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Density and intercohort priority effects on larval *Salamandra salamandra* in temporary pools

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Abstract Priority effects, i.e., effects of an early cohort on the performance of a later cohort, are generally studied between, and not within, species. The paucity of intraspecific assessments does not reflect a lack of ecological importance, but the technical problem associated with differentiating between conspecific cohorts. Here, we examine priority and density-dependent effects on larval *Salamandra salamandra infraimmaculata*. Larvae deposited by their mother early in the season have increased risk of desiccation, as rains at the beginning of the season are less frequent and unpredictable. However, breeding later may incur a high cost through conspecific priority effects, including cannibalism and competition. In an outdoor artificial pool experiment, we established densities of 0, 1, 2, 4 or 6 newly born larvae per pool (~30 l), and 40 days later, added a second cohort of three newly born larvae to each pool. We differentiated between cohorts using natural individual-specific markings. For the early cohort, increasing density decreased survival and size at metamorphosis, and increased time to metamorphosis. For the late cohort, survival was 100% in pools without early-cohort larvae, but ranged between 13 and 33% in the presence of early-cohort larvae. Time to metamorphosis was significantly longer in the presence of low vs high densities of early-cohort larvae. Results suggest that early-cohort larvae are mainly subjected to exploitative competition and cannibalism mediated by food limitation, and that late-cohort larvae are subjected to cannibalism and interference due to size asymmetry between cohorts. The strong priority effects suggest that *Salamandra* females could increase their fitness by adjusting the number of larvae they deposit in specific pools to avoid cannibalism and intraspecific competition.

Keywords Cannibalism · Density dependence · Fire salamander · Intraspecific competition · Temporary ponds

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Introduction

Intraspecific competition often impacts larval performance in aquatic animals through density-dependent mechanisms. High densities cause reduced growth rates, increased time to metamorphosis and decreased metamorphic size in mosquitoes (Gleiser et al. 2000; Agnew et al. 2002; Gimnig et al. 2002), anurans (Semlitsch and Caldwell 1982; Skelly 1995) and urodeles (Harris 1987; Walls and Jaeger 1987; Scott 1990; Smith 1990; VanBuskirk and Smith 1991), leading to increased mortality in some cases (Semlitsch and Caldwell 1982; Loman 2004). For predaceous species, larvae may also be subjected to intraspecific predation, or cannibalism (e.g., Finke 1994; Summers 1999), also resulting in increased mortality at high densities (Walls 1998). Cannibalism is a major factor affecting the behavior, life history and population structure of many species (Polis 1981; Wildy et al. 1999). Progeny that are deposited later in the season may be at even greater risk of competition or predation from earlier cohorts. However, few studies have shown evidence of such intraspecific priority effects (Anholt 1994; Chen et al. 2001).

Studies of interspecific interactions show that priority effects are often strong and negative on the progeny of late breeders. For example, Alford and Wilbur (1985) and Wilbur and Alford (1985) demonstrated reduced survival, reduced size at metamorphosis and prolonged larval periods in later-breeding anuran species. More recent studies have shown similar priority effects in other anurans (Lawler and Morin 1993), *Drosophila* (Shorrocks and Bingley 1994), mosquitoes (Blaustein and Margalit 1996) and salamanders (Boone et al. 2002). These priority effects may influence the timing of oviposition and the selection of breeding sites, which in turn affect community structure (Wilbur and Alford 1985).

Intraspecific priority effects usually are inferred from studies of relationships among cohorts of different size classes, which demonstrate that smaller individuals (representing the late cohort) are less successful in the acquisition of food or cover (Crowley et al. 1987; Szabo 2002), resulting in reduced growth (Gustafson 1994) or increased mortality (Crowley et al. 1987; Sunahara and Mogi 2002). Competition and predation among age or size classes may have complex effects on population dynamics (Polis 1981; Ebenman 1987, 1988; Wissinger 1992; Claessen et al. 2004; Webster 2004). However, there are technical problems associated with differentiating cohorts based on size, as cohort sizes may overlap through development. As such, experimental studies typically do not consider the full period of co-occurring cohorts (e.g., Sunahara and Mogi 2002), and therefore, probably do not give a true estimate of the priority effects. In the current study, we differentiate between cohorts of larval fire salamanders, *Salamandra salamandra* L. *infraimmaculata*, by individual-specific identification of tail-spot patterns (Eitam and Blaustein 2002), allowing us to follow both cohorts throughout the larval period.

