



Visual cues contribute to predator detection in anuran larvae

ATTILA HETTYEY^{1,2*}, FRANZISKA RÖLLI¹, NINA THÜRLIMANN¹, ANNE-CATHERINE ZÜRCHER¹ and JOSH VAN BUSKIRK¹

¹*Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, CH-8057, Zürich, Switzerland*

²*Konrad Lorenz Institute of Ethology, Department of Integrative Biology and Evolution, University of Veterinary Medicine Vienna, Savoyenstrasse 1A, A-1160 Vienna, Austria*

Received 29 January 2012; revised 13 March 2012; accepted for publication 13 March 2012

The ability of prey to detect predators directly affects their probability of survival. Chemical cues are known to be important for predator detection in aquatic environments, but the role of other potential cues is controversial. We tested for changes in behaviour of *Rana temporaria* tadpoles in response to chemical, visual, acoustic, and hydraulic cues originating from dragonfly larvae (*Aeshna cyanea*) and fish (*Gasterosteus aculeatus*). The greatest reduction in tadpole activity occurred when all cues were available, but activity was also significantly reduced by visual cues only. We did not find evidence for tadpoles lowering their activity in response to acoustic and hydraulic cues. There was no spatial avoidance of predators in our small experimental containers. The results show that anuran larvae indeed use vision for predator detection, while acoustic and hydraulic cues may be less important. Future studies of predator-induced responses of tadpoles should not only concentrate on chemical cues but also consider visual stimuli. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, 106, 820–827.

ADDITIONAL KEYWORDS: anti-predator behaviour – induced defence – sensory modality – tadpole.

INTRODUCTION

Responding appropriately to predation threat is of fundamental importance for individual fitness (Sih, 1980; Lima & Dill, 1990). The first stage of response involves detecting risk accurately. In aquatic environments, the most important sensory modalities for predator detection are olfaction and vision (Tollrian & Harvell, 1999). Tactile cues, sensed by mechanoreceptors embedded in the skin, can also help detect immediate threats. Further modalities in some taxa include electric and hydraulic cues, sensed by electro- and mechanoreceptors located in the lateral line system. Acoustic cues (also referred to as sonic or auditory cues) may also play a role in predator detection if sound is generated by the predator itself or by prey under attack (e.g. Hoy, 1992; Natale *et al.*, 2011; Wilson *et al.*, 2011).

In anuran larvae, chemical cues play a major role in predator detection (e.g. Kiesecker, Chivers & Blaustein, 1996; Laurila, 2000; Benard, 2006), but the importance of other sensory modalities is poorly known and controversial. Tadpoles are near-sighted (Hoff *et al.*, 1999) and their habitat often consists of turbid water and dense vegetation; consequently, vision has rarely been studied in the context of predation and is often dismissed as unimportant (Stauffer & Semlitsch, 1993; Kiesecker *et al.*, 1996; Jowers *et al.*, 2006; Parris, Reese & Storfer, 2006; Saidapur *et al.*, 2009). Nonetheless, tadpoles do use vision in other contexts, such as adjusting their swimming movements to those of conspecifics (Wassersug, Lum & Potel, 1981; Rot-Nikcevic, Denver & Wassersug, 2005; Gouchie, Roberts & Wassersug, 2008). Also, anuran larvae respond to tactile stimulation (Rot-Nikcevic *et al.*, 2005), and functional mechanoreceptors in the lateral line system allow them to sense water movements (Lannoo, 1999; Simmons, Costa &

*Corresponding author. E-mail: hettyeyattila@yahoo.de

Gerstein, 2004; Schmidt, Knowles & Simmons, 2011). One study suggests that hydraulic cues may help tadpoles to detect predators (Stauffer & Semlitsch, 1993). Anurans are unable to sense electric cues because they lack electroreceptors (Lannoo, 1999). Whether tadpoles exploit acoustic cues in predator detection is largely unexplored, although they do have a functional inner ear (Lannoo, 1999) and some species exhibit intraspecific acoustic communication (Natale *et al.*, 2011; Reeve *et al.*, 2011).

The present study examines whether tadpoles use visual, acoustic, and hydraulic cues for predator detection. Acoustic and hydraulic cues are difficult to separate from each other in practice, so we tested their effects together. We predicted that tadpoles sensing the presence of a predator, regardless of the cue, would decrease activity and move away from the predator (Skelly & Werner, 1990; Stauffer & Semlitsch, 1993; Parris *et al.*, 2006). Behavioural responses can vary with the predator species (Van Buskirk, 2001; Teplitsky *et al.*, 2005; Hettyey *et al.*, 2011), so we included two different predators to increase the likelihood of detecting what we anticipated to be relatively subtle responses to visual, acoustic, and hydraulic cues.

