

Trait-mediated indirect effects and complex life-cycles in two European frogs

Res Altwegg*

Institute of Zoology, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

ABSTRACT

Most animals actively avoid predators. If such a reaction reduces competitive ability, for example by reducing food intake, predator presence can lead to trait-mediated indirect effects. Because predator avoidance typically leads to reduced growth rather than reduced survival, its effect on population processes is difficult to assess. This is especially true for organisms with complex life-cycles, where predator avoidance during one stage is expected to lead to trait-mediated indirect effects if it has effects reaching into the following life stages. I experimentally investigated the effect of caged (thus non-lethal) dragonfly larvae on the competition between tadpoles of two frog species (*Rana lessonae* and *R. esculenta*) and on juvenile frog survival during the subsequent terrestrial stage. In response to caged predators, *R. lessonae* delayed metamorphosis more than *R. esculenta*, but they both metamorphosed heavier. These differences suggest the possibility of a competitive disadvantage for *R. lessonae* in the presence of predators, which could lead to trait-mediated indirect effects. However, the presence of predators did not modify competitive effects and had no measurable consequences on terrestrial survival. Regardless of the presence of predators, competition during the larval stage had large effects on metamorphosis and led to strongly decreased survival in the subsequent terrestrial stage. These results suggest that trait-mediated indirect effects are not important in this system, because the predator reaction of the tadpoles in both species had no measurable effect on the following life stage and, therefore, probably no strong effect on community dynamics.

Keywords: Akaike's information criterion, *Anax imperator*, competition, food web, higher-order interaction, interaction modification, metamorphosis, model selection, predators, *Rana lessonae*, *Rana esculenta*, trait-mediated indirect effects.

INTRODUCTION

Indirect effects, where more than one trophic link is involved, play an important role in food webs (Schoener, 1993; Wootton, 1994; Menge, 1995; Abrams *et al.*, 1996). There are two types of indirect effects (Abrams *et al.*, 1996). First, density-mediated indirect effects occur when a change in density of one species affects another species through changes in density of a third species. This type of indirect effect has received much attention in community

* e-mail: altweggr@zool.unizh.ch

Consult the copyright statement on the inside front cover for non-commercial copying policies.

ecology. A second type of effect, termed trait-mediated indirect effect, occurs when a species modifies the interaction between two others by changing the per capita effects (Abrams *et al.*, 1996). An example is the change in the competitive relationship caused by adaptive behavioural or morphological reactions of prey individuals to the presence of predators (Werner, 1992; Relyea, 2000). In principle, density-mediated indirect effects can be calculated if the direct effects between species pairs are known (Abrams, 1991, 1993). However, the occurrence of strong trait-mediated indirect effects makes it impossible to predict the dynamics of the community from the study of isolated sub-units (Werner, 1992). Therefore, the identification of trait-mediated indirect effects is an important task in ecology.

The strength of trait-mediated indirect effects in a community critically depends on how predator avoidance and competition interact to determine the population size of all competitors. For instance, if an organism changes its growth in reaction to predators but maintains the same schedule of reproduction and experiences the same mortality as in the absence of predators, this reaction may not lead to a trait-mediated indirect effect. In organisms with complex life-cycles, a reduction in growth in an early life stage is important for the population dynamics only if it has fitness consequences during one of the following life stages. Therefore, data on carry-over effects from one life stage into the next are needed to understand the role of competition and predator avoidance for community dynamics. Such data are often difficult to obtain and, therefore, rare. For example, in fish, growth during early life is important for later survival (Ward and Slaney, 1988; Ryding and Skalski, 1999). In insects, the predator-induced reduction in growth can have equal or even stronger effects on population dynamics than direct predator-induced mortality (McPeck and Peckarsky, 1998). In amphibians, survival during the early terrestrial stage appears to be tightly linked to population dynamics on theoretical grounds (Taylor and Scott, 1997; Hellriegel, 2000; Som *et al.*, 2000). Nevertheless, few empirical studies have investigated the effect of larval competition on performance during the terrestrial life stage (Scott, 1994; Beck and Congdon, 2000; Morey and Reznick, 2001) and, to my knowledge, no study has investigated the effect of larval predator avoidance on later survival.

Trait-mediated indirect effects are likely to be important in larval amphibian communities. Larval amphibians show strong adaptive behavioural and morphological reactions when exposed to predators (Skelly and Werner, 1990; Van Buskirk *et al.*, 1997; Van Buskirk and McCollum, 1999), and competition and predation are important factors shaping these communities (Wilbur, 1980, 1984; Morin, 1983; Smith, 1983; Morin and Johnson, 1988; Van Buskirk and Smith, 1991). Considering the larval stage exclusively, several studies have found that the non-lethal presence of predators can reverse the outcome of competition among larval anurans (Werner and Anholt, 1996; Peacor and Werner, 2000; Relyea, 2000). However, the general importance of trait-mediated indirect effects in amphibian communities is still unknown, because few communities have been investigated and because the connection between larval traits and performance during the later life stages is not yet well established.

The goals of this study were two-fold. First, I examined whether predators affected the outcome of competition among larvae of two closely related frog species, *Rana lessonae* Camerano and *R. esculenta* Linnaeus. Specifically, I wished to determine (1) whether the presence of caged dragonflies affects age or size at metamorphosis differentially in the two species, and (2) whether they modify the effect of competition on age and size at metamorphosis. Second, I investigated how these effects propagated into the following life stage by analysing the consequences of predator presence and competition during the larval

stage on post-metamorphic survival. The larval ecology of the two species suggests that trait-mediated indirect effects might be important in this system, since competition in the absence of predators is strong (Semlitsch, 1993a) and *R. lessonae* shows stronger predator avoidance behaviour than *R. esculenta* (Semlitsch and Reyer, 1992a; Stauffer and Semlitsch, 1993).

METHODS

Study species

The frogs I studied belong to the *Rana esculenta* species complex and are widely distributed across Europe, with many types of mixed populations containing two or three species (Graf and Polls Pelaz, 1989). Around Zürich, Switzerland, *Rana lessonae* and *R. esculenta* occur in mixed populations with species composition varying between sites (Blankenhorn *et al.*, 1973). *Rana esculenta* is originally an interspecific hybrid between *R. lessonae* and *R. ridibunda* (Berger, 1964), with a reproductive system known as 'hybridogenesis' (Schultz, 1969; Berger, 1988; Graf and Polls Pelaz, 1989; see Som *et al.*, 2000, for a recent description of the *Rana esculenta* complex in Switzerland). The larvae of the two species almost always co-occur. Since the two species develop simultaneously and are similar in size, they are exposed to the same predators and are thought to compete commonly in natural ponds. The most important predators of amphibian larvae in my study area were aeshnid dragonfly larvae (Van Buskirk and Schmidt, 2000).

