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Tadpoles' responses to risk of fish introduction

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Abstract The introduction of predatory species, such as fish, in amphibian breeding sites is one of the many likely causes of amphibian population decline. The existence of inducible or constitutive (permanent) defences is expected to temper the lethal effects of fish on tadpoles. According to current theories on the evolution of phenotypic plasticity, the amphibian species that occur in habitats that are mostly or often fish-free were expected to display inducible defences, while the species that reproduce mainly in fish ponds ought to present constitutive defences. The tested species were *Rana dalmatina*, *Hyla arborea* and *R. ridibunda*, respectively.

As expected, *R. ridibunda* tadpoles were less vulnerable to fish predation than the other species. Nevertheless, all three species exhibited morphological responses in the presence of fish. Their increases in tail area and decreases in body depth were similar. However, behaviour was only modified in *R. dalmatina*, which exhibited lower activity rates and higher refuge use in the presence of fish cues. Such lower activity rates were related to lower growth and developmental rates. While not detected in this experiment, the existence of inducible defences in the three species suggests the existence of costs of anti-predator defence. Those costs may have delayed effects so that increasing the frequency of fish ponds may exacerbate the impact of delayed costs whatever the species, suggesting that the dynamics of species that are not fish-adverse could also suffer from the introduction of fish.

Keywords Behaviour · Morphology · Plasticity · Predation · Vulnerability

Introduction

During the past 10 years, the decline of amphibian populations has grown to a world-wide concern (Blau-stein and Wake 1990; Wake 1991; Delis et al. 1996; Stallard 2001). Among various causes of decline, fish introductions are of major concern because of the keystone role of fish in the food webs of freshwaters, and the strong impact of predatory fish on most amphibian communities (Brönmark and Edenhamn 1994; Wellborn et al. 1996; Meyer et al. 1998; Adams 1999; Goodsell and Kats 1999; Lawler et al. 1999). Amphibian communities are assumed to be structured by an ecological gradient of habitats defined by water duration and predation risk (Wellborn et al. 1996). At the one end of this gradient are ephemeral predator-free waters, while at the other end are permanent waters with insects and fish. Temporary waters with only insects as main predators occupy an intermediate position along this gradient. Only a few “fish-tolerant” species are distributed ubiquitously along the gradient while predation risk compels most species to occupy only a part of this gradient. The species that usually breed in permanent ponds where the risk of predation by fish is high can be defined as “fish-prone” species. By contrast, species restricted to fishless habitats can be defined as “fish-adverse”.

While fish introduction should not represent an important threat for the persistence of fish-prone populations, such introductions may result in a considerable loss of suitable breeding habitats for fish-adverse-species, leading ultimately to population decline (Brönmark and Edenhamn 1994; Meyer et al. 1998; Lawler et al. 1999). Nevertheless, the direct and dramatic effects of predation on naive tadpoles could be alleviated by constitutive defences (i.e. defences displayed whatever the environmental conditions) or inducible defences (i.e. defences expressed according to the presence of predators in the habitat, Adler and Harvell 1990; Tollrian and Harvell 1999).

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Within the framework of evolutionary theory, the existence of inducible defences is predicted to be constrained by:

1. reliable cues that allow the prey to perceive predation risk (Harvell 1990). Chemical cues appear reliable for prey since they are produced by the predator itself, or else by damaged prey (Petranka et al. 1987; Kats et al. 1988; Laurila et al. 1998).
2. a cost of the defence (e.g. lower growth and developmental rates) that prevents the acquisition of permanent defences (Smith 1987; Berven 1990; Relyea 2002).
3. variability in predation risk. Theory predicts that plasticity is promoted when the frequencies of alternative environments are similar or when the fitness advantage of the phenotype suited to the rarer environment is great (Moran 1992).

In this context, we predict that fish-tolerant species that breed with equal frequency in ponds that contain or do not contain fish predators should possess inducible defences. For the fish-prone and the fish-adverse species, the existence of inducible defences should depend upon the selective pressures in the rarer environment. For the fish-prone species, defences should be inducible if the cost of the fish-induced phenotype strongly reduces fitness in the predator-free habitats. Otherwise, we expect defences to be permanent. Similarly, fish-adverse species should present inducible defence when the benefit of the induced defence is high and the frequency of fishless habitats is low, and no defence otherwise. In the present study, we addressed the following questions: (1) how vulnerable are tadpoles of the different species to fish predators, (2) do fish induce plastic responses in those species, and (3) are the responses different among the species and in agreement with our habitat-related hypothesis (i.e. fish occurrence)?

