

Morphological and Developmental Responses of Anuran Larvae (*Physalaemus albonotatus*) to Chemical Cues from the Predators *Moenkhausia dichoroura* (Characiformes: Characidae) and *Belostoma elongatum* (Hemiptera: Belostomatidae)

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Valeria I. Gómez and Arturo I. Kehr (2011) Morphological and developmental responses of anuran larvae (*Physalaemus albonotatus*) to chemical cues from the predators *Moenkhausia dichoroura* (Characiformes: Characidae) and *Belostoma elongatum* (Hemiptera: Belostomatidae). *Zoological Studies* 50(2): 203-210. Animals constantly face various predators in diverse environments. The phenotypic changes induced in prey by different predators may differ quantitatively but not qualitatively, possibly because similar defense strategies are effective against different predators. Also, species inhabiting more-permanent habitats tend to exhibit defense strategies that enable them to coexist with potential predators. We examined phenotypic plasticity responses to different predators. We tested differences in the morphology and growth rates of mewing frog *Physalaemus albonotatus* tadpoles raised in the presence of chemical cues from water-bug (*Belostoma elongatum*) and fish (*Moenkhausia dichoroura*) in order to determine if this species has generalized or specialized responses to different predators. The experiment was performed under microcosm conditions, and the experimental design consisted of 3 treatments: chemical cues from fish and from water-bug, and a control group. Each container held a single larva in order to obtain independent data for different variables. Each treatment was replicated 30 times, with 90 total experimental units. The main findings were as follows: 1) tadpole morphology was significantly affected by the presence of predator cues; 2) tadpoles reared with fish cues were significantly larger than those subjected to the other 2 treatments (water-bug cues and the control), while those reared with water-bug cues were also larger than the control; and 3) tadpoles exposed to chemical cues of predators exhibited accelerated growth rates and development stages. Our results suggest that the presence of predaceous fish and water-bug has a major effect on morphology, growth rate, and development of *P. albonotatus* tadpoles. Morphological variables, growth rates, and developmental stages followed the same pattern, and all of these variables showed increases in tadpoles exposed to chemical cues of predators, possibly because *P. albonotatus* larvae develop in temporary and semi-permanent ponds and are able to exploit different habitats, and therefore their responses to chemical cues from different predators are similar.
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Most natural communities are both spatially and temporally heterogeneous, and include multiple predators feeding on multiple prey species (McCoy and Bolker 2008). Under such circumstances, the ability of an organism to undergo phenotypic changes in response to environmental conditions

can be critical for its survival (Scheiner 1993, Via et al. 1995). In nature, prey species face different predators in different environments. These different predators may induce phenotypic changes in their prey that differ quantitatively but not qualitatively (Relyea 2000), possibly because

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similar defense strategies are effective against different predators. The degree to which tadpoles develop any such defenses is related to habitat-induced requirements as opposed to specific predatory threats (Relyea 2001).

Also, in tadpoles, the growth rate is usually considered to be a result of a balance between selection for faster growth that will decrease the high mortality risk (from predators and desiccation), and selection for slower growth, which demands less energy per unit time and consequently allows for a larger ultimate size (Kehr 1998). Prey species that do not normally coexist with a given predator often do not have effective antipredatory responses against it (Relyea 2001). Several studies that tested for induction of different larval phenotypes by different predators found that the induced phenotypes were similar or differed only quantitatively between predators (Relyea 2000, Van Buskirk 2001).

At the population level, predation assemblages may vary from insect dominated to fish dominated along a gradient of water period duration (Wellborn et al. 1996). In short-lived aquatic habitats, predators are relatively uncommon (Babbitt et al. 2003). Such environments are occupied by invertebrates like coleopterans, hemipterans, and odonates. Species inhabiting ephemeral sites have little time available for growth and development; thus, tadpoles that occur in temporary wetlands tend to be relatively active, constantly foraging, rapidly growing, and trying to reach metamorphosis before the water disappears (Woodward 1983, Wellborn et al. 1996).

In contrast, anuran tadpoles from wetlands with long hydroperiods have slower growth rates and tend to be less active than those in temporary wetlands (Gunzburger and Travis 2004). Species that inhabit more-permanent habitats tend to have defense strategies that enable them to coexist with potential predators (Woodward 1983).

