

# Thermal characteristics of ten Andean lizards of the genus *Liolaemus* in central Chile

Características térmicas de diez lagartijas andinas del género *Liolaemus* en Chile central

JOHN H. CAROTHERS<sup>1</sup>, STANLEY F. FOX<sup>2</sup>, PABLO A. MARQUET<sup>3</sup>  
and FABIAN M. JAKSIC<sup>3</sup>

<sup>1</sup>Department of Zoology and Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA. Current address: Department of Biology, Cabrillo College, Aptos, CA 95003, USA

<sup>2</sup>Department of Zoology, Oklahoma State University, Stillwater, OK 74078, USA

<sup>3</sup>Departamento de Ecología, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

## ABSTRACT

We studied the ecology of ten species of tropidurid lizards in the genus *Liolaemus* on an altitudinal transect in the central Chilean Andes, from 1500 to 3000 m elevation, to determine whether physiological factors may be setting distribution limits. Detailed data on thermal biology are presented here. There was a lack of association between lizard thermal tolerance and elevation, thus suggesting that these temperature relationships did not set distributional limits within the elevations of the study transect. Some physical factors did influence the thermal biology of *Liolaemus*. Body mass determined thermal inertia, thus influencing rates of cooling and heating. Larger body size and its consequent thermal inertia in part may determine diel activity periods, with smaller individuals active earlier and larger individuals active later. Non mass-related differences in heating rates also existed among the species: those at higher elevations heated more slowly. The cooler ambient temperatures at higher elevations did not produce interspecific differences in body temperature, but most high-elevation species showed an intraspecific decrease in body temperature with elevation.

**Key words:** Thermoregulation, critical temperature, body size, altitudinal gradient, Chile

## RESUMEN

Estudiamos la ecología de diez especies de lagartijas tropidúridas del género *Liolaemus* en un transecto altitudinal en los Andes centro-chilenos, entre 1 500 y 3 000 m sobre el nivel del mar, para determinar si algunos factores fisiológicos pudieran estar definiendo sus límites distribucionales. Aquí presentamos datos detallados sobre la biología térmica de estas lagartijas. Hubo falta de asociación entre las tolerancias térmicas y las distribuciones altitudinales de las lagartijas, sugiriendo que dichas tolerancias no determinan los límites distribucionales en el transecto estudiado. Sin embargo, algunos factores físicos influyeron sobre la biología térmica de los *Liolaemus*. El tamaño corporal afectó la inercia térmica, a través de influir las tasas de enfriamiento y calentamiento. Estas dos características asociadas pueden determinar los períodos de actividad diarios, dado que los individuos más pequeños estaban activos más temprano que aquellos más grandes. Por otra parte, hubo características térmicas no asociadas a la masa corporal: las especies de mayor altura se calentaban más lentamente, independientemente, de su masa corporal. Las temperaturas ambientales más bajas que se verificaron a mayores alturas no se reflejaron estadísticamente en diferencias interespecíficas en temperatura corporal, pero la mayoría de las especies de mayores alturas mostraron un decrecimiento intraspecifico en su temperatura corporal con la altitud.

**Palabras clave:** Termorregulación, temperatura crítica, tamaño corporal, gradiente altitudinal, Chile

## INTRODUCTION

Almost all studies of the thermal characteristics of congeneric lizard assemblages have focused on members of the genus *Anolis* inhabiting tropical Caribbean islands (e.g., Ballinger et al. 1970, Corn 1971, Hertz 1977, 1979, 1980, 1983, Hertz & Huey 1981; but see Licht et al. 1966, Spellerberg

1972a, 1972b, and Greer 1980 for Australian desert saurofaunas). This work has shown that variability among lizard species in their thermal characteristics can sometimes be attributed to variation in certain characteristics of their physical environment. For example, some of these and other studies suggest the occurrence of altitudinal trends in various measures of thermal tolerance (review in

Huey & Slatkin 1976, Huey 1982), although sometimes such elevation-related effects upon thermal biology are very limited (e.g., Bogert 1949, Spellerberg 1972b, 1972c, Hertz 1979, Hertz & Huey 1981). But because these studies involve perhaps only two or three species, one at high elevations and one at low elevations, interspecific differences in thermal characteristics attributed to adaptation may well result only from chance: sample sizes of species are too few for statistical analyses. Only intraspecific comparisons are valid in such cases.

The purpose of this study was to investigate some thermal characteristics of a relatively complex lizard assemblage over a broad elevational range in a temperate area. We wished to examine the relations between distributions of the lizards and certain thermal characteristics the different species possess, comparing these results with other studies. The subject of this study was a diurnally active South American Andean tropidurid lizard genus, *Liolaemus*, whose members occur at very high and cold conditions in the Andean cordillera and have been noted for their remarkable ability to withstand what for an ectothermic organism are rather harsh thermal conditions (Pearson 1954, 1977, Pearson & Bradford 1976, Marquet et al. 1989). The species in the present study range in elevational distribution from sea level to over 3000 m (Fuentes & Jaksic 1979a), occupying habitats as diverse as trees, bushes and cacti, grasses, open ground, sand, rocks, and boulders (Donoso-Barros 1966).

A cautionary note is worth mentioning from the beginning. When working with a set of closely related species it is desirable to know the phylogeny of the species in order to make use of the Comparative Method to disentangle purely biophysical or ecological effects from phylogenetic inertia (Felsenstein 1985, Huey & Bennet 1987, Garland et al. 1991, Harvey & Pagel 1991, Martins & Hansen 1996). Unfortunately, no phylogeny is yet available for the *Liolaemus* species here considered, and thus our results will remain inconclusive as to the role of phylogenetic relatedness in the similarities and differences detected in our study of thermal biology.

Only laboratory-measured features of the thermal biology of *Liolaemus* were focused on here; the field thermal biology of these species will be dealt with elsewhere. Of particular interest was how elevational distributions were reflected in tolerances to minimum and maximum temperatures, in order to determine whether one could predict their general elevational distribution from the basic thermal characteristics of the lizards. Because body size is likely to influence heat exchange with the environment for these ectothermic animals, the effect of body size on thermal inertia, with regard to heating and cooling rates, was investigated to determine what if any role they play in contributing to altitudinal distribution limits of the species in question.

#### MATERIAL AND METHODS

##### *Temperature gradient and species*

Only four meteorological stations yielded adequate data for the altitudinal gradient examined (Table 1). Unfortunately, none of these stations reached as high as 3000 m elevation. Nevertheless, it is clear that both mean maximum and minimum temperatures decrease with increasing altitude. The difference observed between the lowest (San José de Maipo) and the highest station (Embalse El Yeso) amounts to a decrease of 0.6°C/100 m for the yearly mean maximum and of 0.2°C/100 m for the yearly mean minimum temperatures (Table 1).