METHODS

EXPERIMENTAL PROCEDURES

The prey in our experiment were tadpoles of the European common frog (*Rana temporaria* Linnaeus, 1758), which are known to show strong behavioural responses to many aquatic predators (Laurila, Kujasalo & Ranta, 1997; Van Buskirk, 2001). The predators were larval dragonflies (*Aeshna cyanea* Müller, 1764) and fish (three-spined sticklebacks, *Gasterosteus aculeatus* Linnaeus, 1758), chosen because they are important predators of amphibian larvae, and because they differ in their hunting behaviour: *Aeshna* is a sit-and-wait predator and *Gasterosteus* is an active forager. We collected six freshly laid clutches of *R. temporaria* from a pond in eastern Switzerland (47°02'N, 9°21'E), and held them separately in 10-litre aquaria until hatching. After hatching, we fed tadpoles ad libitum with rabbit chow and changed water every other day. The predators came from ponds near Zurich, Switzerland. We held 45 dragonfly larvae individually in 200-mL plastic cups, and 45 fish in groups of 15 individuals within 80-litre tubs. Predators were fed twice a week with *R. temporaria* tadpoles, but were unfed for 48 h before an experimental trial. We kept all animals in an unheated room with open windows under natural light conditions and water temperatures between 13 and 28 °C.

The experiment had a 3 × 3 complete factorial design with three combinations of cue crossed with the two

species of predator and a predator-free control. Cues were controlled by manipulating a divider that bisected the experimental chambers (polypropylene boxes; 1.0 litre; 20 × 12 × 7 cm) into two parts of equal size (10 × 12 cm). The divider was either a net with 1.4-mm mesh (assumed to transmit all cues to focal tadpoles), 5-mm-thick transparent Plexiglas (transmitting visual cues but blocking chemical, hydraulic, and possibly acoustic cues), or 0.12-mm opaque and freely vibrating polyethylene foil (assumed to transmit acoustic and hydraulic cues, but blocking chemical and visual cues). Our assumptions about the transmission properties of barriers are untested, but it is reasonable to suppose that a net transmits hydraulic and acoustic cues, Plexiglas blocks both cues, and thin foil transmits these cues to some degree. Experimental chambers were lined with a 0.3-mm polyester filter-paper on the inner surface to minimize sound reflection from the walls or interference from adjacent chambers. Lines drawn on the bottom of each chamber created six equal-sized sectors (1.67 cm wide) at increasing distance from the divider.

Trials were conducted on ten days between 9 and 20 May 2011, 16–27 days after hatching. On each day, we conducted two replicates of the predator-free control for each cue treatment and four replicates of the six combinations of predator species and cue type. These 30 chambers were arranged under two video cameras on a bed of Styrofoam, with treatments assigned at random within each group. The walls of the room were covered with high-frequency-absorbing foam. Animals were acclimatized to the experimental conditions under a dim lamp simulating night for 15 h prior to the trial: tadpoles were in the experimental chambers themselves, and predators were in similar chambers containing a divider of 4-mm opaque Plexiglas. At 09:00 h, we switched on broad-spectrum fluorescent lights, and 5 min later transferred predators to the experimental chambers and turned on the video cameras for 15 min. After each day, we washed experimental and acclimatization chambers and discarded the filter paper. Tadpoles were tested individually and only once, whereas the 45 individual predators of each species were used 2–3 times each, and assigned to treatments haphazardly.

We measured activity and location of both the tadpole and predator at 1-min intervals during the 15 min of trials using the video-recordings. Activity was an appropriate response for this study because much evidence suggests that amphibian larvae react to predation risk by decreasing movement (Lawler, 1989; Skelly, 1994; Van Buskirk & Arioli, 2002). An individual was scored as active if it was visibly feeding or swimming and as inactive if it was motionless. Location was defined as the sector that the animal occupied, with higher values corresponding to increasing dis-

Table 1. The number of trials for each combination of cue treatment and predator treatment available for analyses excluding or including data on predator behaviour

Cue treatment	Predator treatment				
	Without predator behaviour			With predator behaviour	
	Control	Dragonfly	Fish	Dragonfly	Fish
All cues	19	37	34	34	34
Visual cues only	22	39	33	39	32
Acoustic and hydraulic cues	19	27	33	26	33
Total	60	103	100	99	99

The depicted sample sizes represent the number of trials where data on both tadpole activity and tadpole location could be used. Hence, sample sizes in the separate analyses on tadpole activity and on tadpole location were somewhat higher.

tances from the barrier. Several replicates were lost, for various reasons. One chamber with acoustic and hydraulic cues developed a leak and was excluded from all dates. Visual obstructions required us to discard five replicates of tadpole activity, 24 replicates of tadpole location, and five replicates of predator behaviour. In three cases we mistakenly did not add a predator to the chamber, which lowered sample size in the predator treatments and increased the number of trials in the control. In the end, 263 trials were available for analyses of the effects of cue treatment and predator treatment on tadpole behaviour, and 198 trials for analyses of the effects of predator behaviour on tadpoles (details in Table 1).

