

Thermal ecology of a *Liolaemus* lizard assemblage along an Andean altitudinal gradient in Chile

Ecología térmica de un ensamble de lagartijas *Liolaemus* a lo largo de un gradiente altitudinal andino en Chile

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ABSTRACT

We studied the thermal ecology of ten species of *Liolaemus* lizards on an altitudinal transect in the central Chilean Andes, from 1500 to 3000 m elevation, to determine in the field how thermoregulatory factors may be setting distribution limits. All but one species had the same field body temperatures (ca. 35°C). The only exception was the higher body temperature of the darkly colored male *L. nigroviridis*, which appears to result from the interplay of biophysical attributes with the social structure of this species. Most species of lizard selected microhabitats that allowed increased length of diel activity time, choosing in the evenings rock substrates, which held heat even after air temperature dropped. Reproductive condition (particularly gestation) of individuals also resulted in broadened diel activity periods. Thermal relationships set upper distributional limits on egg-laying species, which cannot successfully reproduce at high elevations, where only live-bearing lizards were found.

Key words: thermoregulation, field body temperature, body size, altitudinal gradient, reproductive mode

RESUMEN

Estudiamos la ecología térmica de diez especies de lagartijas *Liolaemus* en un transecto altitudinal en los Andes centro-chilenos, entre 1500 y 3000 m sobre el nivel del mar, para determinar en terreno cómo algunos factores termorregulatorios pudieran estar definiendo los límites distribucionales. Todas excepto una especie tuvieron la misma temperatura corporal en terreno (ca. 35°C). La única excepción fue la mayor temperatura corporal de los machos oscuros de *L. nigroviridis*, la cual parece ser el resultado de la interacción entre atributos biofísicos y la estructura social de esta especie. La mayoría de las especies de lagartijas seleccionaron microhábitats que permitían un incremento en el tiempo de actividad diario, escogiendo durante el atardecer sustratos rocosos que retienen calor aun cuando la temperatura del aire haya bajado. La condición reproductiva (particularmente la gestación) de los individuos también resultó en períodos más ampliados de actividad diaria. Las relaciones térmicas determinaron los límites superiores de distribución de las especies ovíparas, las que no pueden reproducirse exitosamente a grandes altitudes, donde solamente se encontraron lagartijas vivíparas.

Palabras clave: termorregulación, temperatura corporal en terreno, tamaño corporal, gradiente altitudinal, modo reproductivo

INTRODUCTION

Because lizards are ectothermic organisms, their thermal ecology is influenced by the physical environment. Thus, it is no surprise that changes that occur with increasing elevation (slightly increased direct solar radiation along with decreased

air temperatures and diffuse radiation – McCullough & Porter 1971), have numerous effects on lizard physiology and thermal ecology (Bogert 1949b, Spellerberg 1972a, 1972b, 1972c, Huey & Webster 1976, Hertz 1977, 1980, Hertz & Huey 1981). Nevertheless, although lizard species such as *Anolis* show remarkable

thermal differentiation along an elevational gradient (Huey 1982), Australian skinks in the genus *Sphenomorphus* display great conservatism, i.e., no detectable change (Spellerberg 1972a, 1972b, 1972c).

Relating thermal characteristics to the niche characteristics of lizards is hampered when the species being compared differ in phylogeny, because phylogenetic relationships exert a strong effect upon thermal relations (Bogert 1949a, Brattstrom 1965, Licht et al. 1966b, Avery 1982). Studies within a closely-related taxonomic group (especially congeners) can greatly reduce such problems, but to date such research has been limited mostly to assemblages of the tropical genus *Anolis* (e.g., Hirth 1965, Ballinger et al. 1970, Huey & Webster 1976, Hertz 1977, 1979, Hertz & Huey 1981; see Huey & Pianka 1977, Licht et al. 1966a, 1966b for other faunas).