This study is designed to examine: (1) the effects of density on fitness within an age-specific larval cohort of *S. s. infraimmaculata*, and (2) the effects of various densities of an early cohort on the fitness of a later larval cohort. We use the following parameters as proxies of *Salamandra* fitness: (1) percent survival to metamorphosis; (2) time to metamorphosis; and (3) size (length) at metamorphosis. Generally in amphibians, time to metamorphosis has been shown to be negatively correlated with the probability of metamorphosis from short-duration pools (Smith 1983; Newman 1988), postmetamorph survival (Berven 1990), and size at reproductive maturity (Semlitsch et al. 1988). Size at metamorphosis often is correlated with postmetamorph survival, date of first reproduction and/or size at maturity (Berven and Gill 1983; Smith 1987; Semlitsch et al. 1988; Berven 1990; Goater 1994; Morey and Reznick 2001).

Methods

The *Salamandra*-temporary pool system

The fire salamander is an endangered species in Israel and reaches the southern edge of its distribution on Mt. Carmel, Israel (Degani 1996), the site of the current study. Its larvae are top predators in temporary and permanent pools; they have significant impacts on aquatic invertebrates, including large cladocerans, copepods and dipterans, and anurans (Blaustein 1997, Blaustein et al. 1996). Activity of females of temporary pool populations on Mt. Carmel begins in early fall, when rains begin following rainless summers, and normally ends by late January (Warburg 1994; Blaustein, personal observations). Females visit the pools on rainy or misty nights, when they may deposit some or all of their larvae. Because precipitation in fall is, on average, much less than in winter, and highly variable among years, early (October–November) breeders risk a higher probability of desiccation than later (December–January) breeders (Warburg 1994). Conversely, later breeders have a greater risk of cannibalism or competition from older larvae (Degani et al. 1980; Warburg 1994; Reques and Tejedo 1996).

Experimental design

An artificial pool experiment was conducted using 25 plastic tubs (48×27 cm at bottom, 55×33 cm at top, height 19 cm) in a 5×5 array placed in an open field on the campus of the University of Haifa, Israel. On 11 October 2000, the pools were filled with tap water to a level of 15 cm (23 l). On 12 October, we added to each pool 500 cm^3 of *Quercus ithaburensis* Decne leaf litter and approximately 10 cm^3 of fish food pellets as sources of nutrients, and three rocks (each ~250 cm^3) for shelter. On 13 October, we added 30 cm^3 of soil from previously used experimental pools (homogenized and randomly distributed among pools), providing an inoculum of algae, crustaceans and other microfauna. The tubs were filled to their full capacity (30 l) by rain on 24–25 October. To simulate natural pool conditions, the water level was allowed to fluctuate naturally with rainfall and evaporation throughout the study.

On 26 October, we introduced into the pools newly born *Salamandra* larvae, collected from a temporary pool on Mt. Carmel (hereafter referred to as the early cohort). The source pool became inundated for the first time that season from rains the previous 2 days and thus this was the first natural cohort of the season in this pool. Larvae from this cohort that were not collected met the fate of many early cohorts—they all desiccated. Five density levels, zero, one, two, four or six *Salamandra* larvae per pool, were established, with one replicate of each level randomly assigned within each of five rows. Both pool size (Spencer et al. 2002) and *Salamandra* densities (Blaustein, personal observations) used in this study are within the range encountered under natural conditions. Larvae were randomly assigned to pools. Upon introduction, larvae measured (mean ± SE) 3.0 ± 0.03 cm (range 2.5–3.5 cm) and 215 ± 2.5 mg (range 135–316 mg), and did not differ significantly among density levels in either length (ANOVA, $F_{3,16} = 2.77$, $P = 0.07$) or weight (ANOVA, $F_{3,16} = 1.28$, $P = 0.32$).