*Liolaemus altissimus*, *L. chiliensis*, *L. fuscus*, *L. lemniscatus*, *L. leopardinus*, *L. monticola*, *L. nigroviridis*, *L. nitidus*, *L. schroederi*, and *L. tenuis* were studied. These ten species encompass all of the *Liolaemus* species in the central Chilean cordillera near Santiago, Chile. They show distinct patterns of zonation with predictable altitudinal distributions and microhabitat preferences, occurring from below 1500 m to above 3000 m elevation in this region. The body sizes, elevational ranges (from Fuentes & Jaksic 1979a), and the elevations where the specimens used in conducting the following experiments were collected are presented in Table 2.

TABLE 1

Mean maximum and minimum temperatures (°C)  
recorded in Meteorological Stations (MS) in the general study area,  
ordered by altitude (m above sea level)

Temperaturas máximas y mínimas medias registradas en Estaciones Meteorológicas (MS)  
del área general de estudio, ordenadas según su altitud (m sobre el nivel del mar)

MS	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
San José de Maipo (33°39'S, 70°22'W, 1060 m elevation)													
Max	27.8	27.1	25.3	22.3	18.2	15.5	15.5	16.0	18.5	20.6	23.8	27.0	21.5
Min	10.6	10.2	8.3	6.1	4.9	2.5	2.4	2.4	4.1	5.6	7.4	9.4	6.2
Queltehues (33°49'S, 70°12'W, 1365 m elevation)													
Max	27.1	28.8	27.0	25.1	19.4	14.7	10.7	15.9	16.7	20.2	22.9	27.3	21.3
Min	11.8	13.7	12.1	10.7	8.0	7.4	3.5	4.4	5.9	8.3	10.2	14.5	9.2
Las Melosas (33°55'S, 70°13'W, 1600 m elevation)													
Max	28.3	28.2	27.5	22.3	16.5	13.9	13.2	16.1	16.0	20.4	22.3	26.6	20.9
Min	11.4	11.5	11.3	8.4	5.8	3.4	3.3	4.6	4.3	6.3	8.4	11.4	7.5
Embalse El Yeso (33°40'S, 70°06'W, 2475 m elevation)													
Max	20.2	20.2	18.9	15.4	10.8	6.9	5.9	6.8	9.3	12.4	15.8	18.7	13.4
Min	8.2	7.9	7.2	4.9	1.8	-1.3	-2.1	-2.3	-0.6	1.7	4.5	7.0	3.1

TABLE 2

Mean adult and juvenile sizes (g and mm, n = sample size), elevational range (m)  
where the species is known to occur, and elevation collection (m)  
of the 10 *Liolaemus* species used in this study

Tamaño medio de adultos y juveniles (g y mm, n = tamaño muestral), rango altitudinal (m)  
en que se sabe que la especie se encuentra y altura de colecta (m) de las 10 especies  
de *Liolaemus* usadas en este estudio

Species	Adults		Juveniles		Elevation range m	Elevation of collection m
	$\bar{x} \pm SD$ (n) g	$\bar{x} \pm SD$ (n) mm	$\bar{x} \pm SD$ (n) g	$\bar{x} \pm SD$ (n) mm		
<i>L. altissimus</i>	11.9 ± 3.2 (141)	71.0 ± 6.5 (143)	5.4 ± 2.3 (78)	55.0 ± 8.2 (77)	2100-3000	2850
<i>L. chiliensis</i>	25.1 ± 7.0 (6)	89.6 ± 9.2 (6)	5.0 ± 0.0 (1)	55.0 ± 0.0 (1)	1500-1800	1500
<i>L. fuscus</i>	3.1 ± 0.7 (71)	47.4 ± 3.5 (77)	1.9 ± 0.6 (24)	39.3 ± 3.9 (24)	1500-2100	1200
<i>L. lemniscatus</i>	3.4 ± 0.7 (297)	49.7 ± 3.6 (302)	1.9 ± 0.5 (42)	40.0 ± 3.3 (43)	1500-2400	1200
<i>L. leopardinus</i>	20.7 ± 4.9 (84)	86.9 ± 9.3 (84)	6.6 ± 2.9 (23)	57.6 ± 8.7 (23)	2100-3000	2850
<i>L. monticola</i>	7.3 ± 1.8 (135)	61.3 ± 5.3 (141)	2.9 ± 0.9 (82)	45.4 ± 4.6 (82)	1500-2450	2200
<i>L. nigroviridis</i>	8.7 ± 3.6 (257)	64.8 ± 7.3 (273)	3.3 ± 1.9 (82)	46.7 ± 9.2 (84)	1700-3000	2675
<i>L. nitidus</i>	21.5 ± 7.8 (83)	84.6 ± 10.2 (89)	6.0 ± 2.5 (65)	55.6 ± 7.6 (67)	1500-2450	2200
<i>L. schroederi</i>	4.9 ± 2.3 (12)	54.2 ± 6.3 (13)	2.3 ± 0.0 (1)	42.0 ± 0.0 (1)	1800-2590	2350
<i>L. tenuis</i>	4.8 ± 1.2 (36)	55.1 ± 4.5 (37)	2.3 ± 0.5 (9)	43.7 ± 3.8 (10)	1500-2040	1500

### *Heating and cooling rates*

In the cooling rate experiments only one species, *L. altissimus*, was used, whereas for the heating rate experiments all but *L. schroederi* and *L. chiliensis* were used. Individuals were caught over a two day period and maintained in separate, numbered plastic bags at room temperature in the laboratory in Santiago under the prevailing photoperiod for one day. The experiments then were conducted the following three days, so that no more than five days elapsed between capture and experimentation. Because the time of day can have an effect on thermal characteristics (Kosh & Hutchison 1968, Mahoney & Hutchison 1969), all experiments were performed within restricted periods: cooling rate experiments were performed from 1000 h until 1500 h, and heating experiments were performed from 1800 h until 2200 h.

For both the heating and cooling rate experiments, the lizards were placed in a cylindrical aluminum container 180 mm in diameter and 200 mm deep. In the bottom was placed a thin (15 mm) layer of Styrofoam covered by a thin sheet of cardboard, to prevent thermal conductance from the metal can bottom. A thermocouple (covered with a thin layer of silicone and lubricated with petroleum jelly for easing insertion) was inserted 1 cm into the cloaca of each experimental lizard, taped in place at the tail base of the lizard to prevent it from being dislodged, and routed out the center of the can's bottom through a 10 mm hole. The thermocouple was connected to a digital readout which displayed the lizard's body temperature to the nearest 0.1°C.

In the heating rate trials, individuals of each *Liolaemus* lizard species were first cooled to 13°C, then heated by a 75 watt lamp suspended 10 cm above the container, following the methods of Hertz (1977). Lizards were timed with a stopwatch, started when their body temperatures warmed to 15°C, recording the time elapsed for their bodies to reach 35°C. In the cooling rate trials, lizards were first warmed to 37°C, then placed in a refrigerator maintained between 4°C and 6°C. Lizards were timed with a stopwatch, started when their body

temperatures decreased to 35°C, recording the time elapsed for their bodies to attain a temperature of 15°C. The time it took for an individual lizard to heat up or cool down was called, respectively, heating and cooling rate.

