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Taylor L. Hall

Stephen F Austin State University

Daniel Saenz

U.S. Forest Service Wildlife and Silviculture Laboratory, Southern Research Station

Matthew Kwiatkowski

Stephen F Austin State University, kwiatkowm@sfasu.edu

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Differential jumping performance in newly metamorphosed Blanchard's cricket frogs, *Acris blanchardi* (Anura: Hylidae), from fish- and invertebrate-dominated ponds

Taylor L. Hall^{1,3}, Daniel Saenz², and Matthew A. Kwiatkowski¹

¹ Department of Biology, Stephen F. Austin State University, Nacogdoches, Texas 75962, USA. E-mails: thall@angelina.edu, kwiatkowm@sfasu.edu.

² U.S. Forest Service Wildlife and Silviculture Laboratory, Southern Research Station, Nacogdoches, Texas 75965, USA. E-mail: dsaenz@fs.fed.us.

³ Department of Science and Mathematics, Angelina College, 3500 South First Street Lufkin, TX 75904, USA.

Abstract

Differential jumping performance in newly metamorphosed Blanchard's cricket frogs *Acris blanchardi* (Anura: Hylidae) from fish- and invertebrate-dominated ponds.

Organisms that adopt phenotypically plastic anti-predator strategies during larval stages may incur fitness costs later in development. These costs are typically difficult to define in many species. The difficulty of identifying ecological trade-offs may result from experimental comparisons that do not adequately mirror naturally occurring predator-prey relationships. To examine this, we captured 61 newly metamorphosed *Acris blanchardi* from ponds dominated either by fish or invertebrate predators. These predators are known to induce alternate phenotypic anti-predator responses at the larval stage. We used jumping performance as a measure of post-metamorphic fitness, and compared the morphological traits and jumping ability of frogs from ponds with and without fish. Frogs from fishless ponds can jump significantly farther than frogs from fish-dominated ponds. Morphological measurements indicated that overall frog size determined differences in jumping ability, with hind-leg length primarily explaining jumping performance. Differences in hind-leg length positively correlated with overall body size, which differed between the two types of ponds, and did not result from allometric growth between them. Differences in frog sizes presumably are related to differences in developmental anti-predator morphologies in larvae.

Keywords: metamorphosis, morphology, post-metamorphic costs, predators.

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Resumo

Desempenho diferencial no salto em indivíduos recém-metamorfoseados de *Acris blanchardi* (Anura: Hylidae) de lagoas dominadas por peixes e invertebrados. Organismos que adotam estratégias anti-predação fenotipicamente plásticas durante estágios larvais podem sofrer perdas de sucesso reprodutivo nas fases finais do desenvolvimento. Em muitas espécies tais custos são tipicamente difíceis de serem definidos. A dificuldade de identificar balanços ecológicos pode resultar de comparações experimentais que não refletem adequadamente relações predador-presa que ocorrem naturalmente. Para examinar isso, capturamos 61 *Acris blanchardi* recém-metamorfoseados em lagoas dominadas por peixes ou por invertebrados. Esses predadores são conhecidos por induzir respostas fenotípicas anti-predadores alternativas na fase larvária. Utilizamos o desempenho no salto como uma medida de sucesso reprodutivo pós-metamorfose e comparamos características morfológicas e capacidade de salto de indivíduos de lagoas com e sem peixes. Indivíduos de lagoas sem peixes podem saltar significativamente mais longe do que indivíduos de lagoas dominadas por peixes. Medidas morfológicas indicaram que o tamanho total do indivíduo determinou diferenças na capacidade saltatória, com o comprimento da pata sendo o fator primário a explicar o desempenho no salto. Diferenças no comprimento da pata posterior foram positivamente correlacionadas com o tamanho total do corpo, que diferiu entre os dois tipos de lagoas e não resultou do crescimento alométrico entre a pata e o corpo. Diferenças no tamanho dos indivíduos presumivelmente estão relacionadas a diferenças na morfologia anti-predação durante o desenvolvimento das larvas.

