

Ecological aspects of thermoregulation at high altitudes: the case of Andean *Liolaemus* lizards in northern Chile

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Summary. We document activity field temperatures, daily activity patterns, and extent of thermoregulation in four species of *Liolaemus* lizards inhabiting at high altitude (above 3500 m) in the Andes of northern Chile. These four species have similar activity field temperature (T_b near 29° C) despite their being distributed at different altitudinal belts. However, conspicuous differences exist between higher-altitude (*L. alticolor* and *L. jamesi*) and lower-altitude (*L. islugensis* and *L. ornatus*) lizards regarding extent of thermoregulation and activity period. Some differences in morphology, behavior, and patterns of microhabitat occupancy are also apparent among these four species and are seemingly related to the thermal environment to which they are subjected. In comparison to eight low-altitude *Liolaemus* species in central Chile (T_b near 35° C) the four high-altitude species in northern Chile have lower activity field temperature. The latter is apparently due to the constraints imposed by the harsh Andean thermal environment, a hypothesis supported by the fact that high-altitude *Liolaemus* lizards under laboratory conditions demonstrate body temperatures that exceed by 5° C or more, those recorded in the field.

Key words: Andes – *Liolaemus* – Thermal environment – Activity temperature – Thermoregulation

Lizards can compensate for changes in the thermal environment in several ways: from use of behavioral tactics (e.g., differential microhabitat selection at different hours of the day, modification of body posture), through physiological acclimatization, to morphological and/or enzymatic differentiation among populations. Previous studies have identified thermoregulatory behavior as the primary route of thermal adaptation in lizards (Cowles and Bogert 1944; Huey 1974; Huey and Slatkin 1976; Muth 1977). Some of the most useful studies about thermal responses have been those focused on lizards distributed along altitudinal gradients, where the thermal environment changes substantially, thus eliciting behavioral and/or physiological responses of those lizards (Heatwole et al. 1969; Huey and Webster 1976; Hertz 1981; Hertz and Huey 1981).

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Members of the iguanid lizard genus *Liolaemus* have a widespread distribution in the southern cone of South America, and very often they occur on altitudinal gradients along the Andean Mountain Range (Donoso-Barros 1966; Fuentes and Jaksic 1979a). Consequently, this group of lizards is particularly suitable for studies focused on responses associated with changes in the thermal environment, as different species replace each other along different points of an altitudinal gradient.

We provide information on the activity field temperature (T_b), daily activity pattern, and extent of thermoregulation in four *Liolaemus* lizards distributed in two altitudinal belts of the Andes of northern Chile. The results will be discussed with reference to the ecological importance of the thermal environment for these lizards in comparison to that for *Liolaemus* species inhabiting lower altitudes in central Chile.

Material and methods

During our first two stays at the high Andean region of northern Chile, from January through May (Summer through early Fall) and in October (Spring) of 1985, sightings and captures of lizards were made at two altitudinal belts between 18°15' S and 19°42' S. The four species studied were distributed differently. Both *Liolaemus ornatus* and *L. islugensis* inhabited between 3500 and 4000 m elevation, at the altitudinal belt called Puneño (Puna belt), which is characterized by the dominance of a dwarf scrub composed of a physiognomically homogeneous but taxonomically rich assemblage of shrub species (Villagrán et al. 1982). *Liolaemus alticolor* and *L. jamesi*, on the other hand, inhabited between 4000 and 4500 m elevation at the so called high-Andean belt, characterized by the dominance of tussock grasses, interspersed with cushion plants on the rocky slopes (Villagrán et al. 1982). The two belts share a highland-steppe type of climate (Velo and Kalin 1982), characterized by a dry season of eight to nine months and a wet season of three to four months, with a mean annual rainfall of 450 mm, concentrated during Summer months, and with mean temperatures of –12.2° C in July (austral Winter), and 12.9° C in December (austral Summer).

We walked through the field, along randomly chosen transects, from 0700 hours until 45 min had passed without sighting any lizard. For each lizard seen we recorded the time of the day, the microhabitat occupied (only when the

lizard appeared undisturbed by our presence) and, when the capture was possible, its sex, air temperature (shaded bulb 2 or 3 cm above the ground = Ta), and cloacal temperature (activity field temperature = Tb), both with a Schultze's thermometer. Individuals that moved ostensibly because of our presence were not captured. Because no difference in Tb was detected between males and females of any species, data for the two sexes were pooled. Because measurement of cloacal temperature required handling of the lizard for ca. 20 s, it is likely that our readings underestimate the actual Tb of a freely moving lizard. We do not know how biased are our estimates of Tb, but at least they are all systematically biased, thus rendering it possible comparison between different species and localities.

