Nordic Society Oikos

Interactions between Larval Salamanders: A Case of Competitive Equality
Author(s): John E. Fauth, William J. Resetarits, Jr., Henry M. Wilbur
Source: *Oikos*, Vol. 58, No. 1 (May, 1990), pp. 91-99
Published by: Blackwell Publishing on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3565364
Accessed: 25/01/2011 16:28

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=black.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Blackwell Publishing and *Nordic Society Oikos* are collaborating with JSTOR to digitize, preserve and extend access to *Oikos.*

http://www.jstor.org

OIKOS 58: 91–99. Copenhagen 1990

Interactions between larval salamanders: a case of competitive equality

John E. Fauth, William J. Resetarits, Jr. and Henry M. Wilbur

Fauth, J. E., Resetarits, W. J., Jr. and Wilbur, H. M. 1990. Interactions between larval salamanders: a case of competitive equality. – Oikos 58: 91–99.

We used a replicated field experiment to determine the relative intensity of intraspecific and interspecific competition between larvae of *Siren intermedia* and *Notophthalmus viridescens*. These two salamanders possess markedly different morphologies and life histories and belong to distantly related salamander families, but feed on similar prey.

Each species was raised in artificial ponds, alone at either low density (3 larvae per pond, 1.95 m^{-2}) or high density (6 larvae per pond, 3.90 m^{-2}) or together in a 3:3 ratio for a combined density of 6 larvae per pond. These 5 treatments were each replicated 4 times in a total of 20 ponds. The experimental design allowed us to explicitly compare the relative intensities of intra- and interspecific competition under realistic conditions.

Competition affected different components of fitness in each species. Both intraspecific and interspecific competition caused a decline in survival of *Notophthalmus*, but had no detectable effect on body size or length of larval period. Negative density-dependent mortality may regulate *Notophthalmus* populations in the larval stage of their complex life cycle. Intraspecific competition caused a decline in both the survival and growth of larval *Siren*, but interspecific competition caused only growth to decline. Decreased growth rates may increase the vulnerability of larval *Siren* to desiccation and to predation. We found no evidence to reject the null hypothesis that larvae of these two species are equal competitors at the densities we employed.

Our results indicate that, despite dissimilarities in life history and morphology, and a distant phylogenetic relationship, larval *Siren* and larval *Notophthalmus* compete as equals.

J.E. Fauth, W.J. Resetarits, Jr. and H.M. Wilbur, Dept of Zoology, Duke Univ., Durham, NC 27706, USA.

Introduction

One of the central questions in ecology is the importance of competition in natural communities. Recent reviews by Schoener (1983) and Connell (1983) have led ecologists to question the frequency and intensity of competitive interactions. Few experimental studies have measured the intensity of interspecific competition (Connell 1983), despite its fundamental importance in models of community dynamics, coexistence and stability (e.g. Lotka 1932, Levins 1968, May 1973). In addition, experimental studies of competition have typically investigated interactions between closely related species (usually congeners), or species that are similar in terms of morphology and life history (e.g. Gause 1935, Park 1948, Vandermeer 1969, Wilbur 1972, Hairston 1980). In contrast, few studies have investigated competition between dissimilar species, especially those that are taxonomically disparate (Brown and Davidson 1977, Reichman 1979 and references therein; Eadie and Keast 1982, Schluter 1986, Morin et al. 1988). It is often assumed that species which are closely related, share common life histories or are similar morphologically are the most likely to compete.

Taxonomy, morphology and life history are frequently used by ecologists to predict which species

Accepted 23 December 1989

within a given community are potential competitors (Hairston 1987). As an alternative, we used dietary similarities to predict that two species from a temporary pond community are potential competitors. Temporary ponds often harbor suites of predators with diverse morphologies and life histories. Many of these species lack specialized trophic structures and are generalized predators, consuming widely overlapping distributions of prey species; competition for prey is an expected interaction between these opportunistic predators. We experimentally manipulated two such predators, larvae of the broken-striped newt (*Notophthalmus viridescens dorsalis*) and larvae of the lesser siren (*Siren intermedia intermedia*) in a series of artificial ponds to determine the relative importance of intraspecific and interspecific competition. *Siren intermedia* and *Notophthalmus viridescens* are two of the most abundant vertebrate predators in large temporary ponds of the southeastern United States. Larvae of the two species often co-occur at high densities (Harris et al. 1988, Fauth, pers. obs.), and are generalized predators which utilize similar types of invertebrate pray (Hamilton 1940, Bishop 1941, Martof 1973, Taylor et al. 1988). However, *Notophthalmus* and *Siren* possess quite different life histories and morphologies, and are only distantly related (Hecht and Edwards 1977).