Experimental procedures

I studied the non-lethal effects of predators on competition in a large outdoor experiment, using 1100 litre fibreglass cattle tanks as experimental units. I subjected tadpoles of the two species to five competition treatments in these tanks (Underwood, 1986) (Table 1). The experimental design allowed me to estimate and compare the competitive effects of each species on itself and on the other under three total densities. I chose the densities to subject the tadpoles to high and low competition, within the range of densities found in ponds near Zürich (J. Van Buskirk, unpublished data). Each of the five treatments was replicated ten times: five times with caged predators (*Anax imperator* dragonfly larvae) and five times without. The tanks were placed outdoors on a field at the University of Zürich and arranged into five spatial blocks. I randomly assigned the treatments within every block.

The tanks were filled with tap water on 19 May 1998. Between 20 and 27 May, I added to every tank 500 g of air-dried deciduous leaf litter, 7.5 g commercial rabbit chow, and inoculated them with phytoplankton and zooplankton obtained from a natural pond.

For the predator treatments, I added to each tank three late instar larvae of *Anax imperator* kept separately in floating cages. The cages consisted of a 10 cm long piece of plastic tube with a diameter of 10 cm, closed with mosquito net on both sides. Throughout the experiment, I fed each dragonfly with 300 mg *Rana lessonae* and *R. esculenta* tadpoles three times a week to ensure strong predator chemical cue. The non-predator tanks contained empty cages. Whenever I fed the dragonflies, I turned and gently shook the cages in the non-predator tanks to equalize disturbance across treatments.

To obtain tadpoles, I caught adult frogs between 15 and 27 May 1998 in a bog pond near Hellberg, Switzerland. I injected the females with the fish hormone LH-RH (H-7525,

Table 1. Experimental design for studying the effects of non-lethal presence of a predator on competition between two larval anuran species

	Treatment				
	I	II	III	IV	V
<i>R. lessonae</i>	15	15	15	45	75
<i>R. esculenta</i>	75	45	15	15	15
Total	90	60	30	60	90

Notes: Values are numbers of larvae stocked per tank for the two species *Rana lessonae* and *R. esculenta*. Treatments I–III manipulate the density of *R. esculenta* and thus test for the competitive effects of *R. esculenta* on *R. lessonae* and on itself. Similarly, treatments III–V manipulate the density of *R. lessonae* and test for competitive effects of *R. lessonae* on *R. esculenta* and on itself. These five treatments were cross-classified with the absence and presence of caged predatory *Anax imperator* larvae to test for non-numerical effects of the predators on competition between the two species.

Bachem, Inc.) to induce ovulation (Berger *et al.*, 1994), and put one female together with two males in a tub, filled with a few centimetres of water. After they had spawned, I removed all frogs and allowed the eggs to develop in these tubs. On 9 June, when the tadpoles were 5 days old (stage 25; Gosner, 1960), I introduced the appropriate number of tadpoles to each tank. I used eight families of *R. lessonae* and three families of *R. esculenta*. All families were represented in the same proportion in all experimental units. At this time, the species were not significantly different in developmental stage or weight.

The first individual metamorphosed (stage 42; Gosner, 1960) on 20 July. From then until 21 August, I searched the tanks for metamorphs every day. I removed them, dried them with a paper towel and weighed them to the nearest milligram using an electronic balance. I also took a tissue sample from the tail for later identification of the species. I caught some metamorphs at a later stage. I calculated their weights at stage 42 using a linear regression equation of weight on stage obtained from the whole data set. After 21 August, I switched to searching the tanks at least every second day. Finally, between 14 and 18 September, I drained the tanks blockwise and counted the remaining tadpoles. Since the weather turned cold at this time, and tadpoles have very little chance of surviving the winter, the remaining individuals probably would have died.

Due to one misidentified parent, the ratio between the two species was biased towards *R. lessonae* by about 10% compared with the attempted treatments (see Table 2). The mistake affected all experimental units equally and had no effect on the total number of individuals entering each unit. Nevertheless, the mistake made it impossible to calculate species-specific survival rates during the larval stage. However, total survival until metamorphosis averaged 93% and was not significantly related to the experimental treatments (all $P \geq 0.2$). Furthermore, the problem was not critical to the rest of the analysis. I identified the species of all survivors using allozyme electrophoresis on LDH-B (E.C.-No. 1.1.1.27) obtained from the tail tissue (Richardson *et al.*, 1986: chapter 9). Then, I used the number of survivors of each species rather than experimental treatments to characterize the competition regime in the statistical analysis (Table 2). In doing so, I made the assumption

Table 2. Summary of treatment means

Species	Predator	Ratio L/E ^a	Weight ^b	Larval period ^b	n ^c
<i>R. lessonae</i>	no	19/59	658 (132)	55.2 (5.1)	5
		19/36	750 (956)	51.9 (2.0)	5
		15/13	1182 (154)	47.9 (2.2)	5
		44/13	739 (160)	55.9 (3.0)	5
		73/13	539 (85)	66.5 (3.6)	5
	yes	20/62	710 (157)	60.0 (6.7)	5
		17/37	803 (145)	54.2 (4.1)	5
		16/13	1204 (181)	54.8 (1.2)	5
		44/13	742 (63)	62.5 (3.9)	5
		74/13	617 (64)	68.9 (5.1)	4
<i>R. esculenta</i>	no	19/59	617 (109)	66.6 (5.5)	5
		19/36	708 (112)	65.2 (3.9)	5
		15/13	1238 (239)	56.4 (2.2)	5
		44/13	803 (189)	68.1 (6.3)	5
		73/13	589 (114)	74.8 (6.7)	4
	yes	20/62	701 (149)	70.6 (6.7)	5
		17/37	825 (187)	64.2 (4.8)	5
		16/13	1269 (263)	61.2 (2.0)	5
		44/13	844 (91)	70.4 (4.9)	5
		74/13	680 (104)	76.2 (4.0)	4

^a Numbers of *Rana lessonae* and *R. esculenta* (ratio L/E) surviving to the end of the experiment; the contradictions to numbers in Table 1 are due to an experimental mishap (see Methods).

^b Mean values and standard deviations for weight at metamorphosis (mg) and length of larval period (days).

^c Number of replicates per treatment.

that mortality occurred early during the experiment. The results were not sensitive to this procedure: whether I assumed that the 7% dying individuals were all *R. lessonae* or all *R. esculenta*, the results remained qualitatively the same (estimates of competitive effects changed by ~6%).