The lizards in this study are members of the South American tropidurine iguanid genus *Liolaemus*, which contains over 100 small to moderate-sized (3-30 g) diurnally active species occurring over a wide longitudinal, elevational, and habitat span, from the Equator to Tierra del Fuego, from sea level to well over 4000 m elevation, and from the Atacama Desert to the cold, coastal rainforests of southern Chile. Thus, they offer a group in which the effect of phylogeny on ecological differences is controlled, and provide an opportunity to confirm previous results from studies of the tropical *Anolis* (Carothers et al. 1996, 1997). Further, because *Liolaemus* lizards are physiologically able to tolerate a diversity of environments not faced by any other congeneric lizard assemblage (Jaksic & Schwenk 1983, Marquet et al. 1989, Carothers et al. 1996), they offer the possibility of addressing questions not possible with *Anolis*.

The species of *Liolaemus* that are the focus of this study occur along elevational transects in the central Chilean Andes Ranges, occupying habitats as diverse as

bushes, trees, grass, open ground, rocks, and boulders (Donoso-Barros 1966, Jaksic et al. 1980, Jaksic 1997). Questions addressed in this study are divided into three categories, concerning field body temperatures, behavioral thermoregulation, and altitudinal zonation. With regard to field body temperatures, we sought to determine (1) if differences in field body temperature occurred among conspecific lizards living at different elevations, (2) if differences existed interspecifically among lizards dwelling at the same elevations, and (3) if species occupying similar microhabitats had more similar field body temperatures. Questions regarding thermoregulatory behavior over the course of the day were approached to determine (4) how basking site selection changes, (5) whether larger, adult *Liolaemus* lizards, which have greater thermal inertia (Carothers et al. 1997), have diel activity periods that differ from smaller juveniles, and (6) what exceptions to the normal patterns of size-related diel activity patterns would occur. Lastly, because these lizards show pronounced zonation over their elevational range, we sought to determine if distributional limits of any of the species were constrained by thermoregulatory demands, as represented by field body temperatures or other factors related to thermal biology, specifically reproduction.

MATERIAL AND METHODS

Lizard species and study areas

All of the species of *Liolaemus* one encounters in the central Chilean Andes Ranges near Santiago, Chile, were studied: *L. altissimus*, *L. chiliensis*, *L. fuscus*, *L. lemniscatus*, *L. leopardinus*, *L. monticola*, *L. nigroviridis*, *L. nitidus*, *L. schroederi*, and *L. tenuis*. These species show distinct patterns of zonation with predictable altitudinal distributions and microhabitat preferences in this region. Their elevational ranges, body sizes, and preferred

TABLE 1

Microhabitat, morphometric (SVL = snout-to-vent length), and elevational features of 10 species of *Liolaemus* lizards studied. Those two species that have microhabitats described as "Ground (bush)" primarily occupy the ground underneath, and adjacent to, bushes.

All species (except *L. chiliensis* and *L. schroederi*) also occupy rocks that are in close proximity to their preferred microhabitat as described in this table

Características de microhábitat, morfometría (SVL = longitud hocico-cloaca) y elevación de 10 especies de *Liolaemus* estudiadas. Las dos especies cuyo microhábitat está descrito como "Suelo (arbusto)", se encuentran principalmente en el suelo bajo o adyacente a arbustos. Todas la especies (excepto *L. chiliensis* y *L. schroederi*) se encuentran también en rocas que están próximas a sus microhábitats preferidos, según se describe en esta tabla

<i>Liolaemus</i> spp.	Microhabitat	Adult mean mass (g)	Adult mean SVL (mm)	Juvenile mean mass (g)	Juvenile mean SVL (mm)	Elevation range (m)	Elevation mean (m)
<i>L. altissimus</i>	Ground (bush)	11.9	71.0	5.4	55.0	2100-3000	2799
<i>L. chiliensis</i>	Bush	25.1	89.6	5.0	55.0	1500-1800	1517
<i>L. fuscus</i>	Rock & bush	3.1	47.4	1.9	39.3	1500-2100	1609
<i>L. lemniscatus</i>	Ground & bush	3.4	49.7	1.9	40.0	1500-2400	1807
<i>L. leopardinus</i>	Boulder	20.7	86.9	6.6	57.6	2100-3000	2483
<i>L. monticola</i>	Rock	7.3	61.3	2.9	45.4	1500-2400	1692
<i>L. nigroviridis</i>	Ground & rock	8.7	64.8	3.3	46.7	1700-3000	2402
<i>L. nitidus</i>	Ground (bush)	21.5	84.6	6.0	55.6	1500-2400	2133
<i>L. schroederi</i>	Bush	4.9	54.2	2.3	42.0	1800-2590	2153
<i>L. tenuis</i>	Tree	4.8	55.1	2.3	43.7	1500-2040	1500

microhabitats are presented in Table 1, based on data collected chiefly by JHC and field assistants (see Acknowledgments).

