

PREDATOR-INDUCED BEHAVIOURAL RESPONSES: TADPOLES OF THE NEOTROPICAL FROG *PHYLLOMEDUSA TARSIVS* DO NOT RESPOND TO ALL PREDATORS

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Many species show behavioural responses to predators that reduce predation mortality but are assumed to be costly. We tested whether an induced behavioural response is predator-specific and whether the strength is related to the risk of being killed by a predator. We used tadpoles of the neotropical frog *Phyllomedusa tarsivus* as prey, and larvae of an aeshnid dragonfly and belostomatid bugs as predators. Belostomatids killed twice as many tadpoles within 24 hours as aeshnids did. Tadpoles reduced activity in the presence of aeshnids by 30% but did not respond at all to the more dangerous belostomatids. Tadpoles did not show spatial avoidance of predators. We favour the explanation that tadpoles of *P. tarsivus* did not respond to belostomatids because belostomatids are encountered too rarely for evolution to favour an induced response to belostomatids.

Key words: amphibian, distribution, induced response, *Phyllomedusa tarsivus*, predation risk, tadpole

INTRODUCTION

Predators are well-known for inducing antipredator responses in their prey (Tollrian & Harvell, 1999). The responses include changes in life history (Skelly & Werner, 1990; Sih & Moore, 1993; Warkentin, 1995), morphology (Smith & Van Buskirk, 1995; Van Buskirk, McCollum & Werner, 1997; Van Buskirk & Schmidt 2000), and behaviour (Lawler, 1989; Horat & Semlitsch, 1994; Anholt & Werner, 1995). These changes in life history, morphology or behaviour can reduce predation rates but the induced phenotype generally suffers a cost, usually reduced growth rates (e.g., Skelly, 1992; Skelly & Werner, 1990; Van Buskirk et al., 1997; Relyea & Werner, 1999; Van Buskirk 2000).

Because there is a cost to an antipredator response, natural selection should favour precise antipredator responses. The cost of ignoring a dangerous predator is an increased probability of death, whereas the cost of overestimating risk is a loss of opportunities to feed or mate. Therefore, an induced response should be related to the risk of predation and be predator-specific where predators differ in predation risk (Sih, 1987). This prediction has been tested several times with one predator and two prey species. These studies generally showed that the more vulnerable prey species reacted more strongly (see Sih, 1987 for a review). Such studies are at risk of confounding predation risk and interspecific differences between prey species. Several studies have measured behavioural responses of one prey species to

different predators, but only a few have related behaviour to predation risk (Skelly, 1994; Anholt & Werner, 1995; Lefcort, 1996; Van Buskirk & McCollum 2000). This study aims at testing whether one species of prey reacts differently to two species of predator that differ in predation threat.

Tadpoles offer an excellent opportunity to test whether an induced response is related to the risk of predation. They show predator-induced responses in behaviour, morphology, life history or habitat use (Lawler, 1989; Stauffer & Semlitsch, 1993; Warkentin, 1995; Smith & Van Buskirk, 1995). Behavioural responses often include changes in levels of activity (Lawler, 1989; Skelly & Werner, 1990; Horat & Semlitsch, 1994). More active individuals (or species) have a higher probability of being captured by a predator (Cooke, 1971; Woodward, 1983; Azevedo-Ramos, Van Sluys, Hero & Magnusson, 1992; Skelly, 1994; Lefcort, 1996; Van Buskirk & McCollum 2000). Activity level is also related to feeding and growth rates with more active individuals feeding more and growing faster (Skelly & Werner, 1990; Werner, 1991; Skelly, 1992; Relyea & Werner, 1999). Therefore, tadpoles have to trade-off growth and mortality rates that both depend on behaviour.

In this study, we experimentally tested whether tadpoles of the neotropical frog *Phyllomedusa tarsivus* (Anura: Hylidae) reduce activity and spatial distribution in the presence of two predator species. We tested whether the reduction in activity and the change in spatial distribution are predator-specific, and whether the strength of the induced response is related to the risk of predation.