I monitored the survival of 326 juvenile frogs over the first winter in their natural habitat to estimate the effects of larval competition and presence of predators. The individuals were drawn randomly with respect to treatment and time of metamorphosis. After the froglets had completed tail resorption (stage 46; Gosner, 1960), I individually marked them by toe clipping and kept them for a few days in groups of up to ten individuals in plastic 5-litre tubs. The froglets had *ad libitum* access to crickets. Starting on 6 August, I released newly marked individuals once every 2 weeks into field enclosures, so that a maximal density of 4.5 individuals per square metre was eventually reached. The four enclosures consisted of 18 m² of fenced forest floor near Zürich, Switzerland, where frogs are known to hibernate (Holenweg and Reyer, 2000). The fences extended about 40 cm into the soil; a 15 cm wide overhanging plastic strip prevented the frogs from climbing across. Each enclosure had a shallow-bottomed plastic bowl with a diameter of 65 cm that served as a small permanent

pool. Between 5 May and 19 June 1999, I caught and identified all surviving frogs in a total of seven capture events.

Statistical analyses

I structured the statistical analysis in two parts. First, I studied the non-lethal predator effects on larval competition (Part 1). I then examined the consequences of these effects on survival during the subsequent terrestrial stage (Part 2). All analyses were performed on mean values across tanks. I omitted the data for one tank because one of the predator cages broke open and the dragonfly larva escaped into the tank. The total sample size was thus 49.

Part 1. I examined whether predators and competition differentially affected larval growth in the two species using a multivariate analysis of covariance (MANCOVA) and subsequent univariate analysis of covariance (ANCOVA) models in PROC GLM (SAS Institute, Inc., 1996). Since all treatments contained both species, the response variables were [(tank mean *esculenta* length of larval period) minus (tank mean *lessonae* length of larval period)] and [(tank mean *esculenta* weight at metamorphosis) minus (tank mean *lessonae* weight at metamorphosis)]. Here, competition refers to the total number of competitors of both species combined.

Next, I analysed the effects of numbers of conspecific and heterospecific competitors and the effect of caged predators on duration of larval period and weight at metamorphosis. A statistical interaction would indicate a predator-induced modification of competition and possibly trait-mediated indirect effects. I conducted separate analyses on *Rana lessonae* and *R. esculenta*.

I ran regression models using a GLIM framework provided by PROC GENMOD in SAS (SAS Institute, Inc., 1996) to analyse the effects on each of the two response variables separately. Instead of first conducting a multivariate analysis on both responses, I investigated the joint effect of these variables on subsequent survival (see below). Inspection of the residuals showed that the data did not violate the assumptions of equal variance and normality. Thus I did not transform the data before the analysis.

Due to a mistake during the set-up of the experiment (see above), I analysed competition by taking the number of survivors as covariates rather than using the experimental treatments. The possibility that competitive effects could have been equal between the species, and that they could have been linear or non-linear with increasing density, led to four statistical models corresponding to these biological hypotheses. I used model selection based on information-theoretic methods to evaluate the relative fit of the models, because this allowed me to compare all models simultaneously (Burnham and Anderson, 1998). Also, some of the models are not nested in a statistical sense, in which case no significance test exists (Anderson *et al.*, 2000). The analysis involved calculating the small-sample bias adjusted Akaike's information criterion (AICc; Anderson and Burnham, 1999). The lower this criterion, the better the fit to the data of the corresponding model. The Akaike weights estimate the relative support that a particular model has from the data and sum up to one across all models (Burnham and Anderson, 1998: 123). Running the four models with and without an interaction between predators and competition enabled me to estimate the importance of these interactions using the same methods. Finally, I used the regression coefficients to assess the effects of predator presence and competition based on the AICc selected best model. The standard errors are thus conditional on this model.

Part 2. I used the relationship between survival after metamorphosis and age and size at metamorphosis among the 326 froglets that I followed during their early terrestrial life stage to infer expected survival for all individuals. Terrestrial survival decreased with increasing age at metamorphosis and increased with increasing size at metamorphosis. Competition and the presence of predators had no independent effect beyond that which these two metamorphic responses explained (R. Altwegg, unpublished). I used the parameter values obtained from a multiple logistic regression of survival on age and size at metamorphosis in the sub-sample to calculate expected survival of the other individuals:

$$\text{survival} = 1/(1 + \exp^{(-\text{intercept} + a*A + b*W)})$$

where A = age at metamorphosis and W = weight at metamorphosis. The slope parameters were $a = -0.0322$, $b = 0.00230$ and the intercept = -1.5903 for *R. lessonae*, and $a = -0.0474$, $b = 0.0016$ and the intercept = 0.8049 for *R. esculenta*. Since tadpoles almost never survive the winter in my study area (personal observation), individuals that had not metamorphosed by the time I ended the experiment were assumed to have zero survival. I did not analyse the effects on body size of froglets in the spring because poor overwinter survival of small froglets resulted in size and survival being confounded.

I evaluated the importance of competition and presence of predators on expected survival by using the model selection approach outlined above. I compared eight *a priori* models corresponding to the biological hypotheses outlined in the previous section, evaluated their relative fit to the data using AICc, and estimated the magnitude of the regression coefficients from the AICc selected best model.

RESULTS

Differences between species

The results of the MANCOVA on species differences in length of larval period and weight at metamorphosis showed that the two species reacted differently to the presence of predators, but similarly to increased competition (Table 3). Furthermore, the significant intercept term indicated general species differences in metamorphosis. These results suggest that growth of the two species was differentially affected by the predators. This could lead to trait-mediated indirect effects. Table 2 gives a summary of length of larval period and weight at metamorphosis in all treatments.

A univariate ANCOVA model showed that *R. lessonae* metamorphosed sooner than *R. esculenta* (intercept: $F_{1,47} = 331.82$, $P < 0.001$; Fig. 1a), but this difference was smaller when predators were present ($F_{1,41} = 6.95$, $P = 0.011$). Number of competitors had a similar effect on *R. esculenta* and *R. lessonae* ($F_{1,41} = 1.92$, $P = 0.17$), and the two factors affected the difference between the species in an additive way (predator $\times$ density interaction: $F_{1,40} = 0.33$, $P = 0.57$).

Rana lessonae tended to metamorphose at a lower weight than *R. esculenta* (intercept: $F_{1,48} = 5.67$, $P = 0.021$; Fig. 1b), but predators affected weight at metamorphosis to a similar extent in both species ($F_{1,41} = 1.80$, $P = 0.19$). The number of competitors also had a similar effect on *R. esculenta* and on *R. lessonae* ($F_{1,41} = 2.18$, $P = 0.15$), and there was no significant interaction between these two factors ($F_{1,40} = 0.14$, $P = 0.71$).

Table 3. Results of MANCOVA on the effects of presence of predators, total number of competitors and their interaction on relative performance of *Rana esculenta* and *R. lessonae*

	d.f.	Wilk's λ	<i>F</i>	<i>P</i>
Intercept ^a	2,46	0.112	182.21	< 0.001
Predators	2,40	0.838	3.87	0.029
Number of competitors	2,40	0.919	1.76	0.185
Predators*competitors	2,39	0.987	0.26	0.772

Note: Response variables are the differences in tank means in weight at metamorphosis and duration of larval period.