Predator-specific phenotypes are more likely to occur when predators occupy non-overlapping foraging niches or have qualitatively different foraging styles (e.g., sit and wait vs. active foraging), and are less likely to occur when their existence increases prey vulnerability to other predators (Matsuda et al. 1993 1994, Sih et al. 1998). In contrast, in more-ephemeral environments, the generalized defense strategies of prey species have equivocal impacts on inter and intra-specific interactions between predators and the short-term dynamics of prey are expected

to become stable by reducing the initial slope of their functional responses to different predators (Matsuda et al. 1993 1994).

Numerous studies examined the effects of selection on tadpole phenotypes in the presence of predators (McCollum and Van Buskirk 1996, Van Buskirk et al. 1997). McCoy and Bolker (2008) showed that the squirrel tree frog (*Hyla squirella*) exhibits generalized adaptive responses when faced with different predators; in contrast Benard (2006) found that Pacific tree frog (*Pseudacris regilla*) tadpoles exposed to chemical cues from predaceous diving beetles and bluegill sunfish (2 predators that do not typically co-occur) expressed qualitatively different phenotypes; and Teplitsky et al. (2004) showed that tadpoles of *Rana dalmatina* and *R. ridibunda* simultaneously exposed to chemical cues from different predators, expressed phenotypes similar to those expressed only for the predator that inflicted the highest mortality rates in foraging trials.

In this paper, we examined the phenotypic plasticity of the response of mewing frog *Physalaemus albonotatus* tadpoles to different predators. We tested for differences in morphology, growth rates, and development stages of tadpoles raised in the presence of chemical cues from predaceous water-bug (*Belostoma elongatum*) and characin fish (*Moenkhausia dichroua*). Our main goal was to establish if this anuran species displays generalized or specialized responses when raised in the presence of predators from different environments.

MATERIALS AND METHODS

The mewing frog is a geographically widespread anuran found in Brazil, Paraguay, Bolivia, and Argentina (Frost 2010). The species breeds from Sept. to Mar. in ephemeral and semi-permanent ponds, and may coexist with fish although it is more abundant in fishless habitats.

The tadpoles used in this work were obtained from a single *P. albonotatus* foam nest. Foam nests of this species are hemispherical and about 40-60 mm in diameter. Each nest has 240-850 eggs (Schaefer 2007). The foam nest was collected on 14 Jan. 2009 from an artificial semi-permanent pond (4 × 4 × 0.5 m) located on the grounds (with a total surface of 6 ha) of the Centro de Ecología Aplicada del Litoral, 10 km from Corrientes City (27°30'S, 58°45'W) and was transported to the laboratory for hatching. In the

laboratory, the foam nest was placed in a shallow plastic wading pool (33 × 23 × 7.5 cm) filled with well water to 6 cm deep. Two days after hatching, the larvae were randomly assigned to the various treatments. Water-bug were collected at different sites located in the vicinity of Corrientes City (semi-permanent ponds, pools, ditches, etc). Fish were collected using dip nets, aquatic funnel traps, and sieve nets, from a permanent pond located 2 km away from the pond where the *P. albonotatus* foam nest was collected.

The 2 predator species were kept in separate containers. Ten fish (3.5 cm in standard length) were placed in a plastic container (18.5 cm in diameter × 17 cm high) with 3 L of well water in order to obtain chemical cues from them. For the same purpose, 4 water-bug were placed in a similar container with 3.5 L of well water.

The captive predators were fed fish food (Shulet brand, Shulet S.A. 108/A/E, Buenos Aires) and tadpoles every 2 d. The tadpoles were fed boiled lettuce ad libitum twice a week. The containers that held the tadpoles and predators were partially cleaned once a week. Tadpoles that died during the 1st 3 d were removed to reduce the chance that the experiments would be influenced by stress induced by these early individual deaths.

Experimental design

The experiment was performed under microcosm conditions. The temperature ranged 26-29°C, and the photoperiod was 13 of light and 11 h of dark. Tests were carried out in plastic containers (8 cm in diameter × 9 cm high) filled with 300 ml of well water. The experimental design consisted of 3 treatments: chemical cues from fish, chemical cues from water-bug, and a control group, with tadpoles randomly assigned to the various treatments.

The experiment began on 16 Jan. (day 0) when tadpoles that had reached developmental stage 26 (Gosner 1960), and finished 25 d. later when the 1st metamorphic individual was observed. Each treatment was replicated 30 times, resulting in 90 total experimental units. Each container held a single larva in order to obtain independent data for different variables.