Materials and methods

Anuran species

We used three species: *Hyla arborea*, *Rana dalmatina* and *R. ridibunda*, which differ in habitat use with respect to fish presence. According to a study of amphibian assemblages in 82 ponds of the Rhone floodplain (Morand 1996; Joly and Morand 1997), *R. ridibunda* (72.7% co-occurrence with fish) is a fish-prone species, while *H. arborea* (20% co-occurrence) is a fish-adverse species; *R. dalmatina* (50% co-occurrence with fish) stands as a fish-tolerant species.

Ten clutches of *R. dalmatina*, ten clutches of *R. ridibunda* and four clutches of *H. arborea* were collected from several ponds of the French Rhone floodplain close to Lyon, on 7 March, 5 May and 28 May 1999, respectively. Egg sampling was authorised by the French Ministry of the Environment. After hatching, tadpoles of each clutch were kept in laboratory tanks until the beginning of the experiments.

Fish species

Three-spined sticklebacks (*Gasterosteus aculeatus*) and topmouth gudgeon (*Pseudorasbora parva*) were used because of their small body size and their propensity to forage actively on tadpoles (Laurila and Aho 1997). Both species frequently colonise formerly fishless habitats where they are introduced by floods or by man. Fish were collected from two fisheries and then kept in outdoor tanks.

Vulnerability of tadpoles

The vulnerability of tadpoles was estimated by survivorship at the end of 24-h predation trials in outdoor microcosms (40×60×50 cm). Fish (two sticklebacks and one topmouth gudgeon) were introduced in the tanks and starved for 48 h before introducing five tadpoles. For each species, trials were repeated ten times, each time using new fish individuals. We tested the vulnerability of naive tadpoles of all species at developmental stage 38 (according to Gosner's table, Gosner 1960).

Plasticity experiments: experimental design

The plasticity of morphology and life-history traits was investigated in outdoor microcosms, while behavioural responses were investigated in indoor tanks. Both fish and no-predator treatments were replicated 5 times for each of the 3 species (30 tanks for each experiment). We followed a fully randomised design for all the tanks involved in the two experiments.

Outdoor microcosms were established in opaque plastic tanks (40×60×50 cm) filled with 50 l water. For enhancing algal growth, we added 0.5 l soil and 15 ml algae powder (Seramicron) to each tank. Finally, five stems of *Myriophyllum heterophyllum* were added to improve oxygenation. A 1-mm-mesh wire net covered each tank to prevent insect colonisation and tadpoles or fish escaping. The fish were held in a 1-mm-mesh wire-netted cage (40×30×30 cm) that was hung in the upper part of each tank to keep them from eating the tadpoles. However, this cage allowed the tadpoles to perceive visual, chemical and mechanical cues emanating from fish.

The tanks were initiated 3 weeks before introducing the tadpoles and the fish. Ten tadpoles of each species were randomly chosen in the different clutches and introduced in the open water. The experiments started on 29 March for *R. dalmatina*, 14 June for *H. arborea* and 24 June for *R. ridibunda*. On the same dates, three fishes (two sticklebacks and one topmouth gudgeon) were introduced into the cage in the predator treatment. The cage was left empty in the no-predator treatment. Suspecting that the presence of predators is perceived through both predator-produced cues and cues emanating from wounded tadpoles (Laurila et al. 1998), the fishes were fed every 2 days with five tadpoles (≈ 200 mg) of the species investigated in the experiment.

To avoid morphological changes due to metamorphosis, the experiments ended when the tadpoles reached stage 38 (Gosner 1960). Because the three species differed in the length of their larval period (longer for *R. dalmatina*), the experiments lasted 8 weeks for *R. dalmatina* and 4 weeks for *H. arborea* and *R. ridibunda*.

