A Comparative Study of the Relation between Heating Rates and Ambient Temperatures in Lacertid Lizards

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Abstract

It is well known that lizard species from thermally diverse areas differ in their use of thermoregulatory behaviors as a means of making short-term adjustments to differences in ambient conditions. In contrast, the extent of long-term adjustments in thermal physiology is poorly documented and still under debate. In this study we report a clear interspecific relationship between heating rates, measured under standardized laboratory conditions, and environmental temperatures within a small clade of lacertid lizards. Phylogenetically based ANCOVAs demonstrate that species with a northern or montane distribution warm at a faster mass-specific rate than do species from a southern (Mediterranean) climatic zone. Correlational analyses, using phylogenetically independent contrasts, confirm that continuous among-species variation in mass-specific heating rates is negatively related to clinal differences in environmental temperatures. A reduction of the time spent warming, associated with higher heating rates, should be especially advantageous for lizards from cool climates, which bask for large amounts of time. Thus, the observed relation between heating rates and climatic conditions could be a result of adaptive evolution. The behaviorally selected preferred temperatures were lower, but not significantly so, in the northern or montane species set; interspecific correlations with ambient temperatures were positive but not significant. However, the divergence of heating rates and the statistically nonsignificant difference in preferred temperatures have similar impacts on variation in the estimated amount of time spent heating. Thus, differences in both heating rate, a physiological trait, and preferred temperature, a behavioral characteristic, contribute equally to variation in heating times.

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Introduction

Thermoregulation has a pervasive influence on most aspects of the biology of animals. This follows from the direct effects of body temperature (T_b) on the rate of biochemical and physiological processes, which in turn affect whole-animal performance abilities and hence fitness (Huey and Stevenson 1979; Bennett 1987; Huey and Bennett 1987; Huey and Kingsolver 1989). Thus, animals spend considerable amounts of energy and time in the regulation of their T_b's (Avery 1976; Huey 1982). Lizards, and many other ectotherms, exhibit two types of thermoregulatory responses in relation to temporal and geographical variation of the thermal environment. The first consists of fast-acting behavioral adjustments (e.g., restriction of activity times, selection of appropriate microhabitats, and postural modifications that alter rates of heating and cooling; Huey 1982; Stevenson 1985b). Such responses are widespread and well documented (e.g., Hertz 1981; Hertz and Huey 1981; Huey 1982; Van Damme et al. 1987, 1989; Adolph 1990; Bauwens et al. 1996). The second type consists of evolutionary changes in behavior and physiology that increase the time that T_b can be maintained within the preferred range. These include evolutionary shifts in the preferred temperatures and modifications in behavioral or physiological attributes that facilitate the attainment of the preferred temperatures. Surprisingly, few studies have explored whether closely related lizard taxa exhibit evolutionary differences in thermoregulatory attributes and whether this variation shows a relationship with ambient heat loads (Bogert 1949; Heatwole et al. 1969; Spellerberg 1972a, 1972b; Huey and Webster 1976; Hertz 1979, 1981; Hertz and Huey 1981; Huey and Bennett 1987; Van Damme et al. 1989, 1990; Sinervo 1990).

Here we examine interspecific variation of heating rates, a physiological trait, in relation to environmental heat loads, within a clade of lacertid lizards. The hypothesis of evolutionary adjustments of thermal physiology in relation to climatic conditions predicts that heating rates will be fastest in species that inhabit the coolest environments. This prediction is based on the supposition that lizards will minimize the time spent heating, to prolong the time that T_b can be maintained at, or near, the preferred range. Lizards in cool climates will need more time to warm to their preferred temperature and should therefore exhibit compensatory physiological (and behavioral) adjustments that increase the rate of heat gain. We test this prediction for both absolute and mass-specific heating rates. An alternative compensatory adjustment would be to lower the preferred temperatures, so that the difference between preferred and ambient temperature becomes similar in species from different climatic zones. Thus, an implicit assumption of our

prediction, which we also test, is that the preferred temperatures do not vary in concert with ambient temperatures.

We use a comparative approach; that is, we analyze interspecific diversity in heating rates and thus explore the outcome of evolutionary processes (Bartholomew 1987; Huey 1987; Garland and Carter 1994). Our choice of study species and data analyses follow recent recommendations and methodological advances (e.g., Felsenstein 1985, 1988; Huey 1987; Harvey and Pagel 1991; Garland et al. 1992, 1993; Garland and Adolph 1994). Specifically, we study a clade of closely related species that form a relatively homogeneous group with respect to many aspects of their ecology and thermal biology. This reduces the risk that results are induced or confounded by differences in traits that were not under study (Huey and Bennett 1986; Losos 1990; Bauwens et al. 1995). In addition, we analyze our data with statistical methods that make explicit use of phylogenetic information (Felsenstein 1985, 1988; Garland et al. 1992, 1993). Finally, we aim to document clinal variation in organismal traits by choosing species that occur along an environmental gradient. This deviates from the traditional approach of contrasting the physiology of species that inhabit extreme conditions (Bartholomew 1987; Garland and Adolph 1991; Garland and Carter 1994). Thus, we attempt to study subtle patterns of phenotypic variation in relation to environmental variability.

Material and Methods

Species Studied

We studied eight European species belonging to the Old World lizard family Lacertidae. The species studied are similar in body shape, foraging mode, arthropod-based diet, and diurnal activity patterns (Arnold 1987). All species maintain their activity T_b's within a relatively narrow range; they thermoregulate behaviorally by restricting activity times, shuttling between sun and shade, and altering body postures and orientation to the sun (Avery 1976; Arnold 1987; Díaz 1992; Bauwens et al. 1995).