Within the central Andes Range study area we established three elevational transects: at Farellones, Lagunillas, and El Volcán, from 1500-3000 m elevation. Each transect was within 40 km of the neighboring transect, so that latitudinal effects of climate variation were minimized. In general, the habitats at lower elevations consisted of mediterranean-type shrubs ("matorral") and scattered rocks and trees, shifting gradually to scattered low-growing bushes, rocks, and boulders at high elevations.

Field body temperatures and observations

Individuals of all species were stealthily approached in the field, and captured with a pole and noose. If the lizard was captured quickly and not unduly disturbed, its cloacal temperature was immediately taken

with a quick-reading thin-bulb thermometer (to the nearest 0.1°C). The shaded bulb air temperature at 1.0-1.5 m height was also then recorded to the nearest 0.1°C. Along with species identity, age (adult or juvenile, by size), snout-to-vent length (SVL to nearest 1 mm), body mass (to nearest 0.1 g) as measured by a Pesola scale, sex, whether or not the individual was gravid, and the microhabitat the lizard was occupying (rock, dirt, grass, bush, boulder) were recorded. Site elevation measured with an altimeter/barometer (precision of 10 m) was obtained during good weather spells; time of day was recorded with a digital watch. For those individuals not captured, all of the above data were recorded except body temperature, SVL, and mass.

For comparisons of basking site use in the early morning versus late afternoon, only those lizards that generally use a rock substrate as perch site were considered (i.e., all species except *L. schroederi* and *L. chiliensis*). Perch

sites were classified as rocks (including boulders, in the case of *L. leopardinus*) and non-rocks (including grass, bushes, trees, and the dirt ground). In the statistical comparisons of activity periods, lizards were divided by species into juvenile and adult age classes (based on field experience of JHC), and adult non-gravid versus adult gravid reproductive classes (based on direct observation). In comparisons of microhabitat selection and thermoregulation, all individuals of a given species were included. The number of individuals of each class active during the early morning (before 1000 h) as opposed to the late afternoon (after 1800 h) was compared to determine if members of the two classes had similar or differing activity patterns.

RESULTS

Field body temperatures

The *Liolaemus* species in this study demonstrated a high degree of conservatism in field body temperature (i.e., it varied little

from one species to another). Regressions of field body temperatures against body mass showed no significant relationship, except for *L. nigroviridis*, which showed a significant but weakly positive relationship (Table 2). However, a separate analysis of the two sexes of *L. nigroviridis* demonstrated that this trend existed among males ($r^2 = 0.02$, $F = 4.191$, $n = 184$, $P < 0.05$, ANOVA) but not among females ($r^2 = 0.00$, $F = 1.304$, $n = 150$, $P = 0.255$, ANOVA).

A significant negative correlation existed between elevation and air temperature ($r^2 = 0.60$, $F = 1650.99$, $n = 1130$, $P < 0.01$, ANOVA, all species pooled). Despite this typical relationship, within all but two of the species no significant relationship was detected between elevation and field body temperature (Table 2). For those that showed a trend, the relation of body temperature to elevation was negative, reflecting the trend in air temperature. Because the two species showing this trend were at high elevations, the other high elevation species, *L. nigroviridis*, was

TABLE 2

Regressions of field T_b against both body mass and elevation. Sample sizes differ due to missing values in some cases. Regression of T_b against elevation for *L. tenuis* was not performed due to lack of data over an adequate elevational range

Regresiones de T_b versus masa corporal y elevación. Los tamaños muestrales difieren debido a la falta de datos en algunos casos. La regresión de T_b versus elevación para *L. tenuis* no se efectuó por falta de datos que cubrieran adecuadamente el rango de elevaciones