Palavras-chave: custos pós-metamórficos, metamorfose, morfologia, predadores.

Introduction

According to ecological trade-off theory, metabolic investments aimed at increasing survival will incur some level of cost to individuals. The nature or effect of these costs is difficult to observe or define (DeWitt 1998). In amphibian larvae, many species alter morphological and behavioral traits to enhance survival among variable predator regimes (e.g., Komers 1997, Relyea 2001a); however, significantly altering physical traits remains costly, potentially having adverse effects on development, growth, or post-metamorphic fitness in exchange for survival throughout the larval stage (Relyea 2001a, 2002, Van Buskirk and Schmidt 2000). As a result, predator-induced morphologies may incur future costs to fitness, requiring increased energy investments to reverse or alter phenotypes if the environment changes (Van Buskirk *et al.* 1997). However, tadpoles may buffer the costs associated with morphological or behavioral changes by

exhibiting morphological sensitivity to variations in predator type and density gradients (Laurila *et al.* 2004). This sensitivity can maximize phenotypic efficiency while potentially reducing metabolic costs (Kishida and Nishimura 2004).

Typically, the rate of tadpole growth and development decreases as the complexity of the anti-predator phenotype increases (Teplitsky *et al.* 2005). This may cause increased natural mortality due to the costs of phenotypic maintenance (McCollum and Van Buskirk 1996), and also may result in post-metamorphic costs that are not detectable during the larval period (Benard and Fordyce 2003). Although post-metamorphic effects from morphological and behavioral adjustments to larval environments are difficult to quantify, survival, jumping performance, and differential morphologies of newly metamorphosed individuals often are used to assess relative post-metamorphic fitness. However, there may be little correlation between larval predator induction, and post-metamorphic fitness. For example, Van Buskirk

and Saxer (2001) found no metamorphic differences in morphologies or performance between predator-induced and non-induced individuals. Conversely, Tejedo *et al.* (2000) showed that increased competition during the larval stage can affect post-metamorphic performance. Although predator-induced tadpoles may become larger after metamorphosis in contrast to non-induced individuals, these differences reflect variation in time to metamorphosis, rather than predator-induced morphological changes of larvae. However, increased time to metamorphosis may be an indirect effect of predator-induced morphological change (Relyea 2001b). In contrast, Smith (1987) showed that time to, and size at, metamorphosis may have no effect on survival at adulthood. Instead, differences in performance and morphology at metamorphosis more likely result from competition than predator induction, with individuals in low competitive environments exhibiting better post-metamorphic performance, as well as relatively larger morphological traits (Relyea and Hoverman 2003).

While many studies have examined the effects of predator-induced versus non-predator-induced amphibians (i.e., the absence of predators), these comparisons have little ecological application because species capable of phenotypically plastic responses rarely exhibit “non-induced” phenotype in a natural setting. In fact, the evolution of plastic responses to variation in predation-risk exhibits strong correlations to aquatic ephemerality, with individuals inhabiting more permanent ponds exhibiting increases in phenotypically plastic responses (Lardner 2000, Laurila *et al.* 2008). As a result, species that lack predator-induced responses at the larval stage (i.e., ephemeral pond breeders) subsequently avoid the potential costs associated with induced anti-predator mechanisms. Although examining the effects of predatorless systems allows for baseline contrasts to the effects of predators, there also are naturally occurring comparisons known to induce opposing phenotypic responses, such as the

effects of invertebrate predators (Van Buskirk *et al.* 2003) compared to the effects of fish predators (Sosa *et al.* 2009). These represent naturally occurring oppositions that may better facilitate the observation of post-metamorphic costs due to larval induced anti-predator phenotypes. As a result, we contend that post-metamorphic effects of larval anti-predator mechanisms remain difficult to quantify because the correct comparison has yet to be made. We ask the question, does natal pond predator type (fish vs. invertebrate dominated) influence jumping performance and morphology in newly metamorphosed frogs?

