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Juan Espanha Moreira Dias

POTENTIAL DEFENSIVE ROLE OF *BOKERMANNOHYLA SAXICOLA* AND *SCINAX MACHADOI* (ANURA, HYLIDAE) TADPOLE COLORATION AGAINST VISUALLY ORIENTED PREDATORS

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Dissertação apresentada ao Programa de Pós-graduação em Zoologia de Vertebrados da PUC Minas, como requisito parcial para obtenção do grau de Mestre em Zoologia.

Orientadora: Profa. Dra. Paula Cabral Eterovick

Co-orientador: Prof. Dr. Marcelo Ferreira de Vasconcelos

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ABSTRACT

Tadpoles are vulnerable to a wide range of invertebrate and vertebrate predators. Their vulnerability can be influenced by tadpole behavior, morphology, body size, coloration, habitat preferences and palatability. The ability to evade a predator likely depends on the sensory capabilities of the predator and prey and the complexity of the habitat and availability of cover, as well as the locomotor abilities of the tadpole. This study was conducted in two streams at the Serra do Cipó National Park. We tested experimentally how the coloration of *Bokermannohyla saxicola* and *Scinax machadoi* tadpoles may affect their survival when exposed to visually oriented predators. We tested three aquatic invertebrates (Aeshnidae, *Belostoma* sp. and *Lethocerus* sp.) and birds as tadpole predators. We predicted that predation rates would differ depending on the substrate where the tadpoles positioned themselves (light or dark), hypothesizing that each tadpole would use preferentially a background that conferred crypsis and that predation levels would be lower on such backgrounds compared to others. Although *Bokermannohyla saxicola* tadpoles looked more cryptic on light backgrounds, they used preferentially dark backgrounds, but probably because of background characteristics other than the color itself. Predation levels on light backgrounds did not differ from those on dark backgrounds. *Scinax machadoi* coloration looked disruptive on both light and dark background types, and tadpoles showed no preference for a background type or differences in survival rates between them. Predation rates also did not differ between the two species, indicating that a previous hypothesis of aposematic/mimetic coloration for *S. machadoi* tadpoles did not apply. Our results show that colorations that apper to function to impair visual detection may actually not play this role. Such color patterns may have evolved in another context, in which avoiding visual detection by predators was an important selective pressure. Alternatively, such colorations may be a byproduct of evolution guided by selection of other features or they may play another role that remains to be understood.

KEY WORDS: Predation, *Bokermannohyla saxicola*, *Scinax machadoi,* disruptive coloration, cryptic coloration, defensive coloration, Southeastern Brazil

RESUMO

Os girinos de maneira geral são vulneráveis à uma grande variedade de predadores invertebrados e vertebrados. A vulnerabilidade dos girinos pode ser influenciada pelo seu comportamento, morfologia, tamanho do corpo, coloração, preferências de habitat e palatabilidade. A capacidade de fugir de um predador provavelmente depende das capacidades sensoriais do predador e da presa, da complexidade do habitat, da disponibilidade de abrigos, além das habilidades de locomoção do girino. Este estudo foi realizado em dois riachos do Parque Nacional da Serra do Cipó, no qual foi testado experimentalmente como as colorações dos girinos de *Bokermannohyla saxicola* e *Scinax machadoi* podem afetar sua sobrevivência quando expostos a predadores visualmente orientados. Foram utilizados nos testes como predadores de girinos, três invertebrados aquáticos (Aeshnidae, *Belostoma* sp. e *Lethocerus* sp.) e aves. Nós previmos que as taxas de predação seriam diferentes dependendo do substrato onde os girinos tivessem se posicionado (claro ou escuro), levantando a hipótese de que cada girino usaria preferencialmente o fundo que lhe conferiu camuflagem e que os níveis de predação seriam menores em tais fundos comparados com os outros. Apesar de girinos de *Bokermannohyla saxicola* parecerem mais crípticos em fundos claros, eles usaram preferencialmente os fundos escuros, mas provavelmente por causa de outras características, que não a cor do próprio fundo. Os níveis de predação em fundos claros não diferiram daqueles em fundos escuros. A coloração de *Scinax machadoi* pareceu disruptiva tanto no fundo claro quanto no escuro, e os girinos não mostraram preferência por nenhum tipo de fundo ou diferenças nas taxas de sobrevivência entre eles. As taxas de predação também não diferiram entre as duas espécies, indicando que a hipótese prevista de coloração aposemática/mimética para girinos de *S. machadoi* não se aplicava. Nossos resultados mostram que colorações que parecem funcionar para impedir a detecção visual por predadores podem na verdade, não desempenhar esse papel. Esses padrões de cores podem ter evoluído em outro contexto, em que evitar a detecção visual por predadores não fosse uma pressão seletiva importante. Alternativamente, tais colorações podem ser um subproduto da evolução guiada pela seleção de outras características ou podem apresentar outras funções que ainda permanecem incompreendidas.

PALAVRAS-CHAVE: Predação, *Bokermannohyla saxicola*, *Scinax machadoi,* coloração disruptiva, coloração críptica, coloração defensiva, sudeste do Brasil.

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1 INTRODUCTION

Many studies suggest that predation is the major cause of tadpole mortality (Alford, 1999), occurring from the egg stage (Villa *et al.*, 1982), until the end of metamorphosis (Wassersug & Sperry 1977; Arnold & Wassersug 1978). The presence of predators is a limiting factor in the use of ponds by anurans (Woodward, 1983; Kats *et al*., 1988) and may also affect interspecific interactions in tadpole communities (Morin, 1981), for example, reducing interspecific competition (Herreid & Kinney, 1966; Calef, 1973, Cecil & Just, 1979) or affecting their performances and causing size variation (Peacor *et al*. 2007). The main predators of tadpoles include some invertebrates such as Belostomatidae (e.g., *Lethocerus* sp.) Odonata (e.g., *Anax sp.*) and Coleoptera (e.g., *Dysticus sp.*; Herreid & Kinney 1966; DeBenedicts, 1974; Heyer *et al*., 1975), and vertebrates such as fishes, salamanders, and newts (e.g., *Ambystoma* sp.), water snakes, anurans, and birds (Heyer *et al*., 1975; Cecil & Just, 1979).

Tadpole predators use vision to detect their prey in varied degrees. Belostomatidae often lie motionless at the bottom of a body of water, attached to various objects, where they wait for prey to pass by. They then strike, injecting a powerful digestive saliva with their rostrum, and sucking out the liquefied remains (Rafael *et al.*, 2012; Niéser & Melo, 1997). By hiding among vegetation tadpoles can reduce predation risk by water bugs, showing that vision has an important role in prey detection (see Kopp *et al*., 2006). Odonate larvae are visual and tactile predators, and their binocular vision aids in estimating the distance to an object and its size (Corbet, 1999). Although they are specialized to detect movement, odonate larvae are capable of discriminating the shape (Corbet, 1999) and colour (Pritchard, 1965) of immobile prey. Many species of dragonfly nymphs use visual cues as well as tadpole movement and size rather than chemical cues for detection (Pritchard 1965; Rebora *et al*. 2004). Fish, on the other hand, are more efficient than Odonata in detecting immobile prey visually (Nomura *et al.,* 2011).

