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The highland tadpole of the harlequin frog *Atelopus carrikeri* (Anura: Bufonidae) with an analysis of its microhabitat preference

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Abstract. We describe the gastromyzophorous tadpole of *Atelopus carrikeri,* a harlequin frog endemic to the Sierra Nevada de Santa Marta, Colombia. In external morphology and colouration, this tadpole is similar to congeneric larvae with highland distributions yet distinct by its remarkable large size, having a well-developed suctorial ventral disc, and the upper lip usually having bilateral anterior projections that form a conspicuous M-shape. Tadpoles of this species inhabit fast-flowing streams above 3,000 m in altitude where they attach themselves to submerged rocks, especially in areas with low algae cover.

Key words. External morphology, gastromyzophory, Páramo, Sierra Nevada de Santa Marta, Colombia.

Introduction

Atelopus is the largest genus of the Bufonidae and contains at least 97 species (Amphibiaweb 2014, Frost 2014). This genus comprises small cryptically or brightly coloured toads, mainly from higher altitudes in the Andes (La Marca et al. 2005). *Atelopus* are diurnal (except *A. nocturnus*, Bravo-Valencia & Rivera-Correa 2011) and usually found on the ground or perched on lower vegetation, particularly alongside streams (Lötters 1996). Many *Atelopus* species have experienced population declines (Lötters 2007, Stuart et al. 2008), which are particularly dramatic in species that inhabit altitudes above 1,000 m (La Marca et al. 2005).

Of all *Atelopus* recognized, comparatively few tadpoles have been described (Boistel et al. 2005, Coloma & Lötters 1996, Duellman & Lynch 1969, Gascon 1989, Lavilla et al. 1997, Lötters 2001). Forty-four species of the genus have been reported from Colombia (Amphibiaweb 2014), but the tadpoles are currently only known of two: *A. subornatus* (Lynch 1986) and *A. mittermeieri* (Acosta-Galvis et al. 2006). In addition, the tadpoles of *A. ignescens* and *A. spumarius*, species that also occur in Colombia (see Duellman & Lynch 1969), have been described from Ecuadorian populations (Coloma et al. 2000, Lötters et al. 2002). However, these are not included here because both comprise species complexes (Lötters 1996). The tadpole of *A. leoperezii* (suggested to be a junior synonym of *A. carrikeri* according to Coloma 2002) was briefly mentioned by Ruiz-Carranza et al. (1994), nonetheless, the authors did not provide a formal description, detailed illustrations, or even reference museum vouchers.

Moreover, habitat information for harlequin frog tadpoles is likewise sparse, and detailed analyses of microhabitat structure are largely lacking. Relevant information is typically limited to the mentioning of collection sites in some larva descriptions (e.g., Gascon 1989, Coloma & Lötters 1996, Duellman & Lynch 1969, Boistel et al. 2005, Acosta-Galvis et al. 2006). Useful microhabitat details for *Atelopus* tadpoles are those presented by Coloma & Lötters (1996) who specified chemical parameters of the water in which *A. balios* tadpoles live, such as temperature, total hardness, carbonate hardness, pH, and contents of O_2, Fe, NH_4, NO_2, NO_3, and PO_4. In a similar vein, Boistel et al (2005) mentioned details about water depth, current speed, temperature, and described the ecology of *A. franciscus* tadpoles. The absence of basic information on tadpole morphology and ecology of *Atelopus* limit (i) our understanding of the evolutionary history and (ii) hamper in-situ and ex-situ breeding management efforts for these threatened species.

During fieldwork in the Sierra Nevada de Santa Marta, Colombia, a population of *Atelopus carrikeri* Ruthven, 1916 was discovered (Rueda-Solano 2008; Figs. 1, 2), representing the first record of the species since 1994. This species is classified as "Critically Endangered" by the IUCN Red List of Threatened Species (Stuart et al. 2008, www.redlist.org). Given the non-existence of knowledge on the morphology and biology of the larva of *A. carrikeri*, we here provide a detailed description, almost a century after it's the original description of the taxon. We furthermore assess tadpole microhabitat preferences.

