

Patterns of distribution of anurans in high Andean tropical elevations: Insights from integrating biogeography and evolutionary physiology

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Synopsis Among ectothermic tetrapods, amphibians are by far the most diverse group at high elevations in the tropical Andes. This article asks whether this pattern reflects intrinsic aspects of amphibian natural history. An interdisciplinary analysis suggests that amphibians have a long evolutionary history at moderate Andean elevations and that adaptation for activity at low temperature occurred frequently and independently in different taxa. One conclusion is that temperature is unlikely to be the only or the main factor constraining some unrepresented anuran taxa that do not reach high elevations. Other physical variables (*e.g.* the effects of ultraviolet radiation on egg development) could better explain anuran diversity along tropical altitudinal gradients. In contrast, heliothermic taxa, such as lizards, might indeed be constrained by the low and variable temperatures that characterize high tropical elevations. Ecological gradients, therefore, might not affect ectothermic tetrapods in a similar manner, and differential susceptibility to biotic and abiotic factors that change with elevation might help to explain current patterns of distribution and diversity.

Introduction: The challenge of high elevation to tropical anurans

Anurans are particularly diverse in tropical montane environments, even at high elevations, as shown by studies in Andean countries such as Colombia (Lynch, 1987; Lynch *et al.*, 1997). The ecological radiation of anurans along the tropical Andes has occurred despite altitudinal climatic gradients leading to low and variable temperatures that occur all year round in high-elevation biomes. According to general postulates concerning the physiological ecology and thermal relationships of ectotherms (Huey, 1982), these anurans must exhibit ecological, behavioral, or physiological adjustments to counteract the expected reduction in behavioral performance associated with activity at low body temperatures. In amphibians, temperature is known not only to affect behavioral performance but also to affect life-history traits, including growth rates, developmental rates, and adult body size (Berven, 1982; Luddeke, 1997). In addition to low-temperature gradients, high elevations exhibit increased levels of ultraviolet (UV) radiation and a reduction in oxygen partial pressure. UV radiation might produce ontogenetic disorders in anurans and is often considered a

factor in population decline (Broomhall *et al.*, 2000). Altitudinal hypoxia, on the other hand, might limit a number of physiological functions, particularly in extreme-elevation aquatic environments (Hutchison *et al.*, 1976). The altitudinal gradients of the tropical Andes involve also drastic shifts in structural habitat and community constitution; for example, the highest forested environment (the cloud forest, currently at about 3200 m) is being replaced by increasingly depauperate communities, such as páramos and elfin forests, which are more open and less diverse (Baruch, 1984). Altitudinal gradients also encompass changes in the quality, diversity, and density of predators and prey, with the last mentioned known to affect growth rates and related life-history traits in amphibians (Bernardo and Agosta, 2003). All of these physical and biotic variables change simultaneously, so synergistic effects might further increase the ecophysiological challenge for vertebrate ectotherms living at high altitudes.

Detailed reviews focusing on the origins of the high-Andean tropical herpetological fauna or the physiology of high-elevation anurans have been published. The focus of this article, however, is neither to discuss the biogeography of specific Andean anuran taxa (Duellman, 1979; Lynch, 1987) nor to present an

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Fig. 1 Map of northeastern South America showing the general distribution of the tropical Andean mountains.

overview of high-elevation anuran physiology (Hutchison *et al.*, 1976; Navas, 1997). Rather, I focus on the question of why Andean anurans, despite ecological challenges, occur at extreme elevations and are more diverse in the high tropical Andes than any other vertebrate ectotherm taxa. In trying to answer this question I favor integration over detail. First, I present an overview of how anurans colonized high elevations in the tropical Andes (Fig. 1), and then discuss what sort of evolutionary adjustments probably occurred during the process of colonization. Next, I focus on how the patterns of distribution and adaptation observed in high-Andean tropical anurans compare with those of other taxa of vertebrate ectotherms in high-Andean environments, particularly lizards. Finally, I search for novel interpretations of the available data, focusing on whether the success of anurans at high tropical elevations reflects fundamental aspects of their biology.