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MATERIAL AND METHODS

STUDY SITE AND STUDY ANIMALS

The study was carried out in reserve 1501 of the Biological Dynamics of Forest Fragments Project (Instituto Nacional de Pesquisas da Amazônia/Smithsonian Institution), 80 km north of Manaus, Brazil (Gascon, 1991, 1992; Zimmerman & Simberloff, 1996). We used a small area of *terra firme* forest cleared of understory to conduct the experiments under natural light conditions. We chose tadpoles of *Phyllomedusa tarsius* as prey because Azevedo-Ramos *et al.* (1992) showed that less active tadpoles of this species get killed less often by aeshnid dragonfly larvae. We chose larvae of an aeshnid dragonfly and adult belostomatid giant water bugs as predators because (1) given the size difference, they were likely to differ with respect to predation risk; (2) we had previous information about their effects on tadpole communities (Gascon, 1992); (3) both are sit-and-wait predators (Kehr & Schnack, 1991; Pritchard, 1965); (4) both use visual (and tactile) cues for prey detection (Peckarsky, 1984; most invertebrate predators detect moving prey more easily than stationary prey [Wellborn, Skelly & Werner, 1996]); and (5) tadpoles of other species are known to change behaviour in response to both predators (Kiesecker, Chivers & Blaustein, 1996).

Tadpoles and predators were collected from shallow ponds (see Gascon, 1991) a few days prior to the experiment. There were no aquatic plants in the source ponds. Tadpoles were kept together in a large plastic tub prior to the experiments. Tadpoles occurred with both predators. Thus, our tadpoles were unlikely to be predator-naïve (e.g. Chivers, Wisenden & Smith, 1996). We found no belostomatids in ponds where we collected aeshnids and vice versa, but they often do co-exist (Gascon, 1992; Hero, Gascon & Magnusson, 1998). We formed groups of tadpoles from the stock for our experiments. Thus, each group contained some tadpoles that experienced aeshnids and some that experienced belostomatids.

The ponds sampled contained tadpoles of other anurans (*Phyllomedusa tomopterna*, *Hyla minuta*, *Osteocephalus taurinus* and *Bufo marinus*), and various other predators (hemipterans, spiders, and dragonfly and damselfly larvae).

Tadpole snout-vent length was on average 9.6 mm (range: 5.0 to 12.8 mm). Gosner (1960) developmental stages were between 25 and 30. This sample represents the range of sizes and developmental stages of *P. tarsius* tadpoles we encountered in the field in August 1995. Belostomatids had a mass of 6.0 ± 0.97 g (mean \pm SD; $n=10$) and a length 64.1 ± 3.95 mm. The mass of an aeshnid was 0.5 ± 0.27 g and length was 32.6 ± 6.43 mm ($n=9$). Belostomatids were adults whereas aeshnids were at mid- to late-developmental stages. All predators were able to kill all sizes of tadpoles.

EXPERIMENTS

We measured behavioural responses of tadpoles to predators and predation risk in separate experiments during August 1995. We used circular plastic basins (diameter 30 cm, depth 11 cm; Gascon, 1992) filled to a depth of 5 cm with water from the same nearby stream for both experiments (*P. tarsius* never occurs in streams or streamside pools; these have very different, fish-dominated predator communities [Gascon, 1991, 1992; Zimmerman & Simberloff, 1996; Hero *et al.*, 1998]). After every trial, basins were cleaned and refilled. There was no leaf litter, nor aquatic plants in the basins (habitat complexity does not affect the difference in predation rates between aeshnids and belostomatids [Babbitt & Jordan, 1996]). We only added a small piece of twig as a perch for aeshnids.

For measuring the behavioural responses of tadpoles we added two predator cages on opposite sides of the basins. Cages were made of plastic mesh and were large enough for predators to move – tadpoles could therefore detect chemical, visual and tactile cues from predators. We then added one predator to one of the cages (or both cages were left empty for controls) and added ten tadpoles to the basins (tadpoles of *P. tarsius* may form schools [Duellman & Trueb, 1994]). We let the predators and tadpoles acclimatize to the experimental conditions for at least six hours before we started to measure behaviour. We scored each tadpole as being inactive (i.e. no visible movement) or active (i.e. tadpoles either remaining perpendicular in the water column by means of tail movements or swimming [Azevedo-Ramos *et al.*, 1992]; tadpoles are midwater filter feeders [Duellman & Trueb, 1994]). We measured activity of tadpoles seven times at intervals of five minutes. From these data we calculated the proportion of tadpoles active over the course of 30 mins. We also counted in the same way the number of tadpoles that were on the side of the basin opposite to the cage that contained the predator. We used this as our measure of spatial avoidance. We used six groups of ten tadpoles to measure behavioural responses. Groups of ten tadpoles were formed once and were chosen haphazardly from the stock of available tadpoles. Each group was tested with and without each type of predator. We only measured one treatment per group on any one day. Tadpoles were therefore tested over three days. On each day, two groups were subjected to aeshnids, belostomatids or empty predator cages. Groups were rotated through the treatments according to a latin square design.