After the experiment, the tadpoles were weighed live (wet mass) and their developmental stage was established according to Gosner's table (1960). Developmental rates were estimated according to equation (1) and growth rate according to equation (2).

$$\text{Development rate} = \frac{(\text{initial stage} - \text{final stage})}{\text{number of days of experimentation}} \quad (1)$$

$$\text{Growth rate} = \exp \left(\frac{\text{Ln} \left[\frac{\text{final weight}}{\text{initial weight}} \right]}{\text{number of days of experimentation}} \right) \quad (2)$$

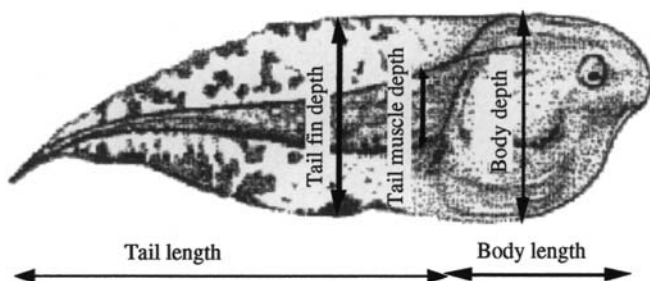


Fig. 1 The five morphological variables measured on tadpoles (modified from McCollum and Leimberger 1997)

Morphological variations were estimated using five variables: tail length, body length, maximum tail-fin depth, maximum tail-muscle depth, and maximum body depth (Fig. 1).

Measurements were performed using a stereoscopic microscope equipped with an ocular micrometer (to the nearest 0.1 mm, measurement error: ± 0.17 mm). Because differences in growth rates between treatments could act as a confounding factor in morphology analysis, we extracted the size effect from our data by means of regression upon each measured value against the cubic-root of mass (McCollum and Leimberger 1997; Van Buskirk et al. 1997). Variation of morphological traits was thus estimated by the residuals of this regression.

Indoor experiments for the analysis of behavioural responses of tadpoles to fish presence were performed under constant and homogeneous conditions (temperature=21°C, artificial photoperiod L:D 14:10). A gravitational flow-through system (Fig. 2) was used. Two 200-l tanks (no-predator treatment, with an empty cage; predator treatment, with a cage containing 4 sticklebacks and 2 topmouth gudgeon) continuously supplied the 30 experimental boxes (30×32×10 cm; 2 treatments×3 species×5 replicates) with aerated tapwater.

Refuges in the experimental boxes consisted of a horizontal, opaque plastic plate (30×16×0.3 cm) fixed 2 cm above the bottom of the box. To avoid any biases, food for tadpoles (rabbit chow) was equally distributed outside and under the plate.

For each species, the experiment began and ended on the same dates as did the outdoor experiments. Six tadpoles (Gosner stage 25) of each species, randomly chosen in the different clutches, were introduced into each experimental box. In parallel, fishes were introduced into the appropriate tank. The tadpoles were fed every 2 days. The fishes were fed every 2 days (4 h before behavioural observations) with 10 tadpoles (≈ 400 mg) of the species investigated during the experiment. All the boxes were scanned every 2 days for 30 min. At 1-min intervals, the number of tadpoles outside the refuge and, among these, the number that were swimming, were counted. For each observation, we considered:

- (1) the cumulative number of tadpoles under the refuge over 30 min, and
- (2) the relative rate of activity outside the refuge (number of swimming tadpoles/number of tadpoles outside the refuge).

Plasticity experiments: statistical analyses

Tadpoles that damaged their tails during the experiment (0–10% maximum) were excluded from the morphological analyses. Relative rates of activity were arcsinus-squareroot-transformed to meet normality (Sokal and Rohlf 1995). Separate nested mixed three-way ANOVAs (Data Desk 4.2) were performed for each variable, testing for species and treatment as fixed effects (and random replicate effect nested within treatment and species). When interactions between predator presence and tadpole species were significant, separate ANOVAs were performed within each species to test for treatment effect.

Results

Vulnerability

While survival was near to zero in both *R. dalmatina* (0.04 ± 0.084) and *H. arborea* (0) in the presence of free-ranging fish, the survival of *R. ridibunda* tadpoles was higher (0.4 ± 0.47). Hence tadpoles of *R. ridibunda* were less vulnerable than tadpoles of *R. dalmatina* and *H. arborea* (Kruskall and Wallis, $n=30$, $H=10.346$, $P=0.0057$). A body-size effect cannot explain this difference in vulnerability because *R. ridibunda* tadpoles were lighter ($0.199 \text{ g} \pm 0.099$) than those of the other species (*R. dalmatina* = $0.567 \text{ g} \pm 0.103$; *H. arborea* = $0.293 \text{ g} \pm 0.101$; Kruskal-Wallis, $n=150$, $H=101.336$, $P<0.0001$).