Biogeography of Andean tropical anurans: Implications for evolutionary physiology

Anuran diversity in the tropical Andes

The ecological success of amphibians in the tropical and subtropical Andes is evident from the 800-plus species (more than 600 endemic), among which

anurans represent 700-plus species. Lynch *et al.* (1997), who studied the distribution and systematic relationships of Colombian Andean anurans, noticed that the west and central branches of the Colombian Andean cordilleras exhibit about 25 species more than the western lowlands, whereas the eastern branch exhibits about the same number of species as the eastern lowlands (*ca.* 85 species). In addition, more than half the total number of species occurs in the Andean cordilleras, where endemism is very high, and species with distributions corresponding to similar altitudes often tend to be phylogenetically related, independent of their absolute geographical distance. These observations led the authors to propose that the biological diversity of Colombian Andean anurans is mainly explained in terms of geographical replacements of species and that the remarkable diversity of the lowland rain forest areas on either side of the Colombian Andean cordilleras is at best only a partial explanation for Andean diversity.

Early anuran communities in the tropical Andes

Understanding the patterns of anuran diversity in the tropical Andes requires information about the origin of this extensive mountain chain. A first rise of the southern and northern Andean mountains, to approximately half their present elevation, occurred in the late Jurassic and roughly coincides with the separation of Laurasia from Pangea (Ramos and Aleman, 2000). This is later than the dates attributed to the first fossils identifiable as anurans, of early Jurassic origin, which are some 200 million years old (Estes and Reig, 1973). These Jurassic anurans gave rise to the South American superfamily Hyloidea, which became well defined after the split between South America and Africa (Feller and Hedges, 1998). In terms of evolutionary physiology, this scenario suggests that anuran adaptation to moderate elevations is likely to be ancient. By the end of the Jurassic a number of anuran taxa were probably well adapted to moderately high elevations. Indeed, various modern Andean anurans are particularly diverse at moderate elevations, including cryptic dendrobatid frogs, such as *Colostethus*, *Epipedobates* and *Cryptophyllobates*, which apparently have experienced several independent local radiations (Coloma, 1995; La Marca *et al.*, 2002; Vences *et al.*, 2003), *Telmatobius*, *Elutherodactylus* (Lynch, 1987), and the bufonids *Osornophryne* (Mueses-Cisneiros, 2003) and *Atelopus*, the latter represented by the striking species *Atelopus carrikeri* found at elevations higher than 4400 m (Rivero, 1963).

The Andean mountains apparently reached their present size through a geologically recent accretion

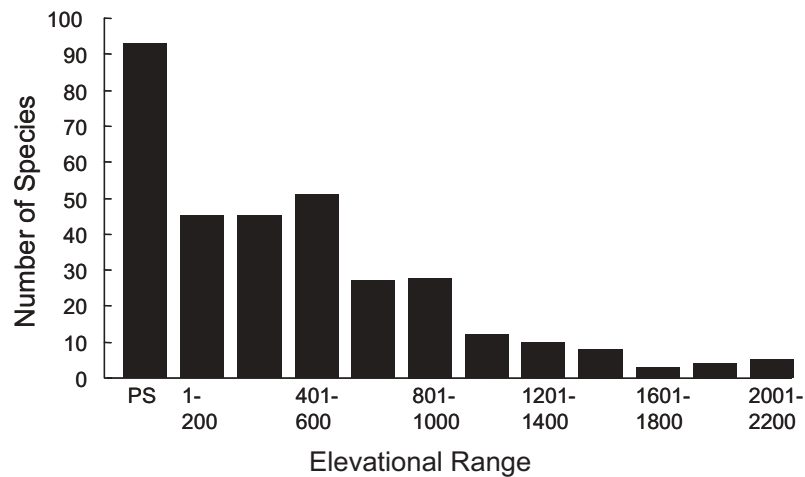


Fig. 2 Frequency distribution of altitudinal intervals (maximum minus minimum reported elevations) for Colombian montane amphibians. Bars to the left indicate species with very narrow altitudinal distributions, and bars to the right indicate species with broad altitudinal distributions. The category PS (presumably small) refers to species that have been reported only at one locality because of either restricted distribution or inadequate data. The subsample used for this plot includes only species found above 1000 m ($n = 331$), representing 5 anuran families (Bufonidae, Leptodactylidae, Centrolenidae, Dendrobatidae and Hylidae) and a salamander in the family Plethodontidae. Data were obtained from a published literature compilation (Acosta-Galvis, 2000).