Material and methods

The population of *A. carrikeri* studied is located in the Páramo Serranía de Cebolleta, Sierra Nevada de Santa Marta, Departamento del Magdalena, Colombia (10°54'03"N, 73°55'05"W; Fig. 1). The Sierra Nevada de Santa Marta is the world's highest isolated coastal massif, reaching an altitude of 5,775 m; it is located just 46 km from the coast of the Caribbean Sea. This massif, isolated from the Andean Mountains, represents the largest biogeographical region with endemic amphibians in Colombia (Lynch et al. 1997, Kattan et al. 2004), and five *Atelopus* species are known to occur in isolates in the Sierra Nevada de Santa Marta, i.e., *Atelopus carrikeri*, *A. walkeri, A. nahumae, A. laetissimus,* and *A. arsyecue* (Rueda-Almonacid 1994, Ruiz-Carranza et al. 1994, Lötters 1996, Coloma 2002).The co-occurrence of other *Atelopus* species with the *A. carrikeri* population reported on here is not confirmed. *Atelopus carrikeri* encountered at the specified site vary in colouration from black to red, yellow, and orange (Rueda-Solano 2012) and are restricted to three streams and their tributaries in an area of approximately 4.5 km^2 ranging from 3,000 to 4,000 m in altitude. Their tadpoles were abundant in these streams.

The tadpole description is based on an individual (CBUMAG-A 306-1) (Fig. 3) at Gosner (1960) developmental stage 34 and comparisons were made with a batch of 12 specimens. One specimen was fully developed and had turned into a froglet (Fig. 2), which facilitated the identification of these tadpoles as being those of *A. carrikeri*. Vouchers were deposited in the herpetological collection of the Universidad del Magdalena-Colombia (lot number: CBUMAG-A 306). Terminology of larval features follows Altig & Johnston (1989) and Mijares-Urrutia (1998). Developmental stages are classified according to Gosner (1960). We took measurements with Mitutoyo Series 500 digital callipers with 0.01 mm precision.