Plasticity experiments

Survivorship during the experiments was high for all species (90% for *H. arborea*, 97% for *R. dalmatina* and 91% for *R. ridibunda*). Survival was not affected by the presence of predator cues (Mann-Whitney; $n=10$, $z=-0.12$, $P=0.9$ for *H. arborea*, $n=10$, $z=-1.49$, $P=0.14$ for *R. dalmatina*, and $n=10$, $z=0$, $P>0.99$ for *R. ridibunda*).

Fig. 2 Gravitational flow-through system used in the behavioural plasticity experiment

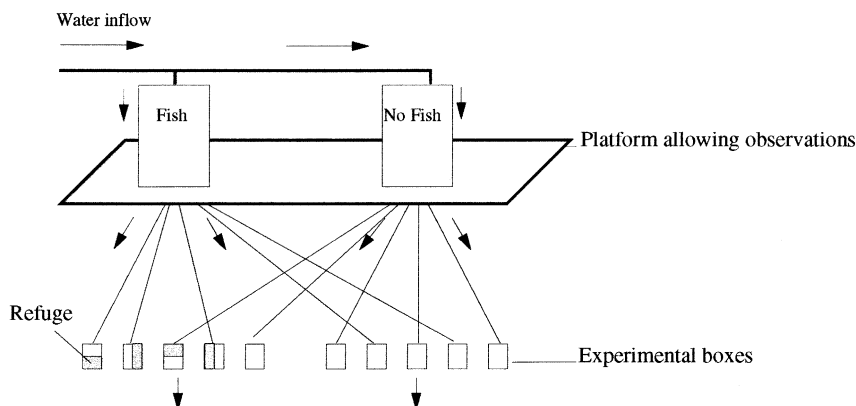


Table 1 ANOVAs on morphological variables (tail-fin depth, tail-muscle depth, tail length, body depth, body length) of tadpoles using the residuals of a regression performed on these morphological variables versus the cubic root of tadpole mass interpreted as a measure of size: results of three-way analyses performed after pooling the three species

Source	df	Tail-fin depth			Tail-muscle depth			Tail length			Body depth			Body length		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Treatment	1	86.3	38.4	<0.0001	6.1	33.2	<0.0001	104.8	6.4	0.019	5.6	5.2	0.0326	0.06	0.04	0.849
Species	2	224.2	99.9	<0.0001	5.6	30.7	<0.0001	361.6	22.1	<0.0001	48.5	44.8	<0.0001	21.5	13.8	0.0001
Replicate	22	2.2	2.9	<0.0001	0.2	2.6	0.0002	16.4	2.2	0.003	1.09	2.9	<0.0001	1.5	1.2	0.279
Treatment×Species	2	12.6	5.6	0.0106	0.9	5.0	0.0161	15.5	0.9	0.404	1.22	1.1	0.3407	4.4	2.8	0.079
Error	222	0.8			0.07			7.6			0.38			1.3		

Table 2 ANOVAs on morphological variables (tail-fin depth, tail-muscle depth) of tadpoles. Separate tests were conducted on each species for tail-fin and muscle-depths because of the significant interaction between predator presence and species

Source	<i>R. dalmatina</i>			df	<i>R. ridibunda</i>			df	<i>H. arborea</i>												
	Tail-muscle depth				Tail-fin depth				Tail-muscle depth												
	MS	F	P		MS	F	P		MS	F	P										
Treatment	1	0.12	0.13	0.7329	2.47	6.77	0.0353	1	81.43	27.77	0.0012	0.15	2.03	0.1975	1	22.05	7.79	0.0235	5.6	46.8	0.0001
Replicate	7	0.96	3.18	0.0052	0.36	3.77	0.0015	7	2.93	5.15	<0.0001	0.07	1.11	0.3692	8	2.82	2.28	0.0305	0.12	2.48	0.0189
Error	76	0.30		0.09				70	0.57			0.07			76	1.24			0.05		