that occurred in an irregular manner between 25 and 4 million years ago, according to latitude (Ramos and Aleman, 2000). Anuran adaptation to high elevations in the tropical Andes, therefore, occurred along or after this geological event. The current distribution of anurans in the tropical Andes suggests that this early radiation might have been biome specific, because many extant species of Andean high-elevation tropical anurans are mainly associated with or endemic to specific biomes (note that biome distributions change over geological time; see the next section). For example, Colombia exhibits 39 species that are truly endemic to the páramo (Lynch, 1987; Lynch and Suárez-Mayorga, 2002), a high-elevation biome characterized by mossy and grassy soils, shrubby vegetation, and abundant plants in the genus *Espeletia* (Asteraceae, Compositae) (Monasterio, 1980; Baruch, 1984). Because this biome is often distributed patchily on mountain tops, it has been considered analogous to an archipelago (Vuilleumier and Monasterio, 1986).

Geologically recent temperature changes in the tropical Andes: Consequences for anuran distribution

Studies performed in Colombia using cluster analyses to analyze fossil pollen samples as biological indicators of environmental conditions, show that the distribution of high-elevation biomes has changed very significantly in recent geological time. According to this study, the forest line, currently at 3200 m, has varied

from *ca.* 1900 to 3400 m over the past 650,000 years. Because of these fluctuations in total area, the degree of isolation and elevation at which high-elevation biomes occurred varied over time, even very recently (Marchant *et al.*, 2002). Likely, this pattern extends to other regions in the tropical Andes, such that high-elevation anurans have been exposed to recent cycles of habitat expansion and contraction. These fluctuations may have increased the possibilities of speciation through vicariance if gene flow across populations became restricted over long periods of time. A survey of the distribution of Colombian frogs that reach elevations higher than 2600 m suggests that most species might be altitude specialists. Indeed, only a handful of anuran species display altitudinal ranges of more than 1500 m, and most exhibit very narrow elevational distributions (Fig. 2).

Biogeography and physiology: Comparison between anurans and other tropical andean ectothermic tetrapods

An important question to evolutionary physiologists concerns the extent to which a long history of adaptation to moderate elevations partially explains the remarkable radiation of anurans along the secondary Andean uplift. Interesting insights emerge from a comparison of anurans with lizards, a group of vertebrate ectotherms that is currently much less diverse at high elevations in the tropical Andes. I focus here on the

autarchoglossans, the lizards that use their tongue and vomeronasal organs to sense chemical cues from the soil and subdue prey with their mouths (Vitt, 2004). These lizards are predators, as are most anurans, and reach higher elevations in the tropical Andes than the other main lizard group, the Iguanians.

New World autarchoglossans radiated to give rise to the teiids and the gymnophthalmids (Vitt and Pianka, 2004), the latter being the most diversified lizard taxa in the tropical Andes. One genus, *Proctoporus*, is a mainly Andean group that is highly diverse at moderate to extreme elevations, including a few species found at more than 4000 m (Doan, 2003). Doan (2003) proposes that *Proctoporus* and other related genera evolved from low-elevation ancestors probably along the first phase of the Andean uplift. If this conclusion is correct, and given that major iguanian radiations apparently were prior to the main autarchoglossan radiations in South America (Estes, 1983), a likely early scenario for the first Andean uplift involves the presence of diverse unrelated systematic groups of anurans and lizards, so that both groups had chances of speciation *in situ*. Currently, however, we see contrasting patterns of diversity at high elevations. High-elevation lizards in the tropical Andes are mainly examples of intense radiations of a few taxa such as *Proctoporus*, whereas a number of anuran families are represented by various genera and many species.

A comparison between anurans and salamanders is also pertinent. In tropical America, the only salamander taxon represented is the supergenus *Bolitoglossa* (Plethodontidae), which radiated extensively late in the history of the clade. This amphibian taxon, despite phylogenetic constraints, has radiated to high- and moderate-elevation biomes, where species are very diverse. Because most species exhibit restricted altitudinal ranges (as in anurans), this diversity is probably better explained by species substitutions over ecological gradients in time and space than by speciation in the context of structural complexity of ecological communities (García-París *et al.*, 2002).

