found no evidence for evolutionary trade-offs.

Alternatively, the observed pattern of interspecific character covariation might be the result of genetic correlations among the traits studied. For instance, traits related because of straightforward biomechanical or physiological interactions (e.g., relative limb length and maximal sprint speed) also should tend to show significant genetic correlations. A sufficient explanation for the correlated evolution of mechanistically linked traits may be selection acting only on one trait or the other, or perhaps genetic drift alone. Either mechanism will tend to cause correlated evolution along the direction dictated by the prevailing genetic correlation (e.g., Felsenstein 1988; Emerson and Arnold 1989; Garland and Carter 1994; Garland and Losos 1994; references therein). However, for traits that are not genetically correlated, hypotheses of correlated selection pressures are suggested. Although we have no quantitative genetic data for the species or combinations of traits studied herein, several of the traits we have studied would seem unlikely to show genetic correlations (at least caused by pleiotropy). For example, we see no obvious physiological or biomechanical reason why preferred body temperature, a behavioral trait, should be genetically correlated with, for example, hind-limb length or thermal-performance breadth. Thus, we do believe that an interpretation of "coadaptation" is warranted: traits at multiple levels of biological organization seem to have evolved together because of correlated selection pressures, as opposed to genetic correlations. Nevertheless, we encourage efforts to perform quantitative genetic analyses with one or more of the species studied, to test our assumption of weak genetic correlations among most of the traits considered here.

The correlated evolution of traits that determine maximum and relative performance levels has resulted in the arrangement of extant species along a continuum of low to high predicted realized sprint speed. From this pattern, we infer that past directional selection for higher sprint performance may have been strong in some lineages and relatively weak in others. In other words, we suggest that the historical "fitness gradient" (Arnold 1983) for higher sprint speed differed in the lineages leading to the extant species we studied. This hypothesis leads to the question: What factors may have resulted in such a phylogenetically variable history of natural selection, and why do some species exhibit traits that result in both low maximum sprinting speed and low relative performance levels? Our study aimed at documenting the patterns of correlated evolution, not elucidating their origin, and we have no direct information on the suite of ecological factors and associated life-history traits that might have molded the link between sprint performance and fitness. However, we can offer some suggestions.

Selection for high sprint speed is likely to have been most intense in species that live in habitats that are sparsely vegetated, exhibit high densities of (specialized) predators, and/or contain profitable prey types that are fast moving. Intense selection for increased sprinting ability should result in the evolution of those morphological (e.g., long hind limbs relative to body length) and physiological (e.g., a high physiologically optimum temperature for sprinting) traits that enable lizards to attain high maximum speeds. As the speed that an ectotherm attains at a given time and place depends also on its body temperature, selection should tend to reduce

the effects of variation in body temperature on sprint performance. This detachment could be achieved by (1) a reduction in the thermal sensitivity of sprinting and/or (2) a reduction in the variability of body temperatures, with their mean centered at the optimal temperature for sprinting.

However, attainment of high speed is probably less important for lizards that inhabit sites with dense vegetation at ground level, that is, where shelter from predation is readily available, that have few predators, and/or where slow-moving prey types are abundant. A relaxed selection regime for sprint speed should allow relatively independent evolution and divergence of the morphological and physiological traits that affect maximum sprinting capacities. Moreover, long hind-legs may even reduce speed in dense vegetation (Pianka 1969; Jaksic and Núñez 1979), such that some ecological contexts may actually constrain the evolution of long hind limbs and hence of maximum sprinting abilities (see also Losos and Sinervo 1989; Sinervo and Losos 1991; Garland and Losos 1994). Dense vegetations may also induce high costs of thermoregulation (Huey and Slatkin 1976; Huey 1982), and therefore favor the maintenance of preferred body temperatures at relatively low and variable levels. Thus, we suggest that some environments may favor the combination of morphological and behavioral characteristics that actually result in reduced levels of sprinting performance. Detailed information on interspecific variation in environmental factors (e.g., habitat openness, predator densities, and prey densities) that might (have) cause(d) variation in selection pressures is needed to test these ideas. Moreover, the development of comparative methods that could allow inferences about lineage-specific histories of selection would be most welcome.

