Journal of Thermal Biology 58 (2016) 91–98

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Thermal ecology of montane *Atelopus* (Anura: Bufonidae): A study of intrageneric diversity

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ARTICLE INFO

Article history:
Received 29 January 2016
Accepted 20 April 2016
Available online 22 April 2016

Keywords:
Activity body temperature
Operative temperature
Thermoregulation
Thermoconformers
Sierra Nevada De Santa Marta

ABSTRACT

Harlequin frogs (Bufonidae: *Atelopus*) are among the most threatened frog genus in the world and reach very high elevations in the tropical Andes and the Sierra Nevada de Santa Marta (SNSM). Learning about their thermal ecology is essential to infer sensitivity to environmental changes, particularly climate warming. We report on the activity temperature and thermoregulatory behavior of three high-elevation species of harlequin frogs, *Atelopus nahumae*, *Atelopus laetissimus* and *Atelopus carrikeri*. The first two mentioned live in streams in Andean rain forests, whereas *A. carrikeri* inhabits paramo streams in the SNSM. We studied the thermal ecology of these species in tree localities differing in altitude, and focused on activity body, operative, substrate and air temperature. A main trend was lower body temperature as elevation increased, so that differences among species were largely explained by differences in substrate temperature. However, this temperature variation was much lower in forest species than paramo species. The *Atelopus* species included in this work proved to be thermoconformers, a trend that not extended to all congenerics at high elevation. This diversity in thermal ecology poses important questions when discussing the impact of climate warming for high-elevation harlequin frogs. For example, forest species show narrow thermal ranges and, if highly specialized, may be more susceptible to temperature change. Paramo species such as *A. carrikeri*, in contrast, may be more resilient to temperature change.

1. Introdution

The body temperature during activity (AT) is influenced by behavior in several lineages of ectothermic animals. Currently, the term "thermoregulation" is loosely applied to all behavioral responses that influence body temperature (BT), but it was originally coined for the specific case of reptiles that maintained elevated and rather constant AT (Cowles and Bogert, 1944; Bogert, 1949). However, the use of a single term to cover different -even contrasting- behaviors obscures diversity among lineages (Angilletta, 2009). Anuran species, for example, may bask while avoiding overheating through regulated evaporation of water (Lylliwhite, 1974), reach high BTs during basking thanks to morpho-physiological traits reducing evaporation (Brattstrom, 1979; Wygoda, 1984; Wygoda and Williams, 1991; Angilletta et al., 2002), use the thermal variability of the substrate to influence AT (thigmothermy) (Hillman et al., 2009), or thermoconform. These responses rarely lead to elevated AT relative to substrate temperature, so that typically AT correlates closely with environmental temperature (Brattstrom, 1979; Navas et al., 2002). This pattern is conspicuous in small species exposed to variable environmental temperatures, and particularly exaggerated in tropical high-elevations (> 3000 m). In these settings anuran microhabitats may encompass shifts greater than 40 °C in 12 h, and body temperatures usually correlate with substrate temperatures (Navas, 1996a; Carvajalino-Fernandez et al., 2011). Under many circumstances this correlation indicates absence of thermoregulation according to the most restrictive sense, but is not incompatible with the concept of behaviorally-modified body temperatures. These considerations are necessary to understand the remarkable diverse behaviors that influence their thermal ecology of anurans in high-elevation tropical Andes.

Even if only few species have been studied, high-elevation tropical anurans display several forms of thermoregulation known for terrestrial amphibians, including basking, thermophilic thigmothemy, thermoconformation, and thermophobic thigmothemy (avoidance of warmest substrates). For example, *Rhinella spinulosa*

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http://dx.doi.org/10.1016/j.jtherbio.2016.04.007
0306-4565/

