

Predator-specific changes in the morphology and swimming performance of larval *Rana lessonae*

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Summary

1. We investigated the morphological responses of larval *Rana lessonae* to the presence of two predators with substantially different prey-detection and capture techniques; larval dragonflies (*Aeshna cyanea*) and the Pumpkinseed Sunfish (*Lepomis gibbosus*).

2. We also examined the functional implications of any predator-induced morphological variation on their swimming ability by assessing performance during the initial stages of a startle response.

3. We found the morphological responses of larval *R. lessonae* were dependent on the specific predator present. Tadpoles raised in the presence of dragonfly larvae preying upon conspecific tadpoles developed total tail heights 5.4% deeper and tail muscles 4.7% shallower than tadpoles raised in a non-predator environment, while tadpoles raised with sunfish possessed tails 2% shallower and tail muscles 2.5% higher than non-predator-exposed tadpoles.

4. Predator-induced morphological variation also significantly influenced swimming performance. Tadpoles raised with sunfish possessed swimming speeds 9.5 and 14.6% higher than non- and dragonfly predator groups, respectively.

5. Thus, the expression of these alternative predator-morphs leads to a functional trade-off in performance between the different environments.

Key-words: Inducible defence, phenotypic plasticity

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Introduction

Phenotypic plasticity should be favoured when reliable cues indicate the state of the environment and a fitness trade-off occurs between phenotypes expressed in each of the environments (Levins 1968; Harvell 1990; Moran 1992). Inducible morphological defences in aquatic organisms have served as excellent model systems for testing these predictions for the evolution and maintenance of phenotypic plasticity. Although most studies of predator-induced plasticity have concentrated on documenting how prey species respond to a single predator and exploring their ecological consequences, several studies have now demonstrated that prey can discriminate among different predators and produce predator-specific phenotypes (Havel 1985; Lawler 1989; Kusch 1995; DeWitt, Robinson & Wilson 2000; Relyea 2001). However, fewer studies have explored the functional implications of these predator-specific morphological responses, and thus elucidated the possible linkages between morphological variation and their

fitness consequences (see DeWitt *et al.* 2000). Combining studies of predator-specific responses with functional analyses of the subsequent morphological variation will help identify not only the targets of selection but also the possible mechanisms of selection on these traits.

Larval amphibians are ideal for studies exploring the functional consequences of variation in predator-mediated responses because they encounter a suite of different predators in their aquatic habitat (Cooke 1974; Wassersug & Sperry 1977; Caldwell, Thorp & Jervey 1980; Formanowicz 1986), exhibit strong behavioural and morphological responses to the presence of predators, and their phenotypes are easily manipulated under controlled experimental conditions (McCollum & Van Buskirk 1996; Van Buskirk 2000; Van Buskirk & Saxer 2001). Importantly, different predators of larval amphibians also vary in their foraging tactics and prey-capture techniques, which may result in selection for different phenotypic characteristics of the tadpoles (DeWitt *et al.* 2000). Not surprisingly, larval anurans exhibit marked variation in their predator-induced morphological responses that are dependent upon the predator species to which they are exposed (Relyea 2001).

The clear benefit of inducible modifications in tadpole tail-fin shape when responding to larval dragonflies is increased survival over non-predator-exposed phenotypes during predator encounters (Van Buskirk & McCollum 1999, 2000). However, the actual mechanisms of selection on tail-fin shape and why tadpoles with relatively higher tail-fins enjoy increased survival has been the source of some debate. Initially it was suggested that increases in tail-fin height should lead to increased tadpole swimming performance, thus allowing effective escape during predator encounters. Support for this hypothesis was based on kinematic studies of fish, suggesting a strong positive association between tail-fin depth and swimming performance (Webb 1984; Weihs 1989). However, recent studies indicate predator-induced variation in tadpole tail shape has very little effect on swimming performance (Hoff & Wassersug 2000; Van Buskirk & McCollum 2000) and small tadpoles have virtually no time to initiate an escape response during an attack by larval dragonflies (Zottoli *et al.* 2001). Instead it seems the larger tails may be used to attract predator-strikes away from the more vulnerable head-body region towards the more expendable tails (Van Buskirk *et al.* 2003). However, previous analyses of predator-induced changes in tadpole swimming performance should still be viewed with some caution as they did not allow detailed high-speed kinematic analyses of initial maximum velocities. Thus, the initial propulsive strokes leading to maximum velocity may still be critical determinants of escape performance. Further analyses of startle responses using high-frequency recordings would undoubtedly add to previous functional analyses of inducible morphological defences in larval amphibians, especially within the framework of predator-specific changes in tail-fin shape.