Several experiments on predator/prey detection and mortality rates have been done involving tadpoles and predatory arthropods (e.g., Gascon, 1992; Takahara *et al.*, 2012; Nomura *et al*., 2013) or fish (e.g., Nomura *et al.,* 2011). However, reports on tadpole predation by terrestrial vertebrates such as birds are occasional (e.g., Garwood, 2006), with some exceptions (Silva and Giaretta, 2008).

Differences in the composition of anuran assemblages and tadpole predator communities result in a set of tadpole adaptations to avoid predation (Woodward, 1983; Kats *et al.,* 1988). These include unpalatability (Voris & Bacon, 1966; Wassersug, 1971), reduction in activity (Caldwell *et al*., 1980; Woodward, 1983; Eklöv & Werner, 2000), cryptic coloration (Wassersug, 1971), chemical repellents (Voris & Bacon, 1966; Brodie *et al*., 1978), changes in activity period (Taylor, 1983), ability to escape (Werner & McPeek, 1994) and ability to seek refuge (Calef, 1973).

Tadpoles can benefit from their coloration associated to behaviors that reduce the risk of detection or predation. Tadpoles of *Bokermannohyla alvarengai,* for instance, choose backgrounds that confer improved crypsis when threatened (Eterovick *et al.*, 2010). A cryptic animal resembles random samples of the habitat background, hampering predator detection (Endler, 2006). Disruptive camouflage is also considered a form of effective protection from predators and is characterized by disruption of the continuity of a surface by a contour of different shape and/or color (Merilaita & Lind, 2005). Background coloration may affect tadpole activity levels in the presence of predators, with tadpoles being less active on contrasting backgrounds (Nomura *et al*., 2013).

The role of cryptic coloration in increasing survival must be associated with appropriate background choice and actual decrease in predation rates. Tadpoles respond behaviorally to background color (Eterovick *et al.,* 2010; Nomura *et al.*, 2013), and reduce movements when they detect predator presence (Takahara *et al*., 2012), but the outcome of such responses against different types of predators must be evaluated to uncover the real role of defensive coloration on survival (Lima & Dill, 1990; Nomura *et al*., 2011; Takahara *et al*., 2012).

Bokermannohyla saxicola (Bokermman, 1964) occurs mostly at altitudes above 1000m in the Espinhaço Mountain Range, is endemic to Brazil and relatively common in its region of occurrence (IUCN, 2012a). It breeds in temporary or permanent streams with rocky bottom. Males call throughout the year on rocks by the stream bed. The spawn is a circular cluster adhered to submerged rocks. Brownish tadpoles are mainly nocturnal and remain in backwaters or on rocky bottoms with some water flow, usually among aquatic vegetation at depths between 5 and 45 cm. Tadpoles are found throughout the year and larval development lasts at least five months (Eterovick & Sazima, 2004).

Scinax machadoi (Bokermann & Sazima, 1973) belongs to the *Scinax catharinae* species group (*sensu* Faivovich *et al*., 2005). *Scinax machadoi* can be found in the Espinhaço and Mantiqueira Mountain Ranges (IUCN, 2012b). It reproduces in permanent streams with rocky bottom surrounded by riparian forests. Males call during the day and at night, throughout the entire year (Eterovick & Sazima, 2004). Tadpoles are dark with a yellowish patch in front of the eyes and a yellowish spot on the dorsal fin (Bokermann & Sazima, 1973). They are active during the day and at night, remaining on the bottom at a range of depths up to 1.60 m, where their coloration looks disruptive (Eterovick & Sazima, 2004). Horta et al. (2010), on the other hand, suggested *S. machadoi* tadpole's color to be aposematic and possibly mimetic with a syntopic naucorid (*Limnocoris porphyrus* Nieser & Lopez Ruf 2001, Heteroptera, Naucoridae) although they did not test this hypothesis.

Bokermannohyla saxicola and *Scinax machadoi* can be abundant as tadpoles in some permanent streams at the montane meadows of the PN Serra do Cipó, and under such circumstances they are likely to be an abundant source of food for potential predators. In this case, defensive colorations would be an important adaptation to reduce tadpole predation rates. This study aims to investigate in field experiments the potential defensive role of the coloration of tadpoles of these two anuran species at two streams where they are by far the dominant species among local anuran larvae. We aimed to investigate the adaptive value of potentially disruptive/aposematic coloration of *Scinax machadoi* and cryptic coloration of *Bokermannohyla saxicola* tadpoles against potential invertebrate (Odonata and Belostomatidae) and vertebrate (birds) predators.

2 MATERIALS AND METHODS

2.1 Study Site

The Parque Nacional (PN) da Serra do Cipó (Serra do Cipó National Park; 19°12'–19° 20'S, 43°30'–43° 40'W) is located at the southern portion of the Espinhaço mountain range in Minas Gerais state, southeastern Brazil. Its higher portions (1095-1485 m alt.) are covered by montane meadow vegetation. The geological formations are quartizitic, with some calcareous outcrops. The climate shows marked dry (April to September) and wet (October to March) seasons. The park harbors the headwaters of many rivers from distinct watersheds and many streams. A total of 42 species of frogs were recorded at the montane meadows of the Serra do Cipó (Eterovick & Sazima, 2004).

We conducted experiments in two third order (*sensu* Strahler, 1957) streams named Água Escura (19°16'02.84"S and 43°30'56.64"W; WGS84, 1236 m alt.) and Salitreiro (19°16'54.99"S and 43°30'50.10"W; WGS84, 1254 m alt.). Both streams have some small falls and rapids (especially in the rainy season) and many backwaters. Their bottoms are covered by a mosaic of whitish pebbles and yellowish rocks or darker sandy or muddy sediment, sometimes with algae or submerged grasses. Dark debris deposit in rock crevices or deeper sections of the bottom.

