

# Priority effects of the early breeding fire salamander on the late breeding banded newt

Ori Segev · Leon Blaustein

Received: 23 October 2006 / Revised: 7 December 2006 / Accepted: 13 December 2006 /  
Published online: 26 February 2007  
© Springer Science+Business Media B.V. 2007

**Abstract** Early breeding intraguild predators may have advantages over late breeding predators via priority effects; early breeding predators may reduce shared prey resources before late breeders appear and may also prey upon the late breeders. Here we show that predatory larvae of the late-breeding predatory banded newt, *Triturus vittatus vittatus*, occupy the same temporary pond toward the end of the developmental period of the early-breeding predatory fire salamander, *Salamandra salamandra*, resulting in a large size disparity between larvae of these two species while they co-occur. We conducted outdoor artificial pool experiments to assess priority effects of large larval *Salamandra* at the end of their larval development period, on recently hatched larval *Triturus*. We also assessed how artificial vegetation may influence larval *Triturus* performance in the presence or absence of *Salamandra*. *Salamandra*, introduced into the experimental pools two weeks prior to the newt larvae, strongly reduced invertebrate prey abundance shared by these two predatory urodeles and with only a one week

period of overlap, strongly reduced abundance of *Triturus* larvae. The artificial vegetation had only a small ameliorating effect on *Triturus* survival when *Salamandra* was present. *Triturus* size at metamorphosis (snout-tail length) was significantly larger in the *Salamandra* pools, presumably due to a combination of a strong “thinning effect” and greater vulnerability of smaller *Triturus* individuals to predation by *Salamandra*. Time to metamorphosis was not significantly affected by *Salamandra*. These results have conservation implications as *T. v. vittatus* is listed as highly endangered and may also explain the largely negative spatial association of the two species.

**Keywords** Habitat heterogeneity · Priority effects · *Salamandra salamandra* · *Triturus vittatus vittatus* · Temporary pools · Predation

## Introduction

Breeding late by amphibians in temporary aquatic habitats has several potential advantages. For example, in Mediterranean climates where there are distinct rainy and dry seasons, breeding early may come at the cost of higher risk of desiccation since rains are less predictable and less frequent at the start of the rainy season (Warburg, 1994), and food resources for amphibians have had less time to become abundant (Steiner & Roy, 2003).

---

Handling editor: K. Martens

---

O. Segev (✉) · L. Blaustein  
Community Ecology Laboratory, Institute of  
Evolution, Faculty of Sciences, University of Haifa,  
Haifa 31905, Israel  
e-mail: segevo@research.haifa.ac.il

However, breeding late also carries the risk of negative priority effects—i.e., the presence of early breeding competitors and intraguild predators may negatively affect larval performance of late breeders (Morin et al., 1990; Blaustein & Margalit, 1996; Brodman, 1999; Walls & Williams, 2001; Eitam et al., 2005). Intraguild predators may not only affect larval success by competition with, and consumption of, these larvae, but there are costs of various responses to risk of predation (Gustafson, 1994; Resetarits, 1995). By reducing the level of food resources, the early breeders may continue to have negative residual effects on late breeders, even after the early breeders have metamorphosed and left the pool.

Vegetation, or other types of habitat heterogeneity, may affect amphibian larval performance in at least two ways: it may provide more substrate for food resources used by the larvae, and it may reduce predation rates by concealing individuals from predators (Sih, 1987; Semlitsch & Reyer, 1992; Jackson & Semlitsch, 1993; Kats et al., 1994; Walls, 1995; Niecieza, 2000, Baber & Babbitt, 2004).

Facultative shifts in larval life history (Werner, 1986; Rowe & Ludwig, 1991), and behavioral changes (Werner, 1991; Semlitsch & Reyer, 1992; Niecieza, 2000), have both been suggested as anti-predator responses in amphibians. Predator presence might have a negative, non-lethal effect on prey developmental rate by affecting prey behavior. Prey behavioral responses might involve a reduction in activity level or a change in microhabitat selection such as an increase in refuge use (Walls, 1995; Turner & Montgomery, 2003). Reduced foraging activity can consequently decrease growth rate and size at metamorphosis, and increase age at metamorphosis (Fauth, 1990; Babbitt, 2001; Barnett & Richardson, 2002). Alternatively, a facultative shift in prey life history might increase the rate of development and thus might reduce time to metamorphosis (Peacor & Werner, 2004).

Predation could also indirectly benefit surviving prey individuals by thinning the number of consumers, thus increasing per capita food density (Abrams et al., 1996; Van Buskirk & Yurewicz, 1998; Brodin & Johansson, 2002).

Hence thinning may ultimately lead to increased growth rate, development and reduced time to metamorphosis. The beneficial effect of thinning on larval life history may be obscured or outweighed by the negative effect of behavioral avoidance from predators.