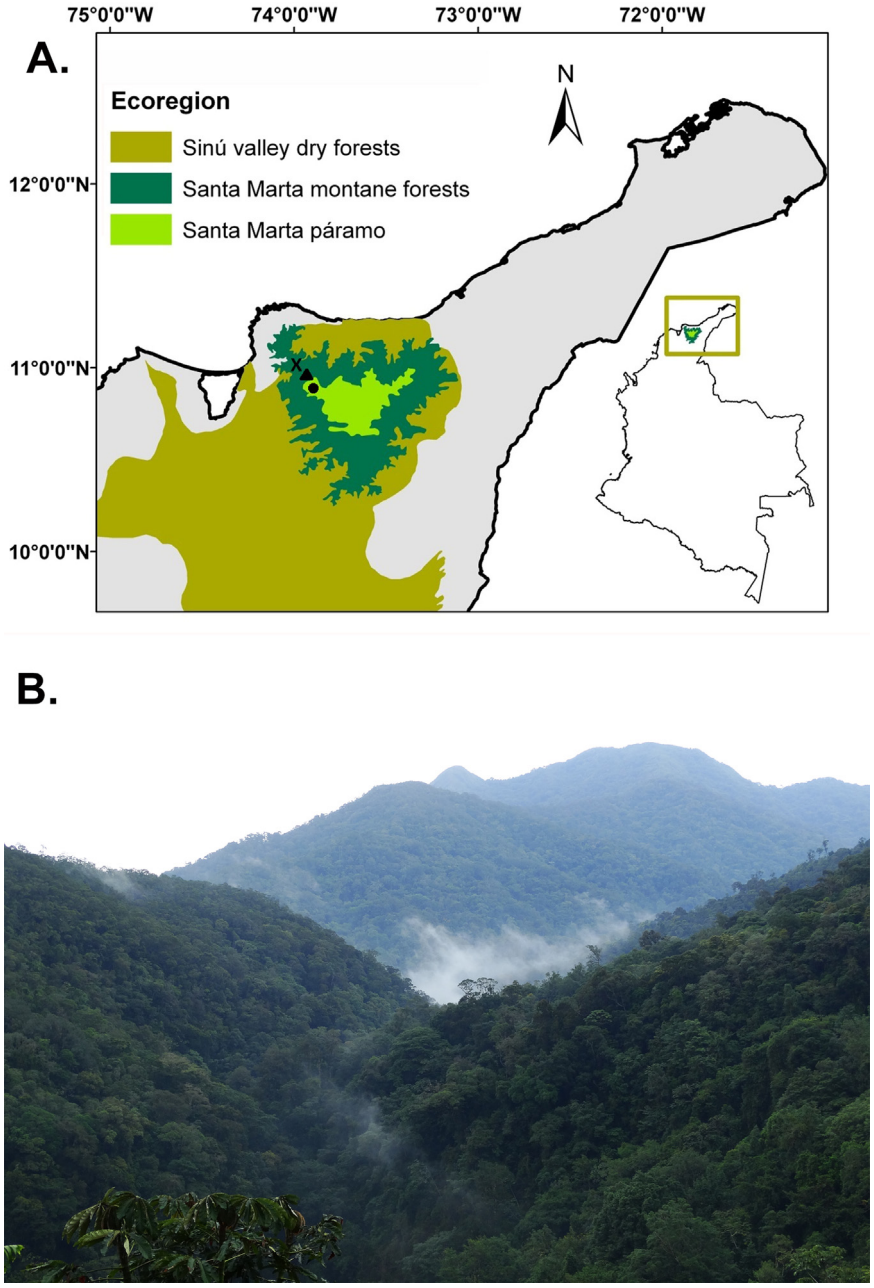

Fig. 1. Sierra Nevada de Santa Marta, Magdalena, North of Colombia, showing study localities. Cascada del rio Gaira 1560 m, locality of *Atelopus nahumae* (x), Quebrada San Lorenzo 2100 m locality of *A. laetissimus* (Δ) and Páramo de Cebolleta 3500 m locality of *A. carrikeri* (●) (A). General view Montane Wet Forest in the Sierra Nevada. Photographs by Luis Alberto Rueda Solano.

elevate AT within ecological constraints by substrate selection (Sinsch, 1989), *Pristimantis bogotensis* increase body temperature during the day using microhabitat selection (Navas, 1996a), tree-frogs *Dendropsophus labialis* bask during the day and are most active at night (Valdivieso and Tamsitt, 1974; Navas, 1996a), and *Atelopus lozanoi* avoids high temperatures by substrate selection (Navas, 1996a, species referred to in this paper as *Atelopus* sp. *nov.*). These types of thermoregulatory behaviors may reflect diversity among the lineages represented, but appear to be expressed in the context of convergent adaptation of thermal physiology improving locomotion at low temperature in all the above mentioned genera (Navas, 1996b). So, exaptation of ancestral thermal behaviors may have played a role in the ecological radiation of tropical anurans to higher elevations. However, two main limitations of actual knowledge are 1) few diurnal species have been studied, and 2) intrageneric diversity has not been addressed. The genus *Atelopus* (Bufonidae), harlequin frogs, is particularly interesting from these two points of view for it is composed by mostly diurnal species and it is speciose at high-tropical elevations. In addition, although the only species studied in detail is a thermophobic thigmotherm (Navas, 1996a), care is needed before generalizing this behavior to other high-elevation harlequin frogs. Indeed, the typically dark coloration of some species at more than 4000 m has prompted the untested hypothesis that some species may be heliothermic (Duellman and Trueb, 1986).

High-elevation *Atelopus* are common in the tropical Andes as well as in non-Andean elevations such as the Sierra Nevada de Santa Marta (SNSM) in Colombia, where the genus is particularly diverse (between 39 and 43 species; Lötters, 2007; Frost et al., 2015). In addition, endemism is high, including five species in the