

# The effect of chemical signal of predatory fish and water bug on the morphology and development of *Elachistocleis bicolor* tadpoles (Anura: Microhylidae)

Valeria I. GÓMEZ & Arturo I. KEHR

Centro de Ecología Aplicada del Litoral (CECOAL-CONICET), Ruta 5, Km 2.5 Corrientes, Argentina C.P. 3400; e-mail: valeria\_vig@yahoo.com.ar

**Abstract:** Changes in environmental conditions can induce organisms to alter their morphology, behavior and life history. Predation is an important factor in many aquatic communities and can strongly select for anti-predator responses. In the present work, we examined the responses in morphology, growth rate and development rate of *Elachistocleis bicolor* tadpoles raised in the presence of chemical cues from two different predators: a water bug (*Belostoma elongatum*) and a fish (*Moenkausia dichroua*). The experiment was performed in microcosm conditions. The experimental design consisted of three treatments: chemical cues from fish, cues from water bugs and a control group. Each treatment was replicated 30 times. Each container held a single larva. The main results were: (1) there were significant differences in body depth between the predator treatments (fish vs. water bug) and between the control group and the water bug treatment, (2) there were significant differences in tail depth between predator treatments (fish vs. water bug) and between the control group and the fish treatment, (3) there were no significant differences in the growth rate and developmental rate among the treatments. Our results suggest that the presence of predaceous fish and water bugs cause different effects on tadpole morphology. In the presence of water bugs, tadpoles decreased body depth, whereas in the presence of fish tadpoles increased tail depth. These responses could be related to the way in which predators capture their prey. Predator chemical cues did not have any detectable effect on the growth rate and development rate of *E. bicolor* tadpoles.

**Key words:** phenotypic plasticity; predators; tadpoles

## Introduction

Theoretical models propose that plasticity evolves when populations face different environments and that there are fitness “trade-offs” between alternative phenotypes, such that there would not be a single phenotype with higher fitness in all environments (Gomulkiewicz & Kirkpatrick 1992; Moran 1992). Predation, which is one of the most important factors that influence the structure of aquatic communities, can select directly for anti-predator defenses.

Prey species frequently demonstrate highly responsive changes in morphology, behavior and life history to modifications in predation risk (Lima & Dill 1990; Schlichting & Pigliucci 1998; Tollrian & Harvell 1999; Laurila et al. 2004).

Several studies have examined how predator species induce morphological responses in their prey (Van Buskirk 2002; Relyea 2003; Kishida et al. 2006) and compared different morphological phenotypes in prey organisms induced by predators with different strategies of attack (Relyea 2001 a-b; Van Buskirk 2001; Benard 2006; Gómez & Kehr 2011).

Previous studies have revealed that tadpoles exhibit a variety of responses when facing different predat-

tors. Relyea (2001a), for example, found that in different tadpole species, prey-specific morphological responses to a given predator are common, and that different species of predators induce different morphological and behavioral responses. Van Buskirk (2001) did not find differences in the morphological response to different species of invertebrate predators, but did find different behavioral responses. This author also showed that *Rana temporaria* (L., 1758) tadpoles develop relatively short bodies and deep tail fins in the presence of different predators. Benard (2006), on the other hand, found qualitative differences between larvae of *Pseudacris regilla* (Baird et Girard, 1852) exposed to bluegill and beetle predators. In a previous experiment, we found quantitative differences between *Physalaemus albonotatus* (Steindachner, 1864) tadpoles exposed to fishes and water bugs (Gómez & Kehr 2011).