STATISTICAL ANALYSES

The behaviour of individual tadpoles and predators did not change over the 15-min observation period (all $P \geq 0.29$ in repeated-measures analyses), so analyses were done on averages for each individual. Tadpole activity and location were not highly correlated, and were therefore analysed independently ($r_s = 0.017$, $N = 263$, $P = 0.78$).

First, we investigated whether the two predators differed in their behaviour and whether behaviour depended on cue treatment or date. Predator activity and location were dependent variables in a multivariate linear model with predator species and cue treatment as categorical factors and date as a continuous covariate. Date was included as a covariate to account for potential directional trends in behaviour due to growth and development of tadpoles and predators. Second, we used two separate linear models to test for the effects of predator treatment, cue treatment, and date on tadpole activity and location. Activity and location were the dependent variables, predator treatment and cue treatment were categorical factors, and date was a continuous covariate. Activity was reciprocally transformed to normalize residuals and equal-

ize error variances. To facilitate interpretation, we reversed the sign of the transformed values of tadpole activity in the analyses. Third, we assessed the relationship between predator behaviour and tadpole activity and location in separate analyses in which predator species and cue treatment were factors, and date and residual activity and location of the predator were covariates. The residuals came from a multivariate model with predator species and cue treatment as factors, and date as a covariate. The second analysis did not include covariates representing predator behaviour because the control treatment contained no predator.

We included all two-way interactions into initial models and performed model simplification by applying a backward stepwise removal procedure to avoid problems because of the inclusion of non-significant terms (Engqvist, 2005). Removed variables were re-entered one by one to the final model to obtain relevant statistics. Wherever necessary for the interpretation of results, we performed Bonferroni-corrected pair-wise comparisons. Statistical models were implemented in SPSS 19.0.

RESULTS

PREDATOR BEHAVIOUR

Predator behaviour depended on predator species, cue treatment, and the interaction between species and cue (multivariate model; species: $F_{2,191} = 594.5$, $P < 0.001$; cue: $F_{4,382} = 9.61$, $P < 0.001$; species \times cue: $F_{4,382} = 3.16$, $P < 0.001$). Fish were more active than dragonfly larvae (univariate model; $F_{1,192} = 1004$, $P < 0.001$) and remained further from the divider ($F_{1,192} = 306.7$, $P < 0.001$; Fig. 1). Date and its interactions did not have an effect on predator behaviour (all $P > 0.2$). Subsequent separate analyses for the two predators revealed that the activity of both predators varied among cue treatments (dragonfly larvae: $F_{2,96} = 13.47$, $P < 0.001$; fish: $F_{2,96} = 5.91$, $P = 0.004$);