On the basis of their geographic distributions, the lacertids studied here can be classified into two arbitrary sets. The first consists of four species (*Psammodromus algirus, Psammodromus hispanicus, Podarcis hispanica, Acanthodactylus erythrurus*) that are confined to the Mediterranean area (low and midaltitude areas in the Iberian Peninsula, Mediterranean coast of France, parts of North Africa). The second set includes species that are restricted to montane and northern areas of the Iberian Peninsula (*Lacerta*

monticola, Lacerta schreiberi), or whose geographic range extends to northwestern Europe (*Lacerta vivipara, Podarcis muralis*).

Overlap of distribution areas (see maps in Arnold and Burton [1978]) between representatives of the two sets is restricted to the midaltitude zones of a few mountain ranges in the Iberian Peninsula; species of both sets only rarely occur syntopically. Thus, geographic areas inhabited by the two species sets are well delimited. Climatic conditions differ clearly between the two geographic regions, although considerable spatial variation exists within each of them. The Mediterranean area experiences the highest temperatures throughout the year, and summer months are particularly dry and hot. The activity season of all species studied here is basically restricted to the months April through September, although individuals of *P. hispanicus* and *P. hispanica,* two species from the Mediterranean area, may be active on warm winter days.

The preferred T_b's for our study species are taken from Bauwens et al. (1995). We use the species' median preferred temperature to index the central tendency of the target range of temperature regulation. We caught our lizards at different sites, but within the same climatic zones sampled by Bauwens et al. (1995), and we assume that preferred temperatures do not vary geographically within species. This assumption is supported by the absence of intraspecific variation in thermal preferences along pronounced climatic gradients in two European lacertid lizards (Van Damme et al. 1989, 1990).

We obtained climatic data from weather stations near the capture sites of the different species. Data retained are 15–30-yr averages of daily mean temperature during the whole year, during the lizards' main activity period (April through September), and in the coldest (April) and warmest (July) months with lizard activity. We explore correlations between organismal traits and different ambient temperature statistics, to assess the sensitivity of our conclusions to the use of particular estimates of environmental heat loads.

Measurements of Heating Rate

We collected subadult or adult lizards of both sexes, with an intact or completely regenerated tail ($n = 6$ for *L. schreiberi, $n = 8$* for all other species). All species except *L. vivipara* were caught during the summer of 1994 in central Spain (provinces of Madrid and Segovia) and transported to the University Complutense of Madrid. Individuals of *L. vivipara* were caught during April 1995 in Belgium (province of Limburg) and transported to the Institute of Nature Conservation at Hasselt (Belgium). To avoid artifacts

induced by a possible treatment difference between the two laboratories, we took special care to duplicate housing conditions and the experimental protocol. Specifically, we used an identical setup, and all experiments were run by the same person.

Lizards were housed in terraria and provided with refuge areas, basking opportunities, and food and water ad lib. In order to avoid acclimation to lab conditions, all lizards were tested within 2 wk of capture; afterward they were released at their site of capture.

Because lacertids are heliothermic lizards, we used radiant heating to determine heating rates. After being measured (snout-vent length) and weighed, each lizard was introduced into a refrigerator at $4°$–$6°C$ until its T_b fell to about $25°C$, which is $5°$–$8°C$ below the lower limit of the preferred temperature range for the species examined (Bauwens et al. 1995). We then inserted a Miller-Weber quick-reading mercury thermometer ($\pm 0.1°C$) into the lizard's cloaca and fixed the lizard to a piece of cardboard (12 cm $\times$ 25 cm) with two bands of transparent adhesive tape; the cardboard provided equal conditions of heat conduction in all experiments. The lizard was subsequently placed below a 100-W lightbulb suspended 20 cm over the midpoint of the lizard's body. From the moment the bulb was switched on, the lizard's T_b was recorded at 15-s intervals. The heating experiment finished when the lizard's T_b reached $37°$–$38°C$, which is close to or above the highest limit of the preferred temperature range for the species studied (Bauwens et al. 1995). The bulb was then switched off, and the lizard was transported to a colder site, where it was allowed to cool. In order to standardize convective heat exchanges, the ambient temperature at the start of each experiment was kept uniform (mean $\pm$ SE: $31.3° \pm 0.1°C$, $n = 62$). Note that our procedure did not allow lizards to use postural adjustments during heating, as we were interested in detecting physiological, rather than behavioral, interspecific differences.

For each individual lizard we plotted $\ln(T_b)$ against time elapsed since the start of the heating experiment. These plots showed that the relation was very close to linear (median $R^2 = 0.996$, range: 0.985–0.999), and we found no indications that lizards had attained an equilibrium temperature at the end of the experiment (i.e., when T_b reached $38°C$). Thus, we cannot use analytical procedures that assume a nonlinear relation between T_b and time during heating (e.g., Spotila et al. 1973; Bakken 1976; Smith 1976). In our experiments, the heating process can best be modeled by a simple exponential relationship between T_b and the time elapsed since the start of the heating experiment (t):

$$T_b = T_0 \cdot e^{bt}. \tag{1}$$

The slope (b) of this relation is the relative heating rate (min^{-1}), and it measures the increase in T_b per unit time, relative to T_0, the T_b at the onset of the heating process. The inverse of the relative heating rate (i.e., $1/b$) is the thermal time constant, which is an estimate of the time (min) required to increase T_b by a factor of 2.718 (= e).