^a The intercept term tests whether the grand mean was different from zero; that is, whether the species were different in the two traits considered.

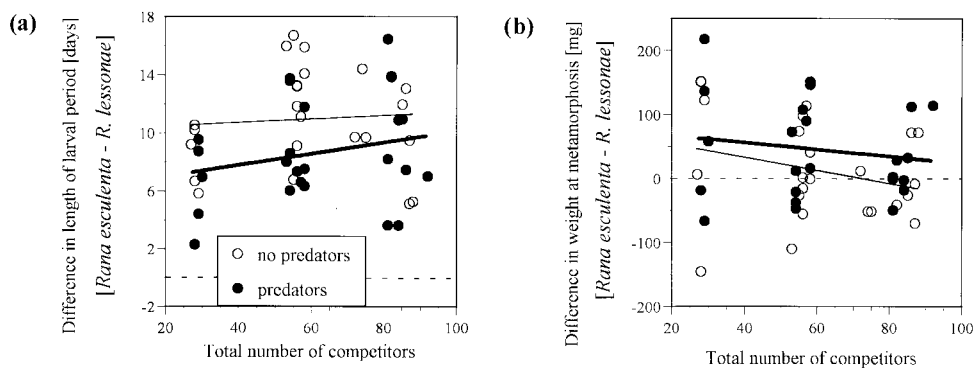


Fig. 1. Differences between *Rana lessonae* and *R. esculenta* in length of larval period (a) and weight at metamorphosis (b). Tank mean values of *R. lessonae* are subtracted from those of *R. esculenta*. Positive values thus mean that *R. esculenta* had a longer larval period and were heavier at metamorphosis than *R. lessonae*. Linear regression lines are shown (thin = no predator, bold = predator). The broken line marks zero differences.

Predator-induced modification of competitive effects: metamorphosis

Length of larval period

For both species, AICc clearly selected the model where the effect of competition on the length of the larval period was linear and different between the two species (Table 4a, Fig. 2a,b). There was no evidence for the presence of predators modifying competition; the Akaike weights for models 5–8, which exclude the interaction between predator presence and competition, summed up to 91.5% and 96.4% for *R. lessonae* and *R. esculenta*, respectively. Therefore, they were 11 times (91.5/8.5 for *R. lessonae*) and 27 times (96.4/3.6 for *R. esculenta*) better supported by the data than models 1–4, which included the interaction. The regression coefficients showed that the per capita effect of *R. lessonae* on its own length of larval period was 0.29 ± 0.02 (mean $\pm$ standard error; $\chi^2 = 205.1$, $P < 0.001$), while the effect of *R. esculenta* on *R. lessonae* length of larval period was 0.10 ± 0.02 ($\chi^2 = 20.6$,

Table 4. Summary of model selection for the effect of competition and presence of predators on (a) length of the larval period and (b) weight at metamorphosis

Model	<i>Rana lessonae</i>					<i>Rana esculenta</i>				
	Log likelihood	K	AICc	ΔAICc	Akaike weight	Log likelihood	K	AICc	ΔAICc	Akaike weight
(a) Length of larval period										
1. les ◇ esc, quadratic, int	-113.503	15	271.552	13.990	0.001	-121.503	15	287.551	14.485	0.001
2. les ◇ esc, linear, int	-116.547	11	262.228	4.667	0.084	-125.107	11	279.349	6.283	0.035
3. les = esc, quadratic, int	-138.293	11	305.721	48.160	0.000	-132.813	11	294.762	21.697	0.000
4. les = esc, linear, int	-139.147	9	300.909	43.348	0.000	-133.877	9	290.369	17.303	0.000
5. les ◇ esc, quadratic	-117.110	11	263.355	5.794	0.048	-123.693	11	276.521	3.456	0.145
6. les ◇ esc, linear	-117.473	9	257.561	0.000	0.867	-125.225	9	273.065	0.000	0.818
7. les = esc, quadratic	-139.098	9	300.810	43.249	0.000	-133.493	9	289.601	16.536	0.000
8. les = esc, linear	-139.843	8	299.287	41.725	0.000	-133.979	8	287.558	14.493	0.001
					Σ = 1					Σ = 1
(b) Weight at metamorphosis										
1. les ◇ esc, quadratic, int	-278.432	15	601.409	15.422	0.000	-291.683	15	627.911	21.298	0.000
2. les ◇ esc, linear, int	-294.845	11	618.825	32.838	0.000	-301.423	11	631.980	25.368	0.000
3. les = esc, quadratic, int	-281.592	11	592.319	6.331	0.023	-291.884	11	612.904	6.291	0.040
4. les = esc, linear, int	-295.932	9	614.479	28.492	0.000	-301.937	9	626.489	19.877	0.000
5. les ◇ esc, quadratic	-278.667	11	586.469	0.482	0.430	-291.842	11	612.820	6.207	0.041
6. les ◇ esc, linear	-295.104	9	612.824	26.837	0.000	-301.762	9	626.140	19.527	0.000
7. les = esc, quadratic	-281.686	9	585.987	0.000	0.547	-291.999	9	606.613	0.000	0.919
8. les = esc, linear	-296.086	8	611.772	25.785	0.000	-302.126	8	623.852	17.240	0.000
					Σ = 1					Σ = 1

Notes: The table lists all fitted models, their log likelihood and their number of parameters, K . AICc gives an estimate of the parsimony of every model and is calculated as $(-2 \log \text{likelihood} + 2K(K+1)/(n-K-1))$, taking into account sample size n (Burnham and Anderson, 1998). ΔAICc is the difference in AICc of a particular model to the most parsimonious model (in **bold**). ‘Akaike weights’ indicate the extent to which the data support a particular model, which were run as regression models in PROC GENMOD (SAS Institute, Inc., 1996). I chose the models to evaluate four hypotheses concerning the effects of competition. Models 1–4 include the interaction between predators and competition, while models 5–8 contain the main effects only. Models 1, 2, 5 and 6 assume competitive effects to be different between the two species. Models 3, 4, 7 and 8 assume equal competitive effects. Models 1, 3, 5 and 7 assume competitive effects to be non-linear with density, while models 2, 4, 6 and 8 assume competition to be linear. Corresponding to the experimental design, all models accounted for the block structure and contained the effects of non-lethal predators and competition.

Abbreviations: les = *R. lessonae*, esc = *R. esculenta*, int = interaction.