Practical Implications

The prospects of global climate warming (Schneider 1993) have increased the practical significance of studies of the evolution of thermal physiology (Bennett et al. 1990; Huey et al. 1991; Dawson 1992). Our empirical results are relevant to this issue. First, we observed interspecific variation in both the position and the shape of the thermal-sensitivity functions. However, these differences are relatively small, especially when considered in combination with the apparently long divergence times within this clade of lizards (e.g., millions of years; see fig. 2). Hence, it is questionable whether lacertid lizards would be able to respond to rapid environmental changes through evolutionary adjustments of their thermal physiology (cf. Bennett et al. 1990; Huey et al. 1991; on organisms with much shorter generation times).

Second, theoretical treatments (e.g., Huey and Kingsolver 1993; Lynch and Lande 1993) exclusively consider abiotic changes in the environment that may alter selection pressures acting on thermal physiology. In the clade of lacertid lizards studied herein, aspects of thermal physiology (optimal temperature and thermal-performance breadth for sprinting) have evolved in close association with thermal preferences, a behavioral trait, and with morphological features that determine maximum sprinting capacities. In the previous section, we hypothesized that the observed pattern evolved as a response to correlated selection on distinct components of sprinting performance, and suggested that biotic factors (e.g., predation

pressure) might have mediated interspecific variation in selection regimes. If true, then we tentatively deduce that shifts in the composition of biotic communities, which could be induced by climatic change, might by themselves constitute changing selection pressures on maximum sprinting ability, and therefore drive evolutionary changes in the thermal physiology of sprint performance.

ACKNOWLEDGMENTS

We thank F. Braña, S. F. Campos, M. Gil, J. S. Martín, and H. Strijbosch for help in capturing lizards, V. Pérez-Mellado for providing lab space at Salamanca, F. Palacios for the loan of equipment, and M. Jagger and M. Turner for inspiration. E. N. Arnold, P. A. Carter, R. M. Díaz-Uriarte, M. Gil, F.-J. Lapointe, and W. Mayer provided advice and discussion; P. E. Hertz, R. B. Huey, J. B. Losos, and B. Van Valkenburgh gave constructive comments that significantly improved the manuscript. This research was funded by the Belgian N.F.W.O., the Spanish M.E.C. (D.B.), C.S.I.C, Generalitat Valenciana, and Ayuntamiento de Castellón (A.M.C.), DGI-CYT (PB88-0009 to D.B. and A.M.C.; PB91-0055 to A.M.C.), and the United States National Science Foundation (IBN-9157268 and DEB-9220872 to T.G.).

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APPENDIX

Reconstruction of Phylogenetic Relations and Divergence Times

We here summarize existing information on phylogenetic relations and divergence times for the lacertid lizards studied. Reconstructions are derived from the phylogeny, based on morphological features, compiled by E. N. Arnold (1989) and from the phylogeny established by W. Mayer and coworkers using immunological data (microcomplement fixation of albumins; Lutz and Mayer 1985; Lutz et al. 1986; Mayer and Lutz 1989, 1990; W. Mayer in litt., June 25, 1990 and October 22, 1990).

Phylogenetic relations of Palearctic Lacertidae are controversial. This controversy is evident at two levels. First, the overall relationships among many groups of primitive Palearctic lacertids are uncertain. This conclusion is brought about both by the analysis of morphological traits (Arnold 1989) and by the immunological results (Mayer, in litt.). Second, the tree based on morphological data differs considerably from that derived from immunology. It is not evident that the controversial issues soon will be resolved. Indeed, both morphological and immunological data suggest that most major branching events among the Palearctic lacertids occurred within a short interval. Hence, it may be difficult to resolve phylogenetic relations, not for methodological reasons, but because of the very nature of the divergence processes that occurred within this lizard group. As noted by Arnold (1989, p. 236) "if the main branching events in the phylogeny occurred swiftly, without much evolutionary change between dichotomies, comprehensive reconstruction of the cladogenetic history of primitive Palearctic and Oriental lacertids may not be possible."