2.2 Experimental design – invertebrate predators

Based on field observations we noticed Belostomatidae, Megaloptera, and Odonata to be the biggest invertebrate predators that could eat tadpoles in the studied streams. Thus we used two species of Belostomatidae (*Lethocerus* sp. and *Belostoma* sp.) and one species of Odonata (Aeshnidae) as invertebrate predators. The family Aeshnidae contains the fastest and largest Anisoptera (Rafael *et. al.*, 2012). The genus *Lethocerus* can reach up to 130 mm in lenght and includes voracious ambush predators of crustaceans, fish and amphibians (Rafael *et al.*, 2012; Niéser & Melo, 1997). We chose these species to study because they were the ones that could be found in large enough numbers to run the experiments *in situ*. We also expected them to represent the greatest threat to tadpoles locally, due to their abundance and predatory habits. Besides the chosen predators we recorded four other species of Odonata (two Zygoptera and two Anisoptera) and two of

Megaloptera (*Corydalus* spp.), but in smaller numbers. There are probably some other aquatic invertebrates that may prey upon tadpoles in the streams, although we did not observe predation events. These are Notonectidae, Corixidae, Naucoridae, and spiders (A. L. Melo, pers. comm.; Galdean *et al*. 2000; Galdean *et al*. 2001; Callisto *et al*. 2001).

Experimental enclosures consisted of transparent plastic boxes (29L, 45.7 cm length, 32.6 cm width, 28.0 cm height) partially submerged in the streams. We made small holes around the walls of the boxes to maintain water flow and covered the bottoms of the boxes with natural substrata from the stream bottom, using rocks as light (yellowish) backgrounds and sand/debris (blackish) as dark backgrounds. Treatments consisted of (1) light, (2) dark, and (3) mixed (half light, half dark) backgrounds. All treatments had three tadpoles of each of the two tadpole species (*B. saxicola* and *S. machadoi*) and one predator. Controls were identical except for the fact that no predator was included. Each run of the experiment consisted of 18 boxes: three replicates of each one of the three treatments and each one of the three controls. We performed the experiment with Aeshnidae three times at Água Escura stream (on April, May and June) and one time at Salitreiro stream (on June). We performed the experiment with *Belostoma* sp. three times at Salitreiro stream (on May, July, and August). Combinations of predator type and stream were determined by availability of predators. After the end of each experiment, all living animals were returned to the stream. All experiments were conducted between April and October 2013.

We captured all tadpoles *in situ* throughout a 100 m section of the stream (what took from 3 to 5 hours) and mounted the experiment right after. We used tadpoles between stages 25 and 35 (sensu Gosner, 1960) to avoid possible interference of large hind limbs on tadpole escape performance. We selected the biggest tadpoles of *S. machadoi* and the smallest tadpoles of *B. saxicola* to standardize tadpole size between the two species. This way we intended to minimize the effect of tadpole size as an influencing factor on tadpole detection or selection by the predator. We kept tadpoles in plastic containers until all individuals necessary for the experiment were collected and then they were randomly distributed among controls and treatments. We captured predators to be used in each experiment at the same night and kept them in individual plastic containers until tadpoles were distributed among all boxes, then we introduced predators in treatment boxes. We also selected predators within the narrowest size range possible to minimize potential predator size interference on tadpole predation rates/preferences. We measured all predators with calipers (to the nearest 0.1 mm). We checked all the boxes in 24h intervals (starting the next day) for 10 days or until one species was eliminated from one box, whatever happened first. We considered that elimination of one species would leave no choice of prey to the predator in that box, and thus cause noise in our results. We recorded the number of surviving tadpoles by the end of each trial. In experiments with Odonata, we noticed that several tadpoles were alive but injured, so we also counted the number of intact tadpoles in these trials. In the experiments with *Lethocerus* sp. we made temporal replicates of treatments and controls because there were not enough predators to conduct spatial replicates of treatments. *Lethocerus* sp. were so voracious that each run of the experiment lasted a single day, two days at most (when one species was eliminated from one box) and we performed other two runs alternating predator individuals among background types. Each experiment was considered as three replicate runs of all treatments and controls. We conducted a total of 6 experiments in June and August 2013.

Because natural backgrounds have different textures that may influence protection provided to tadpoles (e.g., tadpoles may be partially hidden under debris but not on rocks) we also conducted experiments on boxes with the bottoms painted in yellow, black and mixed (half yellow, half black) to test the effect of color alone on predation rates upon the two species of tadpoles. Any differences between results with natural and painted backgrounds could be interpreted as effects of properties of natural backgrounds other than color. The boxes were the same, painted outside so that paint chemicals would not interfere on the behavior of experimental species. Experimental design was the same except for the absence of natural substrate inside the boxes and the use of five tadpoles of each species instead of three. We conducted this experiment twice (on July and August) at Água Escura stream with Aeshnidae as predators and once at each stream (on September) with *Belostoma* sp. as predators. We conducted the experiment four times with *Lethocerus* sp. as predator at Salitreiro stream (on September).

We expected tadpoles of *B. saxicola* to have higher predation rates on dark backgrounds, where they were more visible. These tadpoles have a light hue in the studied streams compared to the range of colors observed for the species (P.C. Eterovick, pers. obs.), thus being very cryptic in light backgrounds (Fig. 1. A, C, E, F).

We expected tadpoles of *Scinax machadoi* not to differ among backgrounds considering predation rates if their coloration is disruptive because their light patches match light backgrounds and their dark body parts match dark backgrounds, interrupting body shape contour in both backgrounds (Fig. 1. B, D, E, F). We expected them to be more predated than *B. saxicola* in light backgrounds, because although disruptive, they are noticeable whereas *B. saxicola* can be very hard to spot in such backgrounds. We also expected them to be less predated than *B. saxicola* on dark backgrounds, where *B. saxicola* is more visible. On the other hand, we expected them to be less predated than *B. saxicola* in all backgrounds if their coloration is aposematic.