Tadpoles that exhibit an induced morphology (e.g., deeper tail, shorter body, longer tail) have an advantage in survival in the presence of a predator (Van Buskirk et al. 1997; Van Buskirk & Relyea 1998). However, this represents a cost when the predator is absent (McCollum & Van Buskirk 1996; Van Buskirk 2000); these costs are usually related to growth rate. Some previous experiments carried out with caged predators re-

vealed that tadpoles exhibit a slower growth and consequently have a smaller size or take a longer time to reach metamorphosis (Wilbur 1997; Kiesecker et al. 2002). However, the majority of previous experiments carried out with caged predators contrast with the prediction proposed by Werner (1986); this works showed that tadpoles exhibit a high growth rate in the presence of predators, and that tadpoles emerge later or at the same time as larvae reared in an environment without predators (Benard 2004; Relyea 2007).

In the present work, we studied anuran tadpoles of *Elachistocleis bicolor* (Guerín-Méneville, 1838) because this species breeds in temporary, semi-permanent and permanent ponds, therefore tadpoles from the same population could coexist with assemblages dominated for insect, fish or both predators.

Our main goals were: (i) to identify morphological responses in tadpoles of *Elachistocleis bicolor* to the presence of different predators: a water bug *Belostoma elongatum* (Montandon, 1908) and a fish *Moenkhausia dichroura* (Kner, 1858), and (ii) to determine the influence of predators on the growth and development of the tadpoles.

## Material and methods

Eggs were obtained from three egg clutches collected on November 11 2009 from an artificial semi-permanent pond ( $4 \times 4 \times 0.5$  m) located in the open lands (total surface = 6 ha) of the Centro de Ecología Aplicada del Litoral, 10 km from Corrientes City ( $27^{\circ}30' S$ ;  $58^{\circ}45' W$ ), Corrientes, Argentina, and carried to the laboratory for hatching. Eggs were placed in a shallow plastic wading pool ( $51 \times 36.5 \times 12$  cm) filled with well water up to 8.5 cm depth. Five days after hatching, the larvae were mixed and randomly assigned to the treatments.

Water bugs were collected at different sites in the vicinity of Corrientes City (semi-permanent ponds, pools, ditches, etc.) and fish were collected using dip nets and aquatic funnel traps, from a permanent pond ( $27^{\circ}28' S$ ;  $58^{\circ}43' W$ ).

The two predator species were kept in separate containers. Ten fish (3.5 cm in standard length) were placed in a plastic container with 3.5 L of well water in order to obtain chemical cues. For the same purpose, four water bugs were placed in a similar container with 3.5 L of well water. The captive predators were fed three times a week; fish were fed fish food (Shulet brand, Shulet S.A. 108/A/E, Buenos Aires), and water bugs were fed tadpoles. We fed the predators in different containers to avoid introducing chemical cues of their food in the containers and not to influence the tadpole responses. The tadpoles were fed boiled lettuce *ad lib.* twice a week. The containers that held the predators were partially cleaned twice a week.

Tadpoles that died during the first three days were removed so that the results of the experiment would not be influenced by individual deaths caused by initial stress. Two tadpoles died and were replaced in the experiment.

### Experimental design

The experiment was performed under microcosm conditions. Temperature ranged between 26 and 29°C and the photoperiod was 13 h of light and 11 h of dark. Tests were carried out in plastic containers (8 cm in diameter  $\times$  9 cm

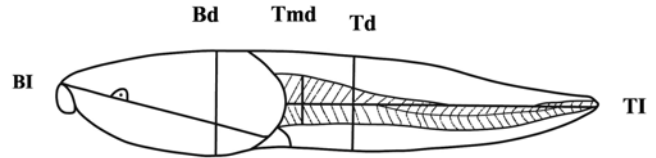


Fig. 1. Hypothetical tadpole illustrated of frog penguin demarcated with the five linear measurements that were used in the morphological analysis: body length (BI), tail length (TI), body depth (Bd), tail depth (Td), tail muscle depth (Tmd).

in height) filled with 300 ml of well water. The experimental design consisted of three treatments: chemical cues from fish, chemical cues from water bugs, and a control group. The containers were arranged in three blocks, each containing 10 replicates of each treatment. The 30 containers in each block were placed randomly.