To measure predation risk we added ten tadpoles and one predator – either belostomatid or aeshnid – to a basin at 0700 hr the first day and at 0800 hr the following day. We then counted the number of tadpoles alive every hour for a period of 16 hr, and again 24 hr after the beginning of the experiment. Predators and tadpoles were used only once. We conducted 12 replicate predation trials for each predator species over a period of three days (three to five trials per predator species and

day). Some trials were excluded from the analysis because belostomatids escaped ($n=3$) or aeshnids moulted ($n=2$).

Clearly, we measured predation risk in an environment much simpler than a natural pond. Therefore, our estimates of risk cannot directly be related to conditions in the field. However, our experimental approach does permit measurement of differences between predators without the confounding effects of predator satiation, prey density, prey size or presence of other predator species. Our experiments therefore permit analysis of the qualitative relationship between predation risk (i.e. which predator is more of a threat) and the tadpole behaviour that we are interested in. If the simple approach of using consumption rate as a measure of predation risk fails, it means that other factors may be important. We will discuss which other factors we believe are important below.

Tadpoles were fed *ad libitum* prior to the behaviour and predation experiments, but could not feed during the experiment. Prior to the behaviour measurements and predation trials, predators were fed tadpoles of both *P. tarsi* and *P. tomopterna*, with *P. tarsi* being more abundant in our samples, but were not allowed to feed for 24 hr prior to their use in the experiments.

RESPONSE VARIABLES AND STATISTICAL ANALYSIS

Using the SAS procedure GLM, we tested for effects of predator identity and group on the activity (proportion of tadpoles active), and spatial avoidance (proportion of tadpoles away from the predator) of tadpoles in an ANOVA after arcsine squareroot transformation of the data. We used the predator x group interaction as our error term for the construction of *F*-tests because groups were not replicated (Potvin, 1993). This way of analysing our data assumes the absence of a predator x group interaction. This assumption seems valid, as groups of tadpoles were assembled haphazardly. Group may be considered a random effect, but the computation of the sums of squares is the same in this analysis (Potvin, 1993). Differences among treatments were tested using Tukey's studentized range test. The critical value of the Tukey test depends on the error df of the ANOVA (Zar, 1999: 211). Thus, we used the predator x group interaction df for the computation of the Tukey test. We tested the effectiveness of the two predators (= number of tadpoles killed within 24 hr) using a Mann-Whitney *U* test (i. e. a Wilcoxon two-sample test in the terminology of SAS procedure NPAR1WAY). Only one belostomatid killed all ten tadpoles. Therefore data are unlikely to be censored.

RESULTS

Belostomatids killed and consumed more than twice as many tadpoles within 24 hr as did aeshnid dragonfly larvae (belostomatids: 7.6 ± 0.57 tadpoles killed [mean \pm SD]; aeshnid: 3.3 ± 0.30 tadpoles killed; Wilcoxon two-sample test, $Z=3.47$, $P=0.0005$; Fig. 1). As belostomatids were much larger than aeshnids, one

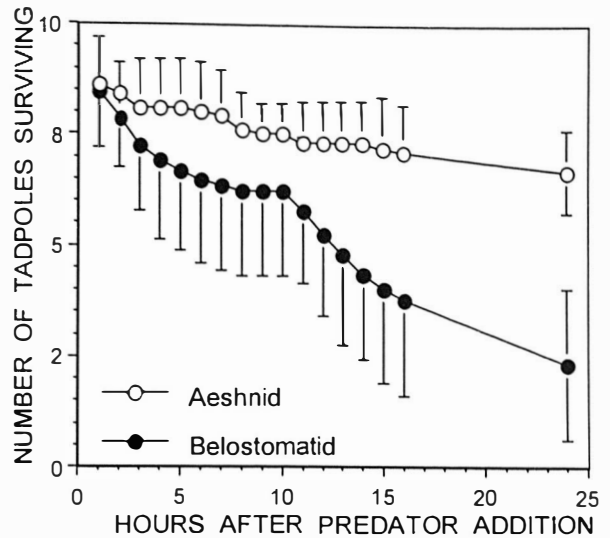


FIG. 1. Survivorship curves for tadpoles in the predation experiment. Open symbols represent predation by dragonfly larvae, filled symbols predation by belostomatids. Means \pm SD are from $n=10$ (aeshnids) and $n=9$ (belostomatids) replicates.

might expect this result. Our intention was to test for a relationship between predation risk and the strength of behavioural responses. We therefore needed an estimate of predation risk. Body size *per se* is not an indicator of predation risk.