On 6 December, 40 days after the introduction of the early cohort and coinciding with another heavy rainfall that re-inundated the natural pool, we added a second cohort of three newly born *Salamandra* larvae (hereafter referred to as the late cohort) to the experimental pools. Two of the late-cohort larvae in each pool came from litters of two different captive mothers (one larva per litter per pool, length 3.3 ± 0.02 and 3.3 ± 0.03 cm, weight 224 ± 2.1 and 232 ± 1.8 mg, for the two litters, respectively). The third late-cohort larva in each pool (length 3.2 ± 0.04 cm, weight 221 ± 7.3 mg) was collected the night after a rain from the same natural pool in which the early cohort and the mothers of the other two late-cohort larvae were collected. All larvae ranged between 2.9 and 3.7 cm in total length and 150 and 310 mg in weight. Larvae of each litter/collection were randomly assigned to pools. Upon introduction to the experimental pools, there were no statistically significant differences in length (ANOVA, $F_{4,20} = 1.00$, $P = 0.43$) or weight (ANOVA, $F_{4,20} = 1.86$, $P = 0.16$) of late-cohort larvae among early-cohort density levels. At this time, early-cohort larvae measured 4.5–6.1, 3.1–5.7 (3.9–5.7 excluding one individual), 3.4–4.7 and 3.4–4.6 cm in length and 690–1,790, 140–1,190 (440–1,190 excluding one individual), 220–880 and 180–910 mg in weight, for densities of 1, 2, 4 and 6 larvae, respectively.

Prior to their introduction into the pools, both sides of the tails of each of these late-cohort individuals were photographed with a Sony DCR-TRV900E digital video camera. Still-image prints allowed for field identification of these individuals based on the tailfin-spot pattern. A full description of this method is presented elsewhere (Eitam and Blaustein 2002).

All surviving *Salamandra* larvae in the pools were examined every 11–15 days through 4 March, then again 8 days later (12 March), and then, because individuals began metamorphosing, every 3–4 days, for a total of 17 inspection dates. Each pool (including those without *Salamandra*) was emptied through a 3-mm mesh net. For each larva, total length was measured and each was then placed in a water-filled glass vial to observe and compare its tailfin pattern with the recorded images of the three late-cohort individuals placed in that particular pool. Thus, the larva was identified either as a specific late-cohort individual or as belonging to the early cohort. Water and larvae then were immediately returned to the pools.

In addition to sampling by emptying pools, individuals exhibiting signs of metamorphosis (yellow markings, reduced gills and shrinking tailfins) were closely monitored to determine as accurately as possible time to, and length at, metamorphosis. Furthermore, because metamorphosis was rapid, from 12 March to the end of the experiment (when the last remaining larva died—2 April), all pools were examined daily for metamorphosed individuals.

In one pool without early-cohort larvae, all three late-cohort larvae disappeared over two observation periods between 4 and 24 January. As this was the only pool in which all larvae (early or late cohort) had died or disappeared at the early stage of the study, and no similar occurrence was recorded in a number of other *Salamandra* experiments with similar tubs (Blaustein et al. 1996; Blaustein 1997; Spencer and Blaustein 2001; Blaustein, unpublished data), it was considered an outlier and removed from the analysis. The deletion of this outlier pool did not affect the observed qualitative relationship between survival and larval density.

To estimate the effect of early-cohort larvae on the availability of invertebrate prey for late-cohort larvae, pools were sampled for invertebrates on 4 December, 2 days prior to the addition of the late-cohort larvae. A single S-shaped sweep through each pool was performed with a 10×7 cm net (mesh size: 250 μm). Samples were preserved in 95% ethyl alcohol, and all individuals were identified and counted under a stereomicroscope.

Statistical analysis

Data were analyzed using MANOVAs on each cohort, with Wilks' λ as the test criterion, followed by univariate tests for each response variable (survival, length at metamorphosis and time to metamorphosis). In the presence of early-cohort larvae, the number of pools with surviving late-cohort metamorphs was low: four, one, two and one pools with surviving larvae for densities of one, two, four and six early-cohort larvae, respectively. Therefore, for the late cohort, we could not perform ANOVAs on time to metamorphosis and length at metamorphosis using all density levels. Consequently, density levels were combined for the MANOVA and these two ANOVAs such that there were three density levels considered—zero, low (one or two larvae) and high (four or six larvae) first-cohort densities. For the ANOVA on survival, all five density levels were maintained. Response variables across densities were compared with the Tukey–Kramer HSD test when *F*-values from the ANOVA were statistically significant ($\alpha = 0.05$).