### *Maximum temperatures and critical thermal minima*

The same individual lizards from the heat rate experiment described above were subjected to continued and uninterrupted heating after they reached 38°C until they initiated panting, at which time heating was stopped. The elapsed time and temperature at which the individual lizards attempted to avoid further heating, as indicated by vigorous movements within the container, indicating discomfort, was recorded. This point was termed the Experimental Voluntary Maximum (EVM). Panting (respiration with the mouth wide open, exposing the moist mouth lining and tongue for evaporative cooling) occurred after individuals reached this temperature, and this temperature (PANT) and the elapsed time to reach it were also recorded. Heating was not continued past this point, so that one measure not taken was what is termed the Critical Thermal Maximum (CTMax). We felt that the temperatures and times to vigorous activity and panting were better indicators of maximum voluntarily-experienced body temperature, and more ecologically relevant, than measurement of CTMax values as indicated by the loss of coordinated activity (absence of righting response when turned upside down), spasms, and death of the individual under study.

The Critical Thermal Minimum (CT-Min) of each species was measured by cooling down individuals of all ten species (in a walk in freezer maintained at -15°C) to such a temperature at which they were incapable of righting themselves when turned on their back. This was deemed an ecologically relevant measurement. Lizards at high elevations must, with the coming of the new day's sun, become active underground in their refuges despite conditions in which a snow pack of more than one meter deep may be present, and crawl up to

the surface in order to bask in the bright sun on emergent boulders (JHC, personal observations).

*Acclimation and elevation*

Various studies have demonstrated effects of acclimation on thermal tolerances of lizards (Lowe & Vance 1955, Kour & Hutchison 1970). As a consequence, acclimation to a common temperature may be needed to detect differences in thermal tolerances not caused by acclimation to differing field temperatures. For comparisons of CTMin temperatures, individuals of each species used in this experiment were maintained at a moderate (20°C) temperature in the laboratory for 10 days before this experiment was performed in order to acclimate all species to a common temperature. The results of the measurements following this period of acclimation would then reduce field acclimation effects as a factor causing differences in thermal minima among the species, especially for those living at higher elevations where, relative to the lower elevation species, colder temperatures are experienced.

Regressions of the various thermal characteristics of these species were performed against two independent measures of elevation: maximum elevation of known occurrence along the transects and elevation from which the specimens examined were collected. The former measure assumes that each species will have little elevationally-related intraspecific variation (either from acclimation, genetic differentiation, or both) in the dependent thermal variables under examination. The latter elevation measure represents how individuals of the various species collected from a given elevation respond, and allows for elevationally-related intraspecific variability in thermal characteristics.

RESULTS

*Heating and cooling rates*

There was a positive and significant relationship between the mass of an individual *L. altissimus* and the time it took to heat up

or cool down (Fig. 1). The same positive relationship of mass to heating rate occurred for all the species (Table 3). In the experiments on heating and cooling rates of *L. altissimus*, for which there was the largest sample size, the rates of change appeared more dependent upon lizard body mass than upon SVL (Table 4).

Because body mass affects heating rate, and because the species vary in mass in these interspecific comparisons, analyses of covariance with body mass as the covariate

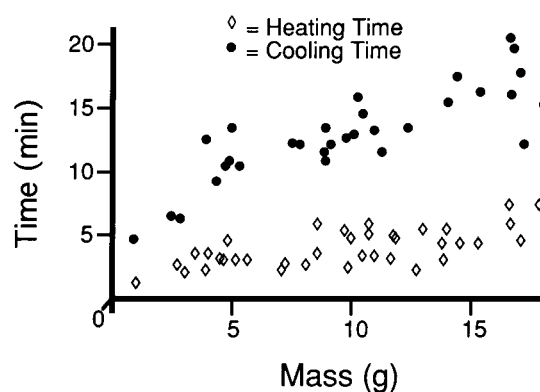


Fig. 1: Time (min) for *L. altissimus* of differing body mass (g) to change in body temperature when heated from 15°C to 35°C and cooled from 35°C to 15°C.

Tiempo (min) para que *L. altissimus* que difieren en masa corporal (g) cambien su temperatura corporal cuando son calentados desde 15°C a 35°C y enfriados desde 35°C a 15°C.

TABLE 3

Y-intercepts and correlation coefficients (r) for heating rates against body mass (g) for eight *Liolaemus* species. n = sample size, \* P<0.05, \*\* P<0.01.

Interceptos y coeficientes de correlación (r) para la tasa de calentamiento versus la masa corporal (g) de ocho especies de *Liolaemus*. n = tamaño muestral, \* P<0.05, \*\* P<0.01.

Species	n	Y-intercept	r
<i>L. altissimus</i>	37	2.918	0.743**
<i>L. fuscus</i>	10	1.555	0.779**
<i>L. lemniscatus</i>	12	1.671	0.555*
<i>L. leopardinus</i>	9	3.961	0.646*
<i>L. monticola</i>	10	2.465	0.721**
<i>L. nigroviridis</i>	16	3.834	0.491*
<i>L. nitidus</i>	11	3.466	0.762**
<i>L. tenuis</i>	12	2.491	0.538*

TABLE 4

Heating and cooling rates of *L. altissimus* in relation to body mass (g) and snout-vent length (mm). n = sample size, \*\*\* P<0.001.

Tasas de calentamiento y enfriamiento de *L. altissimus* en relación a la masa corporal (g) y longitud hocico-cloaca (mm). n = tamaño muestral, \*\*\* P<0.001.

Rates	Body mass r <sup>2</sup> (F)	Snout-vent length r <sup>2</sup> (F)
Heating (n=28)	0.56 (35.46***)	0.43 (21.10***)
Cooling (n=32)	0.66 (61.57***)	0.62 (50.94***)

were performed to look for interspecific differences in heating rates (Table 3). A test of the homogeneity of slopes, which assumes no interaction between mass (the covariate) and species (the treatment) could not detect differences among the species in the slopes of the heating rates (F=1.412, d.f.=7, P>0.2, ANCOVA). However, the elevations of the regressions of heating rates of the species did differ significantly (F=87.288, d.f.=1, P<0.01, ANCOVA). Thus, the heating rates of the species differ from each other in a fashion unrelated to their mass (Table 3).

#### Minimal and maximal thermal tolerances

Considerable differences in mean CTMin values existed among the species (F=2.173, d.f.=7, P<0.05, ANOVA), and Tukey a posteriori tests revealed that various combinations of species pairs differed significantly from one another (Fig. 2).