Our experimental design enabled us to simultaneously investigate the effects of intraspecific and interspecific competition, and to compare their relative strengths at realistic densities of these larval predators. Competition is expected to be intense in the ephemeral larval environment due to extreme fluctuations in habitat quality and the premium placed by natural selection on rapid growth. Consequently, population regulation in most amphibians is believed to occur in this aquatic larval stage (Wilbur 1980). We have therefore focused our attention on larval interactions in this paper. However, because these species remain aquatic as adults, interactions between them may not be confined to their larvae. Competition between juvenile *Siren* and adult *Notophthalmus*, and the complex interactions between adult *Siren* and adult and larval *Notophthalmus*, are the subject of another paper (Fauth and Resetarits, unpubl.).

Methods and materials

Natural history

Siren intermedia (Caudata: Sirenidae) is a large, bizarre, obligately paedomorphic salamander that is permanently aquatic (Martof 1973). Sirenids possess such a unique suite of morphological characters that some workers have consigned the family to its own order, Meantes (= Trachystomata) (Cope 1889, Goin et al. 1978). The natural history of *Siren* is poorly understood. *Siren intermedia* lays large numbers of eggs in a clump on pond bottoms, and females remain at the nest until the eggs hatch (Godley 1983). Larvae grow rapidly after hatching and generally reach sexual maturity in two years (Martof 1973). *Siren* is benthic and nocturnal, and feeds upon a wide variety of aquatic prey, including zooplankton, crustaceans, snails, larval insects and tadpoles (Martof 1973 and references therein; Fauth and Wilbur, pers. obs). Adults can survive long dry periods by burrowing into the pond bottom, secreting a mucus-lined cocoon and estivating until the pond refills (Gehlbach et al. 1973). This trait is especially important because *Siren* is a poor disperser, unable to move overland. When a pond refills, *Siren* emerges from estivation and is soon ready to feed on the aquatic insects and larval amphibians that recolonize the pond.

Notophthalmus viridescens (Caudata: Salamandridae) is a facultatively paedomorphic salamander that generally retains a complex life cycle with two metamorphic events (Gill 1978, and references therein). *Notophthalmus* lays its eggs singly throughout the spring and early summer. Larvae grow rapidly and typically metamorphose into terrestrial juveniles (efts) in late summer or early autumn. Under favorable conditions, some *Notophthalmus* larvae may bypass the eft stage entirely and become paedomorphic, or metamorphose directly into aquatic adults (Harris 1987a). Otherwise, *Notophthalmus* remains in the terrestrial eft stage for 1–9 yr before undergoing a second metamorphosis into the adult stage. *Notophthalmus* survives short periods of pond-drying by burrowing under debris, or by emigrating from the drying pond (Harris et al. 1988, Fauth, Resetarits and Wilbur pers. obs.). *Notophthalmus* is an effective colonizer of new ponds and ponds that have recently refilled after prolonged dry periods. Both larval and adult *Notophthalmus* are voracious predators of zooplankton and other small aquatic prey (Hamilton 1940, Bishop 1941, Taylor et al. 1988). *Notophthalmus* may function as a keystone predator in temporary pond communities, reversing the outcome of competition among anuran tadpoles via selective predation on the competitively dominant species (Morin 1981, 1983, Wilbur 1987).

Field methods

The experiment was conducted in an array of 20 artificial ponds (plastic wading pools 1.4 m in diameter and 0.24 m deep) in an open field at the Duke Zoology Field Station. Ponds were filled to a volume of 375 l with city tap water on 22–23 April, 1986. On 25 April, 0.35 kg of leaf litter raked from the margin of a temporary pond was added to mimic the structure of a natural pond bottom and to provide resting stages of microorganisms and nutrients for the aquatic food chain. Randomized one liter aliquots of a pond water suspension, collected with a 400 μm mesh net from several ponds, were added on 26 and 27 April to provide an additional inoculum of zooplankton, algae and other microorganisms. Tightly fitting lids of fiberglass windowscreen prevented unwanted colonization by ovipositing frogs and insects, and retained metamorphosing newts. A constant water level was maintained by adding water to the ponds as necessary throughout the course of the experiment. Screened drain holes on the sides of the ponds prevented overflow during heavy rains.