The experiment began on November 16, 2009 (day 0), when tadpoles that reached developmental stage 26 (Gosner 1960) were randomly assigned to the treatments, and finished 20 days later when tadpoles reached approximately stage 31. Each container held a single larva, and each treatment was replicated 30 times, resulting in a total of 90 experimental units.

We used a graded plastic syringe to remove 3 ml of water from each container with tadpoles, and then added 3 ml of water with the chemical signal taken from the containers with predators, keeping the water volume constant. This procedure was performed three 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 a container without predators. Twenty days after the start of the experiment, on December 2, the tadpoles were measured, weighed and classified following the standard larval stages of 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 five linear measurements describing morphological traits were taken: body length, body depth, tail fin length, maximum tail fin depth and maximum tail muscle depth (Fig. 1).

### Statistical analyses

Each dependent variable in each treatment was tested for normality (Shapiro-Wilk test) to determine whether the data followed a normal distribution before further analyses were carried out. We performed a two-factor MANCOVA using the treatments as factors and the cube root of the body mass as a covariable (Darlington & Smulders 2001) to eliminate the size effect within morphological measurement. The five morphological variables were included in the analysis. Subsequently, if Wilk's lambda was significant, we performed a one-way ANOVA for each dependent variable. For the significant cases, pair-wise comparisons were made using a Tukey comparison test. In addition, a MANOVA was carried out to determine a possible effect of predators on the growth rate and developmental stage of tadpoles. All statistical tests were performed using SYSTAT 7.0 (SPSS 1997) and XLSTAT 7.5 (Addinsoft 2006). The photographs were measured using Image-Pro Plus 4.5.

## Results

The morphology of tadpoles was significantly affected by the presence of predators (MANCOVA Wilk's

Table 1. Results of MANCOVA tests considering the treatment (factor), cube root of body mass (co variable) and its influence on the five morphological variables of *Elachistocleis bicolor* tadpoles.

MANCOVA Wilk's Lambda = 0.57; $F_{10,138} = 4.40$ ; $P < 0.01$				
ANOVA's				
Body length	Tail length	Body depth	Tail depth	Tail muscle depth
$F_{2, 74} = 7.1$	$F_{2, 74} = 5.1$	$F_{2, 74} = 6.5$	$F_{2, 74} = 11.3$	$F_{2, 74} = 5.1$
$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P = 0.01$
Tukey test results				
1-2: $P < 0.01^*$	1-2: $P < 0.01^*$	1-2: $P < 0.01^*$	1-2: $P < 0.01^*$	1-2: $P = 0.01^*$
1-3: $P = 0.13$	1-3: $P = 0.11$	1-3: $P = 0.03^*$	1-3: $P = 0.08$	1-3: $P = 0.07$
2-3: $P = 0.14$	2-3: $P = 0.43$	2-3: $P = 0.58$	2-3: $P = 0.02^*$	2-3: $P = 0.72$

Explanations: An ANOVA test for each variable and its posteriori comparison (Tukey test) was tested when the probability was significant. The numbers indicated the treatments (1 – water bugs; 2 – fish; 3 – control). ANOVA probabilities according to Bonferroni criteria:  $P < 0.01$ . \* Indicates statistical significance at  $P = 0.05$ .

Lambda = 0.57;  $F_{10,138} = 4.40$ ;  $P < 0.01$ ) (Table 1). The ANOVAs indicated significant differences in body length, tail length and tail muscle depth between individuals subjected to the predator treatments. However, no significant differences were found between each predator treatment against the control treatment for these variables (Fig. 2). Tadpoles exposed to water bugs, that had been previously fed tadpoles, had less depth bodies than those exposed to the fish, which had not been “primed” with tadpoles or control treatments (ANOVA  $F_{2,74} = 6.5$ ,  $P < 0.01$ ). Tadpoles exposed to chemicals from the fish had deeper tails than those exposed to the water bugs or control treatment (ANOVA  $F_{2,74} = 11.3$ ,  $P < 0.01$ ).