<i>Liolaemus</i> spp.	Field T_b (°C) vs. mass (g)				Field T_b (°C) vs. elevation (m)			
	F	P	n	r^2	F	P	n	r^2
<i>L. altissimus</i>	0.349	0.56	219	0.00	19.585	<0.01	262	0.07
<i>L. chiliensis</i>	0.025	0.88	8	0.00	0.002	0.97	9	0.00
<i>L. fuscus</i>	0.284	0.60	100	0.00	1.217	0.27	128	0.01
<i>L. lemniscatus</i>	0.318	0.57	341	0.00	1.069	0.30	381	0.00
<i>L. leopardinus</i>	3.225	0.08	107	0.21	10.406	<0.01	119	0.07
<i>L. monticola</i>	0.088	0.77	216	0.00	0.811	0.37	282	0.00
<i>L. nigroviridis</i>	12.464	<0.01	347	0.03	0.415	0.42	409	0.00
<i>L. nitidus</i>	0.457	0.50	149	0.00	0.005	0.95	181	0.00
<i>L. schroederi</i>	1.588	0.24	13	0.05	2.014	0.18	15	0.07
<i>L. tenuis</i>	0.124	0.73	46	0.00	n/a	n/a	n/a	n/a

again analyzed by sex to determine if there were sexual differences that biased the results away from detecting a similar trend in this species. No significant relationship was found for either males ($r^2 = 0.00$, $F = 0.979$, $P = 0.326$, ANOVA) or females ($r^2 = 0.00$, $F = 0.479$, $P = 0.482$, ANOVA) of *L. nigroviridis*.

In addition to the lack of an intraspecific relation of elevation and temperature, among the ten species, there was no significant relationship between mean elevational distribution and mean body temperature ($F = 1.979$, $P > 0.10$, ANOVA, all species pooled, Fig. 1). Significant differences existed among the species in field body temperatures ($F = 32.004$, P

$<< 0.01$, ANOVA, Fig. 2). However, the mean body temperatures among species spanned a range of less than 2.5°C , from 33.0°C for *L. altissimus* to 35.5°C for *L. nitidus*. Comparison of these results to those of Fuentes & Jaksic (1979) for most of these same species, show striking agreement: mean field body temperatures of the two data sets usually differed by no more than 0.2°C .

There was no association among the species between mean field temperature and microhabitat occupied. Within the 2.5°C range of mean field body

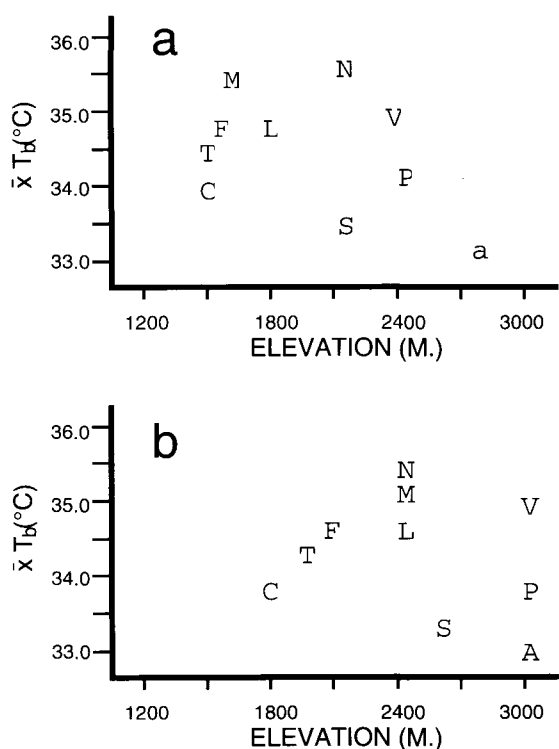


Fig. 1: Relationship of mean body temperature against both mean (a) and maximum (b) elevational distribution. Letters denote species as follows: A = *L. altissimus*, C = *L. chiliensis*, F = *L. fuscus*, L = *L. lemniscatus*, P = *L. leopardinus*, M = *L. monticola*, V = *L. nigroviridis*, N = *L. nitidus*, S = *L. schroederi*, T = *L. tenuis*.

Relación entre temperatura corporal media y elevación (a) media y (b) máxima. Las letras denotan especies según la clave de más arriba.