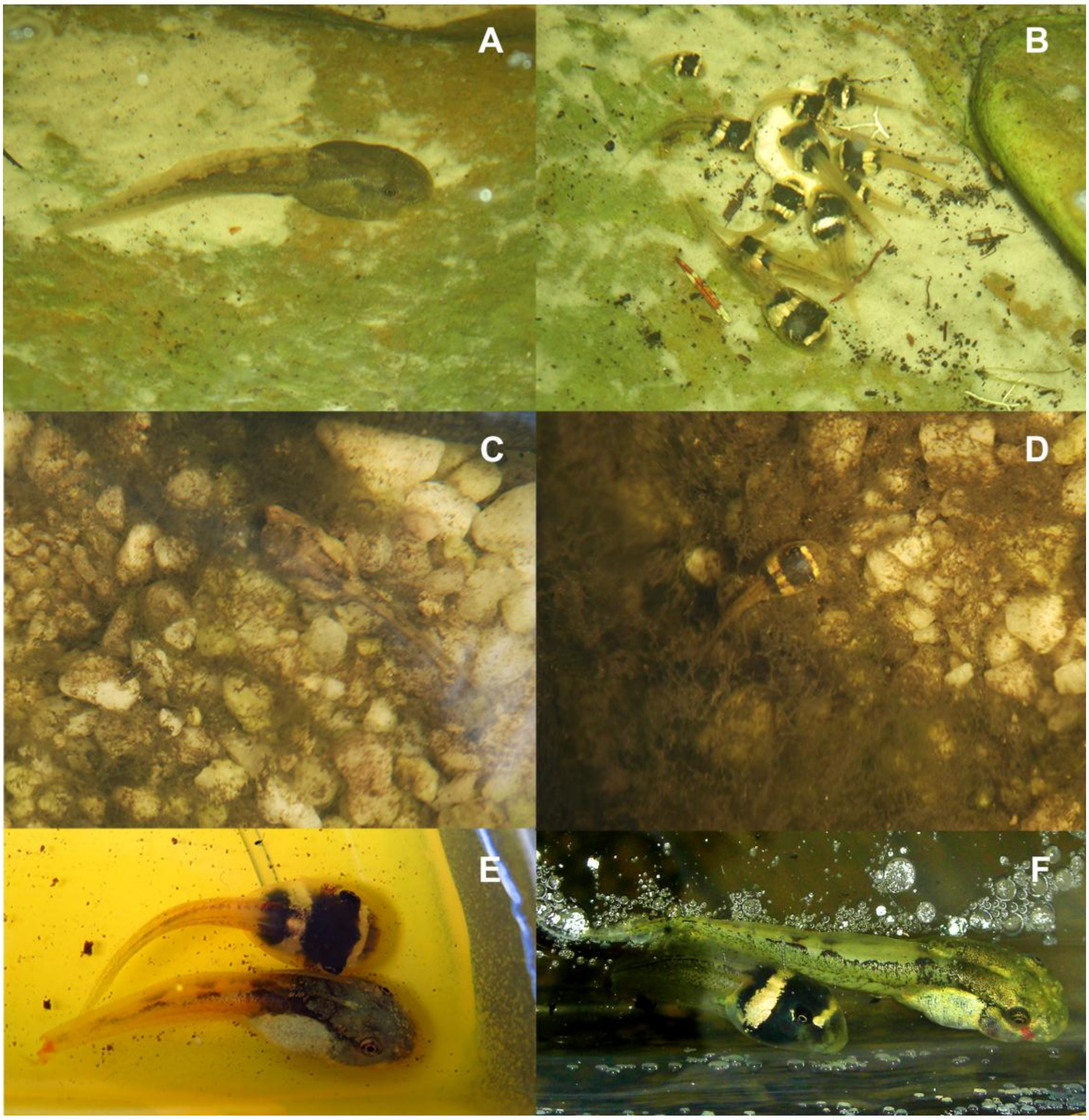

Figure 1. Tadpoles of (A) *Bokermannohyla saxicola* and (B) *Scinax machadoi* on natural light backgrounds at the stream bottom, on the transition of light and dark bottoms in experimental mixed boxes (C, *B. saxicola*; D, *S. machadoi*), and inside trays with (E) and without (F) the yellow cover under the transparent tray (i.e., artificially colored backgrounds).

In order to test for any preference of tadpoles for different backgrounds, we conducted experiments to test for background choice using boxes with mixed backgrounds (exactly as in the mixed background treatment described above) using both natural and painted backgrounds (as described above). We placed five tadpoles of each species in each box and recorded the microhabitat they were on 24h later to test for preferences (considered as a greater number of tadpoles on the preferred background – light or dark). We conducted this experiment with 18 boxes at Água Escura and 12 boxes at Salitreiro streams using natural substrata and 18 boxes at Água Escura and six boxes at Salitreiro streams with painted bottoms. The 12 boxes at Salitreiro with natural substrata had three tadpoles of each species instead of five.

2.3 Experimental design – vertebrate predators

Among vertebrates, birds are the main potential tadpole predators in the studied streams. Thus, we conducted experiments to assess their role on the potential advantages of tadpole defensive colors. First, we used transparent plastic trays (25 x 17 x 5 cm) with a subdivision (in the middle of their longer axis) forming two compartments that we filled with stream water up to about 2 cm. In each compartment we placed one tadpole of each species (*B. saxicola* and *S. machadoi*). Trays were placed on the streams, attached to the closest margin by nylon strings, and left floating for 24h, after what we checked them for predated tadpoles. Because *B. saxicola* tadpoles showed the ability to jump off the trays in some instances, we repeated the experiment with fake tadpoles made of non-toxic clay and painted with non-toxic ink. We tested for effects of dark vs. light backgrounds leaving trays over dark stream bottoms and leaving half (20 trays) with their transparent bottoms and half (20 trays) over a plastic yellow background (made of the tray's yellow plastic cover that we placed under its bottom). We placed trays in groups of four (two with and two without the yellow background). We checked trays every 24 h during two to ten days at each run of the experiment (we planned to check each run of the experiment for 10 days, but some lasted fewer days because of rains that dislodged the trays). Thus, the experiment included 40 models (two per tray) of each tadpole species per run. We conducted this experiment twice at each stream (Água Escura and Salitreiro).

We also conducted visual observations of birds at the stream margins in an attempt to observe events of tadpole predation (totalling about 440 h of observation distributed from 06:00h to 11:00h and from 15:00h to 18:30h). At Água Escura, we mounted mist nets crossing the stream to capture potential species of birds that could be foraging on tadpoles at the stream. Sampling effort consisted of five to seven mistnets mounted for three days at each of three different periods during the rainy season (December 2012, January, and February 2013) and three during the dry season (July, August, and September 2013), totaling a sample effort of 439 h 40 min (216 h 30 min – wet season and 223 h 10 min – dry season). The mist nets (2.5 m height, 9 m length, and 20 mm mesh) were spaced at least 10 m from each other (20 m at most). Nets were opened in the morning and afternoon and checked every 30 min. We weighed captured birds, took measurements and banded them according to CEMAVE specifications (IBAMA, 1994) and then obtained their stomach contents through regurgitation with the use of emetic tartar according to Sabino and Duca (2011). We inspected stomach contents in search for tadpole remains.