Materials and Methods

We captured 61 newly metamorphosed *Acris blanchardi* from six ponds in the Davy Crockett National Forest; the predator content of the ponds was predetermined by multiple predator surveys (Saenz *et al.* unpubl. data). Thirty-one individuals were obtained from three fishless sites (invertebrate-dominated) and 30 individuals from three ponds with sunfish species (*Lepomis* sp.) between 01 and 09 September 2009. These ponds are known to induce alternate phenotypic responses at the larval stage naturally (Hall 2010). In invertebrate-dominated ponds, tadpoles grow to a larger overall size at later developmental stages, possess larger tail fins relative to the tail muscle, and bear a darkly pigmented area on the posterior part of the tail fin. In contrast, tadpoles in fish-dominated ponds are smaller at later developmental stages, possess larger tail muscles relative to the tail fin, and have little or no tail pigmentation. Thus by examining individuals captured from both pond types, we can gain insights as to the post-metamorphic effects of larval phenotypes. Captured individuals were subjected to jump-distance trials at the U.S. Forest Service Wildlife and Silviculture Laboratory Southern Research Station to standardize light exposure and temperature across all replicates. Each frog was placed on a large sheet of paper (7.5 m²) and jumps were

elicited by a slight tap on the sacral region of the frog. The first three jump distances were marked and measured. This was replicated three times per individual, with 10 min. between each replicate. The furthest single jump of the nine total jumps was considered maximum jump distance (Jmax). After the trial, the frogs were anesthetized using MS-222 (0.4g/L), and morphological measurements were taken in the manner of Relyea (2001b; Figure 1).

For statistical analyses, a two-tailed t-test determined if differences in jumping performance occurred between pond types (i.e., fish and invertebrate predators). If differences occurred, principle components analysis (PCA) determined which trait(s) accounted for the observed morphological variation. Analysis of variance (ANOVA) then was applied to a linear model that included pond type, the morphological traits determined by PCA, and all interactions between

these factors to determine if the traits varied between predator types and contributed to the ability of a frog to jump ($\alpha = 0.05$).

To investigate if differences in jumping ability reflected allometric growth of morphological traits, rather than random effects induced by each individual pond, we eliminated the size of the frog from the morphological data by regressing each trait by the weight of the frog, and using the residuals as a set of morphological explanatory variables. We then performed PCA and ANOVA similar to the size-dependant data. All analyses were performed in R 2.9.2 (R Development Core Team 2009).

Results

Individuals from invertebrate-dominated ponds (mean \pm SD = 57.26 \pm 14.77 cm) jumped farther than individuals from fish-dominated