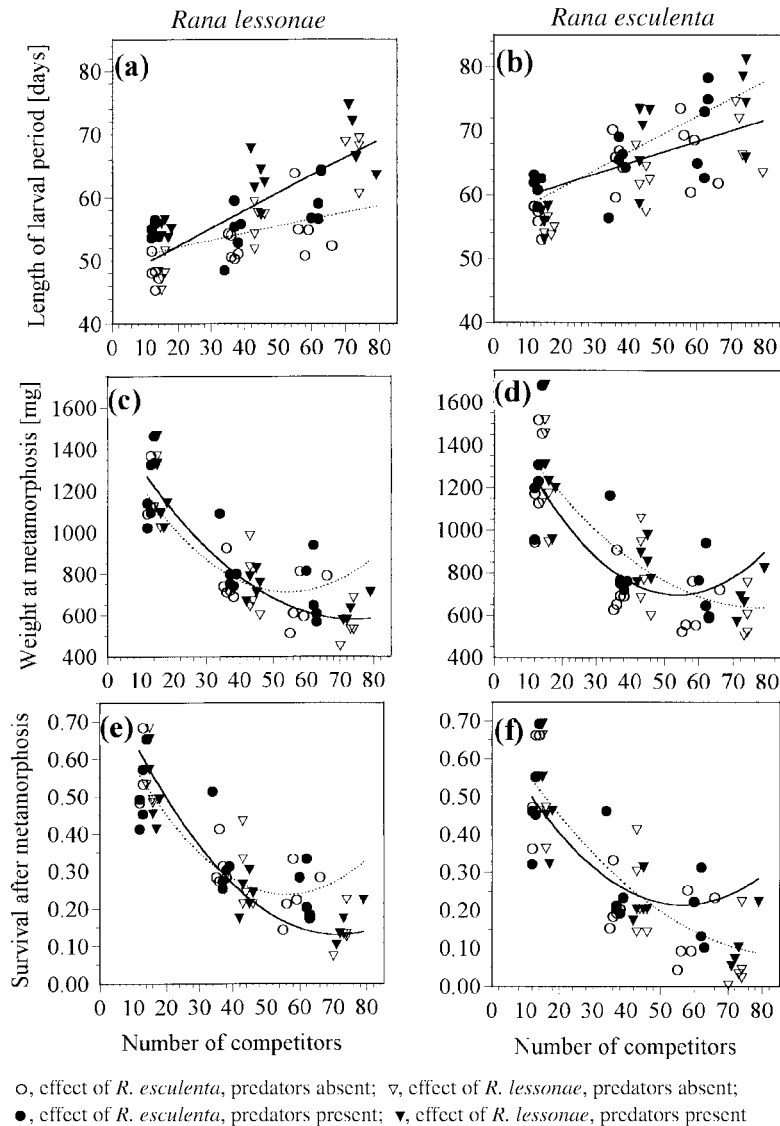


Fig. 2. Effects of competition by *Rana lessonae* (triangles) and *R. esculenta* (circles) on *R. lessonae* (left column) and on *R. esculenta* (right column). Numbers of competitors are in addition to the low competition treatment (15 individuals). The response variables were length of larval period (top row), weight at metamorphosis (middle row) and expected overwinter survival after metamorphosis (bottom row). Open symbols represent no-predator treatments, filled symbols indicate presence of predators. The regression lines show the intraspecific effects (solid) and the interspecific effects (broken).

$P < 0.001$). *Rana lessonae* had a per capita effect of 0.29 ± 0.03 ($\chi^2 = 130.3$, $P < 0.001$) on *R. esculenta*; the effect of *R. esculenta* on its own length of larval period was 0.16 ± 0.03 ($\chi^2 = 35.0$, $P < 0.001$). Predators increased the average length of larval period by $4.6 \pm$

0.8 days ($\chi^2 = 35.8$, $P < 0.001$) in *R. lessonae* and by 2.2 ± 0.9 days ($\chi^2 = 5.4$, $P = 0.02$) in *R. esculenta*.

Weight at metamorphosis

The model selection analysis showed that competition affected weight at metamorphosis in a non-linear way (Table 4b, Fig. 2c,d). The AICc selected best models constrained the intraspecific and interspecific effects to be the same for both species (model 7, Table 4b). But for *R. lessonae*, the fit of the model allowing for differences between these effects was almost as good (models 5 vs 7: $\Delta\text{AICc} = 0.482$). In this case, the data do not clarify whether the intraspecific and the interspecific competitive effects were equal. There was no evidence for an interaction between predators and competition; the Akaike weights show that models 5–8 excluding the interactions were 42 times (for *R. lessonae*) and 24 times (for *R. esculenta*) better supported by the data than models 1–4.

With increasing density, weight at metamorphosis first decreased steeply and then levelled off. The regression coefficients showed that adding x individuals depressed weight at metamorphosis in *R. lessonae* by $-30.1x + 0.18x^2$ mg (standard error = 3.3, $\chi^2 = 82.8$, $P < 0.001$; and standard error = 0.03, $\chi^2 = 39.2$, $P < 0.001$, respectively), while the effect on *R. esculenta* was $-33.3x + 0.2x^2$ mg (standard error = 4.6, $\chi^2 = 51.9$, $P < 0.001$; and standard error = 0.04, $\chi^2 = 25.2$, $P < 0.001$, respectively). The presence of predators increased average weight at metamorphosis by 50 ± 22 mg ($\chi^2 = 5.3$, $P = 0.02$) in *R. lessonae* and by 76 ± 30 mg ($\chi^2 = 6.1$, $P = 0.01$) in *R. esculenta*.

Consequences of predators and competition for post-metamorphic survival

Competition affected post-metamorphic survival in a non-linear way and the effects differed between the species (Table 5, Fig. 2e,f). There was no evidence for an interaction between predators and competition; the Akaike weights showed that models 5–8 excluding the interactions were 110 times (for *R. lessonae*) and 17 times (for *R. esculenta*) better supported by the data than models 1–4.

Generally, adding competitors strongly depressed survival at low densities, but the effect levelled off at higher densities. The per capita effect of *R. lessonae* on its own survival after metamorphosis was $-0.019x + 0.00012x^2$ (standard error = 0.0021, $\chi^2 = 82.5$, $P < 0.001$; and standard error = 0.000023, $\chi^2 = 28.7$, $P < 0.001$, respectively), while the effect of *R. esculenta* on *R. lessonae* was $-0.018x + 0.00016x^2$ (standard error = 0.0024, $\chi^2 = 55.867$, $P < 0.001$; and standard error = 0.000033, $\chi^2 = 23.8$, $P < 0.001$, respectively). *Rana lessonae* had a per capita effect of $-0.013x + 0.00007x^2$ (standard error = 0.0022, $\chi^2 = 35.2$, $P < 0.001$; and standard error = 0.000024, $\chi^2 = 7.3$, $P = 0.007$, respectively) on *R. esculenta*, and the effect of *R. esculenta* on its own survival after metamorphosis was $-0.016x + 0.00013x^2$ (standard error = 0.0025, $\chi^2 = 37.5$, $P < 0.001$; and standard error = 0.000034, $\chi^2 = 15.3$, $P < 0.001$, respectively).