We do not wish to take any position in this controversial issue. Rather, we have compiled two different trees, which we consider as the currently best available and equally likely representations of the true phylogeny.

The species considered here are unequivocal representatives of six species groups: *Psammodromus* group (*Psammodromus algirus* and *Psammodromus hispanicus*); *Archaeolacerta* group (*Lacerta monticola*); *Podarcis* group (*Podarcis bocagei*, *Podarcis hispanica*, *Podarcis muralis*, *Podarcis lilfordi*, and *Podarcis tiliguerta*); the Saharo-Eurasian clade (*Acanthodactylus erythrurus*); *Lacerta vivipara* (a single-species group); and *Lacerta* s. str. group (*Lacerta agilis* and *Lacerta schreiberi*). Both morphological and immunological data agree in the assignment of the species to the groups, and in the existence of these groups. The methods disagree, however, in the phylogenetic relations among the groups. The (putative) relations suggested by both approaches are shown in figure 1.

Divergence times for branching patterns are based on immunological distances (Lutz and Mayer 1985; Lutz et al. 1986; Mayer and Lutz 1989, 1990) and were used for both phylogenetic trees. In the earlier

papers (Lutz and Mayer 1985; Lutz et al. 1986), it was assumed that one unit of immunological distance was equivalent with one amino acid substitution, and to approximately 0.60 million yr of lineage independence (Maxson et al. 1975; Wilson et al. 1977). This time scaling was slightly altered later on, such that "it fits better to the geological facts than the older estimations. If we assume an isolation of 33 million yr for the separation of *Gallotia* from the continental Lacertidae (e.g., *Acanthodactylus*, *Podarcis*, and *Lacerta parva*) we compute isolation times for most *Gallotia* species which perfectly agree with the geological ages of the islands inhabited by them" (W. Mayer, in litt.). We have adopted the most recent estimates throughout.

Tree A—Immunological Data

Psammodromus and *Gallotia* (both are considered "sister" groups (Lutz et al. 1986; Arnold 1989) split from the other Lacertidae during the Oligocene (Mayer, in litt.). The divergence time for *Gallotia* was estimated to be about 33 mya (Lutz et al. 1986; Mayer in litt.). We therefore estimate that *Psammodromus* was separated from all other species 33 mya.

The separation between *L. vivipara* and *Lacerta* s. str. on one side, and *Podarcis*, *Archaeolacerta*, and the Saharo-Eurasian clade on the other, was estimated to have occurred at the transition Oligocene-Miocene (= 24 million yr Mayer, in litt.), and 23–24 mya (Mayer and Lutz 1989, 1990). We have used a divergence time of 24 million yr.

The split leading ultimately to the Palearctic and Saharo-Eurasian clades occurred soon after the former separation (Lutz et al. 1986; Mayer, in litt.). This was estimated to be at 22 million yr.

Estimates for the timing of the separation between *Podarcis* and *Archaeolacerta* were 18–20 million yr (Mayer and Lutz 1990) and 17–20 million yr (Mayer and Lutz 1989; Mayer, in litt.). An estimate of 18 million yr was retained.

The separation of *L. vivipara* from *Lacerta* s. str. took place at 23–24 million yr (Lutz et al. 1986) or 22 million yr (Mayer, in litt.). The latter figure was retained.

Separation of *Psammodromus* species. Although *P. algirus* differs considerably in morphology from the three species in the *P. hispanicus* group (*hispanicus*, *blanci*, *microdactylus*) (Arnold 1973), a direct relationship is supported by several morphological features (Arnold 1989). However, results of protein electrophoresis (Lutz et al. 1986) suggest that the separation between the two groups of *Psammodromus* is fairly ancient, and was estimated at 17 million yr (Mayer, in litt.).

No study is available of the phylogenetical relations among the *Podarcis* species that are treated here. The group is very homogenous in many respects (morphology, ecology, and behavior), and the radiation is probably a recent event. Our hypothetical arrangement is based on a combination of morphological (Arnold 1973, 1989), immunological (Lutz and Mayer 1985), taxonomic, biogeographical, and geological (Arnold 1989) information.