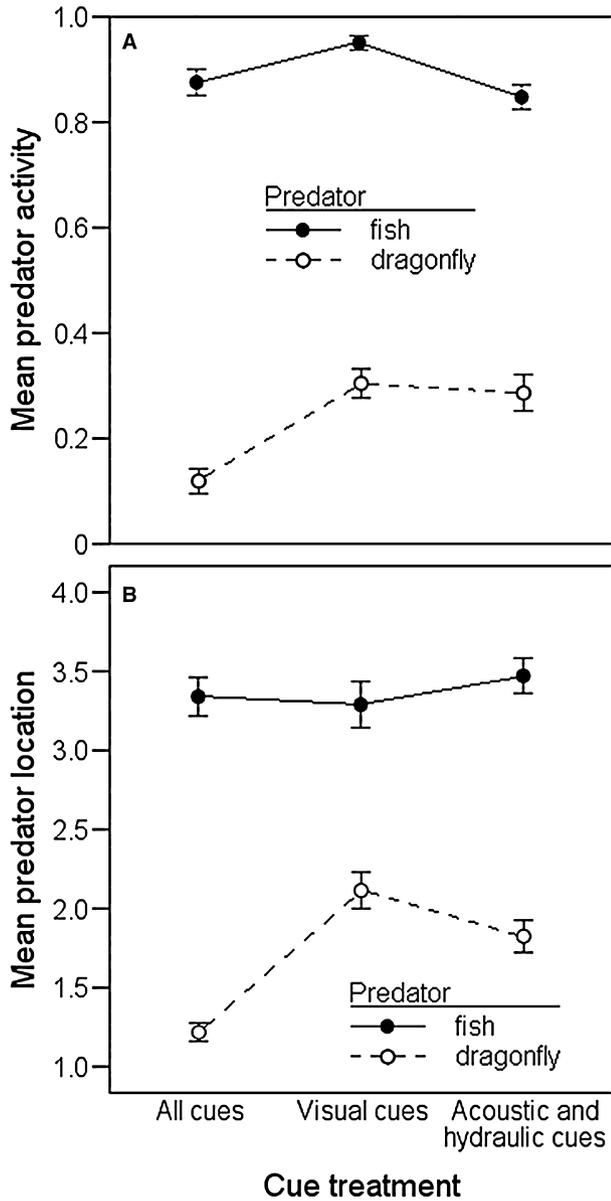


Figure 1. Behaviour of the two predators in the three cue treatments: A, predator activity; B, predator location. Larger values on the y-axis indicate higher activity and locations further from the divider. The figure is based on averages calculated for each individual from observations made once every minute over a 15-min period. Means \pm SE are indicated.

dragonflies were least active when all cues could pass through the divider, and both predator species were most active with only visual cues (Fig. 1A). The location of fish was unrelated to cue treatment ($F_{2,96} = 0.55$, $P = 0.58$), whereas that of dragonfly larvae varied among treatments ($F_{2,96} = 22.58$, $P < 0.001$): the latter were closer to the divider in the all-cues treatment (Fig. 1B).

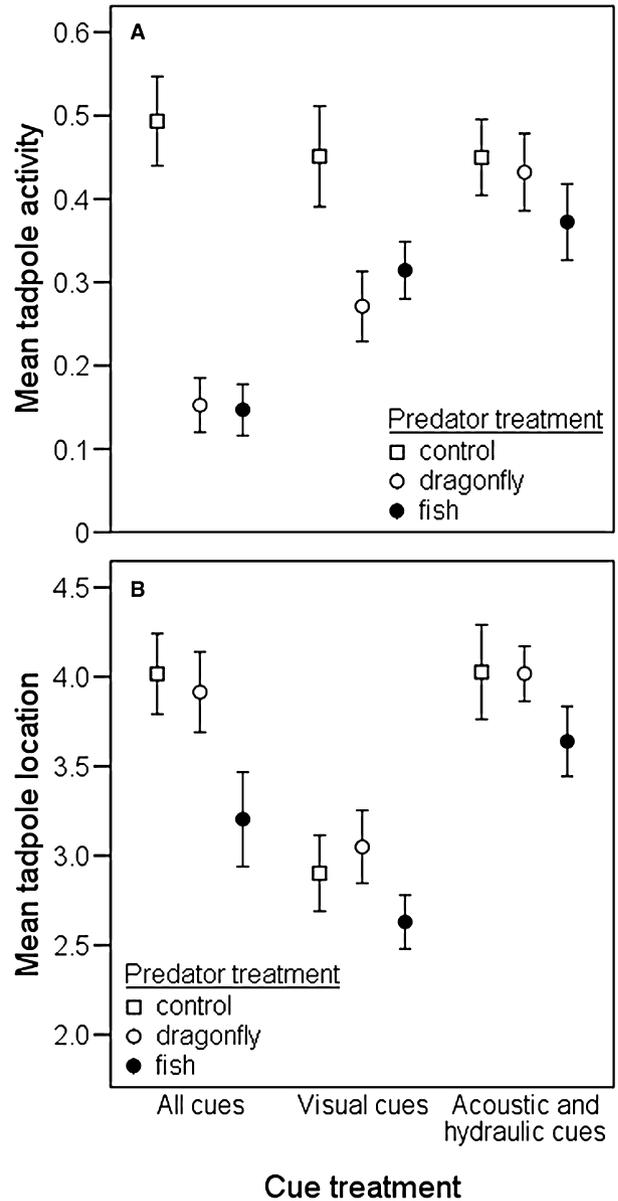


Figure 2. Tadpole behaviour as affected by predator treatment and cue treatment: A, tadpole activity; B, tadpole location. Larger values on the y-axis indicate higher activity and locations further from the divider. The figure is based on averages calculated for each individual from observations made once every minute during the 15-min time period of the experiment. For the ease of interpretation, we present untransformed data on tadpole activity. Means \pm SE are indicated.