Results

Density had statistically significant effects on early-cohort larvae for all three response variables (Table 1, Fig. 1). Survival to metamorphosis ranged from 100% at a density of one larva to 43% at a density of six larvae, with statistically significant differences between the lowest density and all other densities (Fig. 1a). Time to metamorphosis was significantly shorter at a density of one larva than at all higher densities (Fig. 1b). Although the ANOVA for length at metamorphosis was significant (Table 1), post hoc comparisons did not show significant differences among densities. However, when comparing lower (one or two larvae) vs higher (four or six larvae) densities, metamorphosing individuals were significantly larger at lower densities ($t_{18} = 3.253$, $P = 0.004$; Fig. 1c).

Table 1 Results of MANOVA for overall effects of density on survival to, time to and size at metamorphosis of early-cohort *Salamandra* larvae, and ANOVAs for each response variable

Analysis	Dependent variable	df	Wilks' λ	ss	F	P
MANOVA		6, 30	0.26		4.83	0.0015
ANOVA	Survival	3, 16		18,422	4.41	0.019
	Time	3, 16		4,384	6.50	0.004
	Size	3, 16		9.1	3.41	0.043

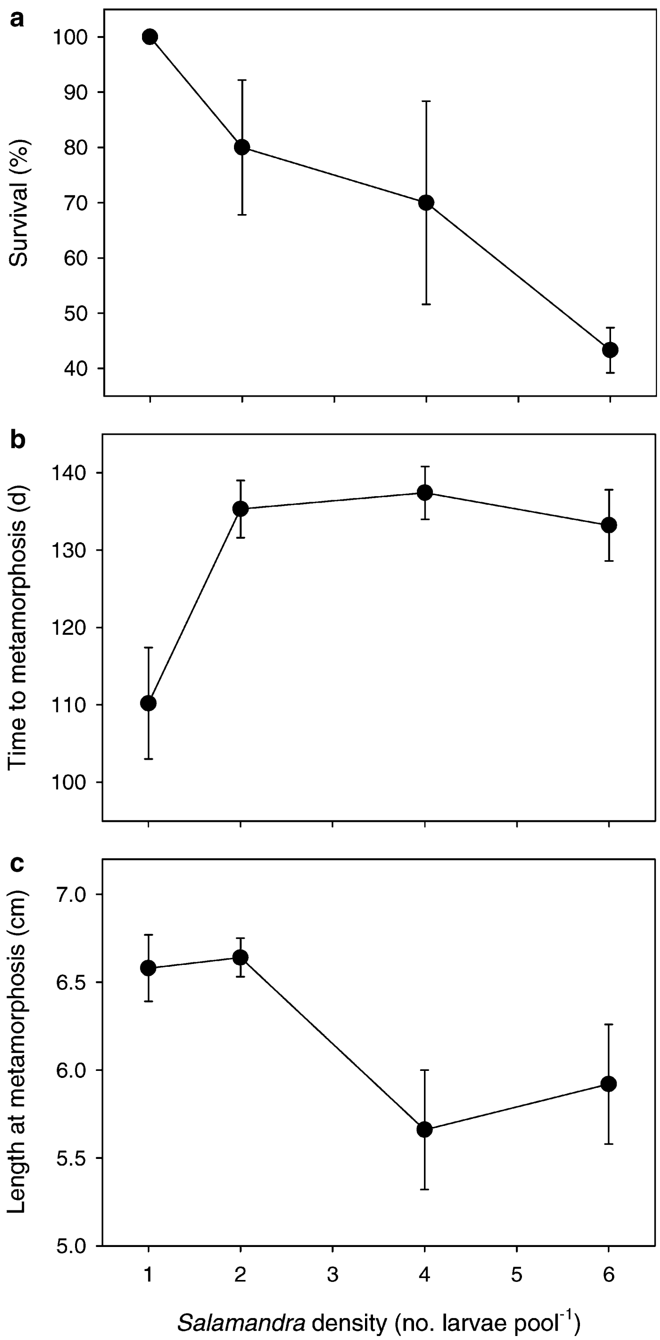

Fig. 1 (**a**) Survival, (**b**) development time and (**c**) body length at metamorphosis of early-cohort *Salamandra salamandra infraimmaculata* larvae at densities of 1, 2, 4 or 6 larvae per pool. Error bars indicate ±1 SE