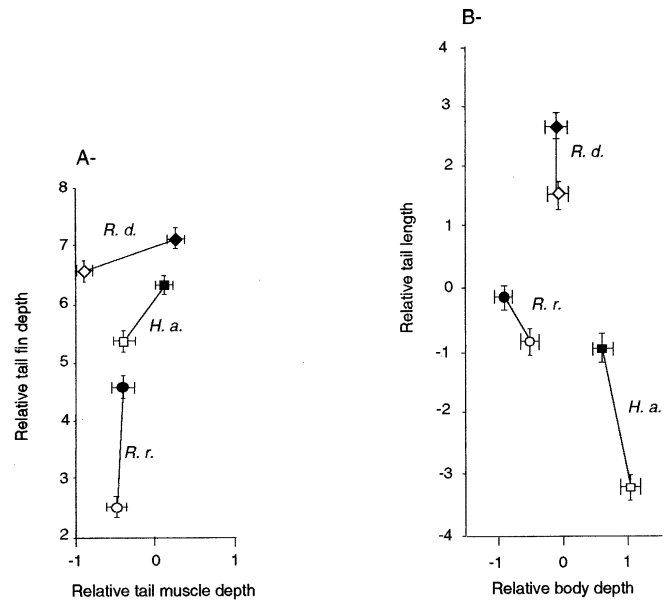


Fig. 3 Bivariate reaction norms of **A** tail morphology and **B** body depth and tail length. *Rana ridibunda* (R. r.) is represented by circles, *R. dalmatina* (R. d.) by diamonds, and *Hyla arborea* (H. a.) by squares. Filled symbols stand for the predator treatment and unfilled symbols for the no-predator treatment. Values correspond to the residuals of a regression of the measured values versus the cubic root of tadpole mass. Values are means of the five replicates (\pm SE)

Impact of the presence of fish on morphology

Most tadpole morphological variables except body length (Tables 1, 2) were modified by the fish treatment. The global trend was an increase in tail area (increased depth of tail muscle and/or of tail fins, as well as increased tail length, Fig. 3A, B) and shallower body (decreased body depth, Fig. 3B).

The three species varied in the expression of tail morphology plasticity (significant species×treatments interactions). Fish presence induced deeper tail fins and deeper tail muscles in tadpoles of *H. arborea*. In contrast, presence of predators induced only deeper tail muscles in *R. dalmatina* tadpoles, or deeper tail fins in *R. ridibunda* (Fig. 3A).

Impact of the presence of fish on tadpole growth and developmental rates

Fish presence had significant effects on tadpoles' growth and development rates in two of the studied species (Tables 3, 4). Both rates were higher in the presence of fish than in their absence for *R. ridibunda* and *H. arborea* (Fig. 4)

Table 3 ANOVAs on growth and developmental rates of tadpoles. Global analysis performed on the three species together

Source	df	Growth rate			Developmental rate		
		MS	F	P	MS	F	P
Treatment	1	0.025	32.5	<0.0001	0.57	17.3	0.0004
Species	2	0.19	255	<0.0001	6.46	196.7	<0.0001
Replicate	22	<0.001	5.7	<0.0001	0.03	8.2	<0.0001
Treatment×Species	2	0.015	0.007	0.0008	0.39	0.19	0.0088
Error	222	<0.001			0.004		

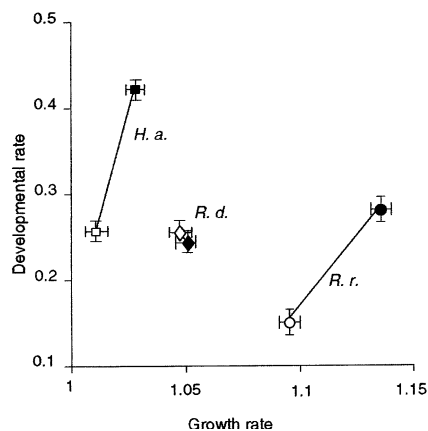


Fig. 4 Bivariate reaction norms of development and growth rates. *Rana ridibunda* (*R. r.*) is represented by circles, *R. dalmatina* (*R. d.*) by diamonds, and *Hyla arborea* (*H. a.*) by squares. Filled symbols stand for the predator treatment and unfilled symbols for the no-predator treatment. Values represent the rates of development (in stage per day) and growth (in grammes per day) over the larval period and are means of the five replicates (\pm SE)