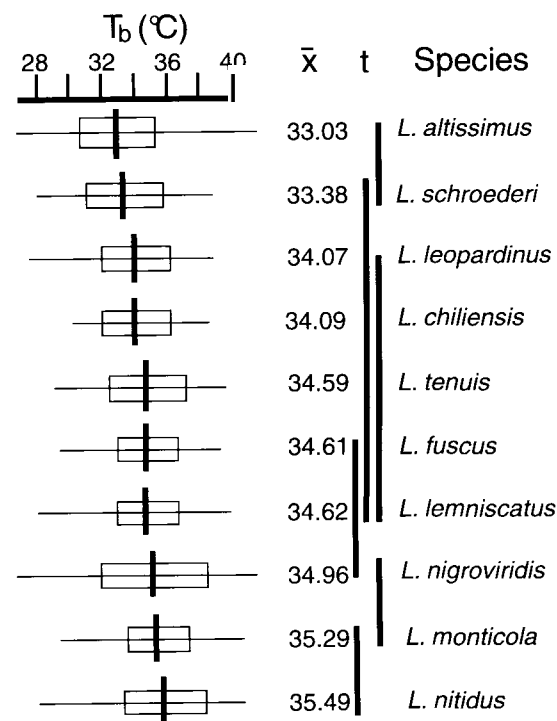


Fig. 2: Field body temperatures, T_b , for each species. In the diagrams, the vertical lines indicate mean, horizontal lines show range, boxes show ± 2 SD. Vertical "t" bars connect those species indistinguishable (by Tukey multiple comparisons tests) from one another at the $P = 0.05$, whereas those unconnected differ at least by $P < 0.05$.

Temperaturas corporales en terreno, T_b , para cada especie. Los diagramas señalan la media con línea vertical, el rango con línea horizontal y ± 2 DE con rectángulo. Las barras verticales "t" conectan aquellas especies indistinguibles entre ellas (mediante pruebas de comparaciones múltiples de Tukey) al nivel de $P = 0,05$, en tanto que aquellas desconectadas difieren en al menos $P < 0,05$.

temperatures encompassed between 33.0°C and 35.5°C, the rock or boulder specialists had mean field body temperatures of 34.1°C, 35.0°C, and 35.3°C, while those of the ground (bush) species were from 33.0°C to 35.5°C and those of the bush-dwelling forms were between 33.4°C and 34.1°C.

Thermoregulation and diel activity

For the eight species that use rocks as basking sites, all used rocks (as opposed to non-rock surfaces) more frequently in the late afternoon (after 1800 h) than in the early morning (before 1000 h) ($P = 0.0039$, Fisher's exact probability test). In five of the eight cases the differences were significant (Table 3). It should be noted that those without a significant change were species that are rock habitat specialists, and hence they do not have the same flexibility and would be biased towards use of rocks in the morning in any case.

In only one species, *L. lemniscatus*, was the frequency of active adults/active

juveniles statistically greater in the afternoon than in the morning ($X^2 = 30.4$, d.f. = 1, $P << 0.01$). However, in each of the eight cases where sufficient data were available (*L. chiliensis* and *L. schroederi* were too rare for meaningful comparisons), the ratio of adults/juveniles active was always greater in the late afternoon than in the early morning ($X^2 = 8$, d.f. = 1, $P << 0.01$). Thus it appeared that juveniles were active earlier than were adults, while adults were active later than were juveniles.

None of the variance ratio tests performed for each species to reveal if gravid females had broader activity periods than non-gravid adults showed significant differences. However, of the nine species for which there were sufficient data (only one gravid female of the rare *L. chiliensis* was encountered), all showed greater variance in activity time for gravid females than for non-gravid adults ($X^2 = 9$, $P < 0.01$). Several of the comparisons approached < 0.05 probability in one-tailed tests, indicating broader activity times for gravid than non-gravid adults.