Third, we conducted some *ex situ* experiments to test *B. saxicola* and *S. machadoi* tadpole palatability for birds and detectability by birds on light and dark backgrounds. For this purpose, we used birds maintained in the CETAS (Centro de Triagem de Animais Silvestres) aviary in Belo Horizonte city. The center maintains native birds recovered from trafic or captivity for recovery and possibly reintroduction. Birds of several species were kept in a common enclosure: *Turdus leucomelas, Turdus rufiventris, Turdus albicolis, Turdus fumigatus* and *Saltator similis* which are potential tadpole predators and also *Paroaria dominicana* and *Icterus jamacaii*. All the species were represented by two or more individuals in the aviary except for *Turdus leucomelas* and *Icterus jamacaii* with just one individual each. We collected tadpoles in the studied streams and took them to the CETAS (about 2-hour-trip in platic bags with stream water in styrofoam boxes). We first offered tadpoles (15 of each species) in a white tray (40 x 28 x 8 cm) filled with stream water up to 2 cm to the birds in the enclosure to test whether they would be willing to feed on the tadpoles and if the tadpoles would be palatable to them. After 30 min we checked for surviving tadpoles. We then offered tadpoles (17 of each species per tray) in a yellow tray and in a black tray (transparent trays of the same size painted in the outside) to test for any differential predation determined by background color. After 2 h we checked for surviving tadpoles. During an attempt to replicate the experiment with colored trays, the tadpoles accidentally died during transportation. Thus we still conducted the same experiment but with dead tadpoles. We used 9 tadpoles of each species per tray and checked for non-eaten tadpoles after 1 h. We added a wook stick to each experimental tray so that birds could perch on it to reach tadpoles (what they did). We removed the commercial bird food usually offered to the birds at CETAS one hour before starting each experiment.

2.4 Statistical analyses

We used analyses of variance mixed models in the software Systat 12.0 (Wilkinson, 2007) to test for differences between numbers of surviving tadpoles on natural and painted backgrounds separately. We also conducted separate analyses for each predator tested (Aeshnidae, *Belostoma* sp., and *Lethocerus* sp.) using "number of surviving tadpoles" as dependent variable, background color (light, dark, or mixed) and tadpole species (*B. saxicola* or *S. machadoi*) as fixed factors and experiment (when experiments were run two or more times) and stream (Água Escura or Salitreiro, when experiments were conducted in both) as random variables. We conducted the same analyses for Odonata considering "undamaged tadpoles" as the dependent variable, because some surviving tadpoles were injured when exposed to odonate predators. Because we recorded a single dead tadpole in a control box during the whole study, we assumed that mortality recorded in treatments could be considered as the result of predation and thus we did not use data from controls in the analyses because they would inflate the amount of large values for the variable "surviving tadpoles" deviating data from normal distribution. In order to achieve normality of the data, we also summed replicates within experiments for analyses, both spatial ones (for experiments with Aeshnidae and *Belostoma* sp.) and spatial ones (for experiments with *Lethocerus* sp.).

In order to test for background preferences, we conducted analysis of variance mixed models for each tadpole species separately using number of tadpoles as dependent variable, background (light or dark) as a fixed factor and experiment (when experiments were run two or more times) and stream (Água Escura or Salitreiro, when experiments were conducted in both) as random variables. Experiments conducted with natural backgrounds at Água Escura stream had three tadpoles of each species instead of five, so we tested these data separately for each species.

3 RESULTS

On natural backgrounds, odonate predators preyed upon *Bokermannohyla saxicola* and *Scinax machadoi* in the same amounts (MS = 0.167, F = 0.074, df = 19, p = 0.788) irrespective of background type (light, dark, or mixed; MS = 5.063, F = 2.249, df = 19, p = 0.150), stream (MS = 0.364, F = 0.162, df = 19, p = 0.692) or different experiment runs (MS = 1.333, F = 0.592, df = 19, p = 0.451) (Fig. 2A). The same result applied when we considered, instead of surviving tadpoles, just undamaged tadpoles as those escaping predation (for species: MS = 4.167, F = 1.262, df = 19, p = 0.275; for background type: MS = 0.562, F = 0.170, df = 19, p = 0.684; for stream: MS = 12.374, F = 3.749, df = 19, p = 0.068; for experiment run: MS = 0.333, F = 0.101, df = 19, p = 0.754 (Fig. 2B).

On painted backgrounds, at Água Escura stream, odonate predators preyed upon *Bokermannohyla saxicola* and *Scinax machadoi* tadpoles in the same amounts (MS = 0.333, F = 0.158, df = 8, p = 0.701) irrespective of background type (light, dark, or mixed; MS = 1.125, F = 0.533, df = 8, p = 0.486) (Fig. 2C), but predation levels were different between the two experiment runs (MS = 85.333, F = 40.454, df = 8, p < 0.0005) because just three tadpoles were preyed upon in the second run of the experiment (August 2013), contrasting to 35 in the first run (July 2013). Considering undamaged tadpoles as the dependent variable, there was no difference in predation between species (MS = 12.000, F = 1.938, df = 8, p = 0.201) irrespective of background type (MS = 3.125, F = 0.505, df = 8, p = 0.498) and experiment run (MS = 8.333, F = 1.346, df = 8, p = 0.279).

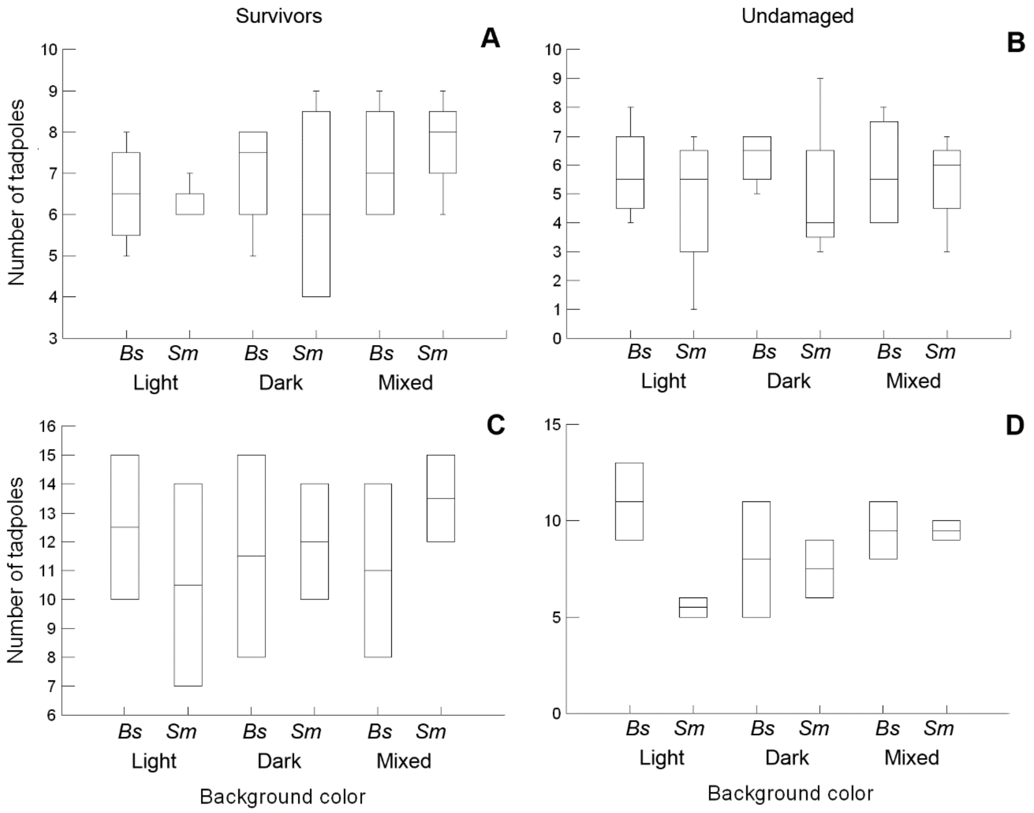

Figure 2. Number of surviving (A, C) and undamaged (B, D) tadpoles of *Bokermannohyla saxicola* (*Bs*) and *Scinax machadoi* (*Sm*) exposed to odonate predators on natural stream bottom backgrounds at both streams (A, B) and on painted backgrounds (C, D) at Água Escura stream. Light backgrounds correspond to rocks (A, B) or yellow paint (C, D) and dark backgrounds correspond to sediments mixed with debris (A, B) or black paint (C, D).