Ecologists use a variety of methods to explore pattern and process in natural communities; each method has strengths and weaknesses (Diamond 1986). Field experiments in container habitats such as ours permit complex, highly replicated and controlled experiments designed to provide sufficient statistical power to test competing ecological hypotheses (Wilbur 1987). A criticism of this method is that biological realism may be sacrificed to gain experimental precision. If high survival in experimental ponds causes larvae to grow for a long period of time at higher densities than they would experience in natural ponds, the importance of competitive interactions might be exaggerated (Petranka and Sih 1986). We deliberately used low initial densities to avoid this artifact.

Each species was introduced alone at a low density, 3 larvae per pond (1.95 ind m^{-2}), and alone at a high density, 6 larvae per pond (3.90 ind m^{-2}). For each species, we tested the null hypothesis of no effect of density on performance of larvae. An additional treatment consisted of the two species raised together, with 3 individuals of each species per pond. The performance of each species in a mixed population could be compared to its performance alone at low density (H_o: no interaction between species), or to its performance alone at high density (H_o: two species are competitive equivalents). In nature, larval densities of *Notophthalmus* can exceed 20 m^{-2} in some years (Harris et al. 1988, Fauth unpubl. data). Larval *Siren* densities are more difficult to estimate, but adult densities rarely exceed 2 m^{-2} (Gehlbach and Kennedy 1978, Wilbur and Fauth unpubl. data). The five treatments were each replicated four times, for a total of 20 experimental ponds. Ponds were arranged in four spatial blocks and each treatment was randomly assigned to a position within each block.

Siren eggs were collected from a pond in Scotland County, North Carolina on 4 April. The eggs probably represent a single clutch, because a large female *Siren* was captured in the same seine haul as the eggs. The eggs hatched in the laboratory and larvae were measured (mean total length = 2.0 cm; range = 1.7 – 2.2 cm) and added to the appropriate experimental ponds on 30 April. *Notophthalmus* larvae were collected from a second pond in Scotland County on 25 May and were measured (mean total length = 1.7 cm; range = 1.4 – 2.3 cm) prior to their addition to the experimental ponds on 26 May. All ponds within a block received *Notophthalmus* larvae of similar initial sizes. Addition of *Notophthalmus* larvae at this later date mimicked the natural breeding phenology of the two species in Scotland County. In addition, larvae of both species were approximately the same size at this time, reducing the likelihood of predation and cannibalism. Thus, any effects on growth and survival could be reasonably ascribed to competition.

Ponds were searched for metamorphosing *Notophthalmus* once per week from 15 June until the first eft appeared on 24 July; thereafter ponds were searched every other night. Metamorphosis was defined by gill resorption. Metamorphs were returned to the laboratory, blotted dry on paper towelling, measured (snout to posterior angle of the vent - SVL), weighed to 0.1 mg precision, anesthetized in 2% chloretone and preserved in 10% formalin. The length of the larval period (measured from the date of introduction) was also recorded for each eft. Ponds were drained and searched for survivors on 19 and 20 October. All individuals of both species remaining in the ponds were returned to the laboratory and weighed and measured as described above; sirens were anesthetized prior to being weighed and measured. These animals have been deposited in the Vertebrate Collection at Duke University (*Notophthalmus viridescens* A18602–A18620; *Siren intermedia* A18621–A18655).

Behavioral censuses

During the weekly searches for metamorphosing efts, it became clear that larval *Notophthalmus* were observed more frequently than larval *Siren*.