TADPOLE BEHAVIOUR

Tadpole activity was significantly affected by predator treatment, cue treatment, and their interaction (Table 2; Fig. 2A). When all types of cue were available, activity declined sharply in the presence of either predator (Fig. 2A; control vs. dragonfly larva:

Table 2. Effects of predator treatment, cue treatment, and date on tadpole activity

Effect	d.f.	<i>B</i>	SE	<i>F</i>	<i>P</i>
Overall					
Predator treatment	2, 275	-0.011	0.003	15.436	< 0.001
Cue treatment	2, 275			10.645	< 0.001
Date	1, 275			15.027	< 0.001
Predator treatment × Cue treatment	4, 275			3.871	0.004
Predator treatment × Date	2, 273			0.586	0.557
Cue treatment × Date	2, 273			2.448	0.088
All cues					
Predator treatment	2, 93	-0.002	0.005	20.138	< 0.001
Date	1, 92			0.279	0.599
Visual cues					
Predator treatment	2, 96	-0.017	0.005	3.642	0.030
Date	1, 96			12.363	0.001
Acoustic and hydraulic cues					
Predator treatment	2, 85	-0.013	0.005	1.299	0.278
Date	1, 87			6.536	0.012

Because the interaction between predator treatment and cue treatment was significant, we also present results of three linear models testing the effect of predator treatment and date on tadpole activity in the three cue treatments separately. Significant results are shown in bold type.

$P < 0.001$; control vs. fish: $P < 0.001$; dragonfly larva vs. fish: $P = 1$). When only visual cues were available, activity again declined in the presence of dragonfly larvae compared with the control, whereas tadpole activity was intermediate in the presence of fish (Fig. 2A; control vs. dragonfly larva: $P = 0.025$; control vs. fish: $P = 0.28$; dragonfly larva vs. fish: $P = 0.73$). When only acoustic and hydraulic cues were present, there were no effects of predator treatment on tadpole activity (Table 2; Fig. 2A). The significant effect of date was caused by a general decline in activity over time (Table 2).

Tadpole location was significantly influenced by predator treatment and cue treatment, but not by their interaction (predator: $F_{2,261} = 5.71$, $P = 0.004$; cue: $F_{2,261} = 18.75$, $P < 0.001$; predator × cue: $F_{4,257} = 0.42$, $P = 0.79$; Fig. 2B). Tadpoles moved closer to the divider in the presence of fish (control vs. dragonfly larva: $P = 1$; control vs. fish: $P = 0.035$; dragonfly larva vs. fish: $P = 0.006$; Fig. 2B), and when only visual cues were available (all cues vs. visual cues: $P < 0.001$; all cues vs. acoustic and hydraulic cues: $P = 0.68$; visual cues vs. acoustic and hydraulic cues: $P < 0.001$; Fig. 2B). Tadpoles tended to move closer to the divider during later experiments, although this was not significant ($F_{1,260} = 3.54$, $B = -0.047$, $SE = 0.025$, $P = 0.061$). All interactions involving date were non-significant ($P > 0.1$).

Residual predator activity was positively related to tadpole activity ($F_{1,188} = 5.4$, $B = 0.153$, $SE = 0.066$,

$P = 0.021$). The main effect of residual predator location ($F_{1,188} = 0.5$, $P = 0.48$) and the interaction terms were non-significant (all $P > 0.09$), except for the interaction between predator type and residual predator location ($F_{1,188} = 4.95$, $P = 0.027$). In the presence of dragonfly larvae, tadpole activity was positively related to residual predator activity ($F_{1,91} = 7.58$, $B = 0.217$, $SE = 0.079$, $P = 0.007$; Fig. 3) and negatively to residual predator location ($F_{1,91} = 4.29$, $B = -0.047$, $SE = 0.023$, $P = 0.041$). In the presence of fish, tadpole activity was not related to residual predator activity or location (both $P > 0.24$). Tadpole location was unrelated to residual predator activity or location ($P > 0.15$).