On natural backgrounds, at Salitreiro stream, *Belostoma* sp. preyed upon *Bokermannohyla saxicola* and *Scinax machadoi* tadpoles in the same amounts (MS = 0.500, F = 0.524, df = 14, p = 0.481) irrespective of background type (MS = 2.083, F = 2.183, df = 14, p = 0.162) and experiment run (MS = 3.000, F = 3.143, df = 14, p = 0.098) (Fig. 3A). On painted backgrounds predation rates did not depend on species (MS = 0.750, F = 4.235, df = 8, p = 0.074) or background type (MS = 0.000, F = 0.000, p = 1.000) (Fig. 3C), but differed between streams (MS = 4.083, F = 23.059, df = 8, p = 0.001). A single predation event occurred at Água Escura stream (on September) against eight predation events at Salitreiro stream (also on September).

On natural backgrounds, at Salitreiro stream, *Lethocerus* sp. preyed upon *Bokermannohyla saxicola* and *Scinax machadoi* tadpoles in the same amounts (MS = 0.214, F = 0.211, df = 38, p = 0.648) irrespective of experiment run (MS = 2.498, F

= 2.465, df = 38, p = 0.125), but predation rates differed among background types (MS = 12.893, F = 12.721, df = 38, p = 0.001). These predators ate more tadpoles on light backgrounds, followed by dark and then mixed ones (Fig. 3B). On painted backgrounds, predation rates did not differ among colors (MS = 8.000, F = 0.913, df = 8, p = 0.367) and still did not differ between tadpole species (MS = 0.083, F = 0.010, df = 8, p = 0.925) or among experiment runs (MS = 24.083, F = 2.749, df = 8, p = 0.136) (Fig. 3D).

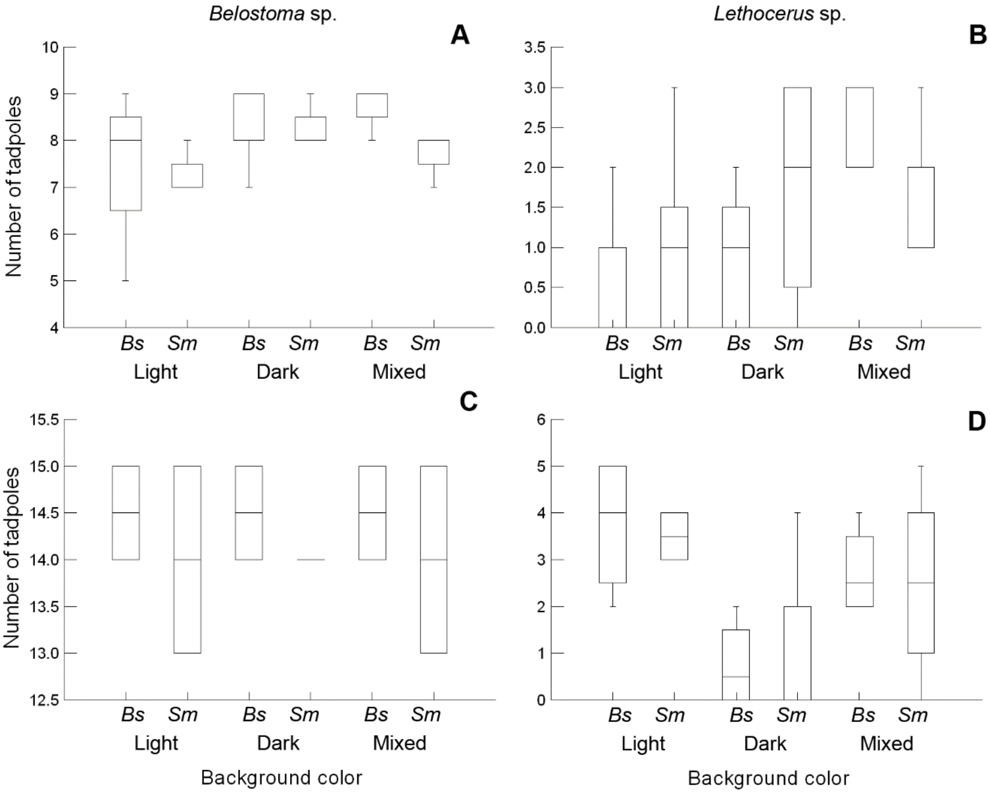

Figure 3. Number of surviving tadpoles of *Bokermannohyla saxicola* (*Bs*) and *Scinax machadoi* (*Sm*) exposed to *Belostoma* sp. (A, C) and *Lethocerus* sp. (B, D) on natural stream bottom backgrounds (A, B) and painted backgrounds (C, D). Experiments were conducted at Salitreiro stream (A-D) and also at Água Escura stream for predation by *Belostoma* sp. on painted backgrounds (C). Light backgrounds correspond to rocks (A, B) or yellow paint (C, D) and dark backgrounds correspond to sediments mixed with debris (A, B) or black paint (C, D).