TABLE 3

Percentages of use of rocks as perch sites, followed by sample size in parentheses. Only sightings of adults were recorded. Chi-square tests were conducted on contingency tables with raw frequencies as entries. NS denotes $P > 0.10$, * denotes $P < 0.05$, ** denotes $P < 0.01$. For *L. tenuis* Fisher's Exact Test was used because one cell size was < 5

Porcentajes del uso de rocas como sitios de percha, seguidos por el tamaño muestral entre paréntesis. Se consignan sólo los avistamientos de adultos. Las pruebas de Chi-cuadrado fueron realizadas en tablas de contingencia usando las frecuencias absolutas como entradas. NS denota $P > 0.10$, * denota $P < 0.05$, ** denota $P < 0.01$. Para *L. tenuis* se usó la Prueba Exacta de Fisher porque una celda tenía frecuencia < 5

<i>Liolaemus</i> spp.	% rock use (n), early morning	% rock use (n), late afternoon	X^2 value
<i>L. altissimus</i>	66.7% (12)	86.5% (96)	4.66*
<i>L. fuscus</i>	68.4% (19)	78.7% (61)	NS
<i>L. lemniscatus</i>	26.3% (99)	44.7% (217)	8.96**
<i>L. leopardinus</i>	80.0% (5)	100.0% (38)	NS
<i>L. monticola</i>	91.3% (23)	100.0% (37)	NS
<i>L. nigroviridis</i>	66.7% (51)	85.1% (141)	6.90**
<i>L. nitidus</i>	55.6% (9)	89.8% (49)	4.44*
<i>L. tenuis</i>	57.1% (7)	100% (11)	$P = 0.043$

DISCUSSION

Field body temperatures

As with other species of lizards (Tracy 1982), in *Liolaemus* there is a strong relationship between size (as measured by mass or by SVL) and the rate at which the lizard heats up or cools down (Carothers et al. 1997). Despite this difference among size classes in thermal inertia, there was almost no evidence of an intraspecific relationship between body size and body temperature in the field. Thus, individuals of a given species had predictable body temperatures regardless of their body size.

The one exception to this rule, *L. nigroviridis*, is exceptional in other ways. In this species a positive relationship of body mass to body temperature was found. The cause of this trend in this species was attributed to the effect occurring in males: females do not show this trend. Another exceptional aspect of this species may explain this sex-biased result. Unlike females, males of this species undergo a dramatic ontogenetic shift in color with increasing body size, from the species-typical cryptic light grey body coloration to one of black with green flecking (hence its Latin name *nigroviridis*). Such black coloration increases heating in lizards (Norris 1967). Coupled with the fact that males of this species are territorial and survey areas from prominent elevated rock perches which exposes them to intense solar radiation (Carothers 1987), their black coloration may cause them to heat up to a higher temperature than they would actually prefer. It has been noted (Huey & Slatkin 1976, Huey 1982) that lizards must make tradeoffs between conflicting demands of thermoregulation to achieve physiologically optimal temperatures and other ecological factors, including requirements of social behavior (in this case, territorial vigilance). As a consequence, lizards may be active at sub-optimal (and likewise super-optimal) body

temperatures (Huey & Slatkin 1976, Huey 1982; but see Regal 1971). Such territorial behavior has been shown to result in elevated body temperatures (Curry-Lindahl 1957, 1979, DeWitt 1967). This type of trade-off, in this case involving territoriality resulting from sexual selection versus physiological optimum, may well explain the anomalously higher body temperatures of adult *L. nigroviridis* males as well. It should be noted that none other of the species studied displayed simultaneously territoriality and dark coloration of the adult males (Carothers 1987).

Some studies on *Anolis* have found a negative relationship of elevation and body temperature (e.g., Huey & Webster 1976), although for some species of *Anolis* (the *cybotes* group on Hispaniola) there is very limited variation (Hertz 1979, Hertz & Huey 1981). In the *A. cristatellus* group there also existed a positive relation between air temperature and field body temperatures of these lizards (Huey & Webster 1976). Given that they also found a decrease in air temperature with elevation, elevation by itself probably does not explain the decrease in field body temperatures, but air temperatures do.

Nevertheless, in the *Liolaemus* of this study, the negative correlation of elevation with air temperature is not reflected in intraspecific patterns of elevation and body temperature within any of the species except for two of the four species that have the highest altitudinal distributions, *L. altissimus* and *L. leopardinus*. Only these two species and the third high elevation species, *L. schroederi*, had r^2 values greater than 0.00, all sharing the same slight r^2 value of 0.07. The fact that the correlation within *L. schroederi* was not significant is probably only due to the very low sample size ($n = 15$). Again, *L. nigroviridis* was the exception to the trend, although in this case the reason is unclear, as it is not the consequence of differences between males and females in body temperature. The radiation-absorbing, black coloration of

males may explain the lack of a decrease in this sex with the cooler temperatures at higher elevations, but the reason for the lack of a decrease in females is not known.