DISCUSSION

Tadpoles of *R. temporaria* reduced activity when they detected predators, as reported in many other anuran species (Lawler, 1989; Van Buskirk, 2002; Laurila, Pakkasmaa & Merilä, 2006). The strongest anti-predator responses have been found when chemical cues are available to tadpoles (Stauffer & Semlitsch, 1993; Kiesecker *et al.*, 1996; Parris *et al.*, 2006). Our results agree with this, because the greatest decline in activity occurred in the treatment with chemical cues, in addition to visual, acoustic, and hydraulic cues. The strength of the response to fish and dragonfly larvae was similar, perhaps because both are important predators of *R. temporaria* (Relyea,

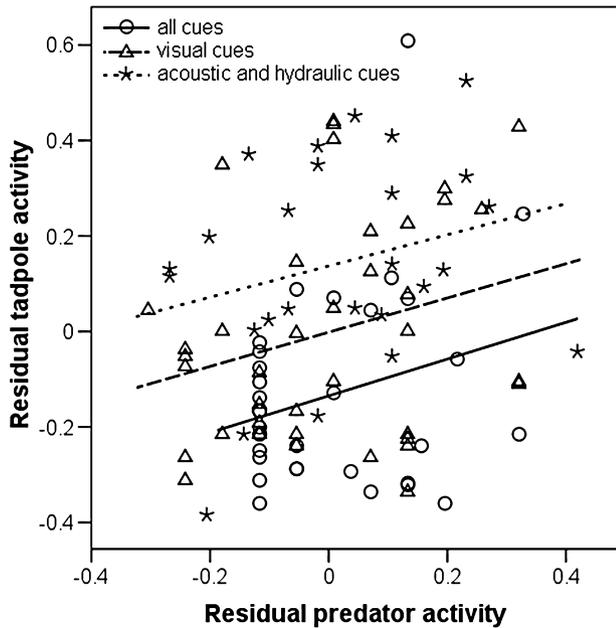


Figure 3. Relationships between tadpole activity and residual predator activity in the presence of dragonfly larvae. Residual values of predator activity originate from the analysis of predator behaviour, whereas residual values of tadpole activity originate from a regression of tadpole activity on date.

2001a; Teplitsky, Plénet & Joly, 2004; Hettyey *et al.*, 2011).

Our most noteworthy result was that when only visual cues were available, tadpole activity was lower in the presence of both predators than in the control (Fig. 2A). Previous studies have found either weak evidence for use of visual cues in anuran predator detection (Stauffer & Semlitsch, 1993; Kiesecker *et al.*, 1996; Jowers *et al.*, 2006; Parris *et al.*, 2006) or no support at all (e.g. Saidapur *et al.*, 2009). Improvements in study design may account for our results. For example, we used smaller experimental chambers to accommodate the near-sightedness of tadpoles (McDiarmid & Altig, 1999), and we used somewhat older animals than had been used previously because tadpole vision improves throughout the larval stage (Lannoo, 1999). Young tadpoles may not use visual cues, but our results suggest that as they become larger they can recognize predators visually.

When only acoustic and hydraulic cues were available, activity was no different from that observed in the control treatment. This agrees with the single previous study that has tested for the use of acoustic and hydraulic cues (Stauffer & Semlitsch, 1993). Stauffer & Semlitsch (1993) argued that water movements may provide information on predator location that augments chemical information on predator

presence. In our study, as well, we cannot exclude the possibility that these cues function in combination with other types of cues during predator recognition and localization. It is also possible that the foil divider in our study weakened or otherwise altered acoustic or hydraulic cues such that they could not be recognized by tadpoles. Thus, further experiments may be necessary to validate our conclusion that acoustic and hydraulic cues are not important.

The relationship between activity of dragonfly larvae and tadpole activity did not differ between cue treatments, as indicated by a lack of a significant interaction between residual predator activity and cue treatment (Fig. 3). A possible interpretation of this result is that tadpoles are able to sense the movements of predators when only visual and when only acoustic and hydraulic cues are available to them, but they recognize predators only using chemical and visual cues but not from acoustic or hydraulic cues. Alternative interpretations are that predators adjust their behaviour to that of tadpoles or that both predators and prey react to other unknown variables. Direct manipulation of predator activity would be required to verify a causal relationship.

We observed no spatial predator avoidance, and in fact tadpoles moved closer to the divider in the presence of fish. Previous studies, conducted in larger arenas, almost always report spatial avoidance of predators (Skelly & Werner, 1990; Relyea, 2001b; Parris *et al.*, 2006). We can only speculate that the small size of the experimental chambers used in the present experiment did not leave much space for tadpoles to express spatial avoidance (also see Parris *et al.*, 2006). The observation that tadpoles were significantly closer to the divider when only visual cues were available might indicate that they misjudged the size of the container in the presence of the completely transparent Plexiglas divider, and attempted to explore and use all of the apparently available space.