The presence of predators during the larval stage had no measurable effect on post-metamorphic survival (-0.009 ± 0.01 , $\chi^2 = 0.34$, $P = 0.6$ on *R. lessonae*; 0.003 ± 0.02 , $\chi^2 = 0.03$, $P = 0.9$ on *R. esculenta*). Apparently, the effect of predator presence on the metamorphic traits had opposite and compensatory consequences for subsequent survival.

Table 5. Summary of model selection for the effect of competitors and presence of predators on expected survival after metamorphosis (see footnotes to Table 4 for details)

Model	<i>Rana lessonae</i>				<i>Rana esculenta</i>					
	Log likelihood	K	AICc	ΔAICc	Akaike weight	Log likelihood	K	AICc	ΔAICc	Akaike weight
Post-metamorphic survival										
1. les ◇ esc, quadratic, int	77.072	15	−109.599	13.609	0.001	76.110	15	−107.674	11.409	0.002
2. les ◇ esc, linear, int	60.750	11	−92.365	30.843	0.000	67.269	11	−105.403	13.679	0.001
3. les = esc, quadratic, int	71.510	11	−113.885	9.324	0.008	71.578	11	−114.020	5.063	0.050
4. les = esc, linear, int	58.648	9	−94.680	28.529	0.000	65.222	9	−107.829	11.254	0.002
5. les ◇ esc, quadratic	76.172	11	−123.208	0.000	0.871	74.109	11	−119.083	0.000	0.633
6. les ◇ esc, linear	59.983	9	−97.350	25.858	0.000	65.769	9	−108.923	10.160	0.004
7. les = esc, quadratic	70.929	9	−119.242	3.966	0.120	70.121	9	−117.627	1.456	0.305
8. les = esc, linear	58.093	8	−96.587	26.621	0.000	63.836	8	−108.072	11.011	0.003
					Σ = 1					Σ = 1

DISCUSSION

This study has shown that the reaction of *Rana lessonae* and *R. esculenta* tadpoles to caged predators leads to different life-history shifts in the two species. This reaction, however, had no detectable survival consequences for the following terrestrial stage. When exposed to the non-lethal presence of predacious *Anax* dragonfly larvae, *R. lessonae* decreased developmental speed more than *R. esculenta*, but both species increased their weight at metamorphosis by a similar amount. The two species showed a strong competitive interaction, which led to substantially decreased terrestrial survival. But the presence of predators did not modify competitive effects. These results suggest that trait-mediated indirect effects are unlikely to be important because, in both species, the presence of caged predators did not affect post-metamorphic survival, which is the response most strongly related to population dynamics.

Theory predicts that trait-mediated indirect effects are expected when two conditions are met: if one competitor shows a large change in a trait in response to the presence of predators, and this change has a large effect on the other competitor (Abrams, 1993; Abrams *et al.*, 1996). This set of circumstances should be common in nature (Lima and Dill, 1990) and, accordingly, the importance of trait-mediated indirect effects has been demonstrated in several of different communities (Turner and Mittelbach, 1990; Wissinger and McGrady, 1993; Werner and Anholt, 1996; Schmitz, 1998; Peacor and Werner, 2000; Turner *et al.*, 2000). Among the classical examples are anuran larvae (Werner, 1991), because they show strong behavioural and morphological responses when exposed to predators; these traits are important for competition (Morin, 1983; Lawler, 1989; Van Buskirk *et al.*, 1997; Relyea, 2000). Therefore, traits such as activity, habitat choice and tail morphology are possible candidates for causing trait-mediated indirect effects in amphibian communities (Werner, 1991). Unfortunately, I could not measure changes in these traits directly, because the tadpoles of *R. lessonae* and *R. esculenta* are visually indistinguishable. Previous studies, however, have shown that the presence of non-lethal predators causes stronger behavioural and morphological reactions in *R. lessonae* than in *R. esculenta* (Semlitsch and Reyer, 1992a; J. Van Buskirk, unpublished data), which led to reduced larval growth in the former but not in the latter species (Van Buskirk, 2000). The results of the present study agree with these findings. *Rana lessonae* showed a stronger growth reaction than *R. esculenta*, as they prolonged their larval period more, but similarly increased metamorphic size.

The results of this study suggest that important conditions for the occurrence of trait-mediated indirect effects were fulfilled: competition between the two tadpole species had a very strong effect on larval growth. And the different consequences of the predator response on metamorphosis could lead to a competitive disadvantage of *R. lessonae* compared with the less responsive *R. esculenta*. However, the species differences were not strong enough to cause trait-mediated indirect effects. The competitive effects were similar, regardless of the presence of predators, as the absence of an interaction between competition and predator presence on all responses suggested. Furthermore, the growth strategies of both species led to the same post-metamorphic survival rates.

Strong trait-mediated indirect effects through the non-lethal presence of *Anax* larvae have been found in two systems similar to the *R. lessonae*–*R. esculenta* system examined here. One consists of *Rana clamitans* and two size classes of *R. catesbeiana* (Werner, 1991; Werner and Anholt, 1996; Peacor and Werner, 1997), and the other consists of *Rana pipiens* and *R. sylvatica* (Relyea, 2000). In both systems, there are strong competitive interactions

between the tadpole species, and the reaction to the presence of predators is strong and asymmetric. However, these studies focused on larval growth rates; none of them investigated metamorphic responses or consequences on later life stages. My results show that larval growth rate is related to the latter fitness components. But within limits, differences in growth rate can be compensated by metamorphic timing. It depends on how the length of the larval period and the size at metamorphosis scale to subsequent survival and growth. In the present study, the reaction to predators delayed metamorphosis in both species. Metamorphosing later is generally a disadvantage, because it has a negative effect on terrestrial growth and survival (Smith, 1987; Berven, 1990; R. Altwegg, unpublished). Furthermore, delaying metamorphosis bears the risk of not being able to metamorphose at all before the onset of winter and almost certain death (personal observation).

On the other hand, later metamorphosis allows more time to grow to a larger size during the aquatic stage, and larger size strongly improves subsequent survival (R. Altwegg, unpublished). In the present study, tadpoles were able to balance the disadvantage of slower larval development by metamorphosing at a larger size. Even though the reaction to predators decreased developmental rate more in *R. lessonae* than in *R. esculenta*, the post-metamorphic survival rates were not affected in either species. Thus the reaction to predators was similar enough in both species that differences in larval growth could be compensated for by the timing of metamorphosis.