The results of the measurements of EVMs gave indications of conservatism as well as divergence among the species. Except for one individual *L. leopardinus*, each species initiated thermal stress avoidance movements at 35°C (Fig. 3). Examination of the ranges and maximum EVMs showed high variation among the species, from almost no variability for *L. leopardinus* (all having EVMs from 34-36°C) to great variability for *L. nigroviridis* and *L. altissimus*, which had EVMs ranging up to 42°C. Although significant differences existed among the species in EVMs (F=2.173, d.f.=7, P<0.05, ANOVA), the range in mean EVMs was slight (from 35.2°C for *L.*

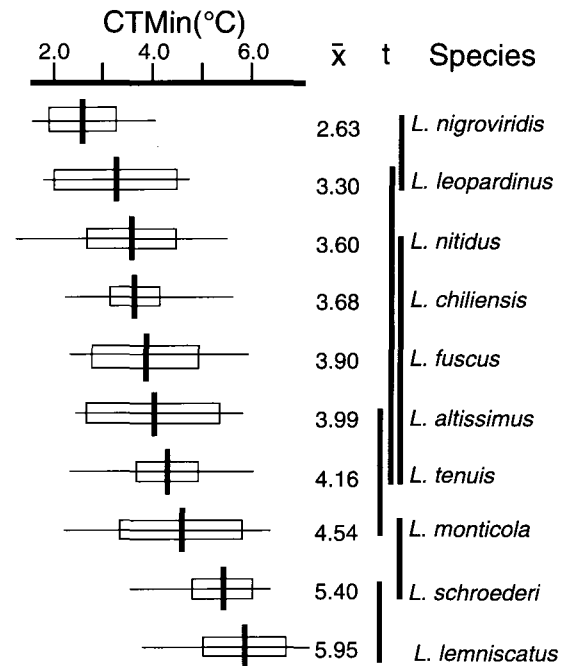


Fig. 2: Mean critical thermal minimum (CTMin) for ten *Liolaemus* species, with ranges and one standard deviation (box). Vertical bars (t) are results of Tukey pairwise-comparisons. Bars connecting species indicate species indistinguishable at the P=0.05, whereas those unconnected differ at least by P<0.05.

Medias de mínimo térmico crítico (CTMin) para diez especies de *Liolaemus*, con sus rangos y una desviación estándar (cajas). Las barras verticales (t) son los resultados de comparaciones pareadas de Tukey. Las barras que conectan especies indican aquellas indistinguibles al nivel de P=0,05, en tanto que aquellas desconectadas difieren en al menos P<0,05.

*leopardinus* to 37.4°C for *L. nigroviridis*) and no species pairs comparisons were significantly different using Tukey tests.

PANTs were always higher than EVMs (Fig. 4). Ranges tended to be similar among the species, although means showed significant differences (F=9.414, d.f.=7, P<<0.01, ANOVA). Tukey paired-comparison tests showed clear differences among various species pair combinations (Fig. 4).

The three temperature tolerance measurements (CTMin, EVM, and PANT; Table 5) were compared to each other using two-tailed Spearman rank correlation to determine if a relationship existed between any of these values. None of the correlations approached significance. In addition,

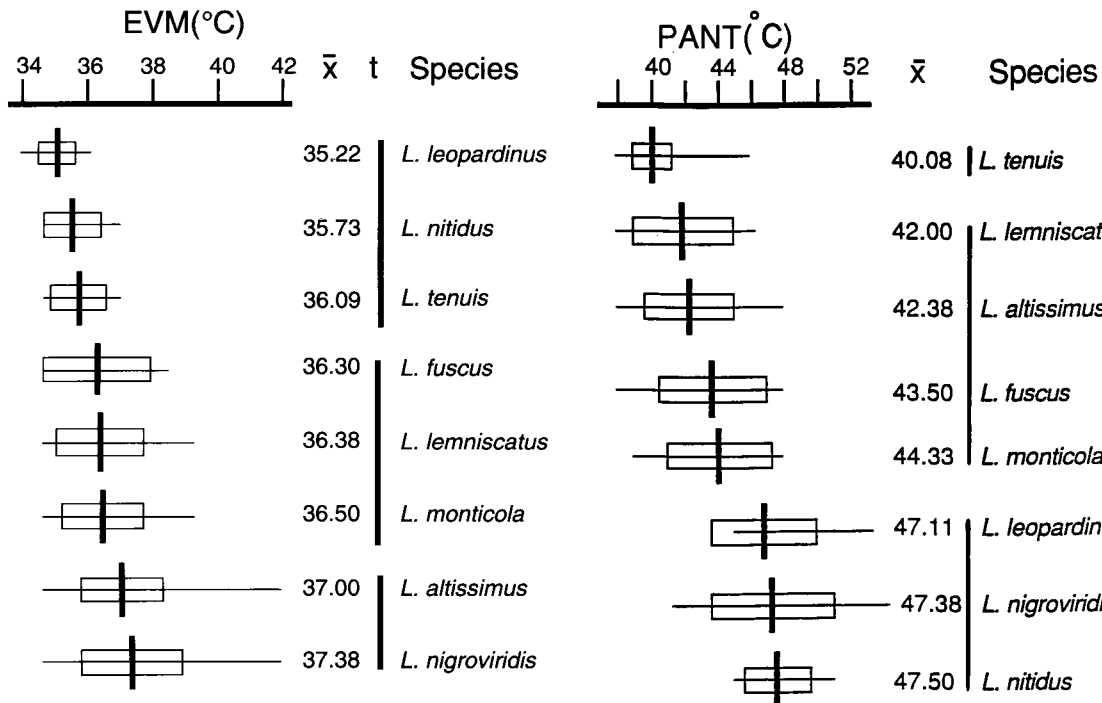


Fig. 3: Mean experimental voluntary maximum (EVM) for eight *Liolaemus* species. Details as in Fig. 2.

Medias de máximo voluntario experimental (EVM) para ocho especies de *Liolaemus*. Detalles tal cual en Fig. 2.

Fig. 4: Mean panting temperatures (PANT) for eight *Liolaemus* species. Details as in Fig. 2.

Medias de temperaturas de jadeo (PANT) para ocho especies de *Liolaemus*. Detalles tal cual en Fig. 2.

TABLE 5

Mean values ( $n$  = sample size) for critical thermal minima (CTM), experimental voluntary maximum (EVM), and panting temperatures (PANT), in °C. Mean field body temperature data ( $T_b$ ) are from Carothers et al. (unpublished data). n/d indicates that data were not obtained.

Valores medios ( $n$  = tamaño muestral) para las temperaturas mínima crítica (CTM), máxima voluntaria experimental (EVM), y de jadeo (PANT), en °C. Los datos de temperatura media de actividad en terreno ( $T_b$ ) provienen de Carothers et al. (datos no publicados). n/d indica que no se obtuvieron datos.