In each of the variables measured, tadpoles reared in the presence of fish cues had higher mean values, whereas tadpoles reared in the presence of water bug cues had lower mean values. The control group always showed intermediate values.

No significant differences were found in the growth rate and developmental stages among the treatments (MANOVA Wilk's lambda = 0.98;  $F_{4,146} = 0.27$ ;  $P = 0.89$ ). Tadpoles exposed to either predator had the same mean values in growth rate (water bugs  $\bar{X} = 1.11$ , SD = 0.26; fish  $\bar{X} = 1.13$ , SD = 0.24; control  $\bar{X} = 1.16$ , SD = 0.19) and development rate (water bugs  $\bar{X} = 0.057$ , SD = 0.028; fish  $\bar{X} = 0.053$ , SD = 0.023; control  $\bar{X} = 0.058$ , SD = 0.026).

## Discussion

Many anuran species, especially those which inhabit temporary ponds, are highly vulnerable to a wealth of predators (Werner & McPeck 1994; Blaustein et al. 1996). Although many tadpole species live in a wide variety of habitats, they typically breed in temporary, semipermanent or permanent ponds and show plastic responses in tail fin depth and a tendency to decrease their growth rates (Wilbur 1997). Many anuran species have also demonstrated a capacity to detect various predators in the same environment (Hews 1988; Blaustein 1999; Skelly 2001).

According to Wojdak & Trexler (2010), the re-

sponse to predators by prey should be flexible, to avoid needless reduction in foraging during relatively safe times or in safe places and to avoid mortality if the larvae are under high risk of predation. This happens because predators have different ways to find, capture, manipulate and consume prey; in addition, different prey species have different traits to avoid the encounter or to escape the attack of predators (Relyea 2001a-b). Since fish are active predators that swim through the water column, a usual anti-predator strategy is to hide in the bottom of the pond (Laurila et al. 2006). On the other hand, water bugs are sit and wait predators typically located in or near the substrate.

In this work, we found that there were significant differences between the treatments with fish and water bugs. However, this does not indicate a response to the presence of predators given that there were no significant differences with the control treatment. Significant differences might be due only to average values, greater in fish and smaller in water bugs; these extreme measures may generate significant differences between treatments without being representative of the effect of predation. The two variables that showed some effects caused by the presence of the predator were body and tail depth. Tadpoles exposed to water bugs had a significantly lower body depth than larvae in the control treatment. Since water bugs capture prey by grasping their bodies and piercing the body with their mouthparts to digest internal tissues of the tadpoles, they need prey of reach a suitable size in order to be able to capture them (Holling 1964). Therefore, reducing the body size is an effective anti-predator strategy to decrease the probability of capture. Nevertheless, our results contrast with most previous studies, which found that tadpoles exposed to invertebrate predators exhibit deeper fine tails, because it is widely known that a deeper tail fin acts as a lure that leads the attack to the less vital part of the body (Benard 2006; Kishida & Nishimura 2005; Teplitsky et al. 2005; Lardner 2000; Relyea & Werner 2000). In this work, we observed that tadpoles exposed to invertebrate predators reduced body depth, in this case, signal of invertebrate predators did not have influences on tail of tadpoles.