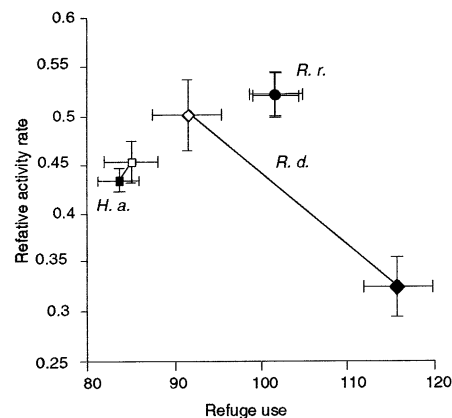


Fig. 5 Bivariate reaction norms of the behavioural response. *Rana ridibunda* (*R. r.*) is represented by circles, *R. dalmatina* (*R. d.*) by diamonds, and *Hyla arborea* (*H. a.*) by squares. Filled symbols stand for the predator treatment and unfilled symbols for the no-predator treatment. Relative activity rate is the number of active tadpoles divided by the number of tadpoles outside the refuge. Refuge use is the cumulated number of tadpoles under the refuge for 30 min. Values are means of the five replicates (\pm SE)

Effects of predator on behaviour

Only the behaviour of *R. dalmatina* tadpoles was significantly modified by the presence of fish, as refuge use increased and relative activity rates decreased in this species (Tables 5, 6, Fig. 5).

Discussion

As expected, the studied species differed in their responses to fish presence according to their habitat preferences (in terms of fish occurrence). These responses varied according to three components: constitutive defence only in the fish-prone species (*R. ridibunda*), morphological plasticity in the three species and, in addition, behavioural plasticity only in the fish-tolerant species (*R. dalmatina*).

The fish-prone species, *R. ridibunda*, was expected to display either inducible or constitutive defences according to the costs of the defence. Naïve tadpoles of *R. ridibunda* were revealed to be less vulnerable to fish predators than tadpoles of the other two species. Lower vulnerability cannot be explained by greater size (refuge size hypothesis, Travis et al. 1985) since *R. ridibunda* tadpoles were smaller than those of the other species. These results suggest a baseline constitutive defence against fish in this

species. The production of repellent chemicals by skin glands may be responsible for this defence. However, despite such a constitutive defence, *R. ridibunda* tadpoles also exhibited induced morphological responses. The absence of constitutive morphological responses nevertheless suggests that their production and maintenance are costly. Data on the costs of phenotypic plasticity are controversial. While some authors found costs for the predator-induced phenotype (McCollum and VanBuskirk 1996; Van Buskirk 2000), others found no costs (Scheiner and Berrigan 1998; Relyea 2002) or even a trend towards increased vigour in individuals reared with predators (Van Buskirk and Saxer 2001). In our study, in the three species, morphological responses included decreased body depth which may result in decreased growth rate, lower body size at metamorphosis, and ultimately lower fitness for these individuals. However, such costs were not detected under our experimental conditions, probably because food conditions were not limiting.

The fish-adverse *H. arborea* and the fish-tolerant *R. dalmatina* displayed predator-induced morphological plasticity. The high vulnerability of naïve tadpoles of these species, as well as their morphological responses to the presence of fish cues, fit our expectation and a selection pressure imposed by frequent co-occurrence with fish, despite selection of fish-free habitats by adult

Table 4 ANOVAs on growth and developmental rates of tadpoles. Because of the significant interaction between predator presence and species, separate tests were conducted for each species

Source	df	<i>R. dalmatina</i>				df	<i>R. ridibunda</i>				df	<i>H. arborea</i>									
		Growth rate		Developmental rate			Growth rate		Developmental rate			Growth rate		Developmental rate							
		MS	F	P	MS		F	P	MS	F		P	MS	F	P						
Treatment	1	0.00012	4.0	0.0846	0.004	1.77	0.2253	1	0.032	31.08	0.0008	0.35	19.7	0.0030	1	0.006	5.23	0.0515	0.60	8.2	0.0210
Replicate	7	0.00003	3.5	0.0028	0.002	2.55	0.0207	7	0.001	3.64	0.0021	0.02	2.64	0.0174	8	0.001	9.79	<0.0001	0.07	15.3	<0.0001
Error	76	0.000009		0.0008	0.0008			70	0.0003			0.006			76	0.0001			0.004		

Table 5 ANOVAs on refuge use (cumulated number of hidden tadpoles) and activity level (number of swimming tadpoles/number of tadpoles outside refuge) of tadpoles. The activity level was normalised through an arcsin square root transformation

