COMMENTARY

Altitudinal zonation among lizards of the genus *Liolaemus*: questions answered and unanswered questions

Zonación altitudinal en lagartijas del género *Liolaemus*: preguntas respondidas y pendientes

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ABSTRACT

We review factors influencing *Liolaemus* distributions in the central Chilean Andes and suggest areas of future research. Our previous studies reveal that lizard parasites (ectoparasitic mites and ticks, and the endoparasite *Plasmodium*) do not set *Liolaemus* altitudinal limits. Thermal tolerances do not appear to limit altitudinal distributions, although cold ambient temperatures dictate that only live-bearing species can occur above 2,400 m elevation. Three *Liolaemus* species specialize on elevationally restricted microhabitats. *Liolaemus tenuis* is found exclusively in or at the base of trees, which are typically below 1,800 m. *Liolaemus leopardinus* specializes on large rocky outcrops found at high altitudes. *Liolaemus monticola* uses smaller rocks: oviparity set its upper distributional limit on two transects, but on one transect this lizard and its rocky habitat virtually disappeared above 1,500 m. Interspecific competition among *Liolaemus* appeared unrelated to elevational distribution. We found no instances of parapatric distributions among pairs of *Liolaemus* species having similar niche requirements. Other researchers have found that predation does not correlate with elevation: its role in determining lizard species distributions depends on both predator and prey identities. We conclude that factors setting distributional limits of *Liolaemus* species vary depending on individual circumstances in time and space: where physiology may be relevant on one transect, preferred microhabitat availability may be important in another.

Key words: altitudinal gradient, central Chile, species distribution, thermal biology, parasite load, microhabitat preference, interspecific competition.

RESUMEN

Revisamos los factores que influyen sobre las distribuciones de *Liolaemus* en los Andes del centro de Chile y sugerimos futuras avenidas de investigación. Nuestros estudios previos revelan que los parásitos (garrapatas y ácaros ectoparásitos y el endoparásito *Plasmodium*) no influyen sobre los límites altitudinales de *Liolaemus*. Las tolerancias térmicas tampoco parecen limitar dichas distribuciones altitudinales, aunque las temperaturas ambientales frías determinan que sólo las especies vivíparas puedan sobrevivir arriba de los 2.400 m de altura. Tres especies de *Liolaemus* se especializan en microhábitats de distribución restringida en el gradiente altitudinal. *Liolaemus tenuis* se encuentra exclusivamente en la base de árboles, los cuales se distribuyen típicamente debajo de los 1.800 m. *Liolaemus leopardinus* se especializa en rocas grandes que se encuentran sólo en altitudes mayores. *Liolaemus monticola* usa rocas pequeñas: la oviparidad determina su límite distribucional superior en dos de los tres transectos examinados, y en el tercero esta especie y su habitat rocoso virtualmente desaparecen arriba de los 1.500 m. La competencia interespecífica entre *Liolaemus* aparentemente no se relaciona con su distribución altitudinal. No encontramos ejemplos de distribuciones parapátricas entre pares de especies de *Liolaemus* con similares requerimientos de nicho. Otros investigadores han encontrado que la depredación no se correlaciona con la altitud: su papel en determinar las distribuciones altitudinales de especies depende tanto de las densidades de predadores como de las presas. Concluimos que los factores determinantes de los límites de distribución de las especies de *Liolaemus* varían dependiendo de sus circunstancias individuales en el tiempo y el espacio: si bien la fisiología puede ser relevante en un transecto, la disponibilidad del microhábitat preferido puede ser importante en otro.

Palabras clave: gradiente altitudinal, Chile central, distribución de especies, biología térmica, carga parasitaria, preferencia de microhábitat, competencia interespecífica.

INTRODUCTION

Carothers et al. (1996) presented a model for the analysis of species distribution patterns along environmental gradients. They emphasized the importance of explaining distributional limits on altitudinal transects, typical of mountainous regions such as the central Chilean Andes, and proposed that lizards were especially fit as model systems, because of their dependence of ambient temperature. In order to answer the questions posed by Carothers et al. (1996), detailed information regarding the thermal relations, reproductive biology, resource distributions, lizard species distributions, and other potentially interacting species distributions was needed. In this context, Carothers et al. (1997, 1998) dealt with the thermal physiological properties and thermal ecology of *Liolaemus* lizards, and Carothers & Jaksic (2001) examined the role of parasite loads in setting distributional limits of the same lizards. The remainder (particularly competition and predation) will have to be studied by others, but we considered that a brief overview was timely, on what has been learned regarding the influence on *Liolaemus* distributions of the factors already analyzed, and commenting upon the likely influence of the other factors. We then conclude with thoughts on how to approach and answer these questions in future studies.