In the Middle East region, temporary pools generally first fill in autumn with the onset of the rainy season. The banded newt, *Triturus vittatus vittatus*, an endangered species in Israel due at least partly to a reduction in quantity and quality of suitable breeding habitats (e.g., Blaustein et al., 1996a; Gafny, 2004), is a late season, temporary pool breeder. Late breeding by *Triturus* may be related to increased temperature or the presence of vegetation, which can be used by the female to wrap her eggs singly (Degani & Kaplan, 1999). In the absence of an early season dominant predator, late breeding often provides a higher abundance of prey (primarily aquatic insects and crustaceans) and abundant submerged vegetation for oviposition. However, some pools inhabited by *Triturus* are also breeding sites of an early season breeder, the fire salamander *Salamandra salamandra* (Degani & Kaplan, 1999). *Salamandra* larvae have strong negative impacts on the biomass of aquatic insects and crustaceans (Blaustein et al., 1996b; Blaustein, 1997; Spencer & Blaustein, 2001; Eitam et al., 2005). Consequently, *Salamandra* larvae may have strong competitive effects on *Triturus* larvae even after *Salamandra* metamorphose and leave the pool. Moreover, since *Triturus* begins its larval life at a time when *Salamandra* larvae are quite large, larval *Salamandra* may potentially be an important predator of *Triturus* where the two species co-occur. In such pools, vegetation may be crucial in reducing predation rates of *Triturus* larvae by *Salamandra*. *Salamandra* and *Triturus* tend to be negatively associated spatially across pools (Degani & Kaplan, 1999). This may be partly due to negative priority effects of *Salamandra* on *Triturus*. This, to date, has not been experimentally examined. In pools where they do coexist, ample submerged vegetation may prevent local extinction of *Triturus* (e.g., Sassa Pond, Degani and Kaplan, 1999).

On Mt Carmel, Israel, we found populations of *Salamandra* and *Triturus* together in a large temporary pool, Secher Pool. *Salamandra* occurs

there naturally while H. Mendelssohn introduced the *Triturus* population in 1985 (H. Lahav, personal communication). Here, we examine the temporal distributions of these two urodeles in this pool. We also report on experiments designed to isolate the effects of *Salamandra* larvae and artificial vegetation on survival and development of *Triturus* larvae.

## Methods

### Urodele survey at Secher Pool

Secher Pool (624 N 690 W) is a large pool (~400 m<sup>2</sup> surface area and ~2 m depth at maximum size in early to mid winter), which generally dries completely by summer but during some years, holds water all year. We periodically sampled the pool for urodeles on 15 dates by sweeping with a D-net (0.3 cm mesh; 0.35 m<sup>2</sup>) between 16 November 1994 and 19 June 1995 (urodeles were no longer found by this last date). The total number of *Salamandra* and *Triturus* collected in 10 net sweeps of one-meter length was recorded. On 9 of those dates, individuals were also measured (total length), and then immediately returned to the pool.

### Artificial pool experiments

In the first experiment, we used a two factorial design—presence or absence of larval *Salamandra* crossed with presence or absence of artificial vegetation—to study the effects of these two factors on larval *Triturus* survival and development. The experiment was conducted on the periphery of the University of Haifa Campus in 20 plastic tubs (length, width, depth: 60 × 40 × 14 cm). *Salamandra* larvae are often found in pools of this size and smaller (Spencer et al. 2002; L. Blaustein, pers. obs.). *Triturus* larvae can also be found in pools of this size. The tubs were arranged in 2 × 10 array under a 90% shaded net suspended at a height of 1.5 m. Distance between neighboring tubs was 0.5 m. On 20 April 2002, we filled pools to a depth of 12 cm with tap water. Water level was then maintained at 12–13 cm (~30 L) to some extent

with rainwater, but mostly with aged tap water and distilled water. To prevent the escape of metamorphosing *Triturus*, an 8 cm wide plastic frame overhang was horizontally attached to the tub edges using Velcro® straps. The pools were otherwise open at the top to allow insect colonization and allochthonous input. To supply metamorphosing *Triturus* with a terrestrial platform for exiting the water, two 10 × 10 × 6.5 cm bricks were placed one on top of the other into the center of each tub (total height: 13 cm).