Early-cohort densities had significant multivariate effects on late-cohort larvae (Table 2). Survival to metamorphosis was 100% in pools without early-cohort larvae, 33% in the presence of a single early-cohort larva, and between 13 and 20% at early-cohort densities ranging between two and six larvae (Fig. 2a). Differences in survival of late-cohort larvae were statistically significant between pools without early-cohort larvae and pools with any density of early-cohort larvae, but not among the various early-cohort density levels. Time to metamorphosis was significantly longer in the presence of low densities (one or two) than high densities (four or six) of early-cohort larvae (Fig. 2b). Although late-cohort larvae tended to be smaller at high densities of early-cohort larvae (Fig. 2c), differences among densities were not statistically significant (Table 2).

Crustacean densities, measured just prior to the introduction of the late cohort, were strongly affected by larval *Salamandra* density (Wilks' λ, $F_{8,38} = 8.4$, $P < 0.0001$). The dominant crustaceans in the pools were the cladocerans *Daphnia magna* Straus, *Ceriodaphnia* sp. and *Moina brachiata* (Jurine) and the copepod *Arctodiaptomus similis* (Baird). *Daphnia*, the largest of the microcrustaceans, was the most numerous prey species in pools without early-cohort larvae, and was nearly eliminated from pools with *Salamandra* larvae (Fig. 3a). The smaller and similarly sized *Ceriodaphnia* and *Moina* (lumped together for analysis) were also most abundant in pools without early-cohort larvae, but were also quite common in pools with one larva (Fig. 3b). Populations of *Arctodiaptomus* were not reduced, and even increased, at low *Salamandra* densities, peaking at a density of two early-cohort larvae (Fig. 3c). In general, high crustacean densities occurred in pools without *Salamandra* larvae, intermediate prey densities at low *Salamandra* densities (one or two larvae) and low prey densities at high *Salamandra* densities (four or six larvae).

Discussion

In this study, we consider the effects of density and priority on the performance of larval *Salamandra*. This examination of the interaction between density and priority allows us insights into the mechanisms driving

Table 2 Results of MANOVA for overall effects of density of early-cohort *Salamandra* larvae on survival to, time to and size at metamorphosis of late-cohort larvae, and ANOVAs for each response variable

Analysis	Dependent variable	df	Wilks' λ	ss	F	P
MANOVA		4, 16	0.12		7.40	0.0014
ANOVA	Survival	4, 19		35,564	8.34	0.0005
	Time	2, 9		379	4.75	0.039
	Size	2, 9		6.9	1.84	0.21

The number of pools with surviving metamorphs was 4, 4, 1, 2 and 1 for densities of 0, 1, 2, 4 and 6 early-cohort larvae, respectively larval performance. Over a natural range of densities, we found strong density-dependent effects of an early cohort of larval *Salamandra* both on itself and on a later larval cohort. While larvae of both cohorts are affected by density, the different patterns for the two cohorts suggest different mechanisms are at work on each of them.

For the early cohort, the larger size of metamorphosing individuals at low densities and the faster growth at the lowest density, coupled with our observation of higher zooplankton densities in pools with low vs high salamander densities, are consistent with a mechanism of exploitative competition (Gill 1979; Petranka and Sih 1986; Walls and Jaeger 1987; Fauth and Resetarits 1991). Furthermore, the observed density-dependent mortality may result from either competition (Fauth et al. 1991) or cannibalism due to food limitation (Walls 1998). A recent