To assess thermal constraints imposed by the high altitude, we collected individuals of *Liolaemus alticolor* and *L. jamesi* during a third visit in Summer 1988. Their preferred body temperature was recorded under laboratory conditions. Laboratory Tb was measured repeatedly during the day in a thermal gradient of 15° to 75° C inside a chamber of 300 cm² with a sand carpet on the bottom. Heat was provided by an infrared lamp. Body temperature was measured with Cu-constantan thermocouples and a Bailey digital multi-channel recorder (for details see Bozinović and Rosenmann 1988). We considered that the thermal environment may be deemed restrictive for lizard thermoregulation if the Tb measured in the field was lower than the Tb recorded in the laboratory.

Breadth of the temporal axis of the niche was estimated

with Levins' (1968) index $B = 1/\sum p_i^2$, where p_i represents the proportion of the i th resource used by a given species, considering each hour of the day as a resource state, given their different thermal characteristics. This index renders values between 1 and n (when n resource states are equally used). We computed regressions of field Tb on Ta to estimate the extent of thermoregulation during a given activity period (Huey and Slatkin 1976), where a slope of $b=1$ indicates complete thermoconformity (see Hertz and Huey 1981, for comments on this estimate). Because *Liolaemus* lizards are heliothermic, we deemed adequate to estimate Ta as the air temperature at the location where the lizards were captured. It should be cautioned however, that other estimates of Ta (e.g., unshaded bulb temperature) may render different readings, and perhaps alter the parametric estimates of the regression equation.

All statistical tests (Snedecor and Cochran 1967) are two-tailed unless otherwise noted (when our hypothesis specified the direction of the expected departure).

Results

Activity field temperatures

In spite of the different altitudinal locations where the animals were collected, and of the different microhabitats used by these four *Liolaemus* lizards (Table 1), they all had relatively similar field Tb near 29° C (Table 2). A one-way Anova, however, shows that there were statistical differences

Table 1. Microhabitat use, expressed as percent frequency of sightings, by four high-altitude *Liolaemus* lizards (SVL = Snout - vent length, $\bar{x} \pm 2SE$; N = sample size)

Species	SVL (mm)	Shrubs ^a				Grasses ^b		Rocks	Boulders	Bare ground	N
		(5-25%) ^c		(1-5%)		(40%)					
		Sun	Shade	Sun	Shade	Sun	Shade				
Higher altitude											
<i>L. alticolor</i>	47.9 ± 2.9	11.5	25.6	-	-	14.1	37.3	3.8	-	7.7	78
<i>L. jamesi</i>	88.3 ± 2.9	23.1	7.7	-	-	-	-	-	46.1	23.1	13
Lower altitude											
<i>L. islugensis</i>	66.4 ± 1.6	13.2	19.8	17.9	-	3.3	2.0	1.3	-	42.5	151
<i>L. ornatus</i>	68.9 ± 1.6	30.9	29.4	-	-	-	-	22.5	-	17.2	58

^a *Adesmia* sp., *Parastrephia* sp., *Baccharis* sp. *Lampaya* sp., *Fabiana* sp.

^b Tussock grasses: *Festuca* sp.

^c Cover values as evaluated with line transects

Table 2. Activity field temperature (field Tb, $\bar{x} \pm 2SE$), air temperatures (Ta, $\bar{x} \pm 2SE$), and preferred body temperatures (lab Tb $\bar{x} \pm 2SE$) for high-altitude *Liolaemus* lizards (N = number of individuals measured; n = number of measurements taken)

Species	Field Tb	Range	Ta	Range	N	Lab Tb	Range	n
Higher altitude								
<i>L. alticolor</i>	29.1 ± 1.2	23.0-34.0	20.8 ± 1.4	14.0-28.5	23	34.5 ± 0.9	25.8-39.5	108 ^a
<i>L. jamesi</i>	29.1 ± 2.2	24.0-33.0	19.3 ± 2.6	13.0-25.0	9	36.0 ± 0.4	27.5-40.4	51 ^b
Lower altitude								
<i>L. islugensis</i>	28.2 ± 1.3	18.5-37.0	23.4 ± 1.4	12.0-32.0	41	-	-	-
<i>L. ornatus</i>	30.7 ± 1.3	21.0-35.0	26.6 ± 2.1	17.5-35.0	24	-	-	-