Using a graded plastic syringe, 3 ml of water was removed from each container with tadpoles, and 3 ml of water with the chemical signals taken from the containers with predators was added to maintain a constant water volume in each container. This procedure was performed 3 times

a week. In the case of the control treatment, the 3 ml of water extracted was replaced with 3 ml of well water from an isolated container with no predators. Fifteen days after the start of the experiment, on 31 Jan., the tadpoles were measured, weighed, and staged following Gosner (1960). In order to quantify morphological phenotypic responses, we photographed all tadpoles from each treatment. Tadpoles were photographed in side view using a glass box with a 1-mm grid, and 5 linear measurements describing morphological traits were taken: body length, body depth, tail fin length, tail fin depth, and tail fin muscle depth.

Statistical analyses

Each dependent variable in each treatment was tested for normality (Shapiro-Wilk test) in order to determine if the data followed a normal distribution before further analyses were conducted.

To compare the tadpole morphology between predator treatments, we performed a principal component analysis (PCA) for each treatment to estimate which variables were more important in relation to the total variance explained by each component. The 2 body dimensions and the 3 tail fin dimensions for every individual were entered into the PCA in order to assess the loading of each variable on the different components and their explained variance. The great proportion of variance explained indicates that all 5 variables were important for each treatment.

Morphological traits were analyzed first through an analysis of covariance (MANCOVA), to eliminate the effect of size in the tadpoles; using the treatment as a factor, weight as a covariable, and the 5 morphological variables as dependent variables. Subsequently, if Wilk's lambda indicated significance, we performed a one-way analysis of variance (ANOVA) for each dependent variable. For significant cases, a posteriori pairwise comparisons were made using Tukey's comparison test. In addition, a multivariate analysis (MANOVA) was used to determine the effect of predator treatments on the growth rate and developmental stages of tadpoles. When these results were significant, an ANOVA was used for each dependent variable; in turn, when the ANOVA results were significant, pairwise differences between means were evaluated by Tukey's test.

All statistical tests were carried out using

SYSTAT 7.0 (SPSS 1997) and XLSTAT 7.5 (Addinsoft 2006). Furthermore, in order to analyze the internal variation of each variable, we calculated the coefficient of variation (CV) of each variable for all treatments. The growth rate of tadpoles for each treatment was calculated by dividing the natural logarithm of the final weight by the natural logarithm of the total experiment duration in days (Kehr 1991).

RESULTS

Morphological plasticity in relation to predator type

The PCA of the 5 morphological variables of *P. albonotatus* tadpoles for each treatment showed that the 5 variables were all important in explaining the variance. The lowest variable score was 0.897 for tail depth in the water-bug treatment. The lowest explained variance also corresponded to the 1st component in the water-bug treatment (85.05%) (Table 1).

The morphology of tadpoles was significantly affected by predator type (MANCOVA Wilk's lambda = 0.238; $F_{10,96} = 10.07$; $p < 0.001$). The ANOVAs indicated significant differences in body and tail lengths of individuals subjected to the 3 treatments. Tadpoles reared in the presence of fish cues always presented higher mean values for each of the 5 variables, while those reared with water-bug cues presented intermediate values for all variables, and those in the control group had the lowest mean values (Fig. 1).

There were significant differences in body depth, tail depth, and tail muscle depth between tadpoles in either predator treatment and tadpoles

in the control group (Table 2).

The CV was calculated for each variable and predator treatment. The greatest variation in the 5 morphological variables was observed in control tadpoles raised without predator cues. The CVs for the variables, tail length and tail muscle depth, were lower for tadpoles reared with water-bug cues (3.3% and 5.3%, respectively, lower variability than the same variables in control tadpoles). Similarly, the CVs for the variables, body length, body depth, and tail depth, were lower in tadpoles reared with fish cues compared to control tadpoles (3.1%, 5.1%, and 2.8%, respectively). Apparently, the presence of water-bug cues had a greater influence on tail length and tail muscle, whereas the presence of fish more strongly influenced those variables related to the overall tadpole body morphology.