The last factor regarding field temperature is the relationship among the ten species in preferred microhabitat and field body temperatures. The lack of a relationship between these two features may be the result of phylogenetic constraint (see below), and the very small range of differences in mean field body temperature likely reflects this close evolutionary association. However, this lack of a relationship also probably illuminates the fact that diverse ecological factors other than microhabitat (e.g., elevation, social structure, body coloration, possible competitive divergence), as well as random non-adaptive physiological differences, are responsible for setting the temperatures at which lizards maintain their bodies in the field.

Thermoregulation and diel activity

Microhabitat selection by each of the *Liolaemus* species showed a consistent diel pattern: all species of lizards that use rocks as a perch and basking site did so more often in the late afternoon than in the early morning. The reason for this is likely associated with the thermal properties of rocks. Other authors (e.g., Christian et al. 1983) have found that by taking advantage of the great thermal inertia of rocks, lizards can extend their activity periods a longer time than they could if they were solely dependent upon solar radiation for maintaining an adequate body temperature. By adopting thigmothermy (absorption of radiant heat through bodily contact with a warm surface) on rocks, *Liolaemus* are able to remain active even when air temperatures in the evening are dropping precipitously. A similar shift in microhabitat use was observed for another Andean *Liolaemus* species, *L. multiformis*. Pearson (1954) suggested that in the early morning these lizards selected basking sites

that he later found (Pearson 1977) were not thermally conductive so as to prevent the loss of heat gained as they basked. This same use of microhabitats such as soil or bushes, which have a much lower thermal conductance than do rocks, occurred among the species in the present study as well. Thus, thermal conductance appears to play an important role in diel patterns of activity and microhabitat selection.

Not only is the thermal inertia of a microhabitat important in diel activity patterns, but the thermal inertia of a lizard itself, as determined by its body mass, also plays a role in its activity patterns. Because smaller lizards heat up more quickly and larger lizards cool down more slowly (Porter et al. 1973), it has been suggested that these physical considerations should play an important role in setting activity patterns of large versus small lizards. This effect of body size on heating and cooling rates has been demonstrated in various lizards, including *Liolaemus* (Carothers et al. 1997). Such an effect has been used to explain why juveniles are active earlier and adults later (Cowles & Bogert 1944, Carothers 1983). As a result, the concept of time as a niche difference (Schoener 1974, Carothers & Jaksic 1984), which was based largely upon ectotherms and especially lizards, has been called into question (Huey 1982, Carothers 1983). Such age-related differences in diel activity patterns is exactly what we observed among the *Liolaemus*, with more juveniles active in the early morning and more adults active in the late afternoon.

Another way that biophysical considerations of body size and thermal inertia may play a role in causing the observed differences in diel activity is related to the exchange of heat energy with the environment. Because of their differing thermal properties (Gates 1962), in the early morning air temperatures rise much quicker than do substrate temperatures, while in the evening substrate temperatures stay high longer than do air temperatures.

Smaller individuals are more affected by convective heat exchange, while larger individuals are more affected by conductive heat exchange (thigmothermy) (Muth 1977). Thus, on this basis, one would expect smaller lizards to heat up faster and become active earlier in the morning, while in the evening large individuals would be able to remain active through thigmothermy while smaller individuals convectively lost heat and retreated.

Nevertheless, size alone does not play a deciding role in activity patterns. Various factors are likely to influence choices of activity times, including social interactions (e.g., Carothers 1981) and reproductive biology (Shine 1980). It is this second factor that we observed to repeatedly play an influential role within *Liolaemus*. Gravid females had wider activity periods during the day than did comparable non-gravid adults. For example, while gravid females of the live-bearing species *L. altissimus* were active very late in the day, absorbing heat from warm rocks, they were also active early in the morning, often when only juveniles could be found active. Because the development of the embryos depends on warm temperatures (Packard et al. 1977), the time that a female carries a clutch of young should be decreased by maintaining an elevated body temperature for the longest time period possible during the day. Such increases in basking activity by gravid females have been observed in other lizard species as well (Shine 1980). This extension of activity time may be especially important for the high elevation live-bearing species where temperatures are cooler. Nevertheless, by extending their diel activity period, gravid females may incur other costs as well, such as reduced mobility and its accompanying decrease in the ability to escape predators (Shine 1980).