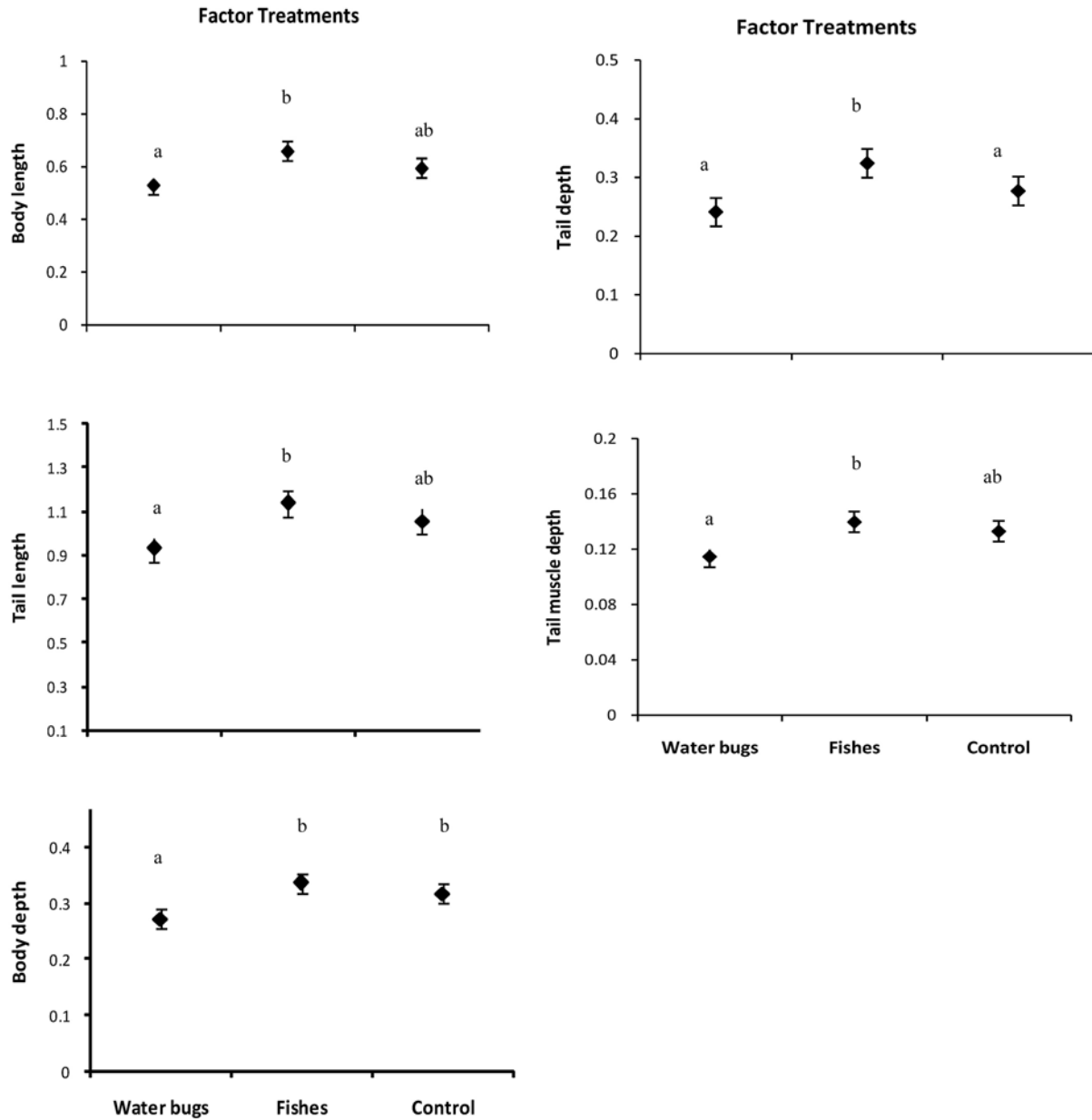


Fig. 2. Effects of the presence of predators chemical cues on morphological variables, in *Elachistocleis bicolor* tadpoles. Each point represent the arithmetic mean  $\pm$  SEM. Treatments data with the same lowercase letter are not significantly different at  $P < 0.05$ .