Anuran adaptation to high tropical elevations

From the standpoint of evolutionary physiology, it is relevant to ask what behavioral, ecological, and physiological adjustments allowed the prominent radiation of anurans in the tropical Andes and how these patterns contrast with those of other ectotherm taxa. Navas (1997) pointed out that the ecological associations and patterns of behavior exhibited by high-selevation anurans might or might not reduce the thermal challenge experienced by individuals. The genus

Eleutherodactylus, for example, tends to be nocturnal and to call all night at any elevation through its range. This pattern of activity increases exposure to the coldest temperatures during peak activity, yet no shifts toward increased diurnal activity are evident at 3500 m (Navas, 1996a). Conversely, high-elevation *Colostethus* are diurnal and associated with humid areas and therefore experience moderate body temperatures during activity. Diurnality, however, is typical of most dendrobatid frogs, and association with humid places characterizes *Colostethus* independently of elevation. As an additional example of intrageneric conservation of patterns of activity, the bufonid genus *Atelopus* includes species from sea level to more than 4400 m, all of them diurnal. A main conclusion derived from these observations is that adaptations involving microhabitat selection and behavior do not seem to be responsible for the extension of altitudinal ranges in tropical Andean anurans.

If general patterns of behavior and ecology remain largely constant within genera and along elevational gradients, body temperatures must decrease. This hypothesis is well supported by the data available; the body temperatures of various typical high-elevation tropical frogs do not differ much from air temperatures, at least during the time of day when vocal activity is most intense, and mean body temperatures for various species decrease monotonically with an increase in elevation (Navas, 1997, 2003). The temperatures experienced by high-elevation tropical anurans would be deleterious for typical tropical frogs, which experience great difficulty in moving when exposed to temperatures near 14°C (Navas, 1996b) and might exhibit inability to move at around 7–10°C (Christian *et al.*, 1988). Given that activity temperatures decrease with elevation (see Fig. 6 in Navas [2003]), physiological adjustments must parallel the extension of altitudinal ranges in tropical anurans. This postulate has been explored mainly in the context of locomotor and metabolic physiology, including the analysis of thermal reaction norms, the functions describing behavioral or physiological performance as a function of temperature (Angilletta *et al.*, 2003). High-elevation frogs exhibit increased capacity for activity at low temperatures with no harm to the ability to move at moderate temperatures (*i.e.*, absence of evident evolutionary trade-offs). Plots of activity metabolic rate (measured in rotatory metabolic chambers) versus temperature show a very similar pattern, such that high-elevation anurans are able to achieve higher energy turnovers at temperatures lower than 15°C in comparison with lowland counterparts, but metabolic rates are similar at moderate temperatures (Navas, 1996b).

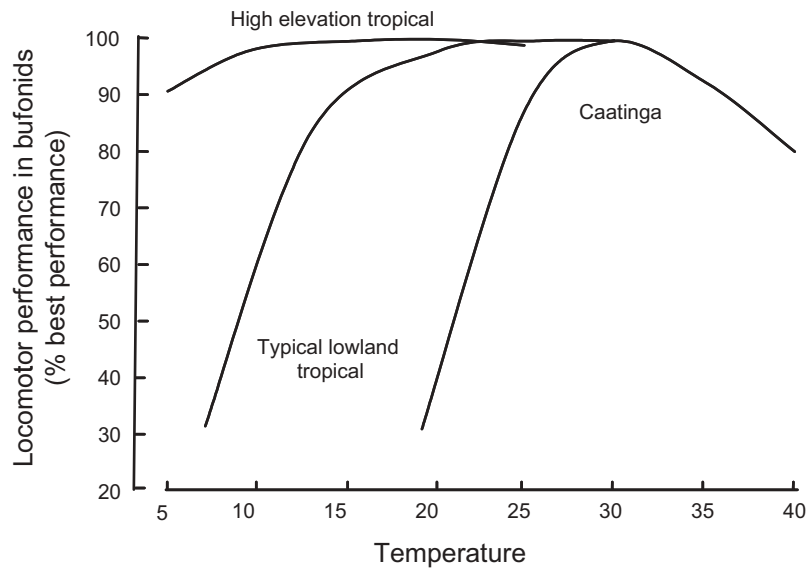


Fig. 3 Smoothed curves of locomotor performance as a function of temperature for 3 bufonids. The curve on the left is for a high-elevation *Atelopus* sp. nov., the central curve for a low-elevation congeneric (Navas, 1996b), and the curve on the right is for *Bufo granulosis* from the Brazilian semiarid (Navas et al., 2004).