In this study, we examined the morphological responses of larval European Green Frogs (*Rana lessonae*) to both predatory sunfish (*Lepomis gibbosus*) and larval dragonflies (*Aeshna cyanea*), and determined the functional implications of this morphological variation on their swimming performance. Both predator species were selected for study because they utilize very different techniques for prey detection and capture, and are thus likely to impose very different selection pressures on the morphology of their prey species. Odonate predators (*Aeshna* sp.) use sit-and-wait tactics for prey location, utilizing their extendable labia to grab hold of the prey item, withdraw it back to the mouth and slowly consume it piece-by-piece (Chovanec 1992). In contrast, like many fish predators, sunfish actively forage for their prey items, and often use fast-start swimming responses for prey capture, and typically suck in and swallow their prey whole (Mittelbach & Osenberg 1994; R. Wilson *et al.*, personal observation). We examined the functional implications of any predator-induced morphological variation in larval *R. lessonae* by using a high-speed camera to assess their

swimming performance during the first 200 ms of their startle response.

Materials and methods

Twelve clutches of the Green Frog *R. lessonae* were collected from several ponds in the areas surrounding Antwerp, Belgium, in May 2001. Eggs were transported to Kalmthout Field Station (University of Antwerp) and maintained indoors in 50-l tanks with constant aeration until 2 days after hatching, when the larvae were free-swimming. All clutches were then mixed together and 168 larvae were selected randomly and distributed evenly among 12 60-l containers (14 per container). Each tank contained 40 l aged water and the base was covered with a 1 cm layer of coarse gravel. For the duration of the experiment, tadpoles were fed *ad libitum* with frozen ground-up lettuce leaves and maintained at a temperature of 20 ± 1.0 °C and photoperiod of 12:12 h (light : dark).

A 25×25 cm² plastic-meshed predator-cage was floated on the surface of each experimental container to a depth of 20 cm. The experiment included three treatments (control, predator dragonflies and predator fish) that were replicated four times. Within four of the predator cages, two larval odonate predators (*Aeshna cyanea*) were kept and fed 1 g live *R. lessonae* larvae each day. In another four of the containers, one sunfish (*Lepomis gibbosus*) approximately 8 cm in total length was placed into each cage and also fed approximately 1 g live *R. lessonae* larvae each day. Densities of both predators were ecologically realistic and within the realms of natural habitat variation (R. Wilson, personal observations). The densities of the two types of predators were different to ensure identical quantities of prey items were consumed each day in all the predator treatment tanks. After 4 weeks, tadpoles from all treatments were between Gosner (1960) stages 27 and 32 (before significant development of hindlegs and eruption of forelimbs), and it was at this stage that the morphology and burst swimming performance of each tadpole were assessed.

Nymphs of the dragonfly *A. cyanea* were selected as the appropriate odonate predator for this study because they were locally abundant and readily consumed tadpoles of *R. lessonae* in the laboratory and their natural environment. Similarly, the sunfish is also abundant throughout Belgium and readily consumes tadpoles in the laboratory and their natural environment. Sunfish are efficient predators and tadpoles use visual stimuli to detect and avoid approaching fish predators. *L. gibbosus* is a native species of North America and was introduced to Belgium and other areas of Western Europe approximately 100 years ago (García-Berthou & Moreno-Amich 2000).