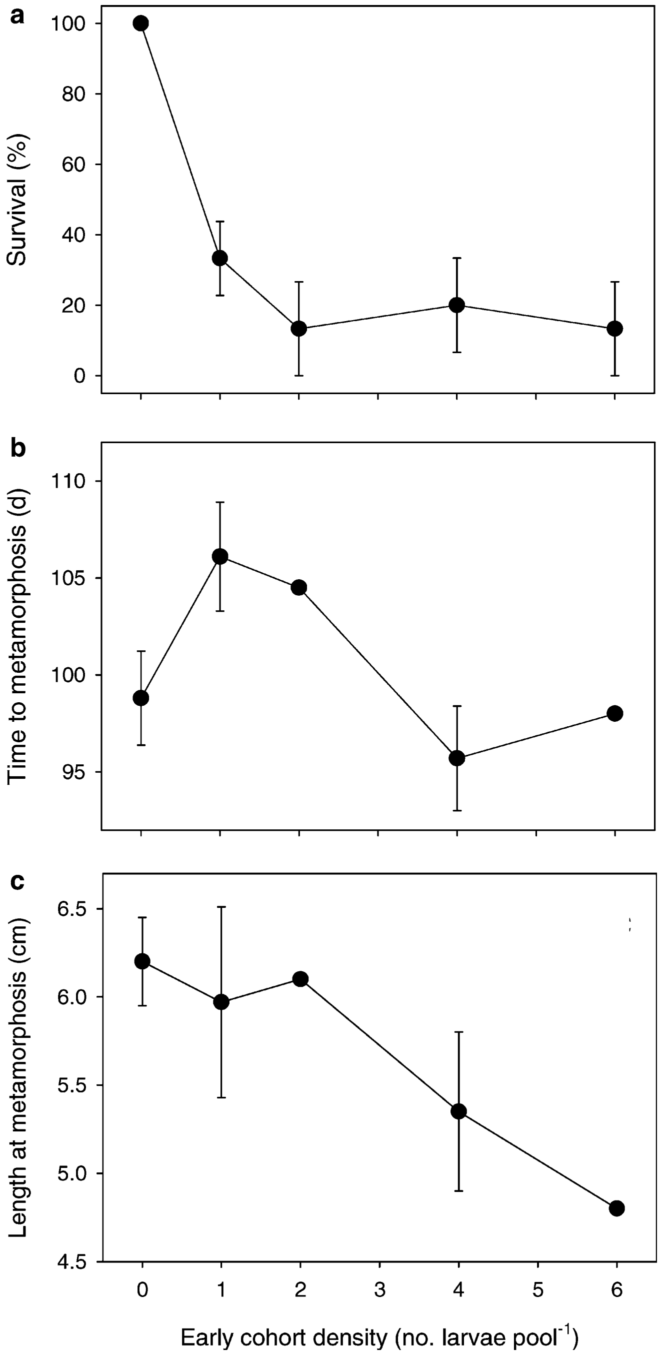

Fig. 2 (**a**) Survival, (**b**) development time and (**c**) body length at metamorphosis of late-cohort *Salamandra salamandra infraimmaculata* larvae at densities of 1, 2, 4 or 6 early-cohort larvae per pool. Error bars indicate ±1 SE