Treatments were randomly assigned to the tubs. On 21 April, three medium sized *Salamandra* larvae (mean total length and standard error: 48.5 mm, 3.4; mean weight and standard error: 0.73 g, 0.12) collected from a nearby spring were added to 10 pools. We placed a bundle of 100 black plastic strips (80 cm long, 3 cm width) tied together at their midpoints, (to simulate a vegetation cover) on one side of five *Salamandra* and five non-*Salamandra* tubs. On 22 April, to provide food resources for the urodeles, we inoculated equal aliquots of invertebrates from other artificial pools containing primarily the crustacean *Arctodiaptomus similis*. Two weeks after introducing the *Salamandra* larvae (2 May), we introduced into each tub, four *Triturus* larvae collected from Secher Pool. Due to limited numbers and high variability in size (mean and standard error of total length: 18.9 cm, 5.9) of *Triturus* found in the natural pool, larvae were sorted by size (4 per tub) in order to get approximately the same mean and range in sizes for all tubs. The groups of four were then randomly assigned to all 20 tubs. At the time of introduction, there were no statistically significant differences in *Triturus* snout-tail length between treatments (Anova:  $F_{3, 16} = 0.246$ ,  $P = 0.863$ ). Adding *Salamandra* larvae two weeks prior to the introduction of *Triturus* was expected to deplete invertebrate resources substantially (Blaustein et al. 1996b; Eitam et al. 2005) prior to the appearance of the *Triturus* larvae. One week after introducing the *Triturus*, several *Salamandra* were observed to start metamorphosis. We then removed all *Salamandra* larvae (8 May). Any *Triturus* larvae surviving in the *Salamandra* tubs should then still be potentially subjected to residual effects of the *Salamandra*—i.e., the depleted invertebrate prey

caused by *Salamandra*. Thus, to reflect the natural phenology of urodeles, our experiment began with a *Salamandra*-only period (2 weeks), a second period of co-occurrence of both urodeles (1 week) and a third period of *Triturus* only.

Invertebrate fauna in the tubs were sampled on April 29th (8 days after the introduction of the *Salamandra* larvae) and on June 10th by sweeping a small rectangular net (size:  $6.4 \times 7.85$  cm, mesh size:  $250 \mu\text{m}$ ) in an S-shape (sample volume:  $0.6 \text{ m}^3$ ) through the water while lifting the artificial vegetation. Mosquito egg rafts on the water surface were counted twice during the *Salamandra*-present period (7 and 8 May) and summed for analysis. Likewise, egg rafts were counted every 2–3 days during the entire post-*Salamandra* period and summed for analysis. Maximum and minimum temperatures, recorded every 3–5 days from max–min thermometers placed at the bottom of three randomly chosen pools, ranged between 13–30°C and 11–26°C, respectively.

*Triturus* larvae were counted on the day that *Salamandra* was removed and then counted and measured (total length) every two weeks beginning 5 days after removing the *Salamandra* larvae. Once the first *Triturus* had emerged from the water (June 3rd), tubs were checked daily for metamorphosing individuals (without gills and generally out of the water), we recorded the metamorphs' length and weight which yielded time to, and size at metamorphosis.

Because the first experiment yielded unclear results of effects of the artificial vegetation on *Triturus* survival, we further assessed *Salamandra* predation on *Triturus* larvae in the presence or absence of artificial vegetation in a second, short-term experiment. The experiment was conducted at the same site and with identical tubs and water depth as the first experiment. The tubs were arranged in a  $3 \times 4$  array placed in the shade of a pine tree (*Pinus halepensis*). The artificial vegetation, randomly assigned to half the tubs, consisted of 50 1-m length black plastic twine sections tied together at their midpoints. On 28 May 2006, we filled pools with tap water. On 30 May, we introduced five *Triturus* larvae (snout-tail length, mean and standard error: 23.23 mm, 3.72) and two *Salamandra* larvae (snout-tail

length, mean and standard error: 61.9 mm, 4.56) into each tub. *Triturus* larvae were sorted by size to get very similar means and ranges for all tubs. The groups of five were then randomly assigned to each of the 12 tubs. We counted the number of *Triturus* larvae surviving for five consecutive days.