Tadpoles of *P. tarsi* were active for $49 \pm 4\%$ of the time when no predator was present. They reduced activity significantly (biologically and statistically) in the presence of aeshnid dragonfly larvae by one third ($33 \pm 4\%$ active), but did not reduce it in the presence of belostomatids ($48 \pm 4\%$ active; Table 1, Fig. 2). Tukey's studentized range test ($\alpha=0.05$) indicated no difference between the response of tadpoles in the control and belostomatid treatment, but activity of tadpoles in the presence of aeshnids was found to be different from that under both other treatments. Groups of tadpoles did not differ significantly in activity (Table 1). This suggests

TABLE 1. Summary of the univariate analyses of variance for activity level (proportion of tadpoles active or showing swimming and tail movement) and microhabitat use (proportion of tadpoles away from predator). The predator x group interaction was used as the error term. Data were arcsine square-root transformed for statistical analysis.

Source of variation	df	Mean squares	<i>F</i>	<i>P</i>
<i>Activity</i>				
Predator	2	0.0516	8.32	0.0075
Group	5	0.0180	2.92	0.0704
Predator x group	10	0.0062		
<i>Spatial Avoidance</i>				
Predator	2	0.0025	0.13	0.8804
Group	5	0.0121	0.62	0.6913
Predator x group	10	0.0197		

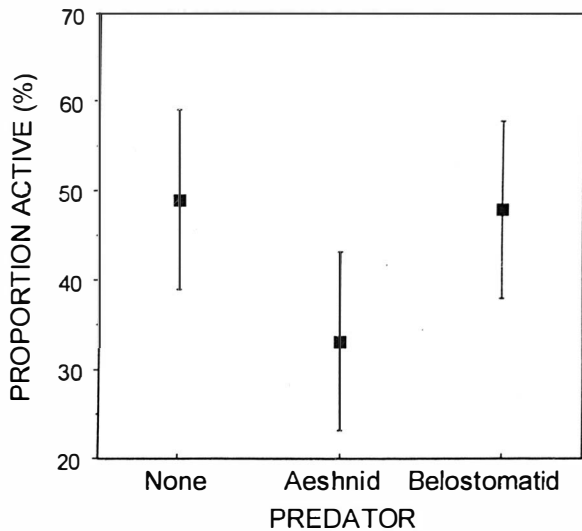


FIG. 2. Effects of predators on activity of tadpoles of *Phyllomedusa tarsius*. Means \pm SD are from six replicates each.

that the order of behavioural measurements did not affect behavioural responses.

Tadpoles of *P. tarsius* did not show spatial avoidance of predators (proportion away from predator: control 59 \pm 6%, belostomatid 63 \pm 4%, aeshnid 64 \pm 6%; Table 1). The Tukey test indicated no statistical difference between treatments. Groups of tadpoles did not differ significantly (Table 1).

DISCUSSION

Behavioural responses of tadpoles of *Phyllomedusa tarsius* to predatory insects were predator-specific. Tadpoles reacted strongly to the presence of aeshnid dragonfly larvae but showed no response to belostomatids. Responses to predators can be specific because tadpoles recognize different species and can discriminate between predators, or because different predators release different amounts of chemical cue and tadpoles respond to the amount of chemical cue available. We suggest that tadpoles of *P. tarsius* can discriminate between predator species. In our behaviour experiment, no cues associated with feeding were available. Only cues released by a predator after a day of starving were available (e.g. metabolic products). Because belostomatids have a mass twelve times greater than that of aeshnids, we would expect that the behav-

ioural response to belostomatids would be stronger if it is based on the amount of cue released. This was not the case. We conclude that the behavioural responses are based on unique cues released by predators and that tadpoles use these cues for predator recognition.

The lack of behavioural response to belostomatids is unexpected for two reasons: (1) it is one of the few studies where prey did not react behaviourally to a predator that is potentially dangerous (for similar results see Sih, 1992; McPeck, 1990; Griffiths *et al.*, 1998); and (2) the response did not depend on predation risk. We first discuss why behavioural responses are not related to predation risk, and go on to discuss why tadpoles of *P. tarsius* did not respond to belostomatids at all.