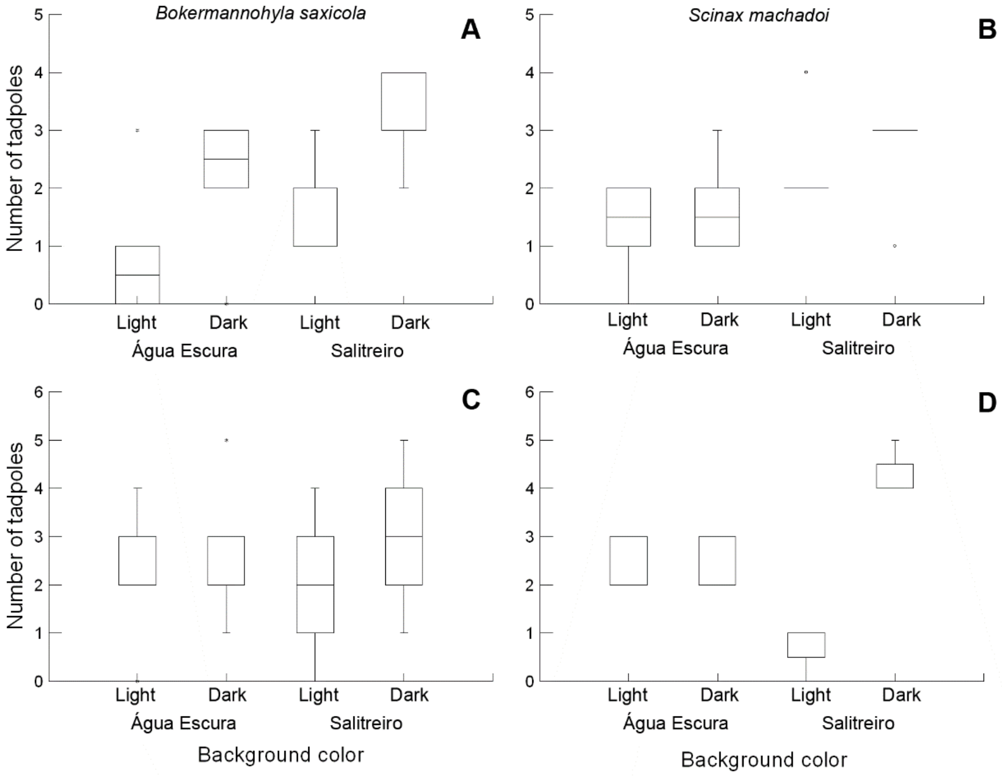

Figure 4. Number of tadpoles of *Bokermannohyla saxicola* and *Scinax machadoi* on light and dark backgrounds from stream bottom (A, B) or painted surfaces (C, D) at Água Escura and Salitreiro streams. Light backgrounds correspond to rocks (A, B) or yellow paint (C, D) and dark backgrounds correspond to sediments mixed with debris (A, B) or black paint (C, D). All experiments started with 5 tadpoles of each species, except for the ones at Água Escura stream natural backgrounds (A, B, first two box plots) that started with 3 tadpoles of each species.

When tested for background preference on natural substrates, *Bokermannohyla saxicola* preferred dark backgrounds at Água Escura (MS = 8.167, F = 24.500, df = 4, p = 0.008) and also at Salitreiro (MS = 9.389, F = 13.520, df = 16, p = 0.002; Fig. 4A) streams. *Scinax machadoi* did not show preference for any background color neither at Água Escura (MS = 0.167, F = 0.500, df = 4, p = 0.519) nor at Salitreiro (MS = 0.056, F = 0.071, df = 16, p = 0.793, Fig. 4B) streams.

On painted backgrounds, *B. saxicola* did not show preference for light or dark backgrounds (MS = 1.500, F = 0.571, df = 20, p = 0.459) irrespective of experiment run (MS = 0.000, F = 0.000, df = 20, p = 1.000) or stream (MS = 0.000, F = 0.000, df = 20, p = 1.000; Fig. 4C). More individuals of *Scinax machadoi* used light backgrounds although the difference was not significant (MS = 4.167, F = 3.817, df = 20, p = 0.065).

In the experiments with clay tadpoles we just recorded one predation attempt on a *Scinax machadoi* model that was partially cut at the base of the tail. The damage could have been done by a beak. We observed no other models to be missing or damaged. Even while we were trying to run these experiments with live tadpoles, we observed no predation after some days until we noticed one tadpole to jump off the tray and thus discarded the data.

We captured 43 birds in mist nets representing 16 species, 9 families and 3 orders. From these, 16 represented potential tadpole predators: eight *Hydropsalis torquata* (Caprimulgidae), six *Turdus leucomelas* (Turdidae), and two *Lochmias nematura* (Furnariidae). We banded them and obtained their stomach contents. We also obtained one additional stomach content from a recaptured *Lochmias nematura*. The only two other birds that might occasionally eat tadpoles were *Saltator similis* and *Fluvicola nengeta*. No remains of tadpoles or adult frogs could be identified in the stomachs. From these potential tadpole predators, we observed one species to forage frequently in both studied streams, the Sharp-tailed streamcreeper (*Lochimias nematura*). However we did not observe any event of tadpole predation by these birds.

In the experiment conducted at CETAS, birds (including individuals from all the species in the enclosure but *Paroaria dominicana* and *Icterus jamacaii*) ate 10 tadpoles of *S. machadoi* and 11 tadpoles of *B. saxicola* from the white tray. In the experiment with colored trays, they ate 11 tadpoles from the yellow tray (6 *S. machadoi* and 5 *B. saxicola*) and 28 tadpoles from the black tray (16 *S. machadoi* and 12 *B. saxicola*). In the other run of the experiment with dead tadpoles they ate 15 tadpoles from each tray (7 *S. machadoi* and 8 *B. saxicola* from the yellow tray and 8 *S. machadoi* and 7 *B. saxicola* from the black tray).

4 DISCUSSION

We hypothesized that the colors of *Bokermannohyla saxicola* and *Scinax machadoi* might have an adaptive value by increasing their chances of survival through hampered tadpole detection by visual predators at their natural habitats. However, we found no difference in tadpoles mortality that could be attributed to predation between background types (light or dark). A similar result was found by Nomura et al. (2013) for tadpoles of *Rhinella schneideri* (Bufonidae) and *Euphemphix nattereri* (Leiuperidae), although this author observed tadpole behavior (movement frequency) to change between light and dark backgrounds. In our study, we did not quantify tadpole movement, however, we tested for background choice. We noticed tadpoles of *B. saxicola* to prefer dark natural backgrounds, but this preference may be related to background properties other than color, because tadpoles did not maintain this preference on artificially colored (painted) backgrounds. *Scinax machadoi* showed no significant background preference either on natural or artificial backgrounds.

We observed no differential predation between tadpole species or between background types and these results were the same for all predator species tested, except for *Lethocerus* sp. that preyed upon more tadpoles on light as opposed to dark natural backgrounds. This may be an effect of the abount of fine sediment (decomposing debris) on dark backgrounds that could confer some protection to tadpoles (although the amount of such sediment in the experimental boxes was not enough to cover the tadpoles). The type of substrate, the presence and distribution of the vegetation, are important factors that have been reported to affect the spatial and temporal distribution of tadpoles among microhabitats (McDiarmid & Altig, 1999; Dickman & Durtsche, 2003).

The runs of the experiment with Aeshnidae on painted backgrounds had different results what is likely to be related to the development of naiads. On August, the naiads were at the end of their aquatic stage and not willing to eat. They just preyed upon 3 tadpoles during this whole trial (10 days) against 35 in the previous trial (5 days on July). Another difference in predation rates was observed among streams for *Belostoma* sp. what can also be explained by the predators willing to eat. In September, when we tested for predation on painted backgrounds, predation rates were low maybe because the bugs were breeding (we found many females with eggs although we did not use them in experiments). A single predation event at Salitreiro stream (against eight at Água Escura) was probably the cause of the difference.