On the other hand, we showed that the change in tail depth was significantly different between fish and control treatments, and that tail depth was significantly greater when the larvae were exposed to fish chemical cues. This result also contrasts with many previous studies (Benard 2006; Teplitsky et al. 2004; Teplitsky et al. 2003), which argued that tadpoles exposed to fish develop longer and shallower tails to increase the swimming speed. However Wassersug (1989) found that deeper tail improve acceleration and not swimming speed. In a previous study, Relyea (2001b) found that different prey responded to a predator fish in a different way. He observed that bullfrogs and tree frogs exposed to fish *Umbra limi* (Kirtland, 1840) did not exhibit responses in tail depth, leopard frogs and wood frogs increased tail depth, and green frogs and toads

decreased tail depth. In another study, Teplitsky et al. (2005) found that tadpoles exposed to fish developed deeper tail fins, but also deeper tail muscle and longer tails, and showed that tail fin depth and body variables did not influence the acceleration responses. However, these authors argued that a deeper tail could be considered a generalized response in tadpoles against all types of predators. In the present work, fish are active predators and *E. bicolor* is tadpole with little movement. Perhaps for that reason this species does not invest energy on the construction of structure to increase its swimming speed, and an increase in tail depth is a good strategy that allows them to escape by means acceleration (Wassersug 1989).

In this study, we did not find significant differences in the growth rate or development stages in any of the

treatments, i.e., tadpoles of *E. bicolor* reached the same weight and development stage at the same time. However, the theoretical prediction was unsuccessful to determine that tadpoles exposed to predators should increase their growth rate and metamorphose smaller and earlier than tadpoles in an environment without predators.

Although some works have corroborated this theory (Kiesecker et al. 2002; Lardner 2000), most previous studies have found no evidence that larvae decrease their growth rate, since it has been observed that tadpoles usually increase their growth rate or develop and grow at the same rate as tadpoles in the absence of predators (Benard 2004; Relyea 2007).

These results are consistent with a previous experience in which we found that *Physalaemus albonotatus* accelerates the growth and development rate in the presence of predators (Gómez & Kehr 2011). In this study, we observed that tadpoles of *E. bicolor* grew and developed at the same rate in all treatments. This could be result of a behavioral shift, due that in an environment with abundant resources; the tadpoles could have a high growth rate at low levels of activities (Peacor & Werner 2004), particularly in this species which feeds almost exclusively in the water column by oral suction since it lacks keratinized mouth parts (Williams & Guldyns 1987).

## Acknowledgements

The English language was improved by Ingles Científico (www.inglescientifico.com.ar).