Burst swimming performance was assessed by filming at least five startle responses for each individual with a high-speed digital camera at 22 °C (± 0.5 °C). Swimming responses were elicited by placing larvae

into the centre of a swimming arena ($0.5 \times 0.5 \times 0.1$ m deep) and touching the tip of the snout with a fine-wire probe. Stimulation of the larvae usually resulted in a C-start and several propulsive beats of the tail. Only responses from a stationary position that led to a C-start were analysed. Swimming sequences were filmed by recording the image reflected off a mirror, suspended at an angle of 45° over the arena, with a high-speed digital camera recording at 200 Hz (Redlake Imaging Corporation, San Diego, California, USA). A sharp silhouette of the larvae was obtained by diffuse lighting from several fluorescent lights.

The accompanying Redlake software package was used for analysis of the first 200 ms of the startle responses by playing back the sequences frame-by-frame. The beginning of a startle response was defined as the frame immediately preceding the frame where movement was first detected. For each frame, both the tip of the tadpole's snout and back of the head-body were digitized. The coordinates from these two points were then used to calculate the mid-point of the head-body region. The raw distance data from this mid-point of the head-body was then smoothed using a Butterworth smoothing function set at 20 Hz (see Walker 1998) (optimal frequency for smoothing function that approximates the tail-beat frequency of larval *R. lessonae*; also see Wilson & Franklin 2000), and then differentiated to calculate speed. The fastest of the swimming responses analysed for each individual was used as a measure of their maximum burst swimming performance. Each swimming sequence was analysed to determine maximum burst swimming speed (U_{\max}), total distance moved throughout the 200 ms (D_{200}), maximum velocity reached during the first 60 ms (U_{60}) and the time taken to reach maximum velocity ($T - U_{\max}$). U_{\max} was calculated by using a moving average of the data over three successive frames (i.e. over 12 ms).

Following recording of swimming performance, each larva was photographed dorsally and ventrally using a JVC digital video camera (DVL 9800). Digital images were then analysed using the Optimas 6.51 Analysis system (Media Cybernetics Silver Spring, Maryland, USA) to obtain measurements of: total length; head-body length; head-body height; tail length, tail muscle depth; maximum tail height; head-body width; and tail muscle width.

STATISTICAL ANALYSES

As swimming performance and all measures of morphology were all highly influenced by body size, we first had to obtain an overall estimate of body size based on several morphological variables. We followed Van Buskirk & McCollum (2000) and defined 'body size' as the first component derived from a principal components analysis (PCA) on the eight morphological variables. The first axis explained 92% of the variance in the data set, and was positively correlated with all traits. Body and tail shape were described by the

residuals of all original eight morphological variables on the estimate of 'body size'. These regressions were highly significant (r^2 ranging from 0.79 to 0.97) and homogeneity of slopes allowed statistical analyses on these residual values. Swimming performance was also described by the residuals of the four swimming parameters on the estimate of body size. Thus, analyses comparing morphology and swimming performance among treatment groups were performed on residuals (relative differences) to remove the overall effects of body size from individual traits.

Statistical comparisons between treatments (two predator and a non-predator-exposed treatment) were performed using a MANOVA design that was followed by univariate ANOVAs to test for significant differences between treatment groups. All experiments were of a nested design; replicates nested within treatment, which meant that each replicate was one independent observation and analysed as such. The association between swimming performance and morphology was analysed using a canonical correlation analysis on two sets of variables representing morphology (all eight parameters) and swimming performance (U_{\max} , D_{200} , U_{60} and $T - U_{\max}$) (see Van Buskirk & McCollum 2000). Canonical correlation analysis is a multivariate extension of standard bivariate correlation analysis and finds the linear combination of each set of variables, called a canonical variate, which maximises the correlation between the two canonical variates. A chi-squared test was used to test the null hypothesis that the correlation among canonical variates representing swimming performance and morphology is zero. All results are presented as means \pm SE. Significance was taken at the level of $P < 0.05$.