Anurans from different thermal environments exhibit contrasting performance curves (Fig. 3), so genetic variation apparently has allowed for evolutionary adjustments in the shape and location of such curves along the temperature axis (as in Fig. 2 in Kingsolver et al. [2004]). High-elevation anurans exhibit a very extensive temperature gradient (from 5 to 30 °C) along which locomotion is barely thermosensitive (Navas, 1996b). These frogs, then, offer an example of absence of thermal trade-offs in the evolution of locomotor performance that is extreme when compared with examples from other ectotherm taxa (Angilletta et al., 2002). Overall, the examples of convergent adaptation to tropical high elevations in various anuran families (Navas, 1996b) suggest a very plastic nature of anuran thermal biology in the moderate to cold direction. The preliminary data available so far, however, suggest that evolution favoring activity in the cold might pose a simpler physiological problem for amphibians than adaptation for activity in hot environments. In the Brazilian Caatinga, a hot semiarid environment that nonetheless is inhabited by some 40 species of anurans in 6 families (Trefaut-Rodrigues, 2000), juvenile *Bufo granulosis* are diurnal and active at high temperatures (Navas et al., 2004). The performance curve for these toads (Fig. 3) is shifted to the right but maintains a typical shape, demonstrating that performance is reduced at moderate temperatures, although such temperatures are also ecologically relevant (Navas et al., 2004).

The pattern of anuran distribution presented in Figure 2 suggests that physiological specialization

along the process of speciation is a more common pattern in anurans than the expansion of altitudinal ranges through the evolution of generalist phenotypes or interpopulational differentiation, although the hypothesis of nonadaptive environmentally induced phenotypic changes cannot be discarded *a priori* (Miaud and Merilä, 2002). Some degree of populational differentiation in aerobic performance between populations at 2600 and 3500 m has been reported for *Eleutherodactylus bogotensis*, a frog that is nocturnal and experiences very low temperatures during calling, but not in other species with similar altitudinal distributions (Navas, 1996b). The tree frog *Hyla labialis* has received particular attention from this point of view as it figures among the Andean frog species (perhaps species complex) with the greatest altitudinal range, from 1900 to more than 3600 m. This species tends to be larger at its upper range, where females produce clutches with fewer but larger eggs (Luddecke, 2002). Studies of vocal behavior suggest moderate effects of temperature on vocal behavior, which has been interpreted as evidence of cold adaptation, particularly in higher-altitude populations (Navas, 1996c; Luddecke and Sanchez, 2002). Regarding physiology, populations at 2600 or 3500 m show similar rates of metabolism during activity (Navas, 1996b), but locomotor performance functions vary among populations. Carolina Ulloa (unpublished data) studied the responses of locomotor performance to acute temperature changes in various populations from 1970 to 3550 m in the Colombian eastern cordillera and found presumably adaptive differences among populations. Similar to

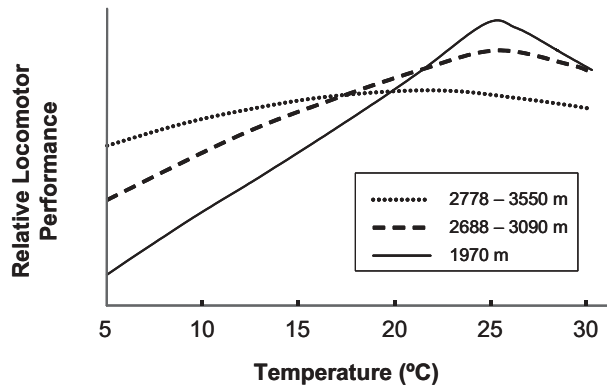


Fig. 4 Three types of smoothed curves of locomotor performance functions that best describe various populations of *Hyla labialis*. The contrast between extremes along the altitudinal range of the species is evident, with higher thermal independence in individuals from higher elevation. Individuals from populations at intermediate elevations are best described by two alternative patterns (C. Ulloa, *et al.*, unpublished data).

the interspecific pattern, at moderate temperatures (15–20°C) performance is similar across populations (Fig. 4). Notice, however, that at temperatures of 25°C and above a decrease in absolute performance is evident for the highest-elevation population, suggesting the eventual role of an absolute performance trade-off limiting intraspecific specialization.