^a Involving 9 different individuals

^b Involving 3 different individuals

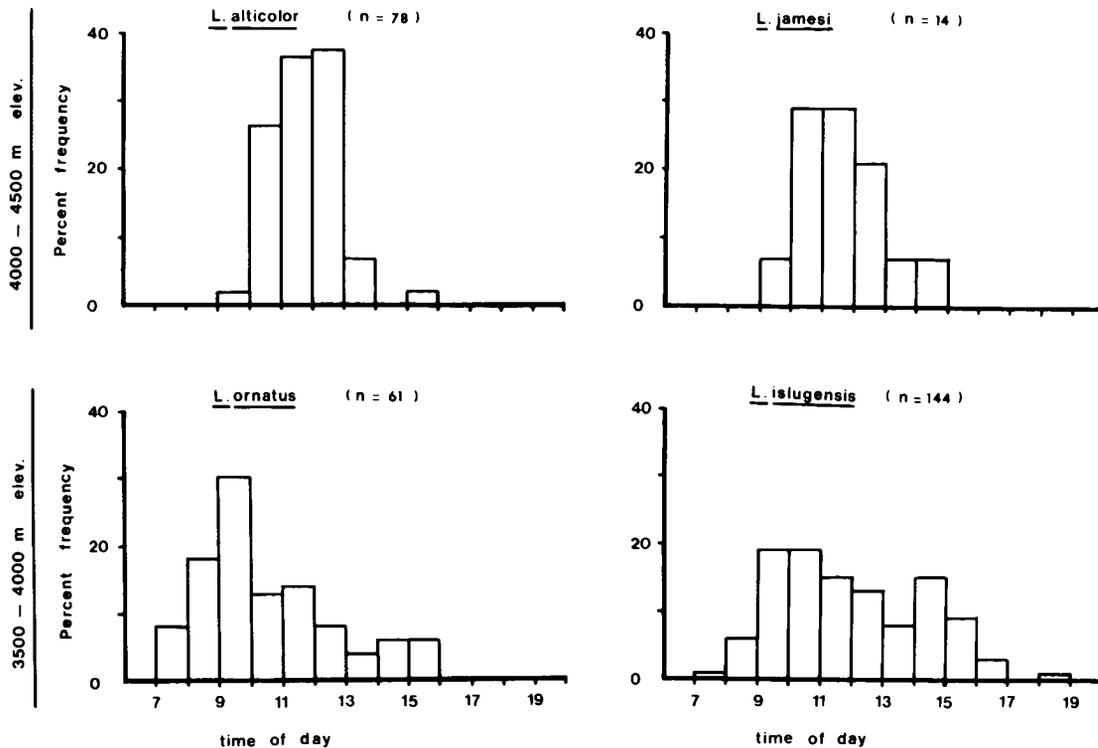


Fig. 1. Daily activity patterns of four high-altitude *Liolaemus* lizards (n = sample size)

among samples ($F=3.59$; $df=3,93$; $P<0.02$), but these were only because *L. ornatus* differed from the syntopic *L. islugensis* (Scheffé a posteriori test, $P<0.05$). Interestingly, there were no statistical differences between species inhabiting at different altitudinal belts, despite their being exposed to contrasting air temperatures (Table 2). Lizards inhabiting the lower Puna belt were active at mean air temperatures above 23°C , whereas lizards inhabiting the higher Andean belt were active at mean air temperatures below 21°C .

Laboratory Tb of *L. alticolor* and *L. jamesi* (Table 2) were higher by 7.3°C and 5.6°C those recorded in the field. We suspect that our handling of lizards in the field may have resulted in a temperature drop, but not as much as that here reported. Actually, Valencia and Jaksic (1981) studying thermoregulation of central Chilean *Liolaemus nitidus* in field and laboratory conditions, did not find evidence of a temperature drop owing to field manipulation. The differences between field and laboratory records for *L. alticolor* and *L. jamesi* were highly significant (Student's t -test, $P<0.001$). Also, the laboratory Tb differed significantly between these two species (Student's t -test, $P<0.001$), which was not the case in the comparison of their field temperatures.

Daily activity patterns

The four species showed unimodal daily activity patterns (Fig. 1), these being more restricted for the lizards inhabiting the high-Andean belt (*L. alticolor* and *L. jamesi*), which was expressed in a narrower temporal niche ($B=3.6$ and 4.4 , respectively). Lizards inhabiting the lower Puna belt (*L. ornatus* and *L. islugensis*) showed a broader daily activity pattern and temporal niche breadth as well ($B=6.0$ and

7.0 , respectively), which may be related to the higher air temperatures experienced by the latter two species in comparison to the former.

Extent of thermoregulation

The lizards apparently differed in their extent of thermoregulation at the two altitudinal belts. The slopes of the regression lines for *L. ornatus* and *L. islugensis* ($b=0.33$ and 0.48 , respectively) indicate that these lower altitude species thermoregulated less carefully than the species at higher altitude (*L. alticolor* and *L. jamesi*, $b=0.14$ and 0.00 , respectively), the former two species being more thermoconformers than the latter. This is also apparent in the statistical significance of Pearson's correlation coefficient between field Tb and Ta for the species at lower altitude ($r=0.54$ and 0.51 $P<0.01$, for *L. ornatus* and *L. islugensis*, respectively) as compared to those at higher altitude ($r=0.15$ and 0.20 , $P>0.48$ for *L. alticolor* and *L. jamesi*, respectively). It is interesting that the species inhabiting the same altitudinal belt showed similar correlation coefficients, which suggests that lizards exposed to similar thermal environments thermoregulate in a similar way despite their use of different microhabitats and their different body sizes (Table 1). This observation stresses the importance of the thermal environment for these lizards.