The tadpoles' lack of response to an apparently high-risk predator was unexpected, but it is possible that the relative danger posed by the two predators in the field was altered in our experimental conditions. Predation rates may be lower for belostomatids in a more natural predation trial and in the field. Indeed, the impact of belostomatids on tadpole communities seems to be lower than our results suggest (most likely because they are rather rare; Hero *et al.*, 1998). Under experimental conditions, however, belostomatids appear to pose more of a threat than aeshnids. Babbitt & Jordan (1996) found in an experiment very similar to ours that juvenile *Belostoma fluminea* (average mass 0.27 g) consumed significantly more tadpoles than larvae of the dragonfly *Anax junius* (average mass 1.36 g) in predation trials (54% and 30% of all tadpoles, respectively, were consumed). Even if we overestimated predation risk, we are confident that belostomatids are potentially dangerous predators. Consequently, a behavioural response would seem beneficial. The toad tadpoles studied by Kiesecker *et al.* (1996) reduced activity in the presence of belostomatids. This suggests that reducing activity in the presence of belostomatids is adaptive because it is likely to reduce the probability of being killed by a belostomatid. Thus, based on potential killing rates and the studies by Babbitt & Jordan (1996) and Kiesecker *et al.* (1996), we expect at least a weak behavioural response. If, as we did, we find no behavioural response at all to a potentially dangerous predator then we must ask either why tadpoles do not change behaviour and which factors are responsible for the lack of a response, or how does a tadpole measure predation risk?

TABLE 2. Distribution and overlap of *Phyllomedusa* tadpoles and their predators at the study site. $n=29$ ponds were surveyed. Data were extracted from Hero *et al.* (1998). Absolute values are given in parentheses.

Predators	Proportion of ponds in which both <i>P. tarsius</i> and predators were found at least once	Proportion of visits in which a predator is encountered, given that it uses the pond (= proportion of time a pond is used)	Proportion of time a predator is present when <i>P. tarsius</i> tadpoles are present in a pond
Aeshnids	1.0 (14/14)	0.5	0.5
Belostomatids	0.42 (6/14)	0.25	0.105

Why do tadpoles of *P. tarsi* not respond at all to a potentially dangerous predator? A variety of factors has been proposed and shown to affect larval amphibian antipredator behaviour, and activity in particular; e.g. resource availability (e.g. Anholt & Werner 1995); predator-naïvety, experience and learning (e.g. Sih & Kats, 1994); predator diet (e.g. Laurila, Kujasalo & Ranta, 1997); presence of constitutive defences such as skin toxins (e.g., Kiesecker *et al.*, 1996); predator speed (Werner & Anholt, 1993) and cues available for predator detection (e.g., Stauffer & Semlitsch, 1993). These factors can affect the strength of a response in an experiment, including the lack of response to a predator. However, they cannot explain the differential behavioural responses that we found. Conditions were the same, and both predator species and tadpoles were collected from ponds where they experienced the same environment previous to the experiment. Similarly, other factors such as feeding style (chewing versus sucking) cannot be responsible because predators could not feed while we were measuring behaviour. We therefore suggest that these factors and the experimental design are not responsible for the results we obtained.

We propose that tadpoles of *P. tarsi* do not respond to belostomatids because they encounter them too rarely. As a consequence, there was no opportunity for natural selection to shape induced behavioural responses. The reasoning is as follows. On the one hand, if organisms always encounter predators then we expect constitutive defences rather than induced defences to evolve. For example, tadpoles of the frog *Pseudacris crucifer* nearly always encounter predators during their larval life. As expected, their antipredator phenotype is such that it confers high fitness in the presence of predators (Skelly, 1995; Smith & Van Buskirk, 1995) but shows weak induced responses (Smith & Van Buskirk, 1995). On the other hand, if organisms never encounter predators then predator-induced responses do not evolve (e.g. Sih, 1986; McPeck, 1990; Parejko & Dodson, 1991; Neill, 1992; Pijanowska, Weider & Lampert, 1993). Salamander larvae that do not have contact with fish do not respond behaviourally to them (Kats, Petranks & Sih, 1988; Sih, 1992). Tadpoles of the frogs *Ascaphus truei* and *Alytes muletensis* respond to predators with which they coexist but do not respond to predators they do not usually encounter (Feminella & Hawkins, 1994; Griffiths *et al.*, 1998). Induced responses will only evolve in a heterogeneous environment: prey must encounter predators sometimes, but predators must be neither ubiquitous nor absent (Via & Lande, 1985; van Tienderen, 1991; De Jong, 1995). There is likely to be an encounter rate > 0 and < 1 , below and above which constitutive absence or presence will be favoured over induced defences despite environmental heterogeneity (e.g. Riessen, 1992). Adaptations should be more precise in common or source environments than in rare or sink environments (Kawecki & Stearns, 1993).