Differences in growth rates and developmental stages with respect to predator type

Growth rates and developmental stages of tadpoles were significantly altered by the presence of predator chemical cues (MANOVA Wilk's lambda = 0.585; $F_{4,104} = 7.990$; $p < 0.001$). The subsequent ANOVAs and a posteriori comparisons of means (Tukey's test) showed that tadpoles reared with predator cues had significantly higher growth rates and reached higher developmental stages than those in the control treatment (Fig. 2). There were no significant differences in growth rates or developmental stages between tadpoles reared with water-bug or fish cues, although the differences were significant when these 2 treatments were compared to the control (Table 3).

The CVs for the growth rates of tadpoles reared with water-bug and fish chemical cues

Table 1. Results of a principal component analysis (PCA) of 5 morphological variables of *Physalaemus albonotatus* tadpoles in each treatment. The factor loadings correspond to the 1st component (PC 1). All variables were important (with factor loadings of > 0.880) in this experiment in order to analyze the response of tadpoles to predator chemical cues. All variables were previously standardized

Variables	Factor loadings		
	Water-bug	Fish	Control
Body length	0.972	0.981	0.983
Tail length	0.900	0.979	0.976
Body depth	0.937	0.968	0.959
Tail depth	0.897	0.978	0.978
Muscle depth	0.903	0.978	0.969
Explained variance	85.05%	95.39%	94.66%

were low (9% and 8%, respectively), while it was higher (28%) for control tadpoles. The influence of predator cues was important given the similar growth rate variations observed. All tadpoles reared in the presence of predator cues responded similarly, with drastic reductions in variations in their growth rates.

DISCUSSION

Many factors, including environmental quality, trophic interactions, and density, were suggested as growth regulators of tadpoles (Alford 1999).

Our results suggest that the presence of predaceous fish and water-bug has major impacts on the morphology, growth, and development of tadpoles of *P. albonotatus*. Although predator-specific morphological responses are common