Species	CTMin $\bar{x} \pm SD$ (n)	EVM $\bar{x} \pm SD$ (n)	PANT $\bar{x} \pm SD$ (n)	$T_b$ $\bar{x} \pm SD$
<i>L. altissimus</i>	3.99 $\pm$ 0.88 (21)	37.00 $\pm$ 2.13 (31)	42.38 $\pm$ 2.66 (31)	33.03 $\pm$ 2.29
<i>L. chiliensis</i>	3.68 $\pm$ 0.39 (6)	n/d	n/d	34.09 $\pm$ 2.22
<i>L. fuscus</i>	3.90 $\pm$ 0.89 (17)	36.30 $\pm$ 1.49 (10)	43.50 $\pm$ 2.92 (10)	34.61 $\pm$ 1.62
<i>L. lemniscatus</i>	5.95 $\pm$ 1.01 (24)	36.38 $\pm$ 1.30 (8)	42.00 $\pm$ 2.92 (10)	34.62 $\pm$ 1.59
<i>L. leopardinus</i>	2.63 $\pm$ 0.65 (32)	35.22 $\pm$ 0.44 (9)	47.11 $\pm$ 2.98 (9)	34.07 $\pm$ 2.12
<i>L. monticola</i>	4.54 $\pm$ 1.32 (40)	36.50 $\pm$ 0.79 (10)	44.33 $\pm$ 2.96 (9)	35.29 $\pm$ 1.52
<i>L. nigroviridis</i>	3.30 $\pm$ 1.25 (29)	37.38 $\pm$ 2.19 (16)	47.38 $\pm$ 3.63 (16)	35.49 $\pm$ 2.08
<i>L. nitidus</i>	3.60 $\pm$ 0.90 (26)	35.73 $\pm$ 0.79 (10)	47.50 $\pm$ 1.90 (10)	34.96 $\pm$ 1.80
<i>L. schroederi</i>	5.40 $\pm$ 0.52 (8)	n/d	n/d	33.38 $\pm$ 2.22
<i>L. tenuis</i>	4.16 $\pm$ 0.46 (16)	36.09 $\pm$ 0.83 (11)	40.08 $\pm$ 5.42 (12)	34.59 $\pm$ 2.04

these three measures were tested for correlation to the measurements of mean field body temperatures for the species (to be reported elsewhere). The correlation between mean field body temperature and CTMin was  $r_s=0.006$ , that for EVM was  $r_s=0.071$ , and that for PANT  $r_s=0.548$ , none of which was significant. Even for those previous correlation comparisons for which a one-tailed test would be appropriate, calculated  $r_s$  values did not exceed the required critical  $r_s(1,8)=0.643$ . In the case of field body temperature against CTMin,  $n=10$ , so that the critical value for  $r_s(1,10)=0.564$ .

#### *Elevational effects and correlations*

The thermal characteristics of the different species were examined for possible elevation-related trends among the species. CTMin results, maximum thermal tolerance measurements (EVM and PANT temperatures), and heating rates of each species were compared to the elevations from which the individuals used in the experiments were collected, as well as to the maximum elevations at which the species are known to occur in the study area of the central Chilean cordillera. These comparisons among the species revealed a significant effect of both collection elevation and maximum elevations on heating rate among the species (Fig. 5a&b). Species with higher elevational distributions heated at lower rates than those occurring at lower elevations, when correlating heating rate to either collection elevation ( $r^2=0.749$ ,  $t=4.229$ ,  $d.f.=6$ ,  $P<0.01$ , 1-tailed t-test) or maximum elevational distribution ( $r^2=0.712$ ,  $t=3.849$ ,  $d.f.=6$ ,  $P<0.01$ , 1-tailed t-test).

The search for elevation-related trends in thermal tolerances was less successful. No relation was found with CTMin values for collection elevation ( $t=-1.424$ ,  $d.f.=8$ ,  $P>0.05$ , 1-tailed t-test) or for maximum elevation ( $t=-0.993$ ,  $d.f.=8$ ,  $P>0.10$ , 1-tailed t-test). Regarding high temperature tolerances, no significant relationship of mean EVMs to either elevation of collection site ( $t=0.235$ ,  $d.f.=6$ ,  $P>0.50$ , 1-tailed t-test) or to maximum elevational distribution ( $t=0.456$ ,  $d.f.=6$ ,  $P>0.30$ , 1-tailed t-test). Likewise, no significant relationship was found between mean PANTs of the species

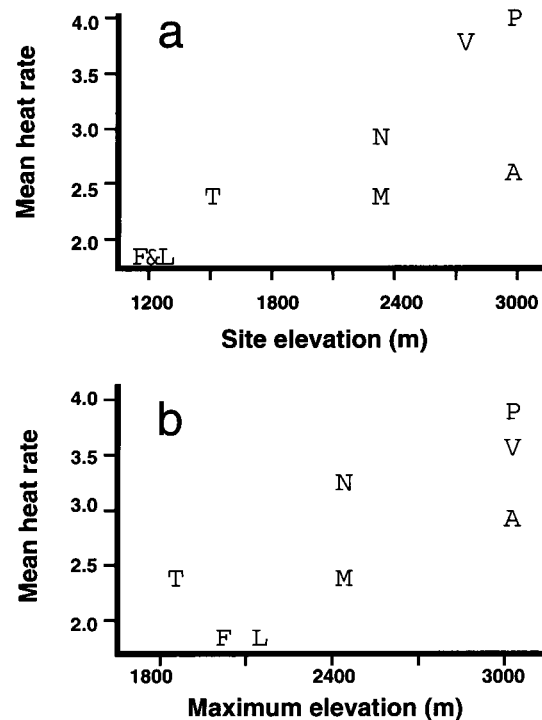


Fig. 5a&b: Mean y-intercepts of plots of heating rates against (a) collection site elevation and (b) maximum elevation of occurrence for eight *Liolaemus* species. Higher mean rates indicate longer periods required to heat up, independent of body mass. Symbols represent species as follows: A = *L. altissimus*, F = *L. fuscus*, L = *L. lemniscatus*, M = *L. monticola*, N = *L. nitidus*, P = *L. leopardinus*, T = *L. tenuis*, and V = *L. nigroviridis*.

Interceptos medios de las tasas de calentamiento versus: (a) altura del sitio de colecta y (b) altura máxima de distribución para ocho especies de *Liolaemus*. Tasas medias más altas indican que se requieren períodos más largos para calentarse, independientemente de la masa corporal. Los símbolos representan las especies de la siguiente manera: A = *L. altissimus*, F = *L. fuscus*, L = *L. lemniscatus*, M = *L. monticola*, N = *L. nitidus*, P = *L. leopardinus*, T = *L. tenuis*, and V = *L. nigroviridis*.

and collection site elevation ( $t=1.778$ ,  $d.f.=6$ ,  $P>0.05$ , 1-tailed t-test) or maximum elevational distribution ( $t=1.647$ ,  $d.f.=6$ ,  $P>0.05$ , 1-tailed t-test).

## DISCUSSION

### *Body sizes and thermal relations*

Simple considerations of the physical properties of solids predict that the time that an



object takes to heat or cool is related to the heat capacity of that object's mass. This relationship is evident in the heating and cooling rate data for *L. altissimus*. A difference in size-related heating rates has been reported anecdotally for a high elevation Peruvian *Liolaemus* species, *L. multiformis* (Pearson 1954). However, biophysical modeling (Porter et al. 1973, Tracy 1982) and experimental studies (Bartholomew 1982) have shown that lizards differ from inanimate objects in that they may exert considerable control over their heat exchange with the environment, and hence the rate of change in body temperature. Dead lizards heat and cool at the same rates, whereas live lizards heat up at rates higher than those at which they cool (Bartholomew 1982). Lizards may physiologically regulate heat exchange rates by modifying their pulmonary evaporation (Templeton 1960, Dawson & Templeton 1963, 1966, Crawford & Kampe 1971), vasomotor activity (Morgareidge & White 1969, Baker et al. 1972, Rice & Bradshaw 1980), cardiac shunting (Tucker 1966, 1967, White 1976), and changing their dermal reflectance (Norris 1967, Porter 1967, Rice & Bradshaw 1980). It follows that variation among individuals in the use of these features will influence those individual's heat exchange rates.