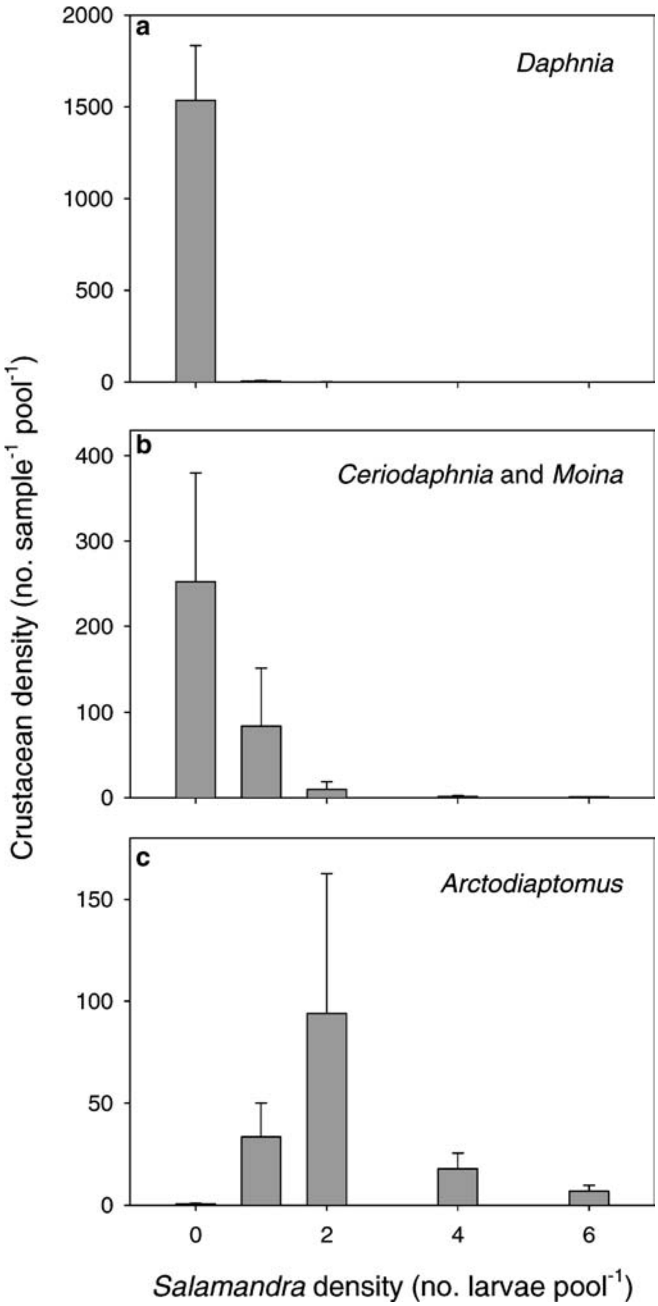

Fig. 3 Densities of crustaceans (**a**) *Daphnia magna*, (**b**) *Ceriodaphnia* sp. and *Moina brachiata* and (**c**) *Arctodiaptomus similis* (number per sample per pool) at various densities of early-cohort *Salamandra salamandra infraimmaculata* larvae, measured just prior to addition of late-cohort larvae. Error bars indicate ±1 SE

field study of *Salamandra* suggests that when resources are unlimited, effects of density are considerably diminished (Csillery and Lengyel 2004).

The late cohort suffered increased mortality (67–87%) relative to the early cohort (0–57%) at all densities of early-cohort larvae. This result suggests a high level of cannibalism, due to greater size asymmetry between cohorts in individual treatment units (Collins and Holomuzki 1984; Reques and Tejedo 1996), and is consistent with other studies showing intercohort priority effects on survival in salamanders (Ryan and Plague 2004) and other cannibalistic species (Crowley et al. 1987).

The observed pattern of time to metamorphosis for late-cohort larvae (later metamorphosis at low density) is consistent with a mechanism of interference. The risk of cannibalism by large early-cohort larvae likely causes reduced foraging activity of surviving late-cohort individuals (Wildy et al. 1999; Ziemba et al. 2000). In low-density pools with relatively high resources, metamorphosis would be delayed to capitalize on high growth opportunities following cessation of feeding or metamorphosis of early-cohort individuals; delayed metamorphosis would not be expected in high-density pools which are low in resources (Wilbur and Collins 1973; Nicieza 2000).

Our results suggest that an early-breeding female could maximize her fitness by adjusting the number of larvae she deposits in a specific pool depending on its size and other attributes, to decrease cannibalism and competition among her progeny (Vasconcellosneto and Monteiro 1993; Kagata and Ohgushi 2002). For late breeders, the dramatic decrease in survival in the presence of early-cohort larvae demonstrates a clear advantage of larvipositing in pools without conspecifics if such pools exist (Summers 1999; Dillon and Fiano 2000; Marsh and Borrell 2001). It also demonstrates the disadvantage of late breeding in urodeles, mirroring similar conclusions for anurans (Morin et al. 1990). However, as discussed by Morin et al. (1990) and Warburg (1994), early breeders risk desiccation in highly ephemeral early-season pools. We have evidence from both natural and experimental pools that *Salamandra* females do not necessarily put all their larvae "in one basket", but rather can spread their larviposition both temporally and spatially (Eitam and Blaustein, unpublished data). Thus, females may increase their fitness by spreading risk among various pool types that differ in ecological properties (Resetarits and Wilbur 1989).

The paucity of studies examining intraspecific priority effects does not imply that such effects are unimportant in ecological systems, but rather reflects the technical obstacles of differentiating between intraspecific cohorts. Our results suggest that priority effects are very important in *Salamandra salamandra*, and once these technical obstacles of identifying individuals in mixed cohort habitats are worked out, we expect intraspecific priority effects to be demonstrated as important phenomena in many other communities.

Previous studies have shown that density dependence has important effects on population dynamics and the evolution of life-history traits in salamanders (Gill 1979; Harris 1987). As mechanisms underlying density dependence effects differ between time-specific cohorts, priority effects are likely to play an important role on the population level. Similar differentiating mechanisms may occur among interspecific cohorts, thus influencing community structure. Future theoretical and empirical studies could further elucidate these complex interactions between priority and density.

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