Our use of the thermal time constant for radiant heating is conceptually analogous to the thermal time constant estimated in step-transfer heating protocols. In step-transfer experiments, lizards are transferred from one environment to another with higher ambient temperature, and the relationship of T_b to time is nonlinear because T_b asymptotically approaches the higher ambient temperature. The heating process (by convection) is then best described by a curve formally identical to the von Bertalanffy growth function (e.g., Spotila et al. 1973). In step-transfer experiments, the thermal time constant equals the time needed to cover 63% of the step-temperature range (Smith 1976) and will thus differ in magnitude from our estimates of the thermal time constant (which measure the time required to increase T_b by a factor ~2.7). This methodological difference should be taken into account when comparing our thermal time constant estimates with those in the literature.

Phylogenetic Analyses

Comparative studies dealing with continuous-valued characters typically use interspecific data to statistically test predictions of evolutionary hypotheses. However, the existence of hierarchical phylogenetic relationships implies that data for different species cannot be regarded as independent and identically distributed data points, so that interspecific data do not meet some basic assumptions of conventional statistical methods (Felsenstein 1985; Garland et al. 1993; Pagel 1993). Consequently, the standard tabulated values of test statistics are not appropriate as critical values for hypothesis testing. Therefore, interspecific comparisons should explicitly account for the phylogenetic relations among the species studied (Felsenstein 1985; Harvey and Pagel 1991; Martins and Garland 1991; Garland et al. 1992, 1993; Pagel 1993).

Within the Lacertidae, phylogenetic reconstructions based on either immunological (Mayer and Benyr 1994) or morphological (Arnold 1989) information are not completely equivalent. We therefore analyzed our data using two phylogenetic hypotheses (Fig. 1). A summary of the available phylogenetic information, and of estimates of separation times between species and clades (i.e., the branch lengths of the putative phylogenetic trees), is given in Bauwens et al. (1995). Some estimates of divergence
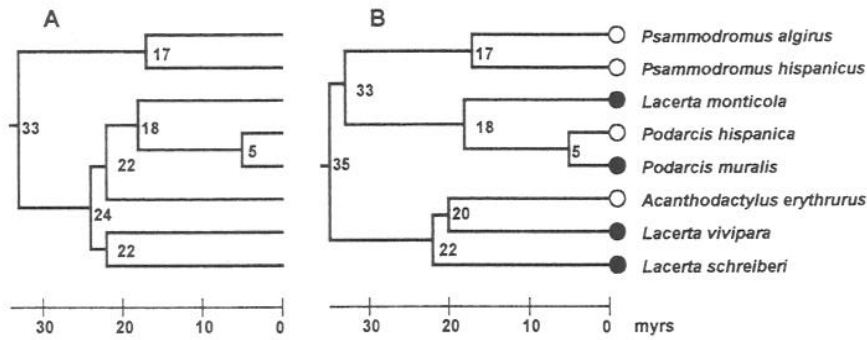
Fig. 1. Hypothesized phylogenetic relationships and estimated divergence times (numbers at nodes, in millions of years) for eight species of lacertid lizards. Branching patterns are based on micro-complement-fixation of albumins (A) and external and internal morphological characteristics (B). Divergence times for main branching patterns are based on immunological distances and were used for both phylogenetic trees (see Bauwens et al. [1995] for details). Species from the Mediterranean climatic zone are indicated by open circles, and species with a northern or montane distribution by dots.

times between species are based on arbitrary choices (see Bauwens et al. 1995). Because of this uncertainty in the assignment of separation times, we performed additional analyses on both phylogenetic trees with all branch lengths set to unit length. By analyzing our data in the context of various phylogenetic hypotheses that differ in both topology and branch lengths, we evaluate the robustness of our results with respect to the phylogenetic hypotheses employed (see Losos 1994; Martins 1996). Note that our analyses are based on phylogenetic reconstructions, so they are not affected by taxonomic incongruencies (e.g., the polyphyletic status of the "genus" *Lacerta;* see Fig. 1).

ANCOVA. We compared the thermal time constants of species with northern or montane distribution ranges to those of lizards with a Mediterranean distribution. We first analyzed the absolute values of the thermal time constants. However, because the heating process is primarily dependent on body mass (e.g., Smith 1976; Claussen and Art 1981; Bartholomew 1982), we also explored variation in size-adjusted thermal time constants. For these purposes, we could use conventional one-way ANOVA and ANCOVA, with distribution range as a factor and body mass as covariate. However, because of the hierarchical phylogenetic relations among species, we cannot adequately assess the statistical significance of the *F* statistic from critical values

in standard tables. To obtain appropriate critical values, we used the simulation procedures described by Garland et al. (1993). This technique simulates character change along a specified phylogenetic tree and generates a phylogenetically correct null distribution of F values, which can then be used for hypothesis testing. This approach has the advantage that character modification can be simulated following different models of evolutionary change (see below).

We averaged estimates of thermal time constant and body mass for each species. Because the relation between thermal time constant and body mass follows a power function, we log-transformed (base 10) the species' averages before all analyses.

The following paragraphs provide details of our implementation of the simulations of character change, which were all generated by the PDSIMUL program of Garland et al. (1993). In unbounded simulations, trait values can become unrealistically large or small; in order to avoid this, simulated trait values were kept within some specified limits, by using the "Replace" option of PDSIMUL. We used limits of 0.35 and 800 g for body mass. The lower limit is close to the size of the smallest known lacertid lizard (*Ophisops beddonii* [~0.5 g]; Arnold 1989); the upper limit is between the mass of the largest extant lacertid (*Gallotia simonyi* [~450 g]) and the estimated mass of the largest extinct species (*Gallotia goliath* [~3,500 g]; Arnold 1989). The limits for the thermal time constant were 5 and 110 min. These values were estimated by substituting the limit values for body mass into the reduced major axis regression equation of the thermal time constant versus body mass for the eight species studied. The regression was calculated by using standardized independent contrasts (see below). For simulations involving the preferred temperatures, we used limits of 27° and 42°C. These values are about 5°C below and above the extreme values for 13 species of European lacertids (Bauwens et al. 1995).