The last factor, dermal reflectance, has been shown to be unimportant in intraspecific rates of heat gain for the species of *Liolaemus* in this study: they fail to display the phenomenon of color change with body temperature observed in many other lizard species (JHC, personal observations). However, the variability among similar-sized individuals seen in both their heating and cooling curves demonstrates that much non size-related individual variation can occur in the rates of temperature change, and these differences can probably be attributed to individual differences in physiology.

#### *Relationships among thermal tolerances*

The lack of correlation between the minimum and maximum thermal tolerance measurements is at first surprising, as one

might expect lizards which are more "cold adapted" (those with a low CTMin) to have a relatively lower threshold tolerance of high temperatures than "warm adapted" species (those with a higher CTMin). However, adaptation of the CTMin characteristics of these lizards seems independent of maximum tolerances. We analyzed the data on CTMin and CTMax for Australian desert reptiles presented in Table 2 of Spellerberg (1972a) encompassing many families of both snakes and lizards, yet found no relationship between these two thermal sensitivity variables within this large data set ( $r_s=0.136$ ,  $n=32$ ,  $P>0.20$ , one-tailed Spearman rank order correlation). There was no relationship within subsets of the data set that Spellerberg (1972a, 1972d) divided into three groups by thermoregulatory behavior of the species (posturing heliotherms  $r_s=0.327$ ,  $n=11$ ,  $P>0.10$ ; shuttling heliotherms  $r_s=0.184$ ,  $n=14$ ,  $P>0.25$ ; thigmotherms  $r_s=0.045$ ,  $n=7$ ,  $P>0.50$ ; all one-tailed Spearman rank order correlations). (Heliotherms absorb solar radiation, whereas thigmotherms absorb heat conductively from surface features). Even when the correlations are performed only within congeneric groups, no significant relations are produced. Thus, this lack of association of CTMin and CTMax values does appear to be a real pattern in a number of unrelated reptile species.

Several factors could produce non-correlation among the species in CTMin values and thermal maximum tolerances. For example, it is likely that thermal maxima are directly related to differences in water loss rates among the species, a characteristic that was not investigated in *Liolaemus*. Because rates of water loss increase with temperature, species with comparatively higher water loss rates may reduce such losses by having lower mean CTMax values. But because water loss rates are diminished at low temperatures they would not similarly influence CTMin values.

In reptiles, the difference between field body temperature and measurements of thermal maximum tolerances are far lower than the difference between field body temperatures and CTMin values (Huey 1982). Maximum values and field body tempera-

tures show a greater correlation, and the former are widely used as an indirect correlate of the latter (Huey 1982). There are reasons to expect the two thermal maxima measures, PANT and EVM, and the field body temperatures to demonstrate correlations among themselves. As noted above, high-temperature thermal characteristics are likely to be related to tolerances of water loss rates, as such temperatures increase water loss rates.

The mean field body temperatures of *Liolaemus* lizard species in central Chile is near 35°C (Fuentes & Jaksic 1979b). For almost all species 35°C is also the temperature at which EVM behaviors were initiated, supporting the validity of the two measures, as they would be expected to be close. Despite this fact, statistical correlations between field body temperature to EVM and PANT temperatures were not significant, although the correlation of mean field body temperatures to mean PANT temperatures approached significance at the  $P < 0.05$  level in a one-tailed test. The lack of strong correlation may result from several factors. First, in each case the correlations were reduced by one (PANT) or two (EVM) species with exceptional rank order; such species may possess unique physiological constraints. Second, because ranking is based upon relative mean temperature measurements which in cases did not differ significantly, rank order between some species is in part arbitrary, perhaps biasing  $r_s$  values away from significance. This problem is particularly relevant for comparisons involving the apparently questionable rank order values of mean EVM temperatures, because no pairs differed significantly from each other in Tukey analyses despite overall differences in means detected in an ANOVA test.

#### *Thermal relations and distributional ecology*

Because air temperatures decrease with elevation, the negative relationship among the *Liolaemus* species of heating rate and elevation is not surprising. At higher elevations solar radiation is more intense, meaning that lizards can heat up faster to their

field body temperature. However, this also means that they would continue past this preferred temperature at a faster rate, and perhaps thus be less able to remain active in the more open habitats of high elevations due to the threat of overheating. Thus, high elevation forms may heat at slower, more controllable rates in order to maintain greater thermal stability. This explanation is, of course, completely ad-hoc, and below we offer arguments to the contrary.

A number of studies, primarily dealing with lizards of the genus *Anolis* from Caribbean islands, have investigated effects of elevation on thermal tolerances. Heatwole et al. (1969) found no differences in PANTS among three anole species from different elevations which were acclimated at a common temperature in the laboratory, although elevation-related differences were found in their CTMax levels. While survival times at low temperatures was correlated to elevation in a non-laboratory acclimated group, acclimation of the species to different field temperatures could not be eliminated as the cause of this pattern. Gorman & Hillman (1976) found that lower elevation populations of *Anolis cristatellus* were more cold-tolerant than were higher elevation populations of *A. gundlachi*. However, because these differences exist for sympatric populations of the two species as well (Huey & Webster 1976), an elevational effect producing such differences is unclear. Hertz & Huey (1981) found a decrease in CTMax with elevation for *A. gundlachi*, but no relation to elevation for the other maximum thermal tolerance measurements. Elevation-related changes have also been observed to be weak or lacking in the *A. cybotes* group (Hertz 1980, Hertz & Huey 1981), as well as in members of the scincid genus *Sphenomorphus* from southeastern Australia (Spellerberg 1972b, 1972c). Better evidence of an influence of elevation upon thermal tolerances of lizards would be an intraspecific shift with elevation in thermal tolerances of laboratory temperature acclimated individuals, or the use of a larger species group in a correlation analysis so as to attain a statistically valid sample size.

In the present study no relation was found among the species between high and

low temperature tolerance measurements and elevation indicators such as maximum elevational range or elevation of collection site, although an effect on field body temperatures will be reported elsewhere. Temperature tolerance characteristics of reptiles have been suggested to influence their distributions (Rand 1964, Heatwole 1970, 1976, Prieto & Whitford 1971, Spellerberg 1972a, 1972b, 1973, 1976, Greer 1980). Several authors (e.g., Heatwole et al. 1969, Spellerberg 1972a) have suggested that because lizards can avoid dangerously high temperatures but not as readily avoid those that are dangerously low, the critical thermal minimum rather than the maximum is likely to set distributional limits. We agree: a warm *Liolaemus* lizard at mid-day can behaviorally escape lethal thermal maximum temperatures by retreating to shade or a burrow, whereas a *Liolaemus* in an underground burrow at night or brumating over the winter cannot seek warmth to avoid lethal thermal minimum temperatures. Indeed, mass mortality of reptiles in the field due to cold stress has been reported (Bailey 1948, 1949, Tinkle 1967), but similar heat-stress mortality has not. Thus, because low temperatures can be extreme at high elevations in the Andes, while temperatures are not unusually high in the area, it is probable that the CTMin values are likely to be those that reflect, and limit, elevation distribution. The fact that anoline lizards show evidence of elevational limitations due to CTMin characteristics has been attributed to the fact that (unlike *Liolaemus* and probably *Sphenomorphus*) at night they fail to seek shelter in crevices of underground burrows (Heatwole et al. 1969). Instead, they remain above ground perching on the terminal branches of trees in a thermal environment that varies far more widely, and where they are subjected to greater fluctuation in air temperature extremes on a short term basis (Heatwole et al. 1969).