The non-lethal presence of predators did not affect per capita competitive effects, neither on age and size at metamorphosis nor on terrestrial survival, as the lack of a statistical interaction between predator presence and competition suggests. Assuming exploitative competition, such an interaction would have been expected if the reaction to predators changed the rate of individual food intake (Peacor and Werner, 2000). The absence of such an interaction over the wide range of densities examined in this experiment suggests that individual feeding efficiency was weakly affected by the presence of predators.

In frogs, age and size at metamorphosis also affected post-metamorphic growth (R. Altwegg, unpublished). If the reaction to predators during the larval stage differentially affected post-metamorphic growth in the two species, this could also lead to trait-mediated indirect effects. Unfortunately, I could not analyse growth of the froglets until the spring because poor winter survival of small froglets resulted in size and survival being confounded. However, among the survivors in both species ($n = 86$), weight in spring was very similar, regardless of predator presence or absence during the larval stage (1577 vs 1539 mg, standard deviation > 900 mg).

The absence of trait-mediated indirect effects in the system of frog larvae and one of their most important predators suggests that this system should be predictable from the knowledge of direct predator-induced mortalities and of competitive effects under different conditions (Abrams, 1991). The results show that increased larval competition strongly lowered survival in the following terrestrial stage (see Fig. 2e,f). There are very few data on the effect of larval competition on survival during the subsequent terrestrial life stage in amphibians. The only other study I am aware of found similarly strong effects in marbled salamanders (Scott, 1994). In the present study, *R. lessonae* appeared to be the stronger competitor. The effect of *R. lessonae* density was stronger, both on *R. esculenta* and on itself. However, compared with the strength of competition in general, differences between the species were small. In nature, this difference may be overridden or reversed by other biotic and abiotic factors. For example, *R. lessonae* performed worse than *R. esculenta* when conditions were harsh (Semlitsch and Reyer, 1992b; Negovetic *et al.*, 2001), and when

exposed to free-ranging dragonfly larvae *R. lessonae* experienced higher mortality (Semlitsch, 1993b).

This study has two major conclusions. First, the results demonstrate a strong effect of the larval growth environment on survival during the following terrestrial life stage. Recent models have shown that population dynamics of amphibians are very sensitive to this fitness component (Taylor and Scott, 1997; Hellriegel, 2000; Hellriegel and Reyer, 2000; Som *et al.*, 2000). However, we still lack detailed data on the relationship between ecological factors and the fitness components of all the life stages and estimates of variability of these fitness components in natural populations. In the face of the global decline in amphibians (Houlahan *et al.*, 2000), such data are sorely needed to identify the factors that generally control amphibian populations. Second, this study suggests that trait-mediated indirect effects are not important in the *Rana lessonae*–*R. esculenta*–*Anax imperator* system. Yet prior knowledge of the anti-predator reaction of the two competing prey species and results from similar systems had indicated that trait-mediated indirect effects are potentially important. This experiment might have led to quite different conclusions regarding the importance of trait-mediated indirect effects if I had terminated it sooner. For instance, predator-induced differences in the early larval growth rate were probably compensated during the less responsive later larval stage or by the timing of metamorphosis. The importance of trait-mediated indirect effects appears to differ between similar communities in nature and requires careful examination in every case.

ACKNOWLEDGEMENTS

Many people helped with fieldwork, including T. Garner, G. Saxer, S. Thurnheer, J. Van Buskirk and Y. Willi. Thanks to S. Röthlisberger for help with the electrophoresis. B.R. Anholt, H.-U. Reyer, M.L. Rosenzweig, G. Saxer, B.R. Schmidt, J. Van Buskirk and C. Vorburger provided very helpful comments on earlier drafts of the manuscript. This work was supported by Swiss NF grant #31-40688.94 to H.-U. Reyer.

REFERENCES

- Abrams, P.A. 1991. Strengths of indirect effects generated by optimal foraging. *Oikos*, **62**: 167–176.
- Abrams, P.A. 1993. Indirect effects arising from optimal foraging. In *Mutualism and Community Organization: Behavioral, Theoretical and Food Web Approaches* (H. Kawanabe, J.E. Cohen and K. Iwasaki, eds), pp. 255–279. Oxford: Oxford University Press.
- Abrams, P.A., Menge, B.A., Mittelbach, G.G., Spiller, D.A. and Yodzis, P. 1996. The role of indirect effects in food webs. In *Food Webs: Integration of Patterns and Dynamics* (G.P. Polis and K.O. Winemiller, eds), pp. 371–395. New York: Chapman & Hall.
- Anderson, D.R. and Burnham, K.P. 1999. Understanding information criteria for selection among capture–recapture or ring recovery models. *Bird Study*, **46**: S14–S21.
- Anderson, D.R., Burnham, K.P. and Thompson, W.L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *J. Wild. Manage.*, **64**: 912–923.
- Beck, C.W. and Congdon, J.D. 2000. Effects of age and size at metamorphosis on performance and metabolic rates of Southern Toad, *Bufo terrestris*, metamorphs. *Funct. Ecol.*, **14**: 32–38.
- Berger, L. 1964. Is *Rana esculenta lessonae* Camerano a distinct species? *Ann. Zool. (Warsaw)*, **22**: 45–61.
- Berger, L. 1988. On the origin of genetic systems in European waterfrog hybrids. *Zool. Poloniae*, **35**: 5–32.