For all simulations we used the means of the real data set, that is, the observed species means, as starting values ("Initial Values" of PDSIMUL) and as the expected means of the generated tip values ("Final Means"). The expected variances of the simulated tip data ("Variances-Tip") were set equal to the variances of the real data. The correlation between the simulated changes for both traits ("Correlation of Input Distribution") was set to 0.

Four different models of evolutionary change were used: (1) gradual Brownian motion (i.e., a model of random and continuous evolutionary changes); (2) speciational Brownian motion (i.e., random evolutionary changes at branching events in the two descendent lines), which is equiv-

alent to gradual Brownian motion along a phylogeny with all branches set to unit length; (3) punctuated equilibrium (i.e., random changes at branching events in only one of the daughter taxa); and (4) the Ornstein-Uhlenbeck model (i.e., a model of quasi-random, continuous changes with a constraint), with an immobile adaptive peak (set equal to the mean of the species values) and a decay constant equal to 10^{-7} (i.e., $\sim$3.5 times the inverse of the height of the phylogenetic tree; Garland et al. 1993). We refer the reader to Garland et al. (1993) and references therein for a detailed account of these evolutionary models.

Correlation Analysis. We also examined whether clinal variation in ambient temperatures is associated with interspecific differences in the thermal time constant. Specifically, we tested the prediction that interspecific variation in the thermal time constant and ambient temperatures are positively correlated. We used partial correlation analysis to account for the effect of body mass. Because statistical tests of standard correlation analyses are invalid in an interspecific context, all correlation coefficients were calculated with the method of phylogenetically independent contrasts (Felsenstein 1985). This method uses information on the phylogenetic relations of the species considered to obtain statistically independent contrasts for each trait studied. One can then employ these contrasts to calculate (partial) correlation coefficients based on regression through the origin (Garland et al. 1992). If the contrasts are appropriately standardized, then the correlation coefficients can be compared with conventional critical values (Martins and Garland 1991; Garland et al. 1992; Díaz-Uriarte and Garland 1996).

We checked for adequate standardization of the independent contrasts by examining correlations between the absolute value of standardized contrasts and their standard deviation (Garland et al. 1992). For the contrasts obtained with the phylogenies with variable branch lengths (i.e., those shown in Fig. 1), negative correlations were evident for several variables; they were appropriately standardized by log (base 10) transforming the original branch lengths. Independent contrasts calculated with all branches set to unit length revealed negative correlations for many variables; no proper standardization can be obtained here.

All data were log-transformed (base 10) prior to obtaining contrasts. Independent contrasts were calculated with the program PDTREE (Garland et al. 1993); statistical analyses, using multiple regression through the origin, were done with SPSS/PC+ (Ver. 5.0). Because we test directional predictions

of character correlations, we use one-tailed tests for all (partial) correlation coefficients.

Results

Table 1 shows the species' means for the thermal time constant, body mass, preferred temperature, and ambient temperature statistics. Our estimate of heating rate for *Psammodromus algirus* (1.2°C min^{-1}) was comparable to those measured during early morning (0700–1000 hours) under field conditions (0.9°–1.8°C min^{-1}; Díaz 1991). Similarly, the estimated heating rate of *Lacerta monticola* (1.6°C min^{-1}) was close to those observed in the field between 0800 and 1000 hours (1.0°–2.2°C min^{-1}; Carrascal et al. 1992). Thus, our laboratory setup simulated conditions encountered by field-active lizards during their early morning warm-up.

We first compared the thermal time constants of lizards with northern or montane ranges to those of lizards with a Mediterranean distribution. Absolute values of the thermal time constant do not differ between the two sets of species (one-way ANOVA: $F_{1,6} = 0.023$, $P > 0.50$ for all four models of evolutionary change and the two hypotheses of phylogenetic relationships). However, independent contrast analyses show that the thermal time constant and body mass are highly and positively correlated: bigger lizards heat more slowly than smaller ones (Fig. 2; for analyses with variable branch lengths: immunological tree, $r = 0.913$, morphological tree, $r = 0.912$, both $P < 0.002$; for analyses with constant branch lengths: immunological tree, $r = 0.964$, morphological tree, $r = 0.956$, both $P < 0.001$). The similarity of the absolute values of the thermal time constant basically reflects the correspondence of body mass between the two species sets (one-way ANOVA: $F_{1,6} = 0.462$, $P > 0.30$ for all simulations). The following analyses examine deviations from the relationship between the thermal time constant and body size.

Slopes of the relationship between the thermal time constant and body mass for the two sets of species are not different ($P > 0.30$ in all analyses), so our data fulfill a basic assumption of ANCOVA. ANCOVA reveal that at a given body mass, species with a northern or montane distribution exhibit lower values for thermal time constant than do lizards with a Mediterranean range (Table 2; Fig. 2). Results from phylogenetic simulations indicate that this difference is highly statistically significant, irrespective of the model of evolutionary change and of the phylogeny employed to simulate character change.