We suggest that although *P. tarsi* does encounter belostomatids from time to time, this happens too rarely for an induced response to evolve. In contrast, aeshnid dragonflies are encountered more often and an induced response has evolved. At our study site, aeshnids occur in twice as many ponds as belostomatids (Table 2; the sources of the distributional data that includes a description of the sampling methods are Gascon, 1992 and personal communication; Hero *et al.*, 1998). Aeshnids are found in all ponds that are used by *P. tarsi* whereas belostomatids are found in only about 40% of the ponds. The overlap between frogs and predators is not 1.0 and 0.4, however. Aeshnids and belostomatids are found only in c. 50% and 25% of the visits to a pond, respectively (Hero *et al.*, 1998; C. Gascon, personal communication). This means aeshnids are using c. 50% of the ponds at a given time whereas belostomatids use only c. 10% of the ponds at a given time (see Table 2). *Phyllomedusa tarsi* will thus only encounter belostomatids in 10% of the ponds it uses for reproduction. Even though the theory of induced responses does not give lower limits for encounter rates below which induced responses do not evolve, the spatiotemporal overlap between belostomatids and *P. tarsi* seems to have been too low for an induced behavioural response to evolve.

However, many evolutionary ecologists would argue that an overlap of 10% between predators and prey is large enough for the evolution of an induced defence (J. Van Buskirk and R. Altwegg, personal communications). Clearly, tadpoles will encounter belostomatids from time to time and there may be selection for an induced defence. The net effect of selection may be weak, however. As expected from the general positive relationship between distribution and abundance, belostomatids are not only less widely distributed than aeshnids, but they are also less abundant within ponds (Hero *et al.*, 1998). Thus, they may have a low selective impact on tadpole populations even when present. Alternatively, belostomatids may have strong effects on tadpole populations (as suggested by Fig. 1). If so, the ponds with belostomatids may represent sinks (Pulliam, 1988). Few frogs will metamorphose from such ponds and most adults will have grown up in belostomatid-free ponds. As a consequence, the effect of selection may be overridden by gene flow from belostomatid-free (source) ponds (Holt & Gaines, 1992; Kawecki & Stearns, 1993; Kawecki, 1995; Holt, 1996; Storer & Sih, 1998). In sum, selection for an induced defence will be in place from time to time, but it is likely to be weak or overridden by the effects of gene flow.

Our hypothesis for the absence of an induced behavioural defence seems plausible but we have no experimental test. However, such a test would be possible – there are other species of *Phyllomedusa* on our study site that are either more and less abundant than *P. tarsi*. In the nearby reserve of 'Adolfo Ducke' belostomatids do not occur at all. Such variation in

abundance and overlap of predators and prey could be used in undertaking a comparative test of our hypothesis.

Our expectation that behavioural responses are predator-specific was met, although in an unexpected way. Rather than showing that the induced response depends on predation risk, we showed that tadpoles of *P. tarsi* do not respond at all to a potentially dangerous predator. The predator appears to be too rare for the evolution of an induced defense. We suggest that the presence and strength of an induced defence does not only depend on predation risk but also on the abundance and distribution in space and time of predators and prey. This calls for theoretical studies that investigate how frequently prey must encounter specific predators if predator-specific induced responses are to evolve, and how abundance and predation rate interact in shaping induced responses.