Source	df	Refuge use				Activity level			
		Refuge use		Activity level		Refuge use		Activity level	
		MS	F	P	P	MS	F	P	P
Treatment	1	9487.4	6.3993	0.0184	0.0184	0.4386	11.039	0.0029	0.0029
Species	2	15099	10.185	0.0006	0.0006	0.5616	14.133	<0.0001	<0.0001
Replicate	22	6686.9	4.5104	0.0616	0.0616	0.3610	9.0849	0.9270	0.9270
Treatment×Species	2	1482.5	1.5025	0.0217	0.0217	0.0397	0.6106	0.0012	0.0012
Error	410	986.74				0.0650			

Table 6 ANOVAs on refuge use and activity level of tadpoles. Separate tests were conducted for each species because of the significant interaction between predator presence and species

Source	df	<i>R. dalmatina</i>				df	<i>R. ridibunda</i>				df	<i>H. arborea</i>									
		Refuge use		Activity level			Refuge use		Activity level			Refuge use		Activity level							
		MS	F	P			MS	F	P			MS	F	P							
Treatment	1	26742	15.1	0.0046	1.35	31.7	0.0005	1	0.86	0.0005	0.9830	0.0002	0.004	0.9533	1	46.9	0.05	0.8262	0.008	0.30	0.5969
Replicate	8	1771.7	1.20	0.2990	0.04	0.42	0.9093	8	1790	2.46	0.0164	0.05	0.939	0.4867	8	910.8	1.67	0.1125	0.027	1.19	0.3096
Error	179	1470.7			0.10			130	728.5			0.05			110	543.8			0.023		

breeders for the fish-adverse species. Such habitat selection might be impeded by difficulties in perceiving fish-specific cues from ponds during breeding migration. Moreover, *H. arborea* often breeds in meadows inundated by floods where fish density may be unpredictable. If such habitats are now rare because of generalised river embankments, they have probably significantly contributed to population dynamics in a recent past, thus leading to the appearance of inducible defences. However, these inducible defences rely solely on morphological modifications, as *H. arborea* did not exhibit any behavioural plasticity.

In contrast, fish-tolerant *R. dalmatina* displayed behavioural plasticity and was the only species that did not exhibit increased growth rates when exposed to fish in the microcosm experiments. This difference among species suggests that using refuges and reducing activity may imply costs that prevent tadpoles from enhancing growth rate in the presence of predators. These data imply that costs associated with behavioural responses would be higher than those associated with morphological defences. This result is important as behavioural traits are considered more plastic than morphological traits (West-Eberhard 1989; Relyea 2001). The existence of such extra costs of behavioural plasticity could explain why only the fish-tolerant species displayed behavioural plasticity, since plasticity is supposed to be more selected in species experiencing the most variable environments.

Response to predator presence needs to be described by several characters before concluding as to the inducible or non-inducible nature of defences (Boersma et al. 1998). Our results confirm that the response to predators can involve multiple traits, each of them displaying specific levels of plasticity. The plurality of defence components emphasises the complexity of genotype-environment interactions that determine the phenotype (Endler 1995). Such plurality makes a modulation of the responses of tadpoles to fish presence possible according to the evolutionary history of each population. However, because our study involves only three species, one for each type of habitat, it does not allow us to generalise on the relationships that have been revealed because we have first to test whether the effects associated with habitat type that we observed are separate specific effects or not. Further comparisons with several species for each habitat type are needed to confirm our conclusions and to investigate the relationships between defence components and habitat selection.

Finally, fish presence may lead to long-term effects on tadpole development. Some studies have revealed some costs in terms of lower growth and developmental rates (Van Buskirk and Yurewicz 1998; Laurila and Kujasalo 1999; Lardner 2000; Van Buskirk 2000). Those costs may have lasting impacts on development. Delayed metamorphosis could lead to lower survival of froglets (Smith 1987; Berven 1990). In species such as *H. arborea* with life-history traits that are different from those of the ranids (e.g. lower fecundity), these delayed costs could have a stronger impact on population dynamics. Never-

theless, increasing the frequency of fish ponds may exacerbate the impact of delayed costs whatever the species, suggesting that the dynamics of species that are not fish-adverse could also suffer from the introduction of fish.

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