TABLE 1

Summary statistics (mean ± SE) for the thermal time constant (τ_r), body mass, median preferred temperature (T_p), and long-term averages of daily mean temperature during the entire year (T_{year}), during the months of lizard activity (T_{act}), during April (T_{apr}), and during July (T_{july}) for eight species of lacertid lizards

Species	τ_r (min)	Mass (g)	T_p (°C)	T_{year} (°C)	T_{act} (°C)	T_{apr} (°C)	T_{july} (°C)
Mediterranean:							
Psammodromus algirus	22.6 ± .8	11.8 ± 1.9	35.4	12.5	18.2	10.3	23.4
Psammodromus hispanicus	9.7 ± .1	1.9 ± .6	35.1	9.8	14.4	7.9	18.8
Podarcis hispanica	12.6 ± .3	3.7 ± .6	34.4	12.5	18.2	10.3	23.4
Acanthodactylus erythrurus	16.2 ± .7	7.0 ± 1.3	37.2	13.7	19.3	12.3	23.9
Northern or montane:							
Lacerta monticola	15.3 ± .5	8.3 ± .9	33.7	6.2	10.9	3.2	15.8
Podarcis muralis	12.3 ± .4	5.6 ± .5	34.2	8.0	12.8	6.2	16.8
Lacerta vivipara	11.0 ± .2	3.4 ± .4	32.5	9.6	14.4	8.8	17.4
Lacerta schreiberi	19.0 ± 1.9	14.0 ± 1.2	35.3	9.8	14.4	7.9	18.8

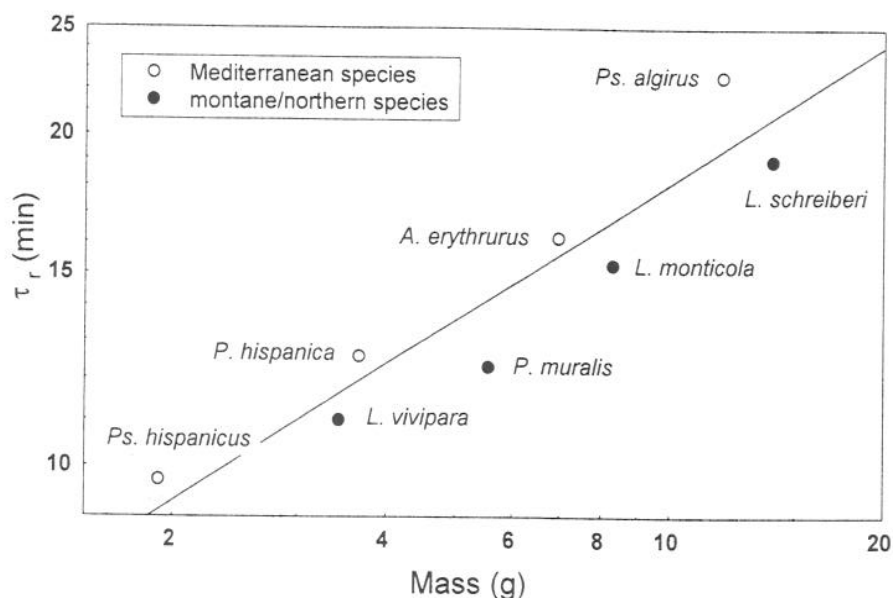Note. Data for T_p are from Bauwens et al. (1995).

Fig. 2. Interspecific relationship between the thermal time constant (τ_r) and body mass in lacertid lizards. Species from the Mediterranean climatic zone are indicated by open circles, and species with a northern or montane distribution by dots. The line represents the reduced major axis regression (slope = 0.41 ± 0.07) calculated with standardized independent contrasts.

The above analyses support the idea that lizards from cooler climate zones have lower mass-specific thermal time constants, and hence heat faster, than similarly sized species from warmer areas. However, this deduction may be criticized on two grounds. First, the species were classified in two well-delimited, but nevertheless arbitrary sets. Second, the distributional range provides, at best, only an indirect index of the prevailing climatic conditions. We therefore used a more refined and direct approach and examined correlations between thermal time constants and ambient temperatures recorded near each species' capture site.

We used partial correlation, holding constant for the effect of body mass, to explore covariation between the thermal time constant and ambient temperatures. Independent contrast analyses show that partial correlations between the thermal time constant and ambient temperature are positive and significant, irrespective of phylogenetic topology, set of branch lengths, or ambient temperature statistic (Table 3). Thus, clinal differences in ambient temperatures are associated with continuous interspecific variation in the size-adjusted thermal time constant. Species that inhabit relatively cool sites

TABLE 2

Phylogenetic ANCOVAs comparing the thermal time constants (log$_{10}$ adjusted) between Mediterranean or northern and montane lacertid lizards, with log$_{10}$ body mass as the covariate

Source of Variation	Gradual Brownian Motion		Speciational Brownian Motion		Punctuated Equilibrium		Ornstein-Uhlenbeck Process	
	Critical Value	P	Critical Value	P	Critical Value	P	Critical Value	P
Immunological phylogeny:								
Factor	6.26	<.001	7.71	.004	6.76	.002	7.25	<.001
Covariate	7.32	<.001	1.92	<.001	14.80	<.001	7.14	<.001
Explained	6.78	<.001	8.84	<.001	9.66	<.001	6.40	<.001
Morphological phylogeny:								
Factor	5.14	.002	4.93	.002	5.64	.002	6.29	.004
Covariate	1.04	<.001	1.31	<.001	14.99	<.001	6.78	<.001
Explained	6.54	<.001	6.50	<.001	9.33	<.001	5.85	<.001

Note. The F values obtained by ANCOVA were 27.46 (1 and 5 df), 256.61 (1 and 5 df), and 128.80 (2 and 5 df) for the effects of factor (i.e., climate zone), covariate (i.e., body mass), and model (variance explained), respectively. These F values would be judged highly significant ($P \le 0.003$) by conventional statistical tables, a procedure that ignores phylogenetic relations. Critical values for F statistics ($\alpha = 0.05$) and significance levels associated with the observed F values were obtained by simulating evolution along two distinct phylogenies (Fig. 1) and under different models of character change. All simulations ($n = 1,000$ in all cases) were bounded (see Material and Methods for details).