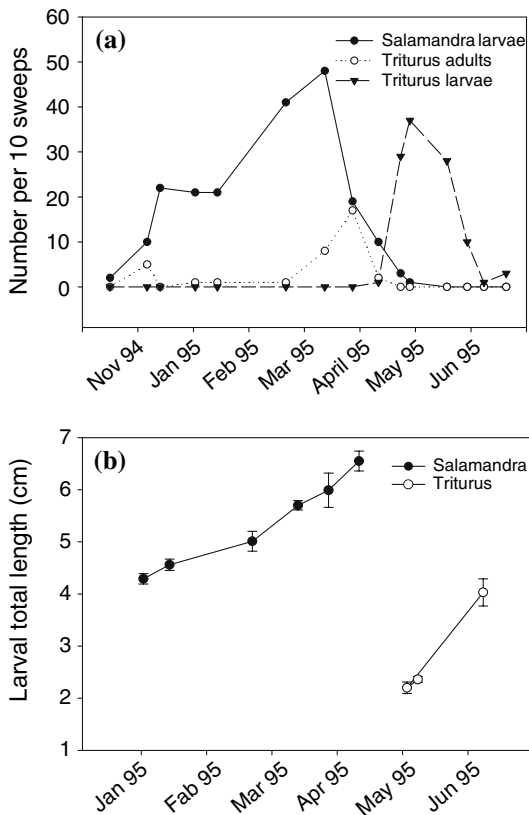
### Statistical analysis

For all *Triturus* variables, analyses were conducted on mean values for each tub. Data were analyzed by analysis of variance when variables met the parametric test assumptions. In all other cases, we used Mann-Whitney *U* tests. Bonferroni-adjusted alpha levels were made when necessary based on numbers of comparisons. In order to further assess a potential effect of vegetation reducing predation rates by *Salamandra* on *Triturus*, we combined data from *Salamandra* treatments of both experiments and tested for the effect of year (block) and artificial vegetation on the proportion of *Triturus* surviving (arcsine-square root transformed) using analysis of variance. Since our a-priori predictions were that *Salamandra* would reduce *Triturus* survival and that survival in the presence of *Salamandra* would be enhanced by vegetation, we used one-tailed tests for survival for these factors. For all other variables and factors, we used two-tailed tests, as there were no specific unidirectional predictions.

### Results

#### Field survey

*Salamandra* and *Triturus* demonstrated strong temporal separation at Secher Pool (Fig. 1a). *Salamandra* larvae were abundant early in the season and disappeared by late April leaving several weeks overlap with *Triturus* larvae. Adult *Triturus* were most abundant in April. During April, when both species co-occurred in the pool, there were large size differences between the larvae of the two species (Fig. 1b).



**Fig. 1** Temporal distributions of *Salamandra salamandra* larvae and *Triturus vittatus* adults and larvae at the temporary pool, Secher Pool: (a) abundance (number caught per ten sweeps); (b) size (total length). Error bars are  $\pm 1$  standard error

Artificial pool experiment 1

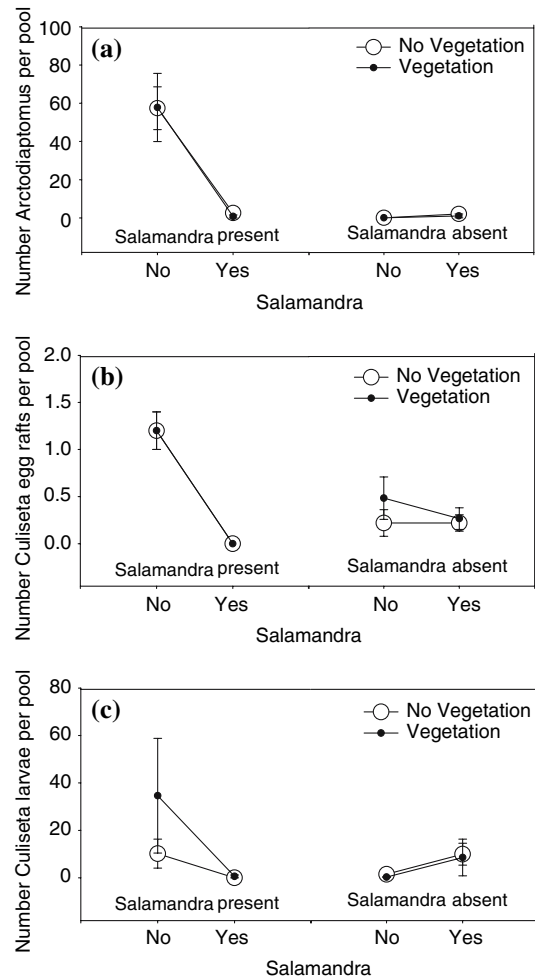
Effects on invertebrates

Two prey species were sufficiently common to assess for treatment effects: the calanoid copepod, *Arctodiaptomus similis*, and the mosquito, *Culiseta longiareolata*. *Salamandra* larvae, while present, virtually eliminated *Arctodiaptomus* ( $U = 100$ ,  $P < 0.0001$ ; Fig. 2a), *Culiseta* egg rafts ( $U = 85$ ,  $P = 0.002$ , Fig. 2b), and *Culiseta* larvae ( $U = 97.5$ ,  $P = 0.0001$ , Fig. 2c). During the post-*Salamandra* period, numbers of these prey types were considerably lower overall and there were no detectable treatment differences (Mann-Whitney tests:  $P > 0.05$  in all cases). During both the *Salamandra* period and post-*Salamandra* period, there were no statistically significant effects of

vegetation on any of the prey categories (Mann-Whitney tests:  $P > 0.05$  in all cases).