Results

DIFFERENCES IN MORPHOLOGY AMONG TREATMENTS

Body size (first axis of PCA) varied significantly between treatment groups (nested ANOVA, $df = 4, 16$, Wilks' $F = 16.6$, $P < 0.001$), with the tadpoles raised in the non-predator-exposed environment significantly larger in body size than both predator-exposed groups. After removing the effects of overall body size from the analysis by taking the residuals of morphological measurements from a regression with 'body size', we found a significant effect of treatment environment on the morphology of larval *R. lessonae* at 4 weeks posthatching (MANOVA, $df = 4, 16$, Wilks' $F = 10.67$, $P = 0.017$). Nested univariate ANOVAs also revealed significant differences among treatment groups for certain morphological variables (Table 1). Body length differed among treatment groups (nested ANOVA, $F_{2,9} = 8.89$, $P = 0.007$), and tail height and muscle height also demonstrated significant differences among treatment groups (Table 1).

Post hoc tests revealed relative tail height and tail muscle depth (based on residual scores against body size)

Table 1. Univariate ANOVA results (nested in design) testing the effect of predator treatment on several morphological traits of larval *Rana lessonae*. Analyses were performed on the relative size of morphological traits to body size that was calculated as the first component derived from a PCA on the eight morphological variables (see methods for details)

Variable	Treatment	
	$F_{2,9}$	P
Head length	1.2	0.44
Tail length	2.43	0.18
Body length	8.89	0.009*
Head depth	3.81	0.06
Tail depth	16.3	0.002*
Muscle depth	17.6	0.0005*
Tail area	1.05	0.35
Muscle area	2.19	0.17
Head width	1.86	0.04*
Tail width	3.42	0.04*

*Significant difference among treatment groups taken at the level of $P < 0.05$.

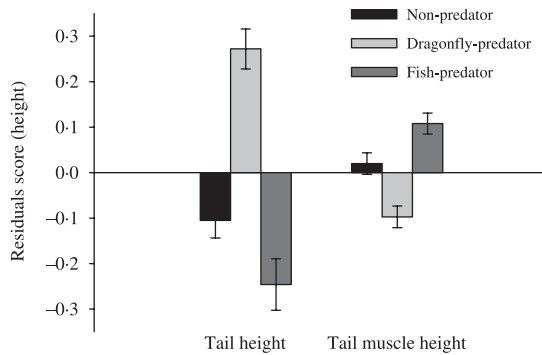


Fig. 1. Relative tail height (includes fin and muscle) and tail muscle depth for larvae of *Rana lessonae* exposed to caged larval dragonflies (*Aeshna cyanea*), sunfish (*Lepomis gibbosus*) feeding on conspecifics of *R. lessonae*, or a non-predator environment. Effects of overall body size were removed from the analysis by taking the residuals of morphological measurements from a regression with 'body size' (first axis of PCA). Significant differences were detected between all three treatments. Data show means \pm SE.

for larvae of *R. lessonae* significantly differed between all treatment groups (Table 1). Larval *R. lessonae* raised with dragonfly larvae possessed tails that were relatively high and tail muscle that was relatively shallow in comparison with larvae raised without predators and with fish-predators (Fig. 1). By contrast, larval *R. lessonae* raised in the presence of fish-predators possessed tail heights that were relatively lower, and tail muscle that was deeper than control and dragonfly group larvae (Fig. 1). Larvae of average body size raised with dragonfly larvae predators possessed a tail height that was 5.4% higher and tail muscle depth that was 4.7% lower than the control group. Thus, despite possessing greater total tail height relative to body size, their tail muscle height relative to body size was lower. By contrast, larvae of average body size raised with fish possessed total tail heights

Table 2. Univariate ANOVA results (nested in design) testing the effect of predator treatment on several measures of swimming performance of larval *Rana lessonae*. Analyses were performed on relative measures of swimming performance after correction for body size calculated as the first component derived from a PCA on the eight morphological variables (see Materials and methods for details)

	Treatment effects	
	$F_{2,9}$	P
D_{200}	12.71	0.002*
U_{\max}	13.14	0.002*
U_{60}	11.7	0.003*
$T - U_{\max}$	9.28	0.006*

*Significant difference among treatment groups taken at the level of $P < 0.05$.

that were 2% lower and tail muscle height 2.5% higher than controls (Fig. 1).