TABLE 3

Partial correlations, based on phylogenetically independent contrasts, between the thermal time constant and statistics describing ambient temperatures and the difference between preferred temperature (T_p) and ambient temperature, holding constant for the effects of body mass, and independent contrast bivariate correlations between preferred temperature and ambient temperature statistics

| | Variable Branch Lengths | | | | Constant Branch Lengths | | | |
| | Immunology | | Morphology | | Immunology | | Morphology | |
	r	P	r	P	r	P	r	P
Thermal time constant:								
Mean annual temperature	.772	.021	.823	.012	.812	.013	.857	.007
Mean temperature of activity season (T_{act})	.806	.014	.850	.008	.845	.008	.881	.005
Mean April temperature (T_{apr})	.624	.067	.688	.044	.697	.041	.750	.026
Mean July temperature	.873	.005	.887	.004	.892	.004	.905	.003
$T_p - T_{act}$	−.904	.003	−.858	.007	−.848	.008	−.835	.010
$T_p - T_{apr}$	−.796	.016	−.715	.036	−.729	.032	−.713	.036
Preferred temperature:								
Mean annual temperature	.567	.071	.568	.071	.584	.064	.591	.062
T_{act}	.547	.081	.546	.081	.584	.064	.592	.061
T_{apr}	.476	.117	.475	.118	.453	.130	.457	.127
Mean July temperature	.613	.053	.615	.052	.661	.037	.670	.035

Note. All variables were $\log_{10}$-transformed prior to analyses. Independent contrast correlations were calculated for two phylogenies (immunology and morphology; Fig. 1) and two different sets of branch lengths (variable and constant) (see Material and Methods for details).

have lower mass-specific thermal time constants and hence heat faster than similar-sized lizards from warmer areas.

During the early morning warm-up, lizards increase their T_b from ambient levels up to the preferred temperature range. The associated time investment in thermoregulatory activities will be highest when the preferred temperature is far above ambient temperature levels. The hypothesis of evolutionary adjustments in heating rates therefore predicts a negative relation between the thermal time constant and the difference between the preferred temperature and ambient temperature, rather than a relation with ambient temperature per se. To test this prediction we calculated two indices that measure the disparity between the preferred and ambient temperatures: (1) the difference between median preferred temperature and the average of the daily mean temperatures for the entire activity season and (2) the difference between median preferred temperature and the average of the daily mean temperatures recorded in April, the coldest month with lizard activity. Our results meet the predictions: independent contrasts correlations, holding constant for the effect of body mass, between the thermal time constant and the difference between preferred and ambient temperature are negative and statistically significant (Table 3). We conclude that mass-specific thermal time constant is shortest, and hence size-adjusted heating rate fastest, in species whose preferred temperature levels are far above the ambient temperatures.

What are the changes in heating time associated with the observed difference in the thermal time constant between northern or montane and Mediterranean lacertids? We estimated size-specific values of the thermal time constant for the two species sets from the independent-contrast relationship between the thermal time constant and mass (Fig. 2). The pooled within-groups slope, estimated by reduced major axis regression, was 0.41 ± 0.07 (estimates were highly similar for both phylogenies). Intercepts were obtained by positioning the regression through the estimated values at the root nodes of each species group (the latter estimate the bivariate means for each species set, weighted by phylogeny; Garland et al. 1993). This gives mass-specific thermal time constants equaling 6.4 min g$^{-0.41}$ for northern or montane species, and 7.5 min g$^{-0.41}$ for the Mediterranean species set. Thus, under identical conditions, heating time will be about 17% shorter in northern or montane species. For instance, the time required to increase T_b from 25° to 35°C is 4.8 min for a 7-g northern or montane species, as opposed to 5.6 min for an equal-sized Mediterranean lizard.

Besides changing the rate of heat gain, lizards may vary heating times by altering their preferred temperature, that is, the target of temperature regulation. The mean (± SD) preferred temperature for northern and montane

species (33.9° ± 1.16°C) was somewhat lower than for Mediterranean lizards (35.5° ± 1.17°C). However, this difference was not statistically significant (ANOVA; significance levels obtained by phylogenetic simulations assuming gradual Brownian motion; immunological tree: $P = 0.110$; morphological tree: $P = 0.070$). A similar result is obtained for a larger set of European lacertid lizards and with different models of character change (D. Bauwens, unpublished data). Preferred temperature was not correlated with body mass (independent contrasts correlations, $P > 0.30$); correlations between preferred temperature and ambient temperatures were positive, as predicted, but only rarely significant (Table 3). Thus, we found no strong statistical evidence for a relation between preferred temperatures and climatic conditions.

The available data allow us to estimate the change in preferred temperatures that would be equivalent, in terms of time spent heating, to the observed difference in the thermal time constant between northern or montane and Mediterranean species. For each northern or montane species we used our empirical time constant estimates and equation (1) to calculate t_p, the time needed to increase its T_b from the preferred temperature minus 10°C to the preferred temperature. We also estimated the expected value of the thermal time constant for an equal-sized hypothetical lizard that heats at a rate typical of the Mediterranean species (estimated thermal time constant $[\tau_r'] = 7.5 \, mass^{0.41}$). Substitution of these values into the equation

$$\ln(T_p/T_0) = t_p/\tau_r', \qquad (2)$$

(see eq. [1]), where T_0 is the T_b at the onset of heating, and solving for T_p, provides an estimate of the hypothetical preferred temperature. This indexes the preferred temperature of a species whose heating time equals that of a northern or montane lizard, while it warms at a rate similar to that observed in Mediterranean lacertids. The estimates of hypothetical preferred temperature were on average 1.7°C (SD = 0.35; range: 1.3–2.2°C) lower than the actual preferred temperatures of the northern or montane species. Thus, by shifting their preferred temperatures 1.7°C below actual levels, the northern or montane species would reduce the time spent heating by an amount equal to that induced by their faster heating rates. This hypothetical difference is similar to the observed difference in preferred temperatures between northern or montane lizards and Mediterranean lizards (1.6°C).