An analysis of covariance (Snedecor and Cochran 1967) revealed that within each altitudinal belt the slopes of the regressions of field Tb on Ta did not differ significantly ($P>0.25$ in the two cases), which is in agreement with the results of the regression/correlation analyses. Also, pooling together data for the two species sympatric at each altitudinal belt, and comparing the two belts, rendered a significant difference between regression slopes ($P<0.05$, one-

tailed test). As expected, lower altitude *Liolaemus* showed larger regression slopes than those at higher altitude. That is, the former allowed their temperature to vary with that of the environment to some extent, whereas the latter did not.

Discussion

Comparative thermal characteristics

The four species studied showed small interspecific differences in their field Tb. This phenomenon is relatively common among species belonging to the same genus, despite their inhabiting areas with different thermal characteristics (Bogert 1949, 1959; Brattstrom 1959; Licht et al. 1966). Similar results have been reported for central Chilean *Liolaemus* (Fuentes and Jaksic 1979b), which despite using a broad range of habitats and microhabitats display little variation in their field Tb. However, a comparison of central and northern Chilean *Liolaemus* shows important differences in their mean field Tb: about 35° C among the former versus 29° C among the latter. This six-degree difference may represent a genetic divergence in preferred Tb or simply reflect the effect of environmental constraints, which do not allow high altitude species to elevate their Tb.

The fact that the Tb measured under laboratory conditions for *Liolaemus alticolor* and *L. jamesi* were significantly higher than those recorded in the field, indicates that these high altitude lizards lived in a harsh thermal environment. Under favorable conditions, they were able to attain high Tb, but the broad range of their field activity temperatures indicates that favorable thermal conditions were not predominant at high altitudes. That high Andean lizards may be able to achieve high Tb under some circumstances, has also been observed in *Liolaemus multiformis* (Pearson and Bradford 1976; Pearson 1977).

In contrast, no thermal constraints are apparent for central Chilean *Liolaemus*, provided that the Tb achieved in the field does not differ from their Tb in laboratory thermal gradients, as has been reported for *L. nitidus* (Valencia and Jaksic 1981). Finally, the field Tb of the four high altitude *Liolaemus* is similar to that reported for a high latitude (i.e., more southerly) species, *L. magellanicus* (field Tb = 27° C ± 0.7; $\bar{x} \pm 2$ SE, $n = 20$; Jaksic and Schwenk 1983).

Ecological implications

Previous studies of *Liolaemus* lizards at high altitude have emphasized the efficiency of the thermoregulatory behaviors shown by these animals (Pearson 1954, 1977; Pearson and Bradford 1976). These behaviors include avoidance of freezing temperatures by retreat into burrows, delayed emergence, selection of thermally suitable microhabitats, and change of the skin reflectance during warming and cooling. Our results, in contrast emphasize the effect of the thermal environment on two important niche axes, time and habitat.

Thermal constraints apparently determined the restriction of the lizards' activity period to those hours of the day with high solar radiation (higher air temperatures). The higher-altitude *Liolaemus alticolor* and *L. jamesi*, which ostensibly lived under harsher environmental conditions than their congeners in the lower Puna belt, had a narrower temporal niche.

The effect of the thermal environment on the spatial niche of the lizards was reflected in a conspicuous pattern of habitat selection. At the higher altitudinal belt, the small body size (high surface/volume ratio) of *L. alticolor* may have accounted for its cryptic behavior in densely covered areas, probably related to the high cooling and warming rates of small ectotherms. The larger *L. jamesi* instead occupied exposed areas, particularly on boulders. At the lower altitudinal belt, *L. ornatus* and *L. islugensis* shared similar body size but showed different patterns of microhabitat occupancy. *Liolaemus ornatus* was found in densely-covered shrub microhabitats, which were more protected from the wind, provided higher Ta, and thus the opportunity to attain higher Tb than *L. islugensis*. This last species was found more often in sparsely covered areas (particularly on bare ground), exposed to the prevailing windy conditions, which may have prevented it from attaining and maintaining a higher Tb. Perhaps the microhabitat differentiation observed between *L. ornatus* and *L. islugensis* was the result of interference competition for suitable places where to attain high Tb (Magnuson et al. 1979; Roughgarden et al. 1981), but it may also be related to segregation in habitat to gain access to other exclusive resources, presumably food (Tracy and Christian 1986).

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