We tested all the potential visual tadpole predators that occur in large enough amounts in the studied streams to cause an important selective pressure. Notwithstanding, there seemed to be no present adaptive value in tadpole coloration associated to background choice to deter predation.

However, it is known that odonates are sensitive to color when foraging. Caldwell (1982) investigated the effect of tail coloration on tadpole predation by odonate naiads (*Anax junius*), and the individuals with dark tails were more common than the ones with light tails when odonate naiads were the dominant predators. Odonates would then direct their attack to the contrasting black tail, giving the tadpole a chance to escape with its body intact. We also observed many tadpoles with damaged tails in the experiments with Aeshnidae. The hypothesis that tadpole tails may be lost to predators with little loss in fitness was supported by an experiment conducted by Wilbur & Semlitsch (1990). Figiel & Semlitsch (1991) demonstrated that tail damage needed to be severe (75% lost) to result in death due to predation by dragonfly naiads (*Tramea lacerta*) on *H. chrysolescelis* larvae. One could argue that the contrasting colors of *Scinax machadoi* tadpoles could function to direct odonate attacks to specific parts of the body. However, we noticed no difference between species regarding number of surviving or undamaged tadpoles, showing this is not the case.

It is also possible that other tadpole features could affect tadpole performance and complement the efficiency of color in deterring predation, resulting in similar performances between *B. saxicola* and *S. machadoi*. For instance, there is a common link between morphology and burst speed in tadpoles so that a deep tail and relatively small body increase burst speed (Dayton *et al.* 2005). *Bokermannohyla saxicola* has a strong muscular tail and actually escapes faster than *S. machadoi* when disturbed (PCE, pers. obs.). Nomura *et al*. (2011) suggests that the antipredator traits of tadpoles can interact with each other, with cryptic tadpoles showing lesser mortality when co-occurring with unpalatable tadpoles and odonate predators. However this is not the case in the present study. Although it has been hypothesized that *S. machadoi* tadpoles might be aposematic (Horta et al., 2010), they are actually palatable to all predators tested (Odonata, Belostomatidae, and birds).

Tadpoles have evolved multiple complex anti-predator defenses, many of which are inducible, such as behavioral, morphological and life-historical responses (Werner & Anholt 1993, Smith and Van Buskirk 1995). There are other factors that could have influenced our results such as the mechanisms by which prey use chemical and visual cues to avoid predation (Takahara, 2012). For instance, tadpoles could be decreasing activity levels to compensate higher visual exposure on contrasting backgrounds (see Nomura et al., 2013).

Although we failed to observe tadpole predation by birds in the studied streams, the experiment conducted at CETAS proved both *B. saxicola* and *S. machadoi* to be palatable to several species of birds that would be willing to feed on tadpoles. Although bird diets are important components of bird ecology, related knowledge is still incipient for the rich Brazilian avifauna (Sabino & Duca, 2011), so reports on tadpole ingestion are mostly anedoctal. Silva and Giaretta (2008) conducted experiments in enclosures with exposed and sheltered (enclosures with debris) tadpoles and noticed that no tadpole was preyed upon by birds (*Turdus amaurochalinus* Cabanis, 1851, Passeriformes) in enclosures with debris, unlike exposed tadpoles. For tadpoles that spend most of the day exposed, defensive coloration may offer alternative protection. According to Bertoluci (2002) *Hyla hylax* tadpoles may rely on their disruptive coloration for protection against visually oriented predators such as birds.

Lopes *et al*. (2005) investigated if passerine birds act as important predators of small vertebrates within the Neotropics by surveying published studies on bird diets, and information on labels of museum specimens, compiling data on the contents of 5,221 stomachs. Eighteen samples (0.3%) presented evidence of predation on vertebrates. Their data suggest that vertebrate predation by passerines is relatively uncommon in the Neotropics and not characteristic of any family. On the other hand, although rare, the ability to prey on vertebrates seems to be widely distributed among Neotropical passerines, which may respond opportunistically to the stimulus of a potential food item.

Based on our data, bird predation upon tadpoles seems to be occasional if it happens in the studied streams. Although we observed the Sharp-tailed streamcreeper (*Lochmias nematura*) foraging in shallow water, we noticed no tadpole capture and found no tadpoles in three stomach contents analyzed for this species. Sharp-tailed streamcreeper is one of the few Brazilian birds that live constantly on the edge of the water. It inhabits the banks of streams with dense vegetation, where it jumps on the soil or on stones, going even in shallow water hunting for insects and larvae. Sometimes they turn fallen leaves and inspect mud in search for prey (Sick, 1997). Piato *et al*. (2012) found Sharp-tailed streamcreeper diet to be mostly (94.8%) composed of invertebrates.

Studies on bird species richness at the Serra do Cipó National Park conducted between 1998 and 2002 recorded 226 species (Rodrigues *et al.* 2005). Most recent studies in areas close to our study site recorded 224 species of birds (Carrara & Faria, 2012) and 151 species (Rodrigues *et al*. 2011). However, the number of species that use streamside habitats and may potentially prey upon tadpoles seems to be much smaller. All the members of the family Turdidae are probably capable to do it (as proved in the experiment at CETAS) as well as members of Tyranidae and Emberezidae, although that would likely be much rarer.

In conclusion, the colors of *B. saxicola* and *S. machadoi* tadpoles do not seem to improve survivorship on backgrounds that increase their cryptic or disruptive potential. Invertebrate predators that are likely to offer more pressure in the studied streams ate both tadpole species in equally large amounts irrespective of background color. Besides, tadpoles showed no background preference that could be attributable to an attempt to improve crypsis or disruptive potential. Birds seem to be occasional tadpole predators at the study site, and even if they do prey upon tadpoles, *ex situ* experiments indicated that they would also prey indiscriminatedly upon both *B. saxicola* and *S. machadoi* on both light and dark backgrounds. If *B. saxicola* and *S. machadoi* tadpole coloration has any adaptive value in the studied streams, it remains to be unvealed. Otherwise, tadpole color may have resulted from past selective pressures and could have evolved in a different context in which avoiding visual detection by predators was an important selective pressure. It is also possible that current tadpole color is plesiomorphic and was not directly selected for. They may be a byproduct of evolution guided by selection of other features. Studies like the present one are important to show that not everything that looks adaptive actually is. The expected outcomes of a potentially adaptive trait must be tested before it is considered as an adaptation to a given function. Our results showed that colorations that apper to function to impair visual detection may actually not play this role, at least in the present context.

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