Discussion

The evolution of thermal physiology in relation to climatic conditions is a central paradigm of physiological ecology. In this study, we tested one pre-

diction of this hypothesis: lizard species that live in cool climates should exhibit higher heating rates than species from warmer areas. Our analysis of absolute heating rates does not seem to support this idea, as we found no differences between northern or montane and southern (Mediterranean) lacertids. However, most of the observed among-species variation in absolute heating rates is induced by differences in body mass (see also Smith 1976; Claussen and Art 1981; Bartholomew 1982), and variation in body size was not associated with climate within the group of species studied. The similarity of absolute heating rates between northern or montane and southern lacertids does therefore not dismiss the evolution of thermal physiology in relation to ambient conditions. It rather indicates that climate, through its effect on the absolute time spent heating, is not of overriding importance in shaping differences in body size among the species studied. This is hardly surprising, because a multitude of factors and processes, including ambient temperatures (Stevenson 1985a), induce variation in body size. As we rarely, if ever, know the distinct factors that affect the evolution of body size, and we seldom have reliable data to document the putative selection pressures, we cannot isolate the contribution of a single agent. A more fruitful approach to assess environmentally induced changes in heating rates consists of examining mass-specific heating rates. The detection of a relationship between interspecific differences in size-adjusted rates and climatic conditions would strongly support the idea of adaptive adjustments.

Relation between Size-Adjusted Heating Rates and
Ambient Temperatures

Our comparative study, conducted in an explicit phylogenetic context, demonstrates a clear-cut relation between variation in size-adjusted heating rates and ambient (environmental) temperatures in a clade of lacertid lizards. Lacertids with a northern or montane distribution exhibit higher mass-specific heating rates than species that are confined to the Mediterranean climatic zone. This conclusion is corroborated by a more refined correlational analysis, using long-term weather records as an index of prevailing climatic conditions: lizards that inhabit relatively cool sites warm at a faster mass-specific rate than species from warmer areas.

Our procedures prevented lizards from using behavioral adjustments during heating, so that the observed variation in heating rates basically reflects physiological differentiation. Field-active lizards, however, can and often do alter heating rates by using postural adjustments (Heath 1965; Muth 1977; Stevenson 1985b; Bauwens et al. 1996). Many lacertids exhibit well-recognizable basking postures, which include dorso-ventral flattening of

the body and a body orientation that provides maximal exposure to the sun (Avery 1976; Van Damme et al. 1987, 1989; Bauwens et al. 1990; Castilla and Bauwens 1991; Carrascal et al. 1992). The adoption of basking postures is most pronounced in cool-climate lacertids (e.g., *Lacerta vivipara, Lacerta monticola, Podarcis muralis*) but is less prominent or even absent in several of our Mediterranean lizards (*Acanthodactylus erythrurus, Psammodromus algirus, Psammodromus hispanicus*). Thus, behavioral adjustments will probably reinforce, rather than counteract, the observed variation in heating rates.

The higher size-adjusted heating rates of the northern and montane species reduce the time spent heating by about 17%. This reduction is likely to be of functional significance, because cool-climate lacertids spend a considerable proportion of their daily time budget in warming. For instance, field-active *L. vivipara* bask for about 45% of their time spent above ground (Van Damme et al. 1990). A further increase in time spent basking would dramatically curtail the time available for other activities (Avery 1976). Increased heating rates should be especially advantageous when cool ambient conditions periodically prevent or hamper the attainment of preferred temperatures. Such situations occur during cool spring months in a lowland habitat of *L. vivipara* (Van Damme et al. 1987) and during the early morning hours in a montane habitat of *Podarcis tiliguerta* (Van Damme et al. 1989) but not in the lowland Mediterranean habitats of *P. tiliguerta* (Van Damme et al. 1989) and *Podarcis hispanica atrata* (Bauwens et al. 1996). Moreover, relatively slow heating rates might be beneficial to Mediterranean lizards, especially during the hot summer months. At high ambient temperatures, retarded warming may prolong the time that T_b's can be maintained within the preferred range. However, this mechanism will be important only when there are few opportunities to reduce T_b by behavioral adjustments, that is, when most of the habitat has operative temperatures above the preferred range. Insufficient data are available to assess whether such conditions occur frequently in the habitats of Mediterranean lacertids (but see Belliure et al. [1996]).

Most biologists interpret a clear pattern of correlation between an organismal character and an environmental factor as evidence for adaptive evolution (e.g., Harvey and Pagel 1991; Miles and Dunham 1993; Ridley 1993). Recent criticism by Leroi and coauthors (1994) has emphasized some weaknesses of this approach. First, information on the phylogenetic relations within a species group might reveal that the organismal trait has changed in state only a limited number of times during the evolutionary history of the group. In the limit, the analysis may deal with only one historical character transition. Inferring adaptation from an essentially single event is, of

course, extremely reckless (Garland and Adolph 1994; Leroi et al. 1994). For continuous-valued traits, a similar problem arises when comparisons are restricted to two species or populations (Garland and Adolph 1994). To avoid these problems, we studied eight species and continuously distributed traits. This allows rigorous statistical testing of the strength and direction of the predicted relationship (Felsenstein 1988; Garland et al. 1992; Garland and Adolph 1994).