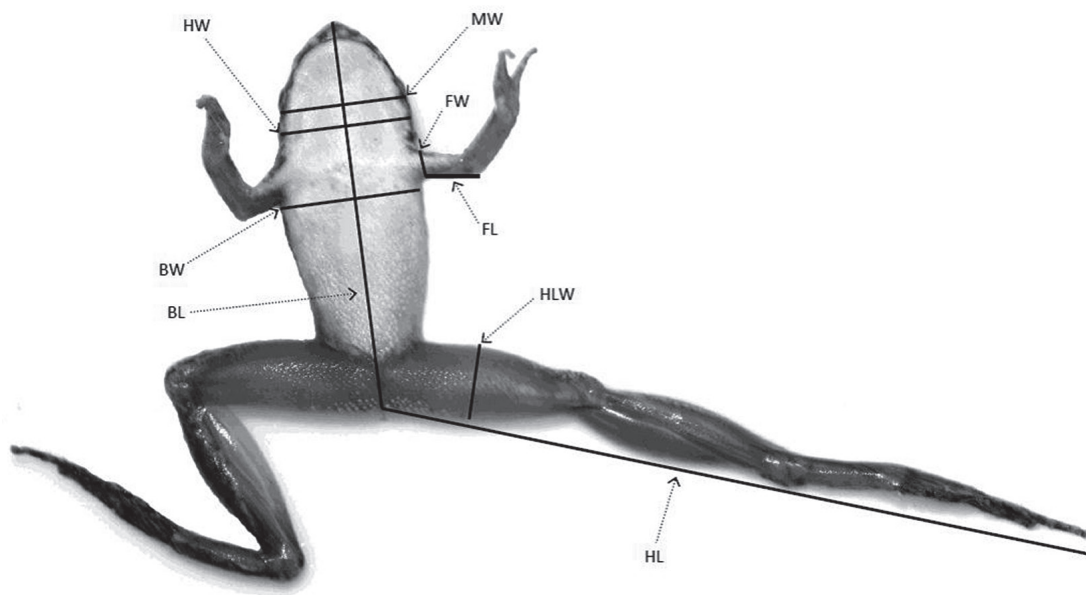


Figure 1. Morphological measurements of each newly metamorphosed *A. blanchardi* captured from ponds in the Davy Crockett National Forest. FL = Forelimb Length, FW = Forelimb Width, BL = Body Length, BW = Body Width, HW = Head Width, MW = Mouth Width, HL = Hind Leg Length, HLW = Hind Leg Width.

ponds (mean \pm SD = 46.16cm \pm 11.53cm, $t = -3.28$, $p = 0.002$). Principle Component 1 (PC1) accounted for 95.2% of the observed variation in the raw morphological data, and primarily resulted from differences in hind-leg length (HL; Table 1), with ANOVA indicating that pond type ($p = 0.039$) and HL ($p < 0.001$) both contributed to a frog's jump ability (Pond Type*HL interaction $p = 0.719$). Size independent PC1 accounted for 82.2% of variation in the standardized morphological data, again primarily resulting from differences in HL (Table 1), however ANOVA indicated that size independent HL was not important to a frog's jump ability ($p = 0.114$), whereas pond predator type was the only determinant factor to jumping performance when frog size influence is removed ($p < 0.001$).

Discussion

Phenotypic plasticity allows organisms to survive sub-optimal environments through alterations of morphological and behavioral traits (Relyea 2001a). These changes may elicit costs to overall fitness, especially among species with complex life histories, such as the ontogenetic shift from aquatic to terrestrial environments in amphibians (Warkentin 1995). Although anti-predator mechanisms of larvae may increase survival to adulthood, post-metamorphic fitness may suffer as a result (Benard and Fordyce 2003). We think that many studies experience difficulty in illustrating these post-metamorphic effects of larval anti-predator phenotypes because they often compare invertebrate-dominated systems with predator-free systems, but this comparison actually yields little information about the potential costs associated with phenotypic plasticity in the natural environment. For example, tadpoles of *Acris blanchardi* in predatorless systems do not differ morphologically from those in invertebrate systems; this suggests that the optimal phenotype in this species is an anti-invertebrate phenotype (Hall 2010). As a result, fish-dominated

Table 1. Contribution of variables to PC1 resulting from Principal Component Analysis of morphological traits on 61 newly metamorphosed individuals of *A. blanchardi*, using raw morphological data (size dependent), and standardized morphological data (size independent). PC1 accounted for 95.2% and 82.2% of the observed variation respectively.

Trait measurement	PC1 (size dependant)	PC1 (size independent)
Forelimb length	0.075203	0.052531
Forelimb width	0.032585	0.028754
Body length	0.344182	0.06552
Body width	0.137127	0.030239
Head width	0.107312	0.027735
Mouth width	0.101525	0.031481
Hind-leg length	0.910985	0.994516
Hind-leg Width	0.06299	0.019601
Weight (g)	0.018236	–

environments, which induce smaller more streamlined tadpoles, may be sub-optimal environments to sustain populations of *A. blanchardi*. In this study, permanent and semi-permanent fishless ponds rarely occurred in a natural setting; thus, Cricket Frogs may be forced to inhabit ponds containing fish. The post-metamorphic costs of adopting phenotypically plastic traits in sub-optimal environments should be more readily observable if comparisons are made to environments that are better suited to the occurrence of the species (i.e., fish vs. invertebrate ponds).