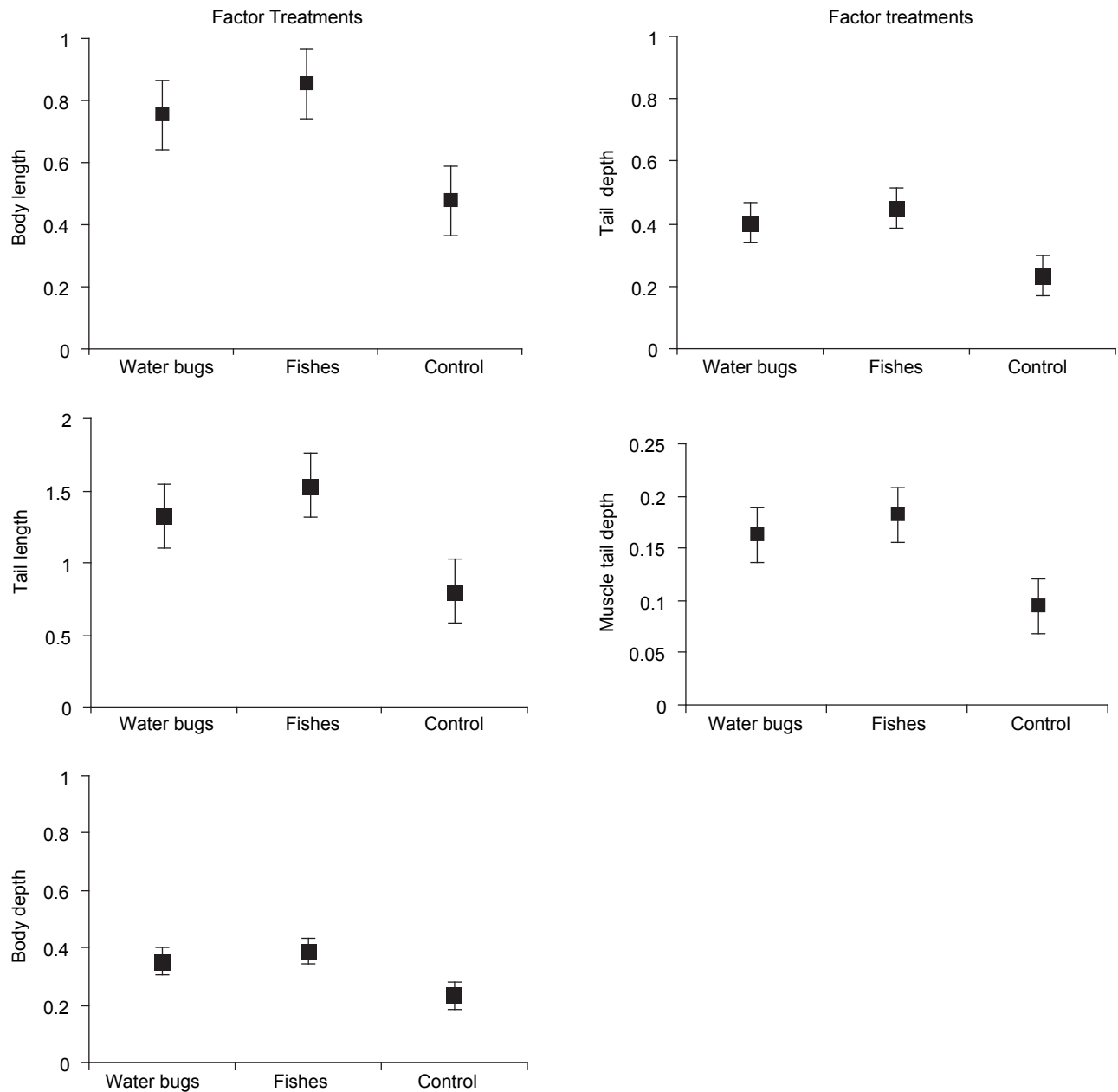


Fig. 1. Effects of the presence of predator chemical cues on morphological variables in *Physalaemus albonotatus* tadpoles. Each point is the arithmetic mean, and the bars indicate the standard error.

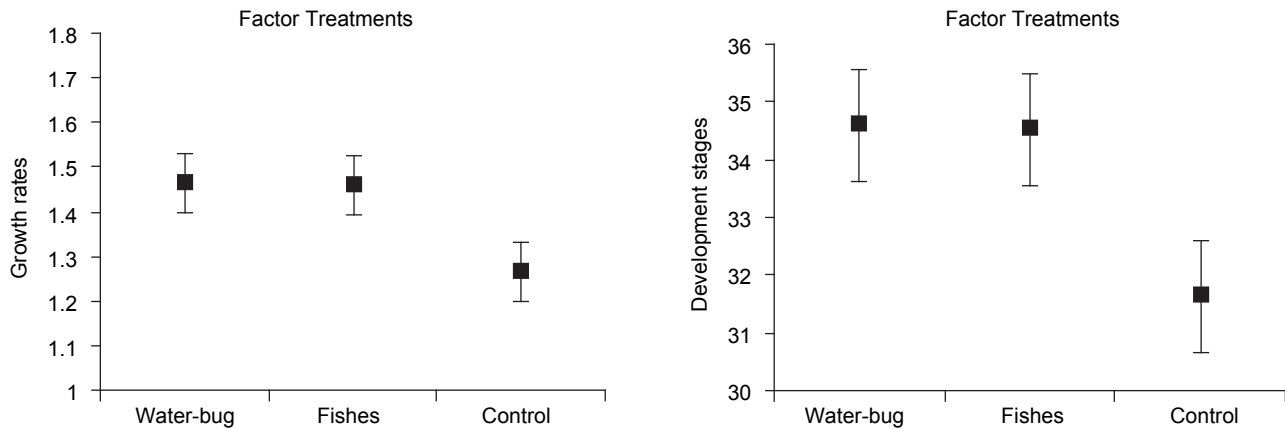


Fig. 2. Effects of the presence of predator chemical cues on morphological variables in *Physalaemus albonotatus* tadpoles. Each point is the arithmetic mean, and the bars indicate the standard error.

Table 2. Results of MANCOVA tests considering treatment (factor), weight (covariable), and its influence on 5 morphological variables of *Physalaemus albonotatus* tadpoles. An ANOVA test for each variable and its posteriori comparison (Tukey’s test) were carried out when the probability was significant. Letters indicate treatments (w, water-bug; f, fish; c, control), and the numbers indicate differences on Tukey’s test (the same number, no significant difference; different numbers, a significant difference). Letters of the treatments are ordinates from the smallest (left position) to largest (right position) arithmetic means recorded. ANOVA probabilities were according to the Bonferroni criteria: $p < 0.01$

Variable	d.f.	F	p
MANCOVA (Wilk’s lambda = 0.238)			
Treatment	10, 96	10.07	< 0.001
ANOVA’s			
Body length c ¹ , w ² , f ³	2, 53	65.4	< 0.0001
Tail length c ¹ , w ² , f ³	2, 53	52.03	< 0.0001
Body depth c ¹ , w ² , f ²	2, 53	48.58	< 0.0001
Tail depth c ¹ , w ² , f ²	2, 53	58.51	< 0.0001
Tail muscle depth c ¹ , w ² , f ²	2, 53	44.59	< 0.0001