Arnold (1973) found that *P. muralis* and *P. hispanica* (which at that time still included *P. bocagei* as a subspecific form) are similar in having the outer sulcal lips of the hemipenis free and that they differed in this respect from all other *Podarcis* species. The absence of the derived feature points to a primitive position of these species within the *Podarcis* group. The "distinct" position of *P. muralis* within its genus is also corroborated by immunological evidence. Lutz and Mayer (1985) stated

that *P. muralis* (and *P. sicula*) were isolated relatively long from six other *Podarcis* species (including *P. tiliguerta*) which they studied. The separation time between both "groups" was estimated at 10 million yr. We therefore postulate that a branching occurred between *P. muralis*, *P. hispanica*, and *P. bocagei* on one side, and *P. tiliguerta* and *P. lilfordi* on the other side. The divergence time between both "groups" has been given an estimate of 10 million yr (Lutz and Mayer 1985; Mayer, in litt.).

Within the *P. muralis* "group," *P. hispanica* and *P. bocagei* are probably more closely related to each other than they are to *P. muralis*. This opinion is based on the fact that *P. bocagei* was considered as a subspecies of *P. hispanica* until very recently when it acquired full specific status (Pérez-Mellado 1981). No direct estimates of separation times between these species are available. Lutz and Mayer (1985) estimated that the main radiation among six *Podarcis* species occurred 4 to 6 mya, at the time of the desiccation of the Mediterranean sea. Accordingly, we have used a figure of 5 million yr for the divergence time between *P. muralis* and *P. hispanica*/*P. bocagei* and between *P. tiliguerta* and *P. lilfordi*. We have assigned an arbitrary value of 3 million yr to the divergence time between the "sister species" *P. hispanica* and *P. bocagei*. The separation time (1 million yr) between both subspecific forms of *P. hispanica* is supported by estimates of the age of the volcanic island archipelago inhabited by *P. hispanica atrata* (Martí et al 1992).

No direct information is available on the divergence time of *L. agilis* and *L. schreiberi*. Lutz and Mayer (1985) estimated the divergence time between *L. agilis* and *L. viridis*/*L. trilineata* to be about 4 to 6 million yr, but considered this to be an underestimate. *Lacerta schreiberi* is probably closely related to *L. viridis* (Arnold 1989). Our estimated divergence time of 10 million yr between *L. agilis* and *L. schreiberi* is considered as very realistic (Mayer, in litt.).

Tree B—Morphological Data

Arnold (1989) proposes an arrangement with two main branches: the first includes *Lacerta* s. str., *L. vivipara*, and the Saharo-Eurasian clade; the second includes all other groups treated here. As Arnold (1989, p. 236) notes, however, the evidence for the reality of the two branches is weak. This main branching event was estimated to have occurred 35 mya ago.

The first main branch probably split into *Lacerta* s. str. on one side, and *L. vivipara* plus the Saharo-Eurasian clade on the other side. By analogy with the postulated separation time of 22 million yr between Palearctic and Saharo-Eurasian groups in tree A, we have assigned a value of 22 million yr to this separation.

Lacerta vivipara and members of the Saharo-Eurasian group often were connected by parsimony analyses, although they nevertheless differ profoundly in morphology (Arnold 1989). We therefore assume that they separated soon after the former branching, and assigned it an arbitrary time estimate of 20 million yr.

The second main branch splits into two parts: (1) *Psammodromus* (and *Gallotia*), and (2) *Podarcis* and *Archaeolacerta*. The timing of this branching was estimated at 33 million yr, by analogy with the estimated separation between *Psammodromus* and the other Lacertidae in tree A.

The separation between *Podarcis* and *Archaeolacerta* was estimated to have taken place 18 mya (see tree A).

Separation of *Psammodromus*, reconstruction of *Podarcis* phylogeny, and separation among *Lacerta* s. str.: see tree A.