Vision may be important for tadpoles living in oligotrophic habitats with little vegetation and clear water, or at very close range in meso- and eutrophic habitats with dense vegetation and murky water. On a longer timescale, chemical cues may provide information on the types of predators present, and on their abundance and dangerousness. Prey clearly adjust their phenotypic responses according to chemical signals from different densities and species of predator (e.g. Van Buskirk & Arioli, 2002; Teplitsky *et al.*, 2005; Hettyey *et al.*, 2011). However, when a predator approaches and an immediate threat develops, the concentration of chemical cues in the water is less relevant than the visual cues immediately available to the prey. Our results suggest that vision does indeed play an important role in eliciting anti-predator behaviour in anuran larvae, at least when

the predator is at close range. Thus, future studies on predator-induced defences of tadpoles should not concentrate solely on chemical stimuli, but also take visual cues into consideration. After all, while chemical cues alone can induce defensive responses in tadpoles (Petranka & Hayes, 1998; Schoeppner & Relyea, 2005, 2009; Fraker *et al.*, 2009), both chemical and visual cues may be required to develop the full suite and magnitude of defences.

ACKNOWLEDGEMENTS

We thank H.-U. Reyer for fruitful discussions and support, to F. Ladich for suggestions regarding the experimental set-up, to the workshop of the Institute of Physics, University of Zurich, for technical help, and to J. A. Allen and four anonymous reviewers for their helpful comments on the manuscript. This study was supported by the Swiss Nationalfonds. The Fachstelle Naturschutz Kanton Zürich, the Fischerei- und Jagdverwaltung Kanton Zürich, and the Veterinäramt Kanton Zürich provided permits (No. 05.0185-13/2011).

REFERENCES

- Benard MF. 2006.** Survival trade-offs between two predator-induced phenotypes in Pacific treefrogs (*Pseudacris regilla*). *Ecology* **87**: 340–346.
- Engqvist L. 2005.** The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour* **70**: 967–971.
- Fraker ME, Hu F, Cuddapah V, McCollum SA, Relyea RA, Hempel J, Denver RJ. 2009.** Characterization of an alarm pheromone secreted by amphibian tadpoles that induces behavioral inhibition and suppression of the neuroendocrine stress axis. *Hormones and Behavior* **55**: 520–529.
- Gouchie GM, Roberts LF, Wassersug RJ. 2008.** The effect of mirrors on African clawed frog (*Xenopus laevis*) larval growth, development, and behavior. *Behavioral Ecology and Sociobiology* **62**: 1821–1829.
- Hettyey A, Vincze K, Zsarnóczai S, Hoi H, Laurila A. 2011.** Costs and benefits of defenses induced by predators differing in dangerousness. *Journal of Evolutionary Biology* **24**: 1007–1019.
- Hoff KvS, Blaustein AR, McDiarmid RW, Altig R. 1999.** Behavior: interactions and their consequences. In: McDiarmid RW, Altig R, eds. *Tadpoles: the biology of anuran larvae*. Chicago: The University of Chicago Press, 215–239.
- Hoy RR. 1992.** The evolution of hearing in insects as an adaptation of predation from bats. In: Webster DB, Fay RR, Popper AN, eds. *The evolutionary biology of hearing*. New York: Springer, 115–129.
- Jowers MJ, Campbell-Palmer R, Walsh PT, Downie JR. 2006.** Intraspecific variation in the avoidance response of stream frog (*Mannophryne trinitatis*) tadpoles to fish and prawn predators. *Herpetological Journal* **16**: 337–346.
- Kiesecker JM, Chivers DP, Blaustein AR. 1996.** The use of chemical cues in predator recognition by western toad tadpoles. *Animal Behaviour* **52**: 1237–1245.
- Lannoo MJ. 1999.** Integration: nervous and sensory systems. In: McDiarmid R, Altig R, eds. *Tadpoles: the biology of anuran larvae*. Chicago: The University of Chicago Press, 149–169.
- Laurila A. 2000.** Behavioural responses to predator chemical cues and local variation in antipredator performance in *Rana temporaria* tadpoles. *Oikos* **88**: 159–168.
- Laurila A, Kujasalo J, Ranta E. 1997.** Different antipredator behaviour in two anuran tadpoles: effects of predator diet. *Behavioral Ecology and Sociobiology* **40**: 329–336.
- Laurila A, Pakkasmaa S, Merilä J. 2006.** Population divergence in growth rate and antipredator defences in *Rana arvalis*. *Oecologia* **147**: 585–595.
- Lawler SP. 1989.** Behavioral-responses to predators and predation risk in 4 species of larval anurans. *Animal Behaviour* **38**: 1039–1047.
- Lima SL, Dill LM. 1990.** Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**: 619–640.
- McDiarmid RW, Altig R. 1999.** *Tadpoles: the biology of anuran larvae*. Chicago: The University of Chicago Press.
- Natale GS, Alcalde L, Herrera R, Cajade R, Schaefer EF, Marangoni F, Trudeau VL. 2011.** Underwater acoustic communication in the macrophagous carnivorous larvae of *Ceratophrys ornata* (Anura: Ceratophryidae). *Acta Zoologica* **92**: 46–53.
- Parris MJ, Reese E, Storfer A. 2006.** Antipredator behavior of chytridiomycosis-infected northern leopard frog (*Rana pipiens*) tadpoles. *Canadian Journal of Zoology* **84**: 58–65.
- Petranka J, Hayes L. 1998.** Chemically mediated avoidance of a predatory odonate (*Anax junius*) by American toad (*Bufo americanus*) and wood frog (*Rana sylvatica*) tadpoles. *Behavioral Ecology and Sociobiology* **42**: 263–271.
- Reeve E, Ndriantsoa SH, Strauß A, Randrianiaina R-D, Rasolonjatovo Hiobiarilanto T, Glaw F, Glos J, Vences M. 2011.** Acoustic underwater signals with a probable function during competitive feeding in a tadpole. *Die Naturwissenschaften* **98**: 135–143.
- Relyea RA. 2001a.** The relationship between predation risk and antipredator responses in larval anurans. *Ecology* **82**: 541–554.
- Relyea RA. 2001b.** Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology* **82**: 523–540.
- Rot-Nikevic I, Denver RJ, Wassersug RJ. 2005.** The influence of visual and tactile stimulation on growth and metamorphosis in anuran larvae. *Functional Ecology* **19**: 1008–1016.
- Saidapur SK, Veeranagoudar DK, Hiragond NC, Shanbhag BA. 2009.** Mechanism of predator–prey detection and behavioral responses in some anuran tadpoles. *Chemoecology* **19**: 21–28.