It is possible that the lack of an observable elevational trend among the *Liolaemus* species studied masks the fact that some of them may be limited while others are not, such that some are at their limits of thermal tolerances. At elevations above the bounds of the study transects (>3000 m elevation),

low winter temperatures are probably very important in setting maximal elevational limits. However, within the elevational range in question (1500 to 3000 m elevation), considerable variation in tolerances exists among these species, which share close phylogenetic alliances. In addition, as noted above, there is no correlation of CTMin and high temperature tolerance measures, so that these latter measures are unlikely to constrain CTMin values. These observations suggest that if *Liolaemus* distributions were influenced by thermal tolerances, then there is enough scope available to any species for the evolution of modified thermal tolerances tuned to the prevailing temperature regimes at differing elevations. As noted by Huey (1982), it is likely that capacity for short-term temperature tolerance is more important for daily activity, whereas resistance to chronic exposure is more valuable in determining survival ability in extreme conditions over a long period. These two measurements may be correlated, but because resistance measurements were not recorded in this study, differences among the organisms cannot be discussed at this time: it is certainly an area worth further pursuit.

Because body size has been shown to influence rates of heat loss and heat gain, it may play a role in setting the distributional limits of the species. At the higher, cooler elevations, larger lizards may be at a thermal advantage, because their higher thermal inertia and the fact that they are less affected by convective or conductive heat loss (Muth 1977, Tracy 1982, Grant & Dunham 1990, Adolph 1990) may allow them to be active in cool microhabitats (e.g., under rocks or shaded in bushes) for longer periods to forage for food. However, there was no significant trend in body size among the species with respect to elevation. In any case, juveniles of the high elevation species are small in body size, yet they exist without apparent problem at high elevations. The only apparent ecological effect of body size, attributable to differences in heating rates, is a modest shift in diel activity periods to be reported elsewhere.

In summary, the temperature tolerances of the *Liolaemus* species in this study fail to

define the limits of their distributions within the elevational confines of the study transect. Of course, the characteristics of the thermal ecology of species may result from short-term acclimation to the environment rather than from long-term genetically-based adaptation. Such acclimation was not controlled for in the thermal maxima experiments, so that if elevation-related patterns occurred they could be artifacts of field acclimation rather than reflect genetically-based adaptations to elevation. Nonetheless, these comparisons failed to indicate significant association with elevation. The ten day period of acclimation used in the CTMin experiments, which also failed to demonstrate elevational effects, may be insufficient to eliminate field acclimation effects. Controlling environmental effects may require standardizing environments during development, a step not yet taken in lizard thermal studies (Greer 1980). Keeping in mind these unexplored aspects of thermal tolerances, other factors (e.g., reproductive biology, distribution of preferred microhabitats, competitors, food, etc.) appear more likely to be important in setting the distributional limits of *Liolaemus* species within the elevational bounds of the transects in this study.

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#### LITERATURE CITED

- ADOLPH SC (1990) Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* 71: 315-327.
- BAILEY RM (1948) Winter mortality in the snake *Storeria dekayi*. *Copeia* 1948: 215.
- BAILEY RM (1949) Temperature toleration of gartersnakes in hibernation. *Ecology* 30: 238-242.
- BAKER LA, WW WEATHERS & FN WHITE (1972) Temperature-induced peripheral blood flow changes in lizards. *Journal of Comparative Physiology* 80: 313-323.
- BALLINGER RE, KR MARION & OJ SEXTON (1970) Thermal ecology of the lizard *Anolis limifrons*, with comparative notes on three additional Panamanian anoles. *Ecology* 51: 246-254.
- BARTHOLOMEW GA (1982) Physiological control of body temperature. In: Gans C & FH Pough (eds) *Biology of the Reptilia*. Volume 12. *Physiological Ecology*, 167-211. Academic Press, New York, New York.
- BOGERT CM (1949) Thermoregulation in reptiles: a factor in evolution. *Evolution* 3: 195-211.
- CORN MJ (1971) Upper thermal limits and thermal preferences for three sympatric species of *Anolis*. *Journal of Herpetology* 5: 17-21.
- CRAWFORD EC & G KAMPE (1971) Physiological responses of the lizard *Sauromalus obesus* to changes in the ambient temperature. *American Journal of Physiology* 220: 569-573.
- DAWSON WR & JR TEMPLETON (1963) Physiological responses to temperature in the alligator lizard, *Crotaphytus collaris*. *Physiological Zoology* 36: 219-236.
- DAWSON WR & JR TEMPLETON (1966) Physiological responses to temperature in the alligator lizard, *Gerrhonotus multicarinatus*. *Ecology* 47: 590-594.
- DONOSO-BARROS R (1966) *Reptiles de Chile*. Ediciones Universidad de Chile, Santiago.
- FELSENSTEIN J (1985) Phylogenies and the comparative method. *American Naturalist* 125: 1-15.
- FUENTES ER & FM JAKSIC (1979a) Lizards and rodents: an explanation for their relative species diversity in Chile. *Archivos de Biología y Medicina Experimentales (Chile)* 12: 179-190.
- FUENTES ER & FM JAKSIC (1979b) Activity temperatures of eight *Liolaemus* (Iguanidae) species in central Chile. *Copeia* 1979: 546-548.
- GARLAND T, RB HUEY & AF BENNETT (1991) Phylogeny and coadaptation of thermal physiology of lizards: a reanalysis. *Evolution* 45: 1969-1975.
- GORMAN GC & S HILLMAN (1976) Physiological basis for climatic niche partitioning in two species of Puerto Rican *Anolis* (Reptilia, Lacertilia, Iguanidae). *Journal of Herpetology* 11: 337-340.
- GRANT BW & AE DUNHAM (1990) Elevational covariation in environmental constraints and life histories of the desert lizard *Sceloporus merriami*. *Ecology* 71: 1765-1776.
- GREER AE (1980) Critical thermal maximum temperatures in Australian scincid lizards: their ecological and evolutionary significance. *Australian Journal of Zoology* 28: 91-102.
- HARVEY PH & MD PAGEL (1991) *The comparative method in evolutionary biology*. Oxford University Press, New York. viii + 239 pp.
- HEATWOLE H (1970) Thermal ecology of the desert dragon, *Amphibolurus inermis*. *Ecological Monographs* 40: 425-457.
- HEATWOLE H (1976) *Reptile ecology*. University of Queensland Press, St. Lucia, Queensland, Australia.
- HEATWOLE H, TH LIN, E VILLALON, A MUNIZ & A MATTA (1969) Some aspects of the thermal ecology of Puerto Rican anoline lizards. *Journal of Herpetology* 3: 65-77.