EFFECT OF TREATMENT ON SWIMMING PERFORMANCE

The startle responses of *R. lessonae* were similar to those reported for other anuran larvae (Hoff & Wassersug 2000; Wilson & Franklin 2000) and consisted of a C-start response, where the larvae turned away from the stimulus and used several propulsive tail-beats to reach a maximum velocity. Apart from $T - U_{\max}$, all performance measures were dependent on body size. U_{\max} ranged from 0.18 m s⁻¹ for a larva with a total body length of 14.2 mm to 0.64 m s⁻¹ for a 42.5 mm tadpole. The time taken to reach maximum velocity varied from 84 to 192 ms.

After size-correction of performance measures, we found a significant effect of treatment environment on the swimming performance of larval *R. lessonae* at 4 weeks posthatching (MANOVA, Wilks' $F = 9.8$, $P < 0.05$). Nested univariate ANOVAs also revealed significant differences in all measures of swimming performance among the treatment groups of larval *R. lessonae* (Table 2). Larvae raised with sunfish possessed the highest swimming performance, while those raised with dragonfly larvae were the poorest performers (Fig. 2). For an average sized larva ('body size' (first axis of PCA) of 0.58), tadpoles raised with sunfish possessed a U_{\max} that was 9.5 and 14.6% higher than control and dragonfly predator groups, respectively.

EFFECT OF SIZE AND SHAPE ON THE SWIMMING PERFORMANCE OF *RANA LESSONAE*

Canonical correlation analysis demonstrated a strong relationship between morphology and measures of swimming performance (Table 3) (canonical root 0, correlation 0.59; $\chi^2 = 98.65$; $r^2 = 0.34$; $df = 50$; $P < 0.0001$). However, chi-squared tests of successive roots shows that when the first (and most significant) root is removed, the remaining roots are no longer significant

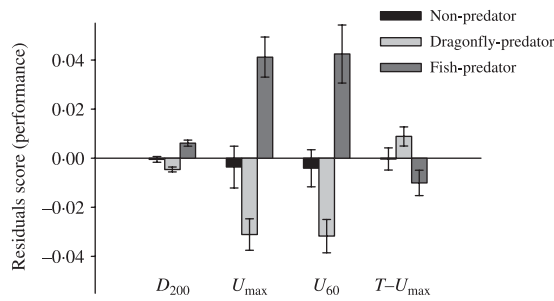


Fig. 2. Relative difference in swimming performance between larvae of *Rana lessonae* exposed to caged larval dragonflies (*Aeshna cyanea*), sunfish (*Lepomis gibossus*) feeding on conspecifics of *R. lessonae*, or a non-predator environment. Effects of overall body size were removed from the analysis by taking the residuals of performance measurements from a regression with ‘body size’ (first axis of PCA). Performance measurements were total distance moved throughout the initial 200 ms of a startle response (D_{200}), maximum burst swimming speed (U_{max}), maximum velocity reached during the first 60 ms (U_{60}), and the time taken to reach maximum velocity ($T - U_{max}$). Significant differences were detected between all three treatments. Data show means \pm SE.