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REFERENCES

- Anholt, B. R. & Werner, E. E. (1995). Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology* **76**, 2230-2234.
- Azevedo-Ramos, C., Van Sluys, M., Hero, J.-M. & Magnusson, W. E. (1992). Influence of tadpole movement on predation by odonate naiads. *J. Herp.* **26**, 335-338.
- Babbitt, K. J. & Jordan, F. (1996). Predation on *Bufo terrestris* tadpoles: effects of cover and predator identity. *Copeia* **1996**, 485-488.
- Chivers, D. P., Wisenden, B. D. & Smith, R. J. F. (1996). Damsel larvae learn to recognize predators from chemical cues in the predator's diet. *Anim. Behav.* **52**, 315-320.
- Cooke, A. S. (1971). Selective predation by newts on frog tadpoles treated with DDT. *Nature* **229**, 275-276.
- De Jong, G. (1995). Phenotypic plasticity as a product of selection in a variable environment. *Amer. Nat.* **145**, 493-512.
- Duellman, W. E. & Trueb, L. (1994). *Biology of amphibians*. Baltimore: Johns Hopkins University Press.
- Feminella, J. W. & Hawkins, C. P. (1994). Tailed frog tadpoles differentially alter their feeding behavior in response to non-visual cues from four predators. *J. North Amer. Bent. Soc.* **13**, 310-320.
- Gascon, C. (1991). Population- and community-level analyses of species occurrences of central Amazonian rainforest tadpoles. *Ecology* **72**, 1731-1746.
- Gascon, C. (1992). Aquatic predators and tadpole prey in central Amazonia: field data and experimental manipulations. *Ecology* **73**, 971-980.
- Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* **16**, 183-190.
- Griffiths, R. A., Schley, L., Sharp, P. E., Dennis, J. L. & Román, A. (1998). Behavioural responses of Mallorcan midwife toad tadpoles to natural and unnatural snake predators. *Anim. Behav.* **55**, 207-214.
- Hero, J.-M., Gascon, C. & Magnusson, W. E. (1998). Direct and indirect effects of predation on tadpole community structure in the Amazon rainforest. *Aust. J. Ecol.* **23**, 474-482.
- Holt, R. D. (1996). Demographic constraints in evolution: towards unifying the evolutionary theories of senescence and niche conservatism. *Evol. Ecol.* **10**, 1-11.
- Holt, R. D. & Gaines, M. S. (1992). Analysis of adaptation in heterogeneous landscapes – implications for the evolution of fundamental niches. *Evol. Ecol.* **6**, 433-447.
- Horat, P. & Semlitsch, R. D. (1994). Effects of predation risk and hunger on the behavior of two species of tadpoles. *Behav. Ecol. Sociobiol.* **34**, 393-401.
- Kats, L. B., Petranks, J. W. & Sih, A. (1988). Antipredator defenses and the persistence of amphibian larvae with fishes. *Ecology* **69**, 1865-1870.
- Kawecki, T. J. (1995). Demography of source-sink populations and the evolution of ecological niches. *Evol. Ecol.* **9**, 38-44.
- Kawecki, T. J. & Stearns, S. C. (1993). The evolution of life histories in spatially heterogeneous environments: optimal reaction norms revisited. *Evol. Ecol.* **7**, 155-174.
- Kehr, A. I. & Schnack, J. A. (1991). Predator-prey relationship between giant water bugs (*Belostoma oxyurum*) and larval anurans (*Bufo arenarum*). *Alytes* **9**, 61-69.
- Kiesecker, J. M., Chivers, D. P. & Blaustein, A. R. (1996). The use of chemical cues in predator recognition by western toad tadpoles. *Anim. Behav.* **52**, 1237-1245.
- Laurila, A., Kujasalo, J. & Ranta, E. (1997). Different antipredator behaviour in two anuran tadpoles: effects of predator diet. *Behav. Ecol. Sociobiol.* **40**, 329-336.
- Lawler, S. P. (1989). Behavioral responses to predators and predation risk in four species of larval anurans. *Anim. Behav.* **38**, 1039-1047.
- Lefcort, H. (1996). Adaptive, chemically mediated fright response in tadpoles of the southern leopard frog, *Rana utricularia*. *Copeia* **1996**, 455-459.
- McPeck, M. A. (1990). Behavioral differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. *Ecology* **71**, 1714-1726.
- Neill, W. E. (1992). Population variation in the ontogeny of predator-induced vertical migration of copepods. *Nature* **356**, 54-57.
- Parejko, K. & Dodson, S. I. (1991). The evolutionary ecology of an antipredator reaction norm: *Daphnia*