Effects of thermal biology and parasite loads

Our studies of the thermal biology of ten species demonstrated that among central Chilean *Liolaemus* there is little variation in thermal tolerances, which relates to altitudinal distributions on the western slope of the Andes (Carothers et al. 1997, 1998). From this we concluded that such tolerances were unlikely to play a major role in setting limits upon the altitudinal distributions of the species in question. However, thermal factors appeared to have a major impact upon reproductive mode of the species: only live-bearing species were able to persist at elevations above 2,400 m. Thus, the thermal environment played a role in setting the upper distributional limits of oviparous species, but not in a manner related directly to thermoregulation.

It should be noted that a recent phylogenetic analysis by Schulte et al. (2000) indicates multiple origins of viviparous reproduction in *Liolaemus*. Under the scenario that viviparity is irreversible, all six origins of viviparity have occurred in cold environments (Schulte et al. 2000), which is suggestive of an adaptive value for lizards in those environments. However, if reproductive mode is considered a reversible character, both gains and losses of viviparity can be identified among the group of taxa currently occupying cold environments, and thus the support for the hypothesis that viviparity is adaptive in cold environments is equivocal. Further work on the interaction between species physiology, ecology, and history in affecting the local radiation of *Liolaemus* inhabiting the altitudinal gradient in central Chile is needed to resolve this issue.

With regard to the effects of parasitic species, the data reported by Carothers & Jaksic (2001) demonstrate that ectoparasites such as mites and ticks occur among *Liolaemus* lizards in patterns apparently unrelated to distributions, and do not increase at elevational limits. Endoparasites such as *Plasmodium* are apparently absent from the populations in question. While it is possible that other undetected parasites may have an effect, the common types of parasites studied in populations of lizards do not appear to be relevant as factors influencing elevational distribution patterns of *Liolaemus*.

Effects of microhabitat specialization

Not explicitly addressed in the papers by Carothers and coworkers is the possible influence of microhabitat spatial patterns on the distributions of the species of *Liolaemus*. Although these data await detailed analysis, we discuss here in a qualitative manner what our data suggest. A number of the species studied appeared to specialize on specific microhabitats: these lizards could predictably be found in quite distinct microhabitat categories despite the presence of many other possible choices.

One such microhabitat specialist is *L. tenuis*, a species found exclusively in or at the base of trees. In the central Chilean Andes, trees are found only at lower elevations, typically no higher than 1,800 m. Likewise, the distribution of *L. tenuis* is tied to the upper limits of trees on each of the transects: on transects where trees occur only to 1,500 m elevation (the El Volcan transect), this limit also marks the boundary of the lizard. But where trees occur up to 1,800 m elevation (on the Farellones and Lagunillas transects), *L. tenuis* occurs this high as well. This species occupies prominent perch sites and males are bright green, blue, and yellow, and are easy to spot. Given the intense level of searching for lizards that took place at each study site over the two-year period of the study, we feel it is likely that very few

individuals of *L. tenuis* were unobserved that may have been occupying alternative microhabitats. Because they are so predictable in their association with trees, it seems safe to tentatively conclude that tree distribution plays a major role in determining the upper elevational limits of *L. tenuis*.

Another species that appears to be a microhabitat specialist is *L. leopardinus*. This species specializes on large rocky outcrops. In the central Chilean Andes, such outcrops are frequent mainly at high elevations, whereas at middle and especially lower elevations they disappear (personal observations). This species is light brown in color, with mottled spots on its back (hence its species name), which causes it to be rather cryptic against the lichens growing on boulders. This species was never found farther than 0.5 m from a boulder outcrop. Because of the close association between its preferred microhabitat and its distribution, *L. leopardinus* may also be assumed to have its altitudinal limits (especially the lower boundary) defined in large part by the distribution of its preferred microhabitat.

Another species that is saxicolous is *L. monticola*, an ant-eating lizard that preferentially perches on smaller rocks. On two transects, this lizard occurred to 2,400 m elevation, where its oviparous reproductive mode appears to set its upper distributional limit (Carothers et al. 1998). However, on one transect its distribution stopped far short of that high elevation. On the Lagunillas transect, rocky habitats virtually disappear above 1,500 m elevation, being replaced by a gently sloping terrain with plenty of soil and very few emergent rocks. Here suitable habitat simply disappeared, and *L. monticola* disappeared as well.

Effects of interspecific competition and predation

Not addressed in the papers by Carothers and coworkers is the possible influence of competition among species of *Liolaemus* with similar niche requirements. While it is widely accepted that species differing in their niche requirements do not compete, the converse assumption that competition occurs among those with similar niches is debatable. Because several *Liolaemus* species are food or microhabitat specialists, competition can tentatively be assumed to play an unimportant role in their distributional limits. This is the case for *L. altissimus*, *L. monticola*, and *L. tenuis*, for each of which microhabitat distributions are adequate to explain their respective limits. But we found no instances of parapatric distributions among pairs of *Liolaemus* species,

which may have similar niche requirements. Such cases —if found— should be investigated for the operation of competition. But up to now, no competitive influences have been detected to affect altitudinal distributional patterns of the lizards studied.