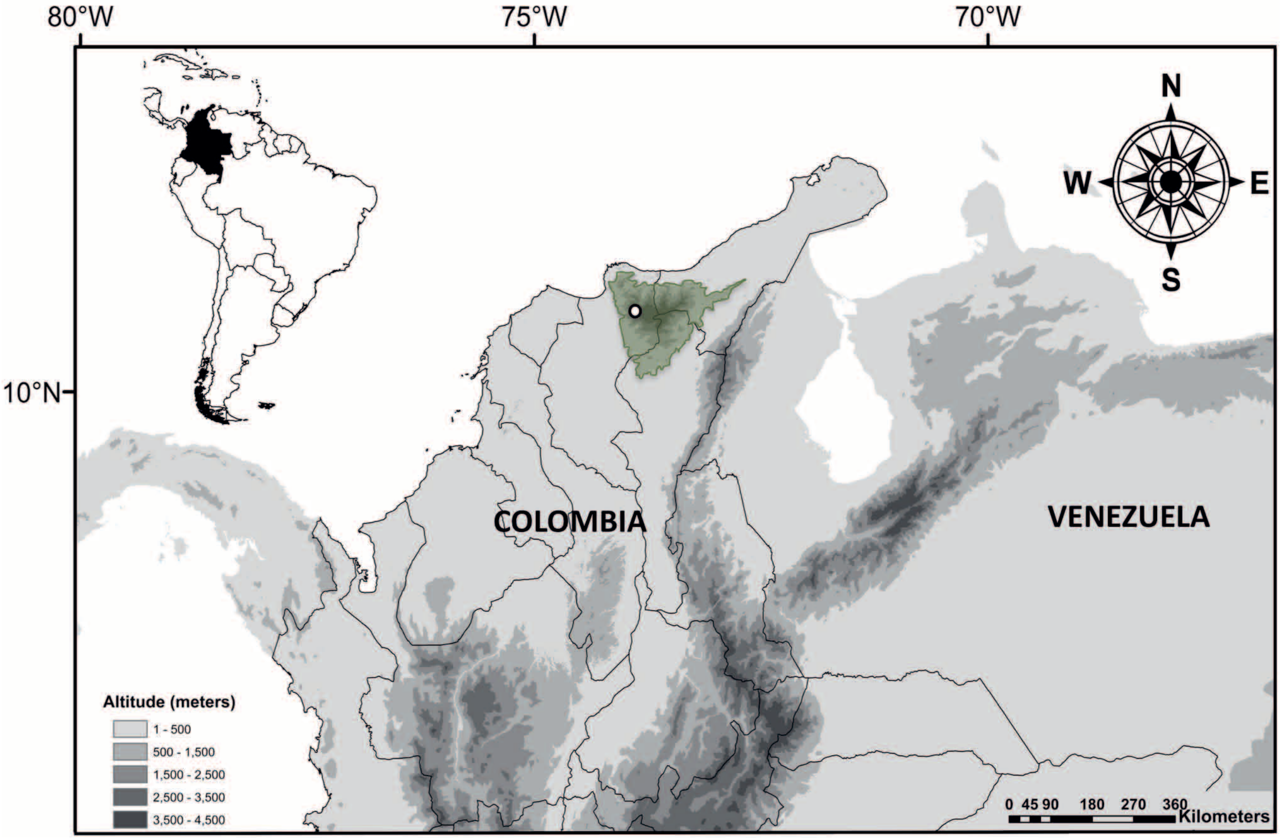

Figure. 1. Geographical position of the Sierra Nevada of Santa Marta in Colombia. The white dot indicates the Páramo de Cebolleta where tadpoles of *Atelopus carrikeri* were observed and collected.

To characterise the microhabitat utilised by larval *A. carrikeri*, we conducted three in-situ studies (September and October 2008, May 2009). Seven randomly selected transects (50 × 2 m) were established along three streams in the study area. Each stream was sampled more than once, and to minimize pseudo-replication, each transect was separated by more than 300 m from the next (as suggested by Rueda-Almonacid et al. 2006). Each transect was divided into 100 squares of 1 m^2, and 15–20 non-adjacent squares were systematically sampled. In each selected square, we took water temperature and dissolved O_2 (mg/l) content with an OAKTON DO 100. We also recorded water depth, mean area size of free bottom substrate, and the percentage of algal coverage. These two later variables were measured by analysing digital pictures with the software Image-J (Scheneider et al. 2012). The visual presence of tadpoles was recorded for every sample unit. All variables recorded in the squares were integrated in a logistic regression model to identify their predictive powers for explaining the presence of tadpoles.

Results

Description of tadpole

Total length 35.9 mm, body elongated ovoid in dorsal view and depressed in lateral view; snout broadly rounded in dorsal view and rounded in profile; chondrocranial elements not detectable; eyes located dorsally and directed dorsolaterally; interocular distance 3.6 mm (taken from the medial edges of the corneas); small semicircular nostrils (cf. Fig. 3c in Mijares-Urrutia 1998) with a flat and non-protuberant margin, closer to eyes than to snout tip. Internarial distance 2.5 mm. Spiracular tube single, sinistral, directed posterodorsally, originating at midpoint of body; diameter of spiracle opening less than half the length of the free tube. Vent tube medial and short; caudal musculature as long as the fin, tip of tail rounded, visible myotomic muscles in the anterior medium section of the tail, straight longitudinal tail axis. Caudal musculature robust anteriorly, narrowing posterior to mid-length portion of the tail. Dorsal fin originates at tail and is narrower than

Figure. 2. Different stages of tadpole development and polychromatism in adults of *Atelopus carrikeri*: Tadpoles at Gosner stages 39 (A) and 42 (B), froglet (C), amplectant adults (D). Photos by L.A. Rueda-Solano.

Table 1. Measurements (mm) of 12 tadpoles of *Atelopus carrikeri* (lot number: CBUMAG-A 306) + (CBUMAG-A 306-1)*; developmental stages sensu Gosner (1960). Mean and standard deviations are given above ranges. N – sample size; BL – body length; TAL – tail length; TL – total length; IND – internarial distance; IOD – interorbital distance; MTH – maximum tail height; TMH – tail muscle height; TMW – tail muscle width.