Effects on *Triturus* during *Salamandra* period

*Salamandra* strongly and negatively affected *Triturus* survival. While present, *Salamandra* reduced *Triturus* larvae by 90% in the non-vegetation pools and by 70% in the pools



**Fig. 2** Effects of larval *Salamandra salamandra* and artificial vegetation on the abundance of: (a) *Arctodiaptomus similis* (number per sweep); (b) *Culiseta longiareolata* egg rafts; (c) *Culiseta longiareolata* larvae (number per sweep). The left hand side of the graph is during the period in which *Salamandra* was present in *Salamandra* pools. The right hand side of the graph is the period after *Salamandra* was removed. Error bars are  $\pm 1$  standard error

**Table 1** Analyses assessing the influences of larval *Sal-amandra salamandra* and artificial vegetation on survival and size (total length) of *Triturus* larvae measured 1 week after the removal of *Sal-amandra* ( $df = 10, 1$ )

Source of variation	Survival ( $N = 20$ )		Length ( $N = 14$ )	
	U	P	F	P
<i>Sal-amandra</i>	100	<0.0001	23.97	0.001
Vegetation	45	0.682	12.33	0.006
<i>Sal-amandra</i> *Vegetation	–	–	11.77	0.006

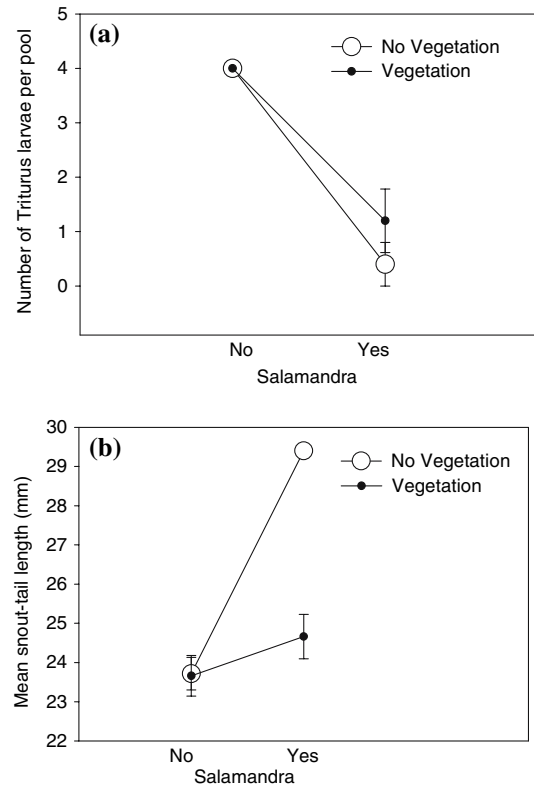
Survival is assessed using Mann-Whitney  $U$  due to nonhomogenous variances. Length is assessed by analysis of variance.  $N$  equals number of pools. There are fewer pools for length because of zero survival in some pools.  $P$ -values are based on two-tailed tests

containing artificial vegetation (Table 1, Fig. 3a). Because a Mann-Whitney  $U$  test cannot test for an interaction term, we also compared for effects of vegetation only in pools with *Sal-amandra* in a separate Mann-Whitney  $U$  test. The lower observed predation rate in the presence of artificial vegetation was not statistically significant (Mann-Whitney  $U = 7.5$ ,  $n = 10$ ,  $P = 0.119$ , one-tailed test).

*Triturus* individuals that survived the *Sal-amandra* period were significantly larger in the tubs containing *Sal-amandra* (Table 1,  $P = 0.001$ , Fig 3b), indicating that *Sal-amandra* predation was greater on smaller individuals. However, the significant vegetation by *Sal-amandra* interaction indicates that smaller individuals were able to escape predation at a higher rate in the presence of vegetation but not in its absence (Table 1,  $P = 0.006$ , Fig. 3b).

#### Overall effects on *Triturus*

*Sal-amandra* strongly reduced survival to and time to metamorphosis, and increased size at metamorphosis of *Triturus* (Table 2, Fig. 4). Neither vegetation nor vegetation by *Sal-amandra* interaction had significant effects on any metamorphosis variables (Table 2, Fig. 4). The presence of a *Sal-amandra* by vegetation interaction on *Triturus* size for the early period ending when *Sal-amandra* was removed, compared with the absence of the interaction for *Triturus* size at metamorphosis, indicates that the smaller surviv-