A second remark concerns the often imprecise definition and quantification of the putative selection regime (Leroi et al. 1994). For instance, climatic conditions are often classified within two broad, partially overlapping categories (e.g., temperate vs. tropical) or are indexed on an indirect scale (e.g., latitude). Such approaches offer little hope to reveal the environmental context of character evolution. Our correlational analyses used long-term weather data to index ambient heat loads. Although climate data recorded in weather stations do not measure the operative temperatures in lizard habitats (e.g., Bakken 1992), they do provide, at the very least, reliable estimates of the relative differences among habitats of different species.

These considerations, and the availability of information on the potential ecological significance of increased heating rates, incline us to consider the observed interspecific relation between mass-specific heating rates and ambient temperature as a convincing example of adaptive evolution. However, processes other than natural selection may generate organismal-environmental correlations (Leroi et al. 1994). Acclimatization may induce phenotypically plastic (i.e., nongenetic) changes of physiological traits in response to seasonal variation in an environmental factor (e.g., ambient temperature) (Prosser 1986). For instance, acclimatization of standard metabolic rate is well documented in lizards (Bennett and Dawson 1976), and such seasonal adjustments may differ among geographically separate populations or species (Tsuji 1988a, 1988b). In addition, continuous exposure to diverging environments may cause long-lasting phenotypic modifications. Such adjustments may induce character-environment correlations of the type we observed in lacertid lizards (Levins 1968). To examine this possibility we should study individuals of different species that were raised in the laboratory from birth (common garden design; Garland and Adolph 1991) or, preferably, that were reciprocally transplanted between sites with contrasting ambient conditions.

Possible Proximate Causes of Variation in Heating Rates

What physiological mechanisms may account for the observed diversity in mass-specific heating rates? Our study was not designed to answer this ques-

tion, but we can offer some suggestions. First, color may be important as a determinant of heat gain rates (Norris 1967; Porter 1967; Stevenson 1985b). Lacertid lizards do not exhibit obvious color changes other than those related to ontogenetic shifts or breeding condition (e.g., Díaz 1993), and they do not appear to use short-term changes in skin reflectance as a thermoregulatory device. However, differences among species in coloration and/or color pattern might partly be responsible for divergence in heating rates (Norris 1967; Stevenson 1985b). Casual observations do not point to a clear-cut difference in coloration between the northern or montane and Mediterranean lacertids studied herein. Nevertheless, we encourage efforts to measure the absorptance of the skin in our study species.

Second, differences in the size, shape and microornamentation of scales can significantly alter heating rates (Soulé 1966; Norris 1967; Ballinger et al. 1970). The possession of large dorsal scales, for instance, has been interpreted as an adaptation to reduce heat gains (Ballinger et al. 1970). Although we lack precise information for the species studied, the possession of relatively large dorsal scales does not follow any well-defined biogeographic pattern within the Lacertidae (Arnold 1989).

Finally, cardiovascular adjustments affect rates of heat exchange and are generally considered as the most important physiological mechanism in reptile thermoregulation (Bartholomew 1982). These adjustments include changes in heart rate (Bartholomew and Tucker 1963; Bartholomew and Lasiewski 1965; Weathers 1971) and peripheral vascular responses (Morgareidge and White 1969; Weathers 1971; Rice and Bradshaw 1980; Tracy et al. 1986). The local heating of lizard skin enhances subdermal blood flow, which in turn increases heating rate, to an extent that is roughly proportional to the magnitude of the heat input (Morgareidge and White 1969; Bartholomew 1982). Hence, all else being equal, short-term circulatory adjustments to ambient heat loads would induce elevated heating rates in species from warmer climates. The resulting character-environment relation would then be opposite to that observed in lacertid lizards.

Evolution of Thermal Physiology Characteristics

In general, reptiles use behavioral rather than physiological adjustments to regulate T_b (Huey 1982; Stevenson 1985b; Bartholomew 1987). When faced with an environmental change, ectotherms should initially respond with short-term compensatory behaviors and by evolutionary changes in behavioral adjustments (Bogert 1949; Hertz 1981; Huey and Bennett 1987). As an extrapolation of this argument, it has been hypothesized that thermal physiology characteristics are evolutionary inert (Bogert 1949); Hertz and coau-

thors (1983) termed this the "static" view of thermal physiology evolution. The antagonistic "labile" view (Hertz et al. 1983) holds that thermal physiology traits evolve readily and that physiological differentiation parallels variation in environmental heat loads. The latter view is supported by observations of interspecific variation in the position and shape of the thermal sensitivity functions for sprint speed in lizards (van Berkum 1986; Huey and Bennett 1987; Bauwens et al. 1995). These studies also show that among-species differences in the optimal temperatures for sprinting, a physiological trait, are usually smaller than variation in preferred or field T_b's, two behavioral characteristics. Thus, thermal physiology traits seem to be evolutionary more conservative than thermal preferences.

Our data bear some relevance to these issues, at least assuming that the observed interspecific differences are genetically determined. First, we demonstrate that size-adjusted heating rates differ among closely related species and that this variation parallels differences in environmental temperatures. Second, we detected statistically significant differences between northern or montane and Mediterranean lacertids in mass-specific heating rates, a physiological trait, but not in preferred T_b's, a behavioral characteristic. This could be interpreted as a counterexample to the paradigm that thermal preferences show greater evolutionary flexibility than thermal physiology traits. However, we reach a different conclusion upon considering the effect on heating times induced by the observed shift in heating rates and by the small, statistically nonsignificant difference in preferred temperatures. Observed differences in these two characteristics have similar impacts on the estimated amount of time spent heating and are therefore of equal biological significance. Thus, both physiological (i.e., heating rates) and behavioral (i.e., preferred temperatures) traits have evolved in relation to ambient temperature within this clade of lacertid lizards, and changes in heating rates and preferred temperatures make equal contributions to reducing heating times of the northern or montane species.

Acknowledgments

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