- Schmidt BP, Knowles JM, Simmons AM. 2011.** Movements of *Rana catesbeiana* tadpoles in weak current flows resemble a directed random walk. *Journal of Experimental Biology* **214**: 2297–2307.
- Schoeppner NM, Relyea RA. 2005.** Damage, digestion, and defence: the roles of alarm cues and kairomones for inducing prey defences. *Ecology Letters* **8**: 505–512.
- Schoeppner NM, Relyea RA. 2009.** Interpreting the smells of predation: how alarm cues and kairomones induce different prey defences. *Functional Ecology* **23**: 1114–1121.
- Sih A. 1980.** Optimal behavior: can foragers balance two conflicting demands? *Science* **210**: 1041–1043.
- Simmons AM, Costa LM, Gerstein H. 2004.** Lateral line-mediated rheotactic behavior in tadpoles of the African clawed frog, *Xenopus laevis*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* **190**: 747–758.
- Skelly DK. 1994.** Activity level and the susceptibility of anuran larvae to predation. *Animal Behaviour* **47**: 465–468.
- Skelly DK, Werner EE. 1990.** Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology* **71**: 2313–2322.
- Stauffer HP, Semlitsch RD. 1993.** Effects of visual, chemical and tactile cues of fish on the behavioral responses of tadpoles. *Animal Behaviour* **46**: 355–364.
- Teplitsky C, Plénet S, Joly P. 2004.** Hierarchical responses of tadpoles to multiple predators. *Ecology* **85**: 2888–2894.
- Teplitsky C, Plénet S, Léna JP, Mermet N, Malet E, Joly P. 2005.** Escape behaviour and ultimate causes of specific induced defences in an anuran tadpole. *Journal of Evolutionary Biology* **18**: 180–190.
- Tollrian R, Harvell CD. 1999.** *The ecology and evolution of inducible defences*. Princeton, NJ: Princeton University Press.
- Van Buskirk J. 2001.** Specific induced responses to different predator species in anuran larvae. *Journal of Evolutionary Biology* **14**: 482–489.
- Van Buskirk J. 2002.** A comparative test of the adaptive plasticity hypothesis: relationships between habitat and phenotype in anuran larvae. *American Naturalist* **160**: 87–102.
- Van Buskirk J, Arioli M. 2002.** Dosage response of an induced defense: how sensitive are tadpoles to predation risk? *Ecology* **83**: 1580–1585.
- Wassersug RJ, Lum AM, Potel MJ. 1981.** An analysis of school structure for tadpoles (Anura: Amphibia). *Behavioral Ecology and Sociobiology* **9**: 15–22.
- Wilson M, Schack HB, Madsen PT, Surlykke A, Wahlberg M. 2011.** Directional escape behavior in allis shad (*Alosa alosa*) exposed to ultrasonic clicks mimicking an approaching toothed whale. *Journal of Experimental Biology* **214**: 22–29.