Medel et al. (1990) studied the correlates of predation on three syntopic low-altitude *Liolaemus* and on two high-altitude ones. They found that local predators did not cue on the more abundant species in either site, that at the lower site they captured the mostly terrestrial *L. lemniscatus* regardless of its small body size, and that at the higher elevation they took the largest lizard (*L. leopardinus*) regardless of its microhabitat use. This study indicates that predation is not a continuous variable that, say, decreases with elevation. Predators seem to take their cues independently of each other and thus their role in determining lizard species distributions may be complex: depending on both predator and prey identities.

Approaches in the pursuit of ecology

In the foregoing discussion, limitations upon altitudinal distributions focused on specific causal factors that appear to play major roles in setting distributional limits. Another way of ordering the discussion could have been to focus upon each species separately, addressing how the different hypothesized factors are influential under different circumstances. Such a Grinnellian niche approach has been used to analyze distributions of other species (e.g., James et al. 1984). The same information can be gotten from either the community approach or the individual species approach, although the two methods are sometimes associated with different preconceptions. In particular, the community approach has often been used by those looking for (and in many cases, expecting) effects of competition among the component species (e.g., Cody & Diamond 1975). In contrast, the individualistic Grinnellian niche approach emphasizes details of the population biology of individual species rather than community ecology and interspecific interactions.

In the preceding papers by Carothers and coworkers and in the discussion above, we have presented data on the biologies of *Liolaemus* species as well as our own interpretations as to the significance of various factors. Interpretation reflects personal biases: our own is that the factors relevant in setting distributional limits should vary dependent upon individual circumstances in time and space (Brown & Lomolino 1998).

Because of such variation in circumstances, we feel that no single factor is likely to predominate for all species. Where physiology may be relevant on one transect, preferred microhabitat availability may be important in another. Nevertheless, because some factors affect deterministically the distribution of species along gradients, we have patterns to explain. In fact, a recent analysis of the altitudinal distribution of 153 species of *Liolaemus* shows that the altitudinal pattern of species richness is nonrandom, showing a significant departure from what would be expected under the null hypothesis that species altitudinal ranges are randomly placed along the gradient (Veech 2000).

Other non-ecological factors certainly are relevant as well, and need to be addressed when adequate data become available. In particular, data on phylogenetic relationships among *Liolaemus* may suggest explanations to some distributional limits, which are alternatives to strictly ecological forces. Indeed, our data on thermal tolerances suggest that phylogenetic constraints may be strong. This idea can be tested by mapping species' thermal characteristics on the phylogenetic reconstructions —based on mitochondrial DNA sequences— proposed by Schulte et al. (2000).

In summary, the completed analyses of available data help in pointing to answers, but more work remains to be done. Experimental approaches testing apparent limiting factors can be used to support or refute our conclusions. Also, to fully answer the questions posed in our study on distributional gradients of *Liolaemus*, one not only needs ecological data but phylogenetic information as well.

LITERATURE CITED

BROWN JH & MV LOMOLINO (1998) Biogeography. Second edition. Sinauer Associates, Inc., Sunderland, Massachusetts. xii + 692 pp.

CAROTHERS JH & FM JAKSIC (2001) Parasite loads and altitudinal distribution of *Liolaemus* lizards in the central Chilean Andes. Revista Chilena de Historia Natural (in press).

CAROTHERS JH, FM JAKSIC & PA MARQUET (1996) A model for species distributions along a gradient: lizards as study systems. Revista Chilena de Historia Natural 69: 301-307.

CAROTHERS JH, SF FOX, PA MARQUET & FM JAKSIC (1997) Thermal characteristics of ten Andean lizards of the Chilean genus *Liolaemus*. Revista Chilena de Historia Natural 70: 297-309.

CAROTHERS JH, PA MARQUET & FM JAKSIC (1998) Thermal ecology of a *Liolaemus* lizard assemblage along an Andean altitudinal gradient in Chile. Revista Chilena de Historia Natural 71: 39-50.

CODY ML & JM DIAMOND, Eds (1975) Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts. xii + 545 pp.

JAMES FC, RF JOHNSTON, NO WAMER, GJ NIEMI & WJ BOECKLEN (1984) The Grinnellian niche of the wood thrush. American Naturalist 124: 17-47.

MEDEL RG, PA MARQUET, SF FOX & FM JAKSIC (1990) Depredación sobre lagartijas en Chile central: importancia relativa de atributos ecológicos y morfológicos. Revista Chilena de Historia Natural 63: 261-266.

SCHULTE II JA, JR MACEY, RE ESPINOZA & A LARSON (2000) Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. Biological Journal of the Linnean Society 69: 75-102.

VEECH JA (2000) A null model for detecting nonrandom patterns of species richness along spatial gradients. Ecology 81: 1143-1149.