## References

- Addinsoft. 2006. XLSTAT version 7. 5. for Excel interface. Addinsoft, U.K.
- Benard M.F. 2006. Survival trade-offs between two predator induced phenotypes in Pacific treefrogs (*Pseudacris regilla*). *Ecology* **87** (2): 340–346. DOI: 10.1890/05-0381
- Benard M.F. 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. *Ann. Rev. Ecol. Evol. Syst.* **35**: 651–673. DOI: 10.1146/annurev.ecolsys.35.021004.112426
- Blaustein L. 1999. Oviposition site selection in response to risk of predation: evidence from aquatic habitats and consequences for population dynamics and community structure, pp. 442–456. In: Wasser S.P. (ed.), *Evolutionary Theory and Processes: Modern Perspectives*. Kluwer Academic Publishers, Netherlands. ISBN: 0792355180
- Blaustein L., Friedman F. & Fahima T. 1996. Larval *Salamandra* drive temporary pool community dynamics: evidence from an artificial pool experiment. *Oikos* **76** (2): 392–402. DOI: 10.2307/3546211
- Darlington R.B. & Smulders T.V. 2001. Problems with residuals analysis. *Anim. Behav.* **62**: 599–602 Part 3. DOI: 10.1006/anbe.2001.1806
- Gómez V.I. & Kehr A.I. 2011. Morphological and developmental responses of anuran larvae (*Physalaemus albonotatus*) to chemical cues from predators *Moenkasia dichrourea* (Characiformes: Characidae) and *Belostoma elongatum* (Hemiptera: Belostomatidae). *Zool. Stud.* **50** (2): 203–210.
- Gomulkiewicz R. & Kirkpatrick M. 1992. Quantitative genetics and the evolution of reaction norms. *Evolution* **46** (2): 390–411. DOI: 10.2307/2409860
- Gosner K.L. 1960. A simplified table for staging anurans embryos and larvae with notes of identification. *Herpetologica* **16** (3): 183–190.
- Hews D.K. 1988. Alarm response in larval western toads, *Bufo boreas*: release of larval chemicals by a natural predator and its effect on predator capture efficiency. *Anim. Behav.* **36** (1): 125–133. DOI: 10.1016/S0003-3472(88)80255-0
- Holling C.S. 1964. The analysis of complex population processes. *Canad. Entomol.* **96** (1–2): 335–347. DOI: 10.4039/Ent963-4
- Kiesecker J.M., Chivers D.P., Anderson M. & Blaustein A.R. 2002. Effect of predator diet on life history shifts of red-legged frogs, *Rana aurora*. *J. Chem. Ecol.* **28** (5): 1007–1015. DOI: 10.1023/A:1015261801900
- Kishida O. Mizuta Y. & Nishimura K. 2006. Reciprocal phenotypic plasticity in a predator-prey interaction between larval amphibians. *Ecology* **87** (6): 1599–1604. DOI: 10.1890/0012-9658(2006)87[1599:RPPIAP]2.0.CO;2
- Kishida O. & Nishimura K. 2005. Multiple inducible defenses against multiple predators in the anuran tadpole, *Rana pirica*. *Evol. Ecol. Res.* **7** (4): 619–631.
- Lardner B. 2000. Morphological and life history response to predators in larvae of seven anurans. *Oikos* **88** (1): 169–180. DOI: 10.1034/j.1600-0706.2000.880119.x
- Laurila A., Pakkasmaa S. & Merila J. 2006. Population divergence in growth rate and antipredator defenses in *Rana arvalis*. *Oecologia* **147** (4): 585–595. DOI: 10.1007/s00442-005-0301-3
- Laurila A., Pakkasmaa S. & Merila J. 2004. Temporal variation in predation risk: stage-dependency, graded responses and fitness costs in tadpole antipredator defenses. *Oikos* **107** (1): 90–99. DOI: 10.1111/j.0030-1299.2004.13126.x
- Lima S.L. & Dill L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68** (4): 619–640. DOI:10.1139/z90-092
- McCollum S.A. & Van Buskirk J. 1996. Costs and benefits of a predator-induced polyphenism in the Gray treefrog *Hyla chrysoscelis*. *Evolution* **50** (2): 583–593. DOI: 10.2307/2410833
- Moran N.A. 1992. The evolutionary maintenance of alternative phenotypes. *Am. Nat.* **139** (5): 971–989.
- Peacor S.D. & Werner E.E. 2004. Context dependent of nonlethal effect of a predator on prey growth. *Isr. J. Zool.* **50** (2–3): 139–157. DOI: 10.1560/KPRR-X1C3-5NHE-QV2N
- Relyea R.A. 2007. Getting out alive: how predators affect the decision to metamorphose. *Oecologia* **152** (3): 389–400. DOI: 10.1007/s00442-007-0675-5
- Relyea R.A. 2003. Predators come and predators go: The reversibility of predator-induced traits. *Ecology* **84** (7): 1840–1848. DOI: 10.1890/0012-9658(2003)084[1840:PCAPGT]2.0.CO;2
- Relyea R.A. 2001a. The relationship between predation risk and antipredator responses in larval anurans. *Ecology* **82** (2): 541–554. DOI: 10.1890/0012-9658(2001)082[0541:TRBPRA]2.0.CO;2
- Relyea R.A. 2001b. Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology* **82** (2): 523–540. DOI: 10.1890/0012-9658(2001)082[0523:MABPOL]2.0.CO;2
- Relyea R.A. & Werner E.E. 2000. Morphological plasticity in four larval anurans distributed along an environmental gradient. *Copeia* **2000** (1): 178–190 DOI: 10.1643/0045-8511(2000)2000[0178:MPIFLA]2.0.CO;2
- Schlichting C.D. & Pigliucci M. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer Associates Publishers, Sunderland, MA, 340 pp. ISBN: 0-87893-799-4
- Skelly D.K. 2001. Distribution of pond-breeding anurans: an overview of mechanisms. *Isr. J. Zool.* **47** (4): 313–332. DOI: 10.1560/BVT1-LUYF-2XG6-B007
- SPSS. 1997. SYSTAT 7.5 for Window. SPSS Inc. Chicago-USA.
- Teplitsky C., Plénet S., Lena J.P., Mermet N., Malet E. & Joly P. 2005. Escape behavior and ultimate causes of specific inducible defenses in an anuran tadpole. *J. Evol. Biol.* **18** (1): 180–190. DOI:10.1111/j.1420-9101.2004.00790.x