To measure salamander activity and microhabitat use, a behavioral census was conducted from midnight on 19 July, through 2100 hours on 20 July. Pools were visually searched for larvae at three-hour intervals. Lids were removed 20 min before each observational period. Each larva encountered was identified and classified as to microhabitat occupied: open water (> 2 cm from the sides of the pool, not in contact with bottom litter), sides of tank (< 2 cm from sides of pool), on bottom (ventral surface resting on the bottom litter), or in the litter layer. It was necessary to estimate the number of larvae of each species hidden from the observer because the number of animals concealed in the litter could not be determined without destroying the artificial pond communities. By assuming that mortality was a constant, linear function of time, it was possible to reasonably estimate the total number of larvae alive at the time of the census; the number concealed in the bottom litter was then determined by subtraction.

Statistical methods

The experimental design enabled us to simultaneously test three null hypotheses: (1) no density-dependent intraspecific competition. (2) no interspecific competition, and (3) larval *Siren* and larval *Notophthalmus* are equal competitors.

We used survival and mass of larval *Siren*, and survival mass and length of larval period of *Notophthalmus* as our response variables. These three response var-

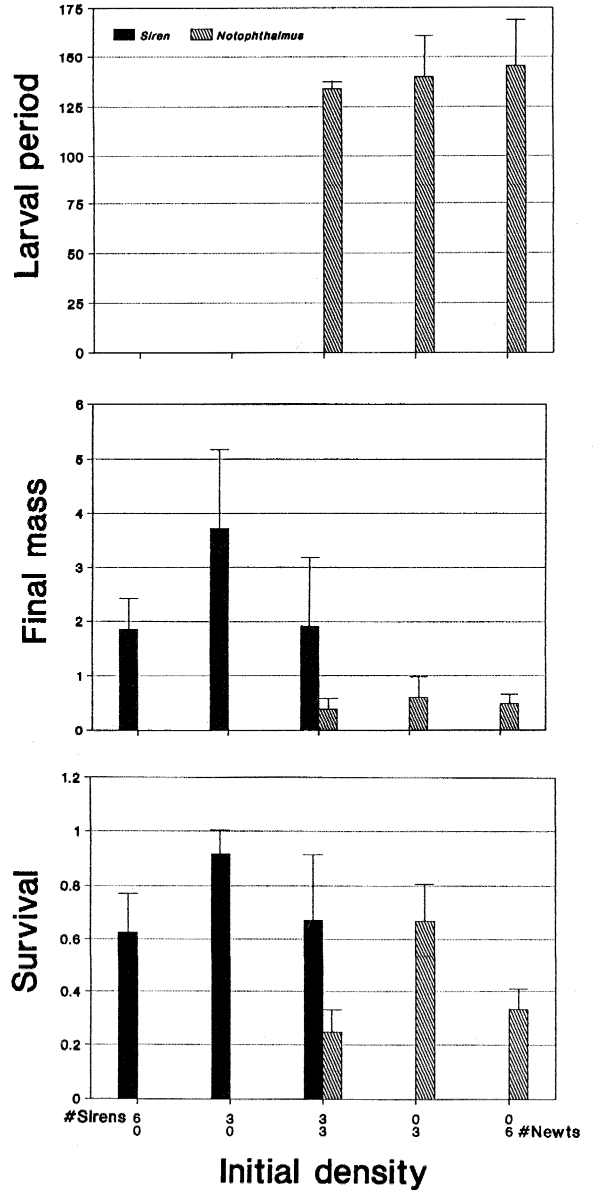

Fig. 1. Summary of treatment means (+ 1 S.E.). Response variables are survival, final mass (g), and length of larval period (d). Solid bars: *Siren* responses. Slashed bars: *Notophthalmus* responses. Paedomorphic *Notophthalmus* were assigned a larval period of 174 days, the duration of the experiment. Since *Siren* never metamorphose, the length of their larval periods could not be determined.

iables are good estimators of fitness components in amphibians and are sensitive measures of the intensity of competition. Fecundity increases with size (mass) in many amphibians (Kaplan and Salthe 1979) and the length of time *Siren* can survive episodes of pond-drying by estivating in the pond bottom is also highly size-dependent (Gehlbach et al. 1973). In *Notophthalmus* female fecundity increases greatly with mass, as does the competitive ability of males during amplectant "wrestling" encounters for possession of females (Verrell 1982, 1986). Date and size at metamorphosis have been shown to influence age at first reproduction and fecundity in a chorus frog (Smith 1987) and a mole salamander (Semlitsch et al. 1988). In amphibians, competition generally causes decreased survival and mass at metamorphosis and lengthened larval periods (Wilbur 1980).