Stage	N	BL	TAL	TL	IND	IOD	MTH	TMH	TMW
25	3	9.43±1.18 (7.83–10.64)	15.12±2.34 (11.83–17.03)	24.56±3.50 (19.66–27.67)	1.83±0.09 (1.7–1.91)	2.61±0.42 (2.02–2.94)	3.49±0.24 (3.18–3.76)	2.32±0.35 (1.82–2.61)	1.55±0.27 (1.17–1.74)
26	2	10.72±0.11 (10.61–10.83)	17.13±1.51 (15.62–18.64)	27.85±1.40 (26.45–29.25)	1.85±0.01 (1.84–1.86)	2.94±0.16 (2.78–3.09)	3.75±0.12 (3.63–3.87)	2.70±0.19 (2.51–2.88)	1.69±0.12 (1.56–1.81)
27	2	10.07±0.08 (9.99–10.15)	16.09±0.43 (15.66–16.52)	26.16±0.51 (25.65–25.67)	2.12±0.00 (2.12)	3.03±0.16 (2.87–3.19)	3.82±0.07 (3.74–3.89)	2.77±0.08 (2.69–2.84)	1.92±0.08 (1.84–1.99)
28	3	10.63±0.32 (10.18–10.88)	16.78±0.25 (16.44–16.98)	27.40±0.57 (26.6–27.81)	2.11±0.28 (1.74–2.41)	3.07±0.14 (2.96–3.27)	4.03±0.30 (3.74–4.44)	2.54±0.09 (2.43–2.64)	2.01±0.09 (1.91–2.12)
33	1	11.23	19.91	31.14	2.55	3.41	4.72	3.27	2.19
34	1*	12.62	23.25	35.87	2.48	3.65	5.16	3.49	2.65

the tail muscle (1.2 and 2 mm, respectively); the ventral fin originates in the tail and is narrower than the caudal muscular tissue (1.5 mm and 2 mm, respectively). Point of origin of legs parallel to the vent tube. No obvious dermal folds, neither knees nor heels on legs.

Mouth ventrally situated, surrounded by well-developed labia that form a complete oral disc, 6.3 mm wide; upper lip with bilateral anterior projections that form a conspicuous M-shaped structure. Marginal papillae short and bluntly tipped; anterior row of marginal papillae complete; posterior papillae and submarginal papillae absent. Labial tooth row formula 2/3, rows equal in length. Jaw sheath partially keratinised in its distal section; the upper jaw sheath arc-shaped, lower jaw sheath V-shaped. Large suctorial ventral disc extending from lower labium to about midbody, forming a complete round disc without papillae.

The tadpoles are uniformly black in life dorsally, with some individuals having small golden spots and blotches, and exhibit a reddish ventral region; oral disc and belly of the suctorial disc are translucent. The iris has a dark brown colouration with small golden reticulations. In preservative, the dorsum and sides of the body are uniformly brown; oral disc and belly of the suctorial disc are translucent, the tail musculature is speckled with brown pigment. Dorsal and ventral fins are translucent. Measurements of the larvae are given in Table 1.

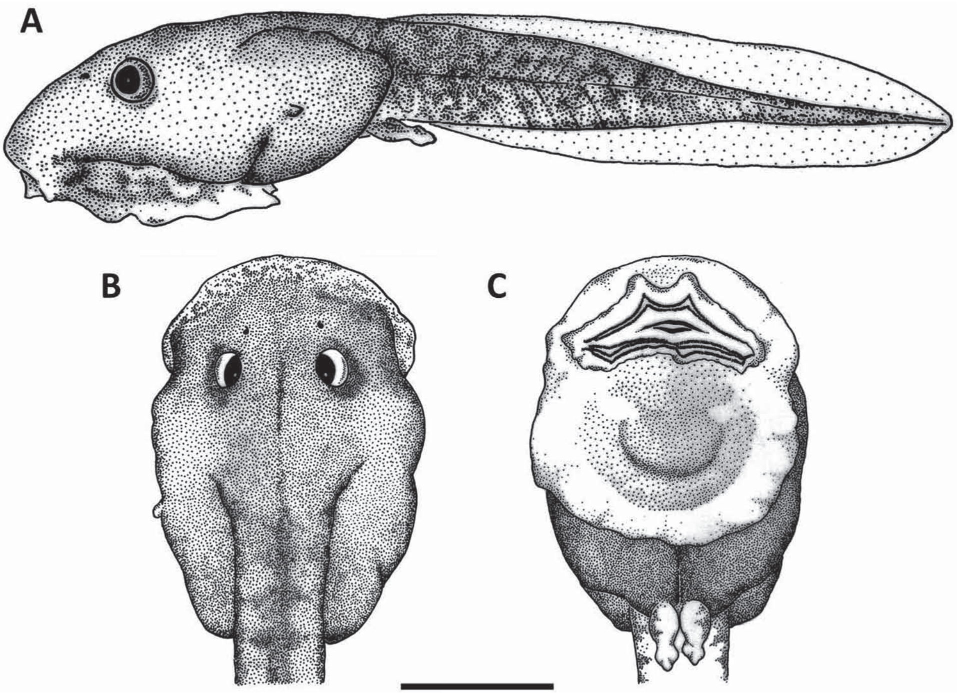

Figure. 3. Tadpole of *Atelopus carrikeri* at Gosner developmental stage 34 (drawings based on specimen CBUMAG-A 306-1) in (A) lateral, (B) dorsal, and (C) ventral views. Scale bar = 5 mm. Drawings by F. Vargas-Salinas.