- Berger, L., Rybacki, M. and Hotz, H. 1994. Artificial fertilization of water frogs. *Amphibia-Reptilia*, **15**: 408–413.
- Berven, K.A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology*, **71**: 1599–1608.
- Blankenhorn, H.J., Heusser, H. and Notter, P. 1973. Zur Verbreitung von *Rana esculenta* Linnaeus und *Rana lessonae* Camerano im Zürcher Oberland. *Rev. Suisse Zool.*, **80**: 662–666.
- Burnham, K.P. and Anderson, D.R. 1998. *Model Selection and Inference: A Practical Information-theoretic Approach*. New York: Springer.
- Gosner, N. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, **16**: 183–190.
- Graf, J.-D. and Polls Pelaz, M. 1989. Evolutionary genetics of the *Rana esculenta* complex. In *Evolution and Ecology of Unisexual Vertebrates* (R.M. Dawley and J.P. Bogart, eds), pp. 289–302. Albany, NY: New York State Museum.
- Hellriegel, B. 2000. Single- or multistage regulation in complex life cycles: does it make a difference? *Oikos*, **88**: 239–249.
- Hellriegel, B. and Reyer, H.-U. 2000. Factors influencing the composition of mixed populations of a hemiclinal hybrid and its sexual host. *J. Evol. Biol.*, **13**: 906–918.
- Holenweg, A.-K. and Reyer, H.-U. 2000. Hibernation behavior of *Rana lessonae* and *R. esculenta* in their natural habitat. *Oecologia*, **123**: 41–47.
- Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H. and Kuzmin, S.L. 2000. Quantitative evidence for global amphibian population declines. *Nature*, **404**: 752–755.
- Lawler, S.P. 1989. Behavioural responses to predators and predation risk in four species of larval anurans. *Anim. Behav.*, **38**: 1039–1047.
- Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**: 619–640.
- McPeck, M. and Peckarsky, B.L. 1998. Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. *Ecology*, **79**: 867–879.
- Menge, B.A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol. Monogr.*, **65**: 21–74.
- Morey, S. and Reznick, D. 2001. Effects of larval density on postmetamorphic spadefoot toads (*Spea hammondi*). *Ecology*, **82**: 510–522.
- Morin, P.J. 1983. Predation, competition, and the composition of larval anuran guilds. *Ecol. Monogr.*, **53**: 119–138.
- Morin, P.J. and Johnson, E.A. 1988. Experimental studies of asymmetric competition among anurans. *Oikos*, **53**: 398–407.
- Negovetic, S., Anholt, B.R., Semlitsch, R.D. and Reyer, H.-U. 2001. Specific responses of sexual and hybridogenetic European waterfrog tadpoles to temperature. *Ecology*, **82**: 766–774.
- Peacor, S.D. and Werner, E.E. 1997. Trait-mediated indirect interactions in a simple aquatic food web. *Ecology*, **78**: 1146–1156.
- Peacor, S.D. and Werner, E.E. 2000. Predator effects on an assemblage of consumers through induced changes in consumer foraging behavior. *Ecology*, **81**: 1998–2010.
- Relyea, R. 2000. Trait-mediated indirect effects in larval anurans: reversing competition with the threat of predation. *Ecology*, **81**: 2278–2289.
- Richardson, B.J., Baverstock, P.R. and Adams, M. 1986. *Allozyme Electrophoresis: A Handbook for Animal Systematics and Population Studies*. San Diego, CA: Academic Press.
- Ryding, K.E. and Skalski, J.R. 1999. Multivariate regression relationships between ocean conditions and early marine survival of coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.*, **56**: 2374–2384.
- SAS Institute, Inc. 1996. *SAS/STAT Software: Changes and Enhancements through Release 6.11*. Cary, NC: SAS Institute, Inc.

- Schmitz, O.J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Nat.*, **151**: 327–342.
- Schoener, T.W. 1993. On the relative importance of direct versus indirect effects in ecological communities. In *Mutualism and Community Organization: Behavioral, Theoretical and Food Web Approaches* (H. Kawanabe, J.E. Cohen and K. Iwasaki, eds), pp. 365–411. Oxford: Oxford University Press.
- Schultz, R.J. 1969. Hybridization, unisexuality, and polyploidy in the teleost *Poeciliopsis* (Poeciliidae) and other vertebrates. *Am. Nat.*, **103**: 605–619.
- Scott, D.E. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology*, **75**: 1383–1396.
- Semlitsch, R.D. 1993a. Asymmetric competition in mixed populations of tadpoles of the hybridogenetic *Rana esculenta* complex. *Evolution*, **47**: 510–519.
- Semlitsch, R.D. 1993b. Effects of different predators on the survival and development of tadpoles from the hybridogenetic *Rana esculenta* complex. *Oikos*, **67**: 40–46.
- Semlitsch, R.D. and Reyer, H.-U. 1992a. Modification of anti-predator behaviour in tadpoles by environmental conditioning. *J. Anim. Ecol.*, **61**: 353–360.
- Semlitsch, R.D. and Reyer, H.-U. 1992b. Performance of tadpoles from the hybridogenetic *Rana esculenta* complex: interactions with pond drying and interspecific competition. *Evolution*, **46**: 665–676.
- Skelly, D.K. and Werner, E.E. 1990. Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology*, **71**: 2313–2322.
- Smith, D.C. 1983. Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. *Ecology*, **64**: 501–510.
- Smith, D.C. 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology*, **68**: 344–350.
- Som, C., Anholt, B.R. and Reyer, H.-U. 2000. The effect of assortative mating on the coexistence of a hybridogenetic waterfrog and its sexual host. *Am. Nat.*, **156**: 34–46.
- Staufer, H.-P. and Semlitsch, R.D. 1993. Effects of visual, chemical and tactile cues of fish on the behavioural responses of tadpoles. *Anim. Behav.*, **46**: 355–364.
- Taylor, B.E. and Scott, D.E. 1997. Effects of larval density dependence on population dynamics of *Ambystoma opacum*. *Herpetologica*, **53**: 132–145.
- Turner, A.M. and Mittelbach, G.G. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology*, **71**: 2241–2254.
- Turner, A.M., Bernot, R.J. and Boes, C.M. 2000. Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails. *Oikos*, **88**: 148–158.
- Underwood, T. 1986. The analysis of competition by field experiments. In *Community Ecology: Pattern and Process* (J. Kikkawa and D.J. Anderson, eds), pp. 240–268. London: Blackwell.
- Van Buskirk, J. 2000. The costs of an inducible defense in anuran larvae. *Ecology*, **81**: 2813–2821.
- Van Buskirk, J. and McCollum, S.A. 1999. Plasticity and selection explain variation in tadpole phenotype between ponds with different predator composition. *Oikos*, **85**: 31–39.
- Van Buskirk, J. and Schmidt, B.R. 2000. Predator-induced phenotypic plasticity in larval newts: trade-offs, selection, and variation in nature. *Ecology*, **81**: 3009–3028.
- Van Buskirk, J. and Smith, D.C. 1991. Density-dependent population regulation in a salamander. *Ecology*, **72**: 1747–1756.
- Van Buskirk, J., McCollum, S.A. and Werner, E.E. 1997. Natural selection for environmentally induced phenotypes in tadpoles. *Evolution*, **51**: 1983–1992.
- Ward, B.R. and Slaney, P.A. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. *Can. J. Fish. Aquat. Sci.*, **45**: 1110–1122.
- Werner, E.E. 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. *Ecology*, **72**: 1709–1720.

- Werner, E.E. 1992. Individual behavior and higher-order interactions. *Am. Nat.*, **140**: S5–S32.
- Werner, E.E. and Anholt, B.R. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. *Ecology*, **77**: 157–169.
- Wilbur, H.M. 1980. Complex life cycles. *Annu. Rev. Ecol. Syst.*, **11**: 67–93.
- Wilbur, H.M. 1984. Complex life cycles and community organization in amphibians. In *A New Ecology: Novel Approaches to Interactive Systems* (P.W. Price, C.N. Slobodchikoff and W.S. Gaud, eds), pp. 196–224. New York: Wiley.
- Wissinger, S. and McGrady, J. 1993. Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. *Ecology*, **74**: 207–218.
- Wootton, J.T. 1994. The nature and consequences of indirect effects in ecological communities. *Annu. Rev. Ecol. Syst.*, **25**: 443–466.