Distributional limits and thermal biology

Thermal factors play a major role in the distribution of reptiles, by effects upon

activity and hence the ability to obtain energy to grow and reproduce (Porter & Tracy 1975). Because the *Liolaemus* in this study occur over such a broad altitudinal range where the potential for temperature variation is great, thermal factors may be influential in setting distributional limits. In fact, there is no doubt that above the 3000-m elevation limit of the transects, thermal constraints set the upper limits on the lizards whose habitats continue into the snowline on the surrounding peaks that reach elevations of 5000 m or higher. However, the question remains whether species whose limits are below 3000 m elevation are constrained by temperature.

Interspecific comparisons showed that no relationship existed between elevation and mean body temperature of the species in question, so that activity per se along the transect was not dependent upon a specific temperature. The very small range of difference among *Liolaemus* in preferred body temperatures also argues against lack of ability to maintain preferred body temperature as a reason for distributional limits below the top of the transects. This indicates that lizards set their thermal optima without an overriding influence of elevation, so that these effects do not seem important. Our previous work (Carothers et al. 1997) has shown that critical thermal minima of the species are also not related to elevation, suggesting that this thermal factor does not set limits upon distributions. In addition, there is no interspecific pattern of body size and elevation, showing that the thermal effects on body size are also unrelated to distributional limits, and neither is there a relation of range or variance in field body temperature and elevation.

It could be argued that a given species is limited in elevation by being particularly sensitive to a particular thermal trait such as critical thermal minimum, but the relatively close phylogenetic relations within the genus and the conservatism among the species in thermal characteristics reduce this

likelihood. It should be noted that it is this feature of phylogeny that acts as a double edged sword. For, while studying any animals which have a common ancestry controls for ecologically irrelevant differences due to differing phylogeny, it also reduces the likelihood of the evolution of adaptive variation.

However, it appears that one feature of lizard biology is likely to play a central role in the thermally related altitudinal distributional limits of a number of *Liolaemus* species: reproduction. As noted by Porter & Tracy (1975), the relationship between potential nest physical environments and reproductive characteristics of egg laying, delayed oviposition, and viviparity are probably far more important than previously acknowledged. A large body of evidence indicates that live-bearing by thermoregulating female reptiles is essential for successful reproduction for species living in colder habitats, where soil temperatures are not warm enough for a long enough period to allow adequate development of embryos in eggs to reach the hatching stage (Weeks 1935, Sergeev 1940, Packard et al. 1977, Tinkle & Gibbons 1977, Shine & Berry 1978, Shine & Bull 1979, Guillette et al. 1980, Blackburn 1982). These authors have postulated that live-bearing is repeatedly seen in high-elevation lizard species because it is a necessary adaptation for reproduction at altitudes where the time available for egg incubation in the soil is quite limited. Retention of the eggs allows the basking female to elevate the temperatures of the embryos, thus speeding developmental rates. It has already been shown above that the female *Liolaemus* have broader activity times, the suggested reason being the benefits of reducing the period of embryonic development.

Along the transects, none of the egg-laying species (*L. chiliensis*, *L. fuscus*, *L. lemniscatus*, *L. monticola*, *L. nitidus*, and *L. tenuis*) occur above 2400 m elevation, while all of those species whose ranges extend beyond this limit (*L. altissimus*, *L.*

leopardinus, *L. nigroviridis*, and *L. schroederi*) are live-bearing. It is not far above this elevation that one finds snow remaining well into Spring. Thus, in an indirect manner, elevation-induced temperature effects apparently limit the distributions of some species that might otherwise easily survive the thermal environment but apparently cannot successfully reproduce due to likely effects of the cold soil decreasing incubation periods and rates to those apparently insufficient for oviparity.

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