Table 2. Summary of microhabitat variables for tadpoles of *Atelopus carrikeri* in streams of the Páramo de Cebolleta, Sierra Nevada de Santa Marta, Colombia. Sample size N = 104 in all cases; SD – standard deviation; CV – coefficient of variation.

Variable	Mean	SD	CV	Range
Water temperature (°C)	9.5	1.081	0.113	7.2–12.8
dissolved O_2 (mg/l)	7.32	0.277	0.037	6.47–7.83
Water depth (cm)	42.69	21.186	0.500	11–117.25
Free bottom substrate (cm^2)	122.80	236.387	1.924	0.01–1758.07
Percent of algae cover	29.46	984.795	1.2162	0–100

Microhabitat preferences

The sites occupied by tadpoles of *A. carrikeri* consisted of rocky areas in streams with a fast current on a slope with approximately 20 degrees incline (Fig. 4). The vegetation cover on the banks was minor wherever tadpoles were present, except for bushes of species such as *Libanothamnus glossophyllus* (Astericeae), *Pentacalia* spp., *Diplostephium* spp (Asteraceae), and *Tillandsia* spp. (Bromeliaceae). Our analyses revealed that the mean area size of free bottom substrate, algae cover, and water depth exhibited higher variability than water temperature and dissolved O_2 (Tab. 2). Our logistic regression analysis that included all variables explained 35–48% of the tadpole distribution in the streams monitored (Cox & Snell $R^2 = 0.358$; Nagelkerke $R^2 = 0.48$). However, algae coverage was the only variable that predicted the presence of tadpoles in the streams: a higher percentage of algae coverage suggested a lower probability of tadpoles occurring (N = 104, Wald = 16.04, $p < 0.001$; Fig. 5). The other variables did not allow predicting the presence of tadpoles (water temperature: N = 104, Wald = 1.052, p = 0.305; dissolved O_2: Wald = 0.042, p = 0.837; depth: Wald = 0.199, p = 0.656; mean area size of free bottom substrate: Wald = 0.018, p = 0.846).

Discussion

The tadpole of *A. carrikeri* exhibits the general morphology, colour pattern, and ecology described for other species of the genus that inhabit lowland ecosystems and is especially similar to those of highlands living in exotrophic lotic situations and have a gastromyzophorous morphology (Altig & McDiarmid 1999). For instance, a tooth row formula of 2/3 is predominant in tadpoles of *Atelopus* (Lötters 1996, Lötters 2001, Acosta-Galvis et al. 2006, but see Rodriguez & Duellman [1994] for a tooth formula of 3/3 in *A. spumarius*). We found no changes in the tooth row formula to take place during ontogeny, suggesting this to be a fixed condition during larval development in *A. carrikeri.* On the other hand, there are proportionally greater musculature sizes and longer tails in Andean species than in lowland species of *Atelopus* (Duellman & Lynch 1969, Gascon 1989, Coloma & Lötters 1996, Lötters 2001). Long tail musculature is interpreted as a morphological adaptation to stream aquadynamics because it will reduce drag from the current in fast-flowing streams (Lötters 2001). A large suctorial ventral disc and a depressed/flattened body also play important roles in this regard (Lötters 2001).

Figure 4. Habitat of *Atelopus carrikeri* in the Páramo de Cebolleta, Sierra Nevada de Santa Marta, Colombia. Photos by L.A. Rueda-Solano.