- pulex* and *Chaoborus americanus*. *Evolution* **45**, 1665-1674.
- Peckarsky, B. L. (1984). Predator-prey interactions among aquatic insects. In *The ecology of aquatic insects*, 196-254. Resh, V. H. and D. M. Rosenberg (Eds). New York: Praeger.
- Pijanowska, J., Weider, L. J. & Lampert, W. (1993). Predator-mediated genotypic shifts in a prey population: experimental evidence. *Oecologia* **96**, 40-42.
- Potvin, C. (1993). ANOVA: experiments in controlled environments. In *Design and analysis of ecological experiments*, 46-68. Scheiner, S. M. and Gurevitch, J. (Eds). New York: Chapman & Hall.
- Pritchard, G. (1965). Prey capture by dragonfly larvae (Odonata: Anisoptera). *Can. J. Zool.* **43**, 271-289.
- Pulliam, H. R. (1988). Sources, sinks, and population regulation. *Amer. Nat.* **132**, 652-661.
- Relyea, R. A. & Werner, E. E. (1999). Quantifying the relation between predator-induced behavior and growth performance in larval anurans. *Ecology* **80**, 2117-2124.
- Riessen, H. P. (1992). Cost-benefit model for the induction of an antipredator defense. *Amer. Nat.* **140**, 349-362.
- Sih, A. (1986). Antipredator responses and the perception of danger by mosquito larvae. *Ecology* **67**, 434-441.
- Sih, A. (1987). Predators and prey lifestyles: an evolutionary and ecological overview. In: *Predation: direct and indirect impacts on aquatic communities*, 203-224. Kerfoot, W. C. and Sih, A. (Eds). Hanover: University Press of New England.
- Sih, A. (1992). Integrative approaches to the study of predation: general thoughts and a case study on sunfish and salamander larvae. *Ann. Zool. Fennici* **29**, 183-198.
- Sih, A. & Kats, L. B. (1994). Age, experience, and the response of streamside salamander hatchlings to chemical cues from predatory sunfish. *Ethology* **96**, 253-259.
- Sih, A. & Moore, R. D. (1993). Delayed hatching of salamander eggs in response to enhanced larval predation risk. *Amer. Nat.* **142**, 947-960.
- Skelly, D. K. (1992). Field evidence for a cost of behavioral antipredator response in a larval amphibian. *Ecology* **73**, 704-708.
- Skelly, D. K. (1994). Activity level and the susceptibility of anuran larvae to predation. *Anim. Behav.* **47**, 465-468.
- Skelly, D. K. (1995). A behavioral trade-off and its consequences for the distribution of *Pseudacris* treefrog larvae. *Ecology* **76**, 150-164.
- Skelly, D. K. & Werner, E. E. (1990). Behavioral and life-historical responses of larval american toads to an odonate predator. *Ecology* **71**, 2313-2322.
- Smith, D. C. & Van Buskirk, J. (1995). Phenotypic design, plasticity, and ecological performance in two tadpole species. *Amer. Nat.* **145**, 211-233.
- Stauffer, H.-P. & Semlitsch, R. D. (1993). Effects of visual, chemical and tactile cues of fish on the behavioral responses of tadpoles. *Anim. Behav.* **46**, 355-364.
- Storfer, A. & Sih, A. (1998). Gene flow and ineffective antipredator behavior in a stream-breeding salamander. *Evolution* **52**, 558-565.
- Tollrian, R. & Harvell, C. D. (Eds) (1999). *The ecology and evolution of inducible defenses*. Princeton: Princeton University Press.
- Van Buskirk, J. (2000). The cost of an inducible defense in anuran larvae. *Ecology* **81**, 2813-2821.
- Van Buskirk, J. & McCollum, S. A. (2000). Functional mechanisms of an inducible defense in tadpoles: morphology and behavior influence mortality risk from predation. *J. Evol. Biol.* **13**, 336-347.
- Van Buskirk, J., McCollum, S. A. & Werner, E. E. (1997). Natural selection for environmentally induced phenotypes in tadpoles. *Evolution* **51**, 1983-1992.
- Van Buskirk, J. & Schmidt, B. R. (2000). Predator-induced phenotypic plasticity in larval newts: trade-offs, selection, and variation in nature. *Ecology* **81**, 3009-3028.
- van Tienderen, P. H. (1991). Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution* **45**, 1317-1331.
- Via, S. & Lande, R. (1985). Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* **39**, 505-522.
- Warkentin, K. M. (1995). Adaptive plasticity in hatching age: a response to predation risk trade-offs. *Proc. Nat. Acad. Sci. U. S. A.* **92**, 3507-3510.
- Wellborn, G. A., Skelly, D. K. & Werner, E. E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.* **27**, 337-363.
- Werner, E. E. (1991). Nonlethal effects of a predator on competitive interactions between two anuran larvae. *Ecology* **72**, 1709-1720.
- Werner, E. E. & Anholt, B. R. (1993). Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Amer. Nat.* **142**, 242-272.
- Woodward, B. D. (1983). Predator-prey interactions and breeding-pond use of temporary species in a desert anuran community. *Ecology* **64**, 1549-1555.
- Zar, J. H. (1999). *Biostatistical analysis* (Fourth edition). Eaglewood Cliffs: Prentice-Hall International Editions.
- Zimmerman, B. L. & Simberloff, D. (1996). An historical interpretation of habitat use by frogs in a central Amazonian forest. *J. Biogeogr.* **23**, 27-46.