Integrating biogeography and evolutionary physiology

Among amphibians, adaptation to fulfill life cycles in high tropical elevations is not only viable but common and has occurred repeatedly and independently in both anurans and plethodontid salamanders. Some of the required evolutionary physiological adjustments allowing anurans to live at moderate tropical elevations are likely to be ancient, because a number of Andean taxa probably evolved *in situ* and adapted to moderate tropical elevations along the first Andean uplift (see above). Many high-elevation anuran taxa probably originated from those moderate-elevation ancestors, although colonization through migration by low-elevation stock cannot be discarded. Adaptation to extreme altitude necessarily accompanied or followed the second Andean uplift and must be recent (not older than some 25 million years) compared with adaptation to the moderate elevations that characterized the first Andean uplift. Recent ecological changes have probably favored speciation through cycles of habitat contraction and expansion that led to speciation events. Given that both anuran and lizard taxa were apparently present at the first rise of the Andes and that the current

patterns of diversity along elevational gradients in the American tropics are quite different, the hypothesis that early adaptation to moderate elevations favors later dispersion of vertebrate ectotherm taxa to high elevations is not supported.

Temperature is often regarded as one of the most important variables limiting diversity at high elevations, even more so in the tropics, where cold conditions are permanent, daily thermal fluctuation surpasses yearly variation (Sarmiento, 1986), and mountain passes are physiologically more challenging (Janzen, 1967; Ghalambor *et al.*, 2005). Anurans, however, contrast with other vertebrate ectotherms in that they maintain conserved general patterns of behavior and ecology and shift their physiology to adjust for activity at lower temperatures at high elevations. This remarkable plasticity, whether evolutionary or phenotypic, suggests that adjustments in thermal biology are fundamental for anurans to invade high elevations, but it raises doubts about the role of temperature as the main constraint for anuran diversity at high tropical elevations. Given that thermal adaptation seems common in diverse taxa, temperature itself might not have been the main factor responsible for the decrease in anuran diversity along Andean altitudinal gradients in the tropics, as previously suggested (Feder and Lynch, 1982; Navas, 1997). Other biotic or abiotic factors might be important. It is worth noting, for example, that genera such as *Hyla*, which apparently originated in the low elevations of central America (Duellman, 1970), are represented at tropical elevations above the timberline only by a few species, but a number of congeners and related species have become adapted for activity at low temperatures during the spring in temperate latitudes (John-Alder *et al.*, 1988). Attributes of high elevations other than cold temperatures, therefore, might constrain anuran altitudinal ranges.

If temperature is not the most likely stressor limiting anuran colonization of high elevations in the tropics, other physical factors must be considered. Oxygen concentration has changed significantly through geological time and was comparatively low in the Jurassic, so that the current concentration might not reflect past eco-physiological challenges (Huey and Ward, 2005). Such geological changes might have helped to shape Andean herpetological communities, but nothing definitive can be stated at this time. Currently, this gas might be an environmental stressor only for anurans living at very high altitudes, as suggested by interpopulational studies showing that *Bufo spinulosus* exhibits blood traits compatible with oxygen deficit only at extreme elevations (Ruiz *et al.*, 1989). Respiratory modifications believed to increase the capacity for oxygen uptake

in high-elevation tropical anurans are reported mainly for aquatic species (Hutchison *et al.*, 1976; Ruiz *et al.*, 1980). The relevance of oxygen concentration to lizard reproduction at extreme elevations, particularly in oviparous species, has not received much attention.

Reproductive constraints are a factor to consider, and one possible explanation for the much lower diversity of anurans at southern Andean elevations than in the tropics is that the variety of potential sites for anuran reproduction decreases with latitude (Navas, 2003). Moreover, some sort of protection against solar radiation (either behavioral or through pigmentation, as in *Hyla labialis*) characterizes the eggs of a number of high-elevation tropical anurans (Lynch and Suárez-Mayorga, 2002), and certain successful high-elevation genera such as *Eleutherodactylus* and *Colostethus* exhibit reproductive modes in which eggs are not exposed to direct solar radiation. Egg protection and the ability to colonize biomes above the timberline might be correlated variables (Lynch and Suárez-Mayorga, 2002). Indeed, amphibian eggs are susceptible to damage by UV radiation, and differences among species are expected according to their reproductive ecology or ability to repair DNA (Blaustein *et al.*, 1998). The issue of whether a jelly coating offers some protection against UV radiation is still not settled (Hansen *et al.*, 2002; Licht, 2003), but behaviors that physically protect the eggs, such as wrapping them in leaves, do reduce significantly UV-induced mortality in newt eggs (Marco *et al.*, 2001). A formal study along these lines would be an important step toward understanding the patterns of distribution of anurans along altitudinal gradients.