Table 3. Phenotypic correlations among swimming performance and morphological traits for tadpoles of *Rana lessonae* from all treatments. Sample size was 152 for swimming performance measures and 155 for morphological parameters. Numbers in bold are statistically significant after Bonferroni adjustment across the 40 tests. Adjusted significance level was $P < 0.001$

	D_{200}	U_{max}	U_{60}	$T - U_{max}$
Body length	0.187	0.184	0.150	-0.031
Head depth	-0.150	-0.175	-0.108	0.061
Head length	0.002	0.01	0.052	0.025
Head width	-0.243	-0.293	-0.116	0.143
Muscle area	0.112	0.109	0.086	-0.124
Muscle depth	0.24	0.295	0.105	-0.139
Tail area	-0.088	-0.106	-0.030	-0.050
Tail height	-0.370	-0.369	-0.271	0.200
Tail length	0.150	0.120	0.182	-0.099
Tail width	0.369	0.302	0.255	-0.180

(canonical root 1, correlation 0.4; $\chi^2 = 39.63$; $r^2 = 0.16$; $df = 36$; $P = 0.31$). The morphology variate from the correlation analysis was dominated by residual tail height (individuals with relatively high tails score high on the axis), residual muscle depth (individuals with relatively small muscles score high on this axis) and residual head width (wide heads score high). The performance variate was negatively correlated with all original swimming performance measures, except $T - U_{max}$. Individuals with relatively high tail-fins, shallow tail muscles and wide heads performed relatively poorly in the measures of swimming performance (Fig. 3).

Discussion

Predator-mediated morphological changes in tadpoles of *R. lessonae* were dependent on the type of predator present during development. Larval *R. lessonae* raised

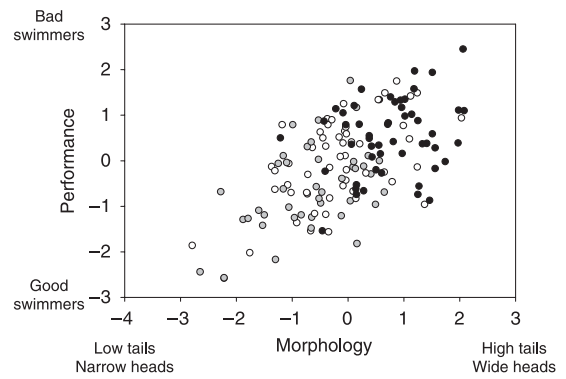


Fig. 3. Relationship between morphology and swimming performance variates taken from the canonical correlation analysis for different larval morphs of *Rana lessonae*. Treatment groups include larval *R. lessonae* exposed to caged larval dragonflies (*Aeshna cyanea*) (solid circles), caged sunfish (*Lepomis gibossus*) (grey circles) and a non-predator environment (open circles). Individuals with relatively high tails, shallow tail muscles and wide heads performed relatively poorly in all measures of swimming performance. Significant differences were detected between treatment groups in the relationship between morphology and swimming performance.

with dragonfly nymphs possessed tails 5.4% deeper and tail muscles 4.7% lower than non-predator-exposed tadpoles. Many previous studies of larval amphibians responding to predatory dragonfly larvae report similar morphological changes (Smith & Van Buskirk 1995; McCollum & Van Buskirk 1996; Van Buskirk & Relyea 1998; Relyea 2001). For example, when raised with dragonfly nymphs, tadpoles of the frog *Hyla chrysoscelis* develop relatively large, bright coloured tail-fins, and tadpoles of *Hyla versicolor* grow relatively short bodies and long, deep tails (Van Buskirk & McCollum 2000). By contrast, larval *R. lessonae* raised with sunfish possessed tails 2% shallower and tail muscles 2.5% higher than non-predator-exposed tadpoles. Few previous studies have reported reductions in tail height with exposure to aquatic predators, but larval *Bufo americanus* exhibited decreases in tail height when exposed to both dragonfly nymphs and fish predators (Relyea 2001).