- HERTZ PE (1977) Altitudinal variation of thermoregulatory strategies, physiological ecology, and morphology of some West Indian anoles. Dissertation, Harvard University, Cambridge, Massachusetts, USA.
- HERTZ PE (1979) Comparative thermal biology of sympatric grass anoles (*Anolis semilineatus* and *A. olssoni*) in lowland Hispaniola. *Journal of Herpetology* 13: 329-333.
- HERTZ PE (1980) Responses to dehydration in *Anolis* lizards sampled along altitudinal transects. *Copeia* 1980: 440-446.
- HERTZ PE (1983) Eurythermy and niche breadth in *Anolis* lizards: a reappraisal. In: Rhodin J & K Miyata (eds) *Advances in herpetology and evolutionary biology: essays in honor of Ernest E. Williams*, 472-483. Museum of Comparative Zoology, Cambridge, Massachusetts.
- HERTZ PE & RB HUEY (1981) Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. *Ecology* 62: 515-521.
- HUEY RB (1982) Temperature, physiology, and the ecology of reptiles. In: Gans C & FH Pough (eds) *Biology of the Reptilia*. Volume 12. *Physiological Ecology*, 25-92. Academic Press, New York, New York. 536 pp.
- HUEY RB & AF BENNETT (1987) Phylogenetic studies of co-adaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41: 1098-1115.
- HUEY RB & M SLATKIN (1976) Costs and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51: 363-384.
- HUEY RB & TP WEBSTER (1976) Thermal biology of *Anolis* lizards in a complex fauna: the cristatellus group on Puerto Rico. *Ecology* 57: 985-994.
- KOSH RJ & VH HUTCHISON (1968) Daily rhythmicity of temperature tolerance in eastern painted turtles, *Chrysemys picta*. *Copeia* 1968: 244-246.
- KOUR EL & VH HUTCHISON (1970) Critical thermal tolerances and heating and cooling rates of lizards from diverse habitats. *Copeia* 1970: 219-229.
- LICHT P, WR DAWSON & VH SHOEMAKER (1966) Heat resistance of some Australian lizards. *Copeia* 1966: 162-169.
- LOWE CH & VJ VANCE (1955) Acclimation of the critical thermal maximum of the reptile *Urosaurus ornatus*. *Science* 122: 73-74.
- MAHONEY JJ & VH HUTCHISON (1969) Photoperiod acclimation and twenty-four hour variations in the critical thermal maxima of a tropical and a temperate frog. *Oecologia* 2: 143-161.
- MARQUET, PA, JC ORTIZ, F BOZINOVIC & FM JAKSIC (1989) Ecological aspects of thermoregulation at high altitudes: the case of Andean *Liolaemus* lizards in northern Chile. *Oecologia* 81: 16-20.
- MARTINS E & HANSEN (1996) The statistical analyses of interspecific data: a review and evaluation of phylogenetic comparative methods. In: Martins E (ed) *Phylogenies and the Comparative Method in animal behavior*. Oxford University Press, Oxford.
- MORGAREIDGE KR & FN WHITE (1969) Cutaneous vascular changes during heating and cooling in the Galapagos marine iguana. *Nature* 223: 587-591.
- MUTH A (1977) Thermoregulatory postures and orientation to the sun: a mechanistic evaluation for the zebra-tailed lizard, *Callisaurus draconoides*. *Copeia* 1977: 710-720.
- NORRIS KS (1967) Color adaptation in desert reptiles and its thermal relationships. In: Milstead WW (ed) *Lizard ecology: a symposium*, 162-229. University of Missouri Press, Columbia, Missouri.
- PEARSON OP (1954) Habits of the lizard *Liolaemus multiformis multiformis* at high altitudes in southern Peru. *Copeia* 1954: 111-116.
- PEARSON OP (1977) The effect of substrate and of skin color on thermoregulation of a lizard. *Comparative Biochemistry and Physiology* 58A: 353-358.
- PEARSON OP & D BRADFORD (1976) Thermoregulation of lizards and toads at high altitudes in Peru. *Copeia* 1976: 155-170.
- PORTER WP (1967) Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. *Ecological Monographs* 37: 273-296.
- PORTER WP, JW MITCHELL, WA BECKMAN & CB DEWITT (1973) Behavioral implications of mechanistic ecology. *Oecologia* 13: 1-54.
- PRIETO AA & WG WHITFORD (1971) Physiological responses to temperature in the horned lizards, *Phrynosoma cornutum* and *Phrynosoma douglassii*. *Copeia* 1971: 498-504.
- RAND AS (1964) Ecological distribution in anoline lizards of Puerto Rico. *Ecology* 45: 745-752.
- RICE GE & SD BRADSHAW (1980) Changes in dermal reflectance and vascularity and their effects on thermoregulation in *Amphibolurus nuchalis* (Reptilia: Agamidae). *Journal of Comparative Physiology* 135: 139-146.
- SPELLERBERG IF (1972a) Temperature tolerances of southwest Australian reptiles examined in relation to reptile thermoregulatory behavior and distribution. *Oecologia* 9: 23-46.
- SPELLERBERG IF (1972b) Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. I. The environment and lizard critical temperatures. *Oecologia* 9: 371-383.
- SPELLERBERG IF (1972c) Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. II. Physiological aspects of thermoregulation. *Oecologia* 9: 385-398.
- SPELLERBERG IF (1972d) Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. III. Behavioural aspects of thermoregulation. *Oecologia* 11: 1-16.
- SPELLERBERG IF (1973) Critical minimum temperatures of reptiles. In: W Weiser (ed) *Effects of temperature on ectothermic organisms*, 239-247. Springer-Verlag, Berlin.
- SPELLERBERG IF (1976) Adaptation of reptiles to cold. In: Bellairs A d'A & CB Cox (eds) *Morphology and biology of reptiles*. Linnaean Society Symposium Series 3, 261-285. London.
- TEMPLETON JR (1960) Respiration and water loss at higher temperatures in the desert iguana, *Dipsosaurus dorsalis*. *Physiological Zoology* 33: 136-145.
- TINKLE DW (1967) The life and demography of the side-blotched lizard. *Miscellaneous Publications of the Museum of Zoology* 132, University of Michigan, Ann Arbor, Michigan.
- TRACY CR (1982) Biophysical modeling in reptilian physiology and ecology. In: Gans C & FH Pough (eds) *Biology of the Reptilia*. Volume 12. *Physiological Ecology*, 275-324. Academic Press, New York, New York.
- TUCKER VA (1966) Oxygen transport by the circulatory system of the green iguana (*Iguana iguana*) at different body temperatures. *Journal of Experimental Biology* 44: 77-92.
- TUCKER VA (1967) The role of the cardiovascular system in oxygen transport and thermoregulation in lizards. In: Milstead WW (ed) *Lizard ecology: a symposium*, 258-269. University of Missouri Press, Columbia, Missouri.
- WHITE FN (1976) Circulation. In: Gans C & WR Dawson (eds) *Biology of the Reptilia*. Volume 5, 275-334. Academic Press, New York, New York.