Table 3. Results of MANOVA tests considering treatment (factor) and its influences on growth rates and developmental stages of *Physalaemus albonotatus* tadpoles. An ANOVA test for each variable and its posteriori comparison (Tukey’s test) were carried out when the probability was significant. Letters indicate treatments (w, water-bug; f, fish; c, control), and numbers indicate differences in Tukey’s test (the same number, no significant difference; different numbers, a significant difference). Letters of treatments are ordinates from the smallest (left position) to largest (right position) arithmetic mean recorded. ANOVA probabilities were according to the Bonferroni criteria: $p < 0.025$

Variable	d.f.	F	p
MANOVA (Wilk’s lambda = 0.585)			
Treatments	4, 104	7.990	< 0.001
ANOVA’s			
Growth rate c ¹ , f ² , w ²	2, 53	4.26	= 0.019
Development stage c ¹ , f ² , w ²	2, 53	16.13	< 0.0001

among anuran tadpoles (Relyea 2001, Teplitsky et al. 2004, Benard 2006), our results are consistent with those of McCoy and Bolker (2008); in this case, there was no strong evidence for predator-specific morphological responses to the 2 different predators.

Although there were significant differences in some morphological variables between the 2 predator treatments, they were only quantitative, and the morphological variables followed the same pattern. The response of all analyzed variables was a tendency for greater growth, with larger dimensions occurring in tadpoles raised in the presence of fish chemical cues; in contrast, no qualitative differences in structure types were observed.

Furthermore, even though we recorded significant differences in some morphological variables in relation to the presence of predator chemical cues, growth rates and developmental stages of tadpoles subjected to the 2 types of predators did not differ from each other, although a significant difference was observed when these were compared to the control group. This could be due to the fact that *P. albonotatus* typically breeds in temporary ponds but is also able to colonize semi-permanent water bodies, and may therefore occasionally come into contact with both types of predators.

The species of water-bug used for this study is a common inhabitant of fluctuating ponds, while characins commonly occur in temporary and semi-permanent ponds; thus, *Physalaemus* tadpoles are likely to encounter both predators in a given pond. Our finding is consistent with theoretical predictions that generalized adaptive responses are more likely when predators co-occur (McCoy and Bolker 2008) or when a species is able to colonize different kinds of habitats.

The responses of different species of tadpoles will likely differ depending on the habitat preference of each species. In opportunistic species that breed in highly variable and/or unpredictable environments, abiotic factors will be more important for the population dynamics of tadpoles, and predator-induced responses affecting their external and internal plasticity will differ from those of other species, the tadpoles of which inhabit more-predictable environments (Kehr and Gómez 2009).

Plasticity in growth and development rates affects the timing of metamorphosis, and subsequently the age and size at metamorphosis, and the age at 1st reproduction in several taxa,

including crustaceans (Hentschel and Emlet 2000), cladocerans (Hwang et al. 2009), fish (Reznick 1990), and amphibians (Wilbur 1980, Pfennig et al. 1991, Newman 1992, Rudolf and Rodel 2007).

Changes in developmental stages can be strongly correlated with activity levels but not with morphological changes, which suggests that morphological changes have little impact on developmental rates (Richter-Boix et al. 2007), although previous work suggested that morphological defenses in response to predators come at the cost of decreased developmental and growth rates (Van Buskirk 2000, Relyea 2002, Teplitsky et al. 2005). These morphological changes affect growth and development, causing individuals to grow and develop more slowly when exposed to predators than in the absence of predators (Lardner 2000, Relyea 2002, Van Buskirk 2002). However, our results agree with those of Hoverman and Relyea (2008), who found that tadpoles grew more in the presence of predators such as crayfish and fish. This could occur because species that persist in temporary ponds commonly face time constraints that limit their ability to delay growth and development (Altwegg 2002). On the other hand, in predator-prey interactions, predation success greatly depends on the balance between the gape size of the predator and the body size of the prey (Kishida et al. 2006). In any case, more studies should concentrate on quantifying changes in phenotypic traits in response to predators and on understanding how those trait changes affect survival across density and water level fluctuations (McCoy and Bolker 2008).

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