- Teplitsky C., Plénet S. & Joly P. 2004. Hierarchical responses to tadpoles to multiple predators. *Ecology* **85** (10): 2888–2894. DOI: 10.1890/03–3043
- Teplitsky C., Plénet S. & Joly P. 2003. Tadpoles responses to the risk of fish introduction. *Oecologia* **134** (2): 270–277. DOI: 10.1007/s00442–002–1106–2
- Tollrian R. & Harvell D. (eds) 1999. *The Ecology and Evolution of Inducible Defenses*. Princeton University Press, Princeton, NJ, 383 pp. ISBN: 0691004943, 9780691004945
- Van Buskirk J. 2000. The cost of an inducible defense in anuran larvae. *Ecology* **81** (10): 2813–2821. DOI: 10.1890/0012–9658(2000)081[2813:TCOAID]2.0.CO;2
- Van Buskirk J. 2001. Specific induced responses to different predator species in anuran larvae. *J. Evol. Biol.* **14**: 482–489. DOI:10.1046/j.1420–9101.2001.00282.x
- Van Buskirk J. 2002. Phenotypic lability and the evolution of predator-induced plasticity in tadpoles. *Evolution* **56** (2): 361–370. PMID: 11926504
- Van Buskirk J., McCollum S.A. & Werner E.E. 1997. Natural selection for environmentally induced phenotypes in tadpoles. *Evolution* **51**(6): 1983–1992.
- Van Buskirk J. & Relyea R.A. 1998. Selection for phenotypic plasticity in *Rana sylvatica* tadpoles. *Biol. J. Linn. Soc.* **65** (3): 301–328. DOI: 10.1111/j.1095–8312.1998.tb01144.x
- Wassersug R.J. 1989. Locomotion in amphibian larvae (or “Why aren’t tadpoles built like fishes?”). *Amer. Zool.* **29** (1): 65–84. DOI: 10.1093/icb/29.1.65
- Werner E.E. 1986. Amphibian metamorphosis: growth rate, predation risk, and optimal size at transformation. *Am. Nat.* **128** (3): 319–341.
- Werner E.E. & McPeck M.A. 1994. Direct and indirect effect of predators on two anuran species along an environmental gradient. *Ecology* **75** (5): 1368–1382. DOI: 10.2307/1937461
- Wilbur H.M. 1997. Experimental ecology of food webs: complex systems in temporary ponds. *Ecology* **78** (8): 2279–2302. DOI: 10.1890/0012–9658(1997)078[2279:EEOFWC]2.0.CO;2
- Williams J.D. & Gudynas E. 1987. Descripción de la larva de *Elachistocleis bicolor* (Valenciennes 1838) (Anura: Microhylidae). *Amphibia-Reptilia* **8** (3): 225–229. DOI: 10.1163/156853887X00261
- Wojdak J.M. & Trexler D.C. 2010. The influence of temporally variable predation risk on indirect interactions in an aquatic food chain. *Ecol. Res.* **25** (2): 327–335. DOI: 10.1007/s11284–009–0664–8

Received August 18, 2011

Accepted May 2, 2012