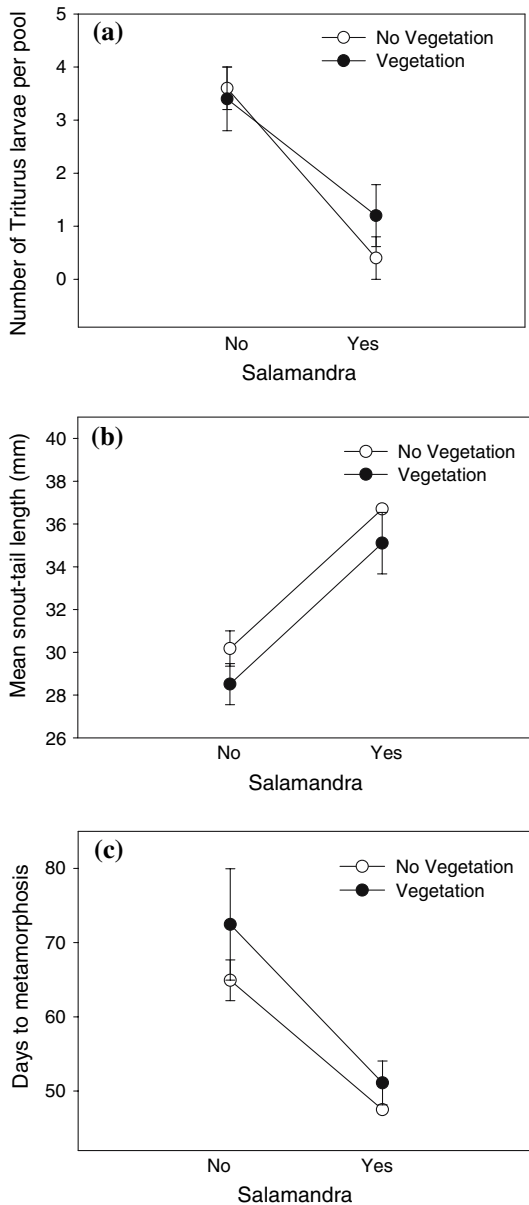
**Fig. 3** Effects of larval *Sal-amandra salamandra* and artificial vegetation on larval *Triturus vittatus* (a) survival and (b) size (total length) five days after the removal of *Sal-amandra salamandra*. Error bars are  $\pm 1$  standard error

ing larvae in the vegetated pools caught up in size (Fig. 4b). This result should be treated with caution because the high predation rate by *Sal-amandra* resulted in few remaining *Triturus* larvae to make this comparison.

**Table 2** Mann-Whitney  $U$  for measures of *Triturus vittatus* at metamorphosis: survival, size and development time

Source of variation	Survival to ( $N = 20$ )		Size at ( $N = 14$ )		Time to ( $N = 14$ )	
	U	P	U	P	U	P
<i>Sal-amandra</i>	97.5	<0.0001	0.0	0.005	39	0.007
Vegetation	43	0.578	25	0.897	23	0.897

$N$  gives number of pools. There are fewer pools for size and time to metamorphosis because of zero survival in some pools.  $P$ -values are two tailed



**Fig. 4** Effects of larval *Salamandra salamandra* and artificial vegetation on *Triturus vittatus* survival to (a), size at (b), and time to (c) metamorphosis. Error bars are  $\pm 1$  standard error

#### Artificial pool experiment 2

As in the first experiment, in the presence of *Salamandra* larvae, the measured increase in *Triturus* survival in the presence of vegetation (from 23.3 to 43.3%) was not statistically significant (Mann-Whitney  $U = 10.5$ ,  $n = 12$ ,  $P = 0.107$ , one-tailed test).

#### Combined results of Experiments 1 and 2

To further increase statistical power, we conducted a statistical analysis combining the same two treatments from the 2002 and 2006 experiments into a single analysis. Neither year nor year  $\times$  *Salamandra* interaction was statistically significant ( $P \gg 0.05$  in both cases) but the overall increase in survival in the presence of vegetation was statistically significant ( $F_{1,18} = 3.02$ ,  $P = 0.049$ , one-tailed test).

#### Discussion

Our observations in a natural pool reported here and in other observations of other pools (Degani & Kaplan, 1999) indicate that where *Salamandra* and *Triturus* co-occur, strong interspecific priority effects should be expected. By the time *Triturus* larvae are in the pool, *Salamandra* larvae are quite large and *Triturus* larvae are vulnerable to being preyed upon by the larger *Salamandra* larvae. Moreover, *Salamandra* will deplete resources that *Triturus* utilize (Blaustein et al., 1996b; Eitam et al., 2005) both before and during *Triturus* is in the pool. The results of the experiment presented here support these predictions. The strong decline in invertebrate numbers observed during the post-*Salamandra* period in the absence of *Salamandra* is likely due to predation by *Triturus* larvae. In the non-*Salamandra* tubs, *Triturus* larvae had nearly 100% survival and are predators of *Arctodiaptomus similis* and *Culiseta*.

In the outdoor artificial pool experiment, *Salamandra* larvae had a strong negative effect on *Triturus* survival. *Triturus* larvae were almost completely eliminated in the *Salamandra* pools without artificial vegetation but the plastic strips caused a marginally significant increase in *Triturus* larval survival in the presence of *Salamandra*. The increased survival is probably due to a partial refuge from predation afforded by the vegetation as has been shown with other predators and prey in aquatic systems (e.g., Morin, 1986; Babbitt & Jordan, 1996; Kupferberg, 1998).