Why only a few lizard taxa have been particularly successful at high tropical elevations in the Andes is a difficult question that cannot be definitively answered with the data available. In contrast with the anuran case, temperature might be the most important stressor for high-elevation tropical lizards and other heliothermic ectotherm vertebrates. Lizards exhibit a conserved thermal biology, at least regarding some relevant aspects of physiology (Angilletta *et al.*, 2002), perhaps because they use mainly behavioral thermoregulation to expand altitudinal ranges (Huey *et al.*, 2003). Therefore, activity temperatures tend to remain constant along elevation (Navas, 2003), but the number of hours available for thermoregulation and proper activity must decrease, a situation that might generate energetic constraints in lizards (Sears and Angilletta, 2004). Studies of the energy budgets of tropical lizards along altitudinal gradients would be helpful to test the appealing hypothesis that reduced energy expenditure, higher efficiency of prey acquisition, and higher quality of prey items are part of the suite of adaptations of the

few lizard taxa that have succeeded at high tropical elevations.

The most diverse high-elevation lizard taxa in the tropical Andes may owe their success to an ancestral natural history that involves activity at low temperatures for lizard standards. Indeed, Vitt and Pianka (2004) considered this hypothesis and noted that some gymnophthalmids work at rather low temperatures in comparison with teiids, their sister taxa, with mean temperatures of about 27°C in forested environments (Vitt, Sartorius *et al.*, 1988; Vitt, Zani *et al.*, 1998). Yet geckos (Autumm *et al.*, 1994) and *Anolis* (Hertz, 1992) are also active at comparatively low temperatures for lizards, and none of these groups is particularly diverse at high elevations. A key unanswered question is whether the activity temperatures of high-Andean lizards in tropical areas are warm and comparable with those of low-elevation lizards, and to what extent lizard taxa such as *Anadia* exhibit an atypical thermal biology. Genera that reach elevations above 2500 m such as *Phenacosaurus*, *Proctoporus*, *Anolis*, and *Stenocercus* are usually regarded as heliothermic, and they might maintain warm body temperature by compensating behaviorally for altitudinal gradients, as described for *Liolaemus* in the southern Andes (Carothers *et al.*, 1998). If this generalization holds, it would be clear that also in the tropical Andes lizards exhibit a strong tendency to adapt to high elevations mainly through behavioral means, as reported for other altitudinal gradients (Navas, 2003).

Concluding remarks and perspectives

This review suggests that the ability of different taxa of ectotherm tetrapods to adapt along tropical altitudinal gradients varies according to the plasticity of their thermal physiology and that such plasticity might be related to the evolutionary history of a taxon. Lizards, for example, rely largely on behavior to colonize colder environments. The absence of selection toward a modified thermal physiology over evolutionary time could limit lizards' scope for thermal adaptation (Huey *et al.*, 2003) because physiological traits would evolve to be highly integrated, thus limiting plasticity (Levins, 1968). This premise remains as a tentative postulate because very little is known about even the most basic aspects of the thermal biology of high tropical Andean lizards. This topic needs urgent attention and might lead to interesting discoveries regarding the evolution of lizard thermal biology.

Temperature might be a fundamental factor for explaining the distribution of lizards and perhaps other ectotherm tetrapod taxa, but it does not seem

to be the main factor limiting anuran altitudinal distribution. Amphibians, in contrast with lizards, exhibit a plastic thermal biology and historically have relied on physiological adaptation to extend their altitudinal ranges. Direct tests of such hypotheses of evolutionary inertia would be difficult, but a number of predictions could be evaluated based on the comparative analysis of thermoregulation and performance reaction norms (Huey *et al.*, 2003; Kingsolver *et al.*, 2004). It is possible that some anuran taxa are constrained by biome-specific specialization that prevents the occupation of areas above the timberline. If this is the case, other environmental stressors may be more important than temperature. Water pH, intensity of UV radiation, and other variables that may impact egg development emerge as likely candidates. These hypotheses could be tested by studying the physiology, diversity, and distributional ranges of ectothermic tetrapods along other altitudinal gradients in other geological ranges, for example montane environments in Africa and Asia. Such integrative and comparative studies of biogeography and evolutionary physiology are important to understanding both the historical events leading to the current distribution of organisms and the causal explanations behind the differential success of taxa along ecological gradients.

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