Predator-specific morphological changes have been previously reported for several invertebrate taxa, including gastropods (DeWitt *et al.* 2000), protozoans (Kuhlmann & Heckmann 1994; Kusch 1995) and cladocerans (Dodson 1988; Black 1993). However, fewer examples of predator-specific morphological responses have been reported for vertebrate taxa (but see Relyea 2001). Tadpoles of the frog *Rana temporaria* exhibited no specific morphological responses to different pond predators, but did show predator-specific behavioural responses (Van Buskirk 2001). By contrast, Relyea (2001) examined the morphological and behavioural responses of tadpoles from six different anuran species to five different predator environments and found that the tadpoles of each species exhibited specific responses to each of the different predators (Relyea 2001). Although the functional consequences of these

varied morphological responses were not examined, a flexible predator-mediated response that is tailored to the type of predator present in the immediate environment would clearly be beneficial for increasing survival (Relyea 2001).

Predator-mediated morphological variation also significantly influenced the swimming performance of larval *R. lessonae*. From the canonical analysis, we also found that individuals possessing relatively high tail-fins, shallow tail muscles and wide heads (general dragonfly exposed phenotype) performed relatively poorly in all measures of swimming performance by comparison with individuals with relatively low tail-fins, deep tail muscles and narrow heads (sunfish-exposed phenotype). Although previous studies of larval amphibians did not report any effect of predator-induced morphological changes on burst swimming performance (Van Buskirk & McCollum 2000), we found tadpoles with deep bodies, deep tail heights and long-tails (typical dragonfly nymph-induced predator-morph) generally swam slower than the typical non-predator phenotype. Given also the minimal effect of substantial tail ablations on the swimming performance of larval anurans (Hoff & Wassersug 2000; Van Buskirk & McCollum 2000), it appears that the function of predator-mediated morphological responses of larval amphibians to dragonfly larvae is not associated with improved swimming performance. Instead, increases in tail-fin height may be utilized to either deflect attention away from the vulnerable head-body region, or to act as an expendable appendage that can be lost when grabbed by a dragonfly predator (Doherty, Wassersug & Lee 1998; Van Buskirk & McCollum 2000), thus allowing escape using a system analogous to caudal autotomy in lizards. Recent studies supporting this prediction found tadpoles escaped more readily from predatory larval dragonflies when struck on the tail rather than the head, and tadpole models with deeper tails were attacked more readily on the tail region (Van Buskirk *et al.* 2003). By contrast with tadpoles raised with dragonfly larvae, the shallower tails and deeper tail muscle of larval *R. lessonae* raised with sunfish predators were associated with higher performance for all recorded swimming parameters. The greater swimming performance of the sunfish-induced tadpoles is probably the result of their greater muscle mass allowing increased power production during an escape response. Further analyses should investigate whether these increases in swimming performance also lead to a greater ability to escape predation during encounters with fish-predators.

Specific predator-mediated responses are probably costly because in the absence of costs their expression should be constitutive rather than inducible (Levins 1968; Harvell 1990). Most models assume costs emanate from shifts in resource allocation to support the new structures or behaviours, transferring energy away from processes supporting growth or developmental rates (Rhoades 1979; Harvell 1990; Clark & Harvell

1992). Although the costs of induced defences in larval amphibians have not always been detected, they seem to be predominantly associated with reductions in growth rate and larval survival (McCollum & Van Buskirk 1996; Van Buskirk 2000).

Larval *R. lessonae* responded to different types of predators by modifications in the same morphological structures but in opposite directions, causing a direct functional conflict in phenotypic expression between the two predator environments. These predator-mediated responses may also lead to costs of defensive structures that are not shifts in resource allocation. If the expression of these alternative predator-morphs also leads to increased survival in their respective environments, this would also lead to decreased survival in the alternate predator environment. A direct survival trade-off would result between morphs expressed in the different environments. In a similar system, DeWitt *et al.* (2000) reported the freshwater snail *Physa heterostropha* develops a more rotund shell when exposed to sunfish and a more elongate shell when exposed to crayfish predators. The rotund-phenotype reduces fish predation but increases susceptibility to crayfish predation, and *vice versa* for the elongate-snail phenotype. Future studies of inducible morphological defences will clearly profit from investigations involving several different predator environments that induce opposing shifts in morphological structures.

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