Although *Triturus* survival was drastically reduced in the presence of *Salamandra*, those

that did survive metamorphosed at a larger size. We suggest two reasons for this. One is that the few remaining *Triturus* larvae in the presence of *Salamandra* enjoyed reduced intraspecific competition. Several anurans have previously been shown to be larger in the presence of *Salamandra*, again presumably because of reduced competition (Blaustein et al., 1996a). A second explanation that likely contributes to this is that as a gape-limited predator, *Salamandra* larvae appeared to demonstrate size-specific predation, resulting in higher predation on the smaller *Triturus* and greater survival of the larger *Triturus* larvae.

Although *Salamandra* and *Triturus* were in the same pools for only 1 week, given the quick and strong negative impact *Salamandra* has on larger invertebrates (Blaustein et al., 1996b; Eitam et al., 2005), we predicted that *Salamandra* presence should influence *Triturus* larvae well past the date of the *Salamandra* removal via priority effects. We would expect that *Salamandra*'s reduction of invertebrate prey shared by the two predators should have contributed to slower growth and perhaps a smaller size at metamorphosis. We found the opposite. Given that *Triturus* metamorphosed at a much larger size in the *Salamandra* pools, we suggest that the reduced intraspecific competition caused by thinning was considerably more important than the negative effect of *Salamandra* in reducing invertebrate prey. We interpret reduced time to metamorphosis in the *Salamandra* pools to both survivors of the *Salamandra* period being bigger plus reduced intraspecific competition due to the thinning.

This study has several conservation implications. First it may supply at least a partial explanation for the apparent negative spatial association observed between the two endangered species, *Triturus vittatus* and *Salamandra salamandra*, in Israel (Degani & Kaplan, 1999). Second, it suggests that increased habitat heterogeneity may increase the likelihood of coexistence between the two urodeles. Although the increased survival of *Triturus* in the presence of *Salamandra* when vegetation was present was statistically insignificant, this may be due simply to insufficient statistical power. Further studies may indicate that a higher density of vegetation or different kind of vegetation, e.g., the filamentous algae, may provide a higher degree

of refuge for the *Triturus* larvae and support richer and more abundant communities of invertebrate prey resources.

**Acknowledgements** We thank Shai Anuka for technical help, Tamar Krugman and Eden Orion for logistical help, Moshe Kiflawi, Avi Eitam, Naomi Hill, Nir Peleg, Alon Silberbush, Oren Pearlson, Gad Degani and Shirli Bar-David and two anonymous reviewers for critiquing an earlier version of the manuscript. The research was funded by a Vataat doctoral fellowship awarded to O. Segev and U.S.-Israel Binational Science Foundation grants 98–390 and 02–365 awarded to L. Blaustein and M. Mangel.

## References

- Abrams, P. A., O. Leimar, S. Nylin & C. Wiklund, 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *American Naturalist* 147: 381–395.
- Babbitt, K. J. & F. Jordan, 1996. Predation on *Bufo terrestris* tadpoles: Effects of cover and predator density. *Copeia* 2: 485–488.
- Babbitt, K. J., 2001. Behaviour and growth of southern leopard frog (*Rana sphenoccephala*) tadpoles: Effects of food and predation risk. *Canadian Journal of Zoology* 79: 809–814.
- Baber, M. J. & K. J. Babbitt, 2004. Influence of habitat complexity on predator-prey interactions between the fish (*Gambusia holbrooki*) and tadpoles of *Hyla squirella* and *Gastrophryne carolinensis*. *Copeia* 1: 173–177.
- Barnett, H. K. & J. S. Richardson, 2002. Predation risk and competition effects on the life-history characteristics of larval Oregon spotted frog and larval red-legged frog. *Oecologia* 132: 436–444.
- Blaustein, L., 1997. Non-consumptive effects of larval *Salamandra* on crustacean prey: Can eggs detect predators? *Oecologia* 110: 212–217.
- Blaustein, L., N. Engert, E. Steiner, E. Nevo & M. R. Warburg, 1996a. Israel's endangered Urodele species: Preliminary studies on their distribution across Mount Carmel and their influence on community structure of temporary pools. In Steinberger, Y. (ed.), *Preservations of Our World in the Wake of Change*. Vol. 6A/B. ISEEQ publishing, Jerusalem, Israel.
- Blaustein, L., J. Friedman & T. Fahima, 1996b. Larval *Salamandra* drive temporary pool community dynamics: Evidence from an artificial pool experiment. *Oikos* 76: 392–402.
- Blaustein, L. & J. Margalit, 1996. Priority effects in temporary pools: Nature and outcome of mosquito larva toad tadpole interactions depend on order of entrance. *Journal of Animal Ecology* 65: 77–84.
- Brodin, T. & F. Johansson, 2002. Effects of predator-induced thinning and activity changes on life history in a damselfly. *Oecologia* 132: 316–322.
- Brodman, R., 1999. Food and space dependent effects during the interactions of two species of larval