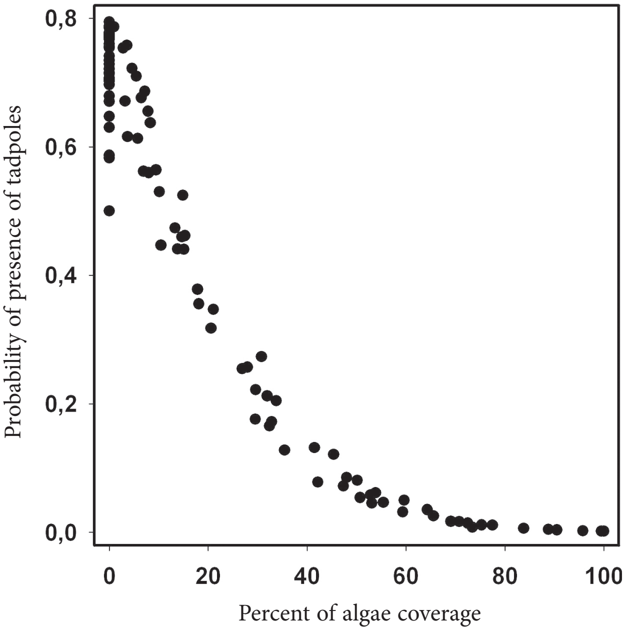

Figure 5. Logistic regression showing the relationship between algae cover and the probability of presence of tadpoles of *Atelopus carrikeri* in streams of the Páramo de Cebolleta, Sierra Nevada de Santa Marta, Colombia.

While *Atelopus* tadpoles exhibit limited interspecific variation in morphology, they greatly differ in colouration. Tadpoles of several *Atelopus* species are dark brown or black overall (e.g., Lötters 1996, Coloma 2002, Acosta et al. 2006). In ectothermic organisms like amphibians, colouration can play an important role in thermoregulation, with dark colours having the potential of increasing the rate of heat absorption and help to reach a higher thermal load than light colours (Iga & Bagnara 1975, Hutchison & Dupré 1992). Hence, it is plausible that the dark brown body colouration observed in tadpoles of *A. carrikeri* is a phenotypic character that brings about a thermal advantage for individuals living in cold streams at higher altitudes (Ruiz-Carranza 1980). This hypothesis may apply to Andean congenerics with dark body colourations such as *A. ignescens, A. peruensis, A. quimbaya, A. muisca, A. nanay, A. nicefori,* and *A. mittermeieri* (Duellman & Lynch 1969, Gray & Canatella 1985, Coloma 2000, 2002, Acosta et al. 2006). Larval colouration has also been suggested as a potentially useful trait for distinguishing *Atelopus* species groups and assessing phylogenetic relationships (Coloma & Lötters 1996, Vélez-Rodríguez & Ruiz-Carranza 1997, Coloma et al. 2000). However, there is little confirmation for this hypothesis in the molecular phylogeny of the genus established by Lötters et al. (2011).

The occurrence of five species of *Atelopus* in the Sierra Nevada de Santa Marta is remarkable not only because of this representing a locally high intrageneric species richness and degree of endemism, but also because some of these species are suggested to occur syntopically, which is uncommon in the genus (Ruiz-Carranza et al. 1994, Lötters 1996). This raises an interesting question regarding niche partitioning and the evolutionary history of these toads. Ruiz-Carranza et al. (1994) suggested a biogeographical relationship between the Sierra Nevada de Santa Marta and the Serranía de Perijá (Cordillera Oriental of Colombia) although this hypothesis has not been tested yet. Tadpole characters and life history may help to answer these questions, but so far the only *Atelopus* larva known from this region is the one described herein.

Algae coverage proved to be the best predictive variable for the presence of tadpoles in streams. An inverse relationship between algae coverage and tadpole presence has also been reported, but not quantified for *A. balios*, a lowland species from Ecuador (Coloma & Lötters 1996). This relationship could be explained because adherence of the suctorial ventral disc is less effective on algae than on a nude rock surface; however, it could just as well be explained as a consequence of the scraping behaviour of tadpoles. Tadpoles of *A. carrikeri* can occur at high densities, which may limit the abundance (standing crop) and composition of algae in some parts of the streams, as has been reported for anurans whose tadpoles develop both in lentic and lotic aquatic habitats (Alford 1999, Ranvestel et al. 2004). An alternative possibility explaining our result is that tadpoles respond negatively to defence mechanisms against herbivory produced by algae, but as far as we know, there is no data to support such a hypothesis. The absence of a relationship between tadpole presence, temperature, and dissolved O_2 could be due to the low microclimatic variability of aquatic microhabitats in highland streams compared with terrestrial microhabitats in Páramo (Navas 1999). Main gravel area and water depth exhibit higher variability than temperature and dissolved O_2 content. Apparently, tadpoles of *A. carrikeri*, like the tadpoles of other species in this genus, can live on rocky, gravel, and sand substrates at different depths (Lötters 1996). The study results described herein contribute a detailed quantification of biotic and abiotic factors of the microhabitat utilised by these highland harlequin frog tadpoles.

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