This study showed that individuals from fish ponds cannot jump as far as individuals from fishless environments. Similarly, allometric morphological growth is not a factor; thus, jump differences primarily result from overall differences in size between populations (Table 2). This is consistent with previous data for this species, suggesting that tadpoles from fishless environments attain larger sizes just prior to

metamorphosis (Hall 2010). These size discrepancies between the two pond types (fish vs. invertebrate) provide further evidence that invertebrate systems provide a more optimal environment for this species; thus, tadpoles in fish ponds may incur an observable cost (decreased post-metamorphic size) resulting from induced anti-predator traits or behavior in larvae. While post-metamorphic survival is unknown for these populations, we know that the size of the organism, and its ability to jump and escape predators, affects predator-prey interactions; where in most cases, larger individuals survive better (Caldwell *et al.* 1980, Formanowicz *et al.* 1981, Scharf *et al.* 2000). Because adult frog size and jumping performance were not measured for this study, it is unclear if these post-metamorphic size differences between populations converge later in development. If so, the cost of larval morphological plasticity of frogs in fish ponds may be a temporary disadvantage; alternately, selective pressures may be driving populations of frogs in fish-pond toward smaller adult sizes.


Anti-predator behaviors used by larvae may carry over into adulthood. When capturing frogs for this study, we observed distinct behavioral differences of frogs at each type of pond.

Although anecdotal, these escape behaviors mirrored known larval anti-predator behaviors. For example, at fishless ponds, frogs tended to jump away continuously (four or five consecutive jumps), and remain visible. Conversely, frogs at fish ponds tended to make two or three short jumps and hide amidst vegetation at the surface of the pond or at the pond's edge. These strategies resemble larval anti-predator behaviors, whereby individuals in invertebrate-dominated habitats tend to struggle with and swim away from predators after an attack (Van Buskirk *et al.* 2003), and individuals from fish ponds rarely move, and presumably hide amidst vegetation to escape fish predators (Sosa *et al.* 2009). In fact, differences in adult anti-predator behaviors may buffer the costs associated with larval anti-predator morphologies, and may nullify differences in survival between pond types, although future research is needed to determine if this is the case. Similarly, future research should investigate the post-metamorphic effects of larval phenotypic plasticity for contrasting predator regimes affecting other amphibian species; this would enhance our understanding of the carry-over effects in organisms that cope with varying environmental conditions through phenotypically plastic responses.

Table 2. Mean \pm SD of morphological traits measured on 61 newly metamorphosed *A. blanchardi* from environments with dissimilar predation pressures, invertebrate ponds ($N = 31$) and fish dominated ponds ($N = 30$).

Trait measurement	Invertebrate ponds	Fish ponds
Forelimb length (mm)	2.21 \pm 0.46	2.20 \pm 0.32
Forelimb width (mm)	0.99 \pm 0.21	0.95 \pm 0.13
Body length (mm)	14.26 \pm 1.97	13.08 \pm 0.80
Body width (mm)	5.07 \pm 0.91	4.60 \pm 0.42
Head width (mm)	4.81 \pm 0.61	4.45 \pm 0.32
Mouth width (mm)	4.64 \pm 0.58	4.30 \pm 0.30
Hind leg length (mm)	23.26 \pm 4.59	21.06 \pm 2.77
Hind leg width (mm)	2.51 \pm 0.38	2.33 \pm 0.37
Weight (g)	0.26 \pm 0.10	0.19 \pm 0.04

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