- salamanders. *Journal of Freshwater Ecology* 14: 431–437.
- Degani, G. & D. Kaplan, 1999. Distribution of amphibian larvae in Israeli habitats with changeable water availability. *Hydrobiologia* 405: 49–56.
- Eitam, A., L. Blaustein & M. Mangel, 2005. Density and intercohort priority effects on larval *Salamandra salamandra* in temporary pools. *Oecologia* 146: 36–42.
- Fauth, J. E., 1990. Interactive effects of predators and early larval dynamics of the treefrog *Hyla chrysoscelis*. *Ecology* 71: 1609–1616.
- Gafny, S., 2004. Threatened amphibians in Israel. In Dolev, A. & A. Perevolotsky (eds), *The red book - vertebrates in Israel*. Israel Nature and Parks Authority and The Society for the Protection of Nature in Israel, Jerusalem, Israel.
- Gustafson, M. P., 1994. Size-specific interactions among larvae of the Plethodontid salamanders *Gyrinophilus-Prophyriticus* and *Eurycea-Cirrigera*. *Journal of Herpetology* 28: 470–476.
- Jackson, M. E. & R. D. Semlitsch, 1993. Pedomorphosis in the salamander *Ambystoma talpoideum* – effects of fish predator. *Ecology* 74: 342–350.
- Kats, L. B., J. A. Breeding, K. M. Hanson & P. Smith, 1994. Ontogenic changes in California newts (*Taricha-Torosa*) in response to chemical cues from conspecific predators. *Journal of the North American Benthological Society* 13: 321–325.
- Kupferberg, S. J., 1998. Predator mediated patch use by tadpoles (*Hyla regilla*): Risk balancing or consequences of motionless? *Journal of Herpetology* 32: 84–92.
- Morin, P. J., 1986. Interaction between intraspecific competition and predation in an amphibian predator-prey system. *Ecology* 67: 713–720.
- Morin, P. J., S. P. Lawler & E. A. Johnson, 1990. Ecology and breeding phenology of larval *Hyla-andersonii*-the disadvantages of breeding late. *Ecology* 71: 1590–1598.
- Niecieza, A. G., 2000. Interacting effects of predation risk and food availability on larval anuran behavior and development. *Oecologia* 123: 497–505.
- Peacor, S. D. & E. E. Werner, 2004. Context dependence of nonlethal effects of a predator on prey growth. *Israel Journal of Zoology* 50: 139–167.
- Resetarits, W. J., 1995. Competitive asymmetry and coexistence in size-structured populations of Brook trout and spring salamanders. *Oikos* 73: 188–198.
- Rowe, L. & D. Ludwig, 1991. Size and timing of metamorphosis in complex life cycles: Time constraints and variation. *Ecology* 72: 413–427.
- Semlitsch, R. D. & H. U. Reyer, 1992. Modification of anti predator behavior in tadpoles by environmental conditioning. *Journal of Animal Ecology* 61: 353–360.
- Sih, A., 1987. Prey refuges and predatory stability. *Theoretical Population Biology* 31: 1–12.
- Spencer, M. & L. Blaustein, 2001. Hatching responses of temporary pool invertebrates to signals of environmental quality. *Israel Journal of Zoology* 47: 397–417.
- Spencer, M. S. S. Schwartz & L. Blaustein, 2002. Are there fine-scale spatial patterns in community similarity among temporary freshwater pools? *Global Ecology and Biogeography* 11: 71–78.
- Steiner, C. F. & A. H. Roy, 2003. Seasonal succession in fishless ponds: effects of enrichment and invertebrate predators on zooplankton community structure. *Hydrobiologia* 490: 125–134.
- Turner, A. M. & S. L. Montgomery, 2003. Spatial and temporal scales of predator avoidance: Experiments with fish and snails. *Ecology* 84: 616–622.
- Van Buskirk, J. & K. L. Yurewicz, 1998. Effects of predators on prey growth rate: Relative contributions of thinning and reduced activity. *Oikos* 82: 20–28.
- Walls, S. C., 1995. Differential vulnerability to predation and refuge use in competing larval salamanders. *Oecologia* 101: 86–93.
- Walls, S. C. & M. G. Williams, 2001. The effect of community composition on persistence of prey with their predators in an assemblage of pond-breeding amphibians. *Oecologia* 128: 134–141.
- Warburg, M. R., 1994. Population ecology, breeding activity, longevity, and reproductive strategies of *Salamandra salamandra* during an 18-year long study of an isolated population on Mt. Carmel, Israel. *Mertensiella* 4: 399–421.
- Werner, E. E., 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist* 128: 319–341.
- Werner, E. E., 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. *Ecology* 72: 1709–1720.