We used analysis of variance with a priori contrasts (Draper and Smith 1981: 425–426, Mardia et al. 1979: 337–338) to test each of our three null hypotheses. Separate ANOVA's were performed for each response variable and individual pool means constituted the unit of statistical analysis. Contrasts were tested over the error term remaining after variation due to spatial blocks and treatments had been partitioned from the model. Survivorship was arcsine-square root transformed to meet assumptions of the analysis of variance (Sokal and Rohlf 1981). Newt larval period was analyzed with a nonparametric test for a randomized block design (Friedman's Method; Sokal and Rohlf 1981) because variances remained heterogeneous after transformation. We also used nonparametric G-tests (Sokal and Rohlf 1981) to test for treatment differences because the small number of animals in each pond resulted in a limited number of discrete responses instead of a continuous distribution. Nonparametric statistics do not rely on an assumption of a continuously distributed response variable, as does the analysis of variance (Sokal and Rohlf 1981). All statistical analyses were performed using SAS (SAS Institute Inc. 1982) maintained at the Triangle Universities Computation Center.

Results

Larval performance in experimental ponds

Our experiment was not biased in favor of finding competition, because larval salamanders never became unrealistically crowded. Both initial and final densities of *Notophthalmus* larvae were low, relative to densities observed in a natural pond in North Carolina (Harris et al. 1988, Fauth, unpubl. data). Larval *Notophthalmus* survival in the experiment was low (39.6% overall; Fig. 1). with one pond in Block II failing to produce any survivors. Growth rates of *Notophthalmus* (final mass/length of larval period) varied from 1.9–6.9 mg d^{-1} ($\bar{x}$ = 3.5); individuals attained final masses from 0.19–1.41 g ($\bar{x}$ = 0.54) and metamorphosed after a minimum larval period of 86 d. Survival of *Notophthalmus* was not significantly correlated with mass ($r = 0.38$, $p < 0.25$), nor with the length of larval periods ($r = 0.36$, $p < 0.28$). Mean mass, however, was weakly correlated with the length of larval period ($r = 0.58$, $p < 0.06$) indicating that *Notophthalmus* populations with longer larval periods metamorphosed at a larger average size. The mean size of efts ($\bar{x}$ = 5.01 cm total length) was similar to the

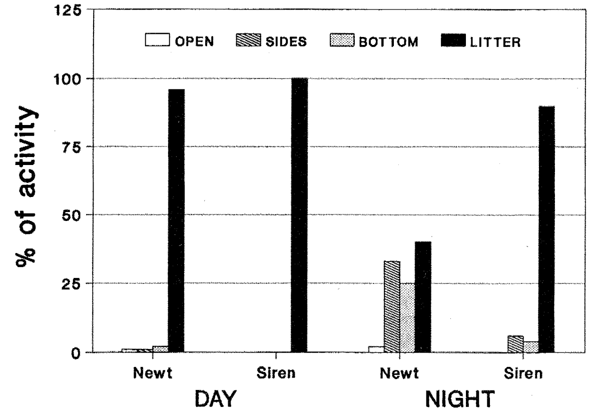

Fig. 2. Microhabitat use by larvae of *Notophthalmus viridescens* and *Siren intermedia* in experimental ponds. Vertical axis is the percentage of individuals utilizing each habitat type: open water, sides of the pools, and resting on bottom (active categories), and in the bottom litter (concealed). No differences were found between treatments in activity patterns or microhabitat use, so all treatments were combined for ease of presentation. Species-specific differences in nocturnal microhabitat use (active vs. concealed) were highly significant ($G = 63.01$, 1 d.f., $p \ll 0.001$).

Tab. 1. ANOVA of siren responses. A priori contrasts test the null hypotheses: (1) no siren density effect, (2) no competition between larval sirens and larval newts, and (3) larval sirens and larval newts are equal competitors.

		Siren survival		
Contrast:	df	SS	F	p›F
(1)	1	1243.3987	1.76	0.23
(2)	1	374.4982	0.53	0.49
(3)	1	253.1250	0.36	0.57
Source				
Block	3	615.8494	0.29	0.83
Treatment	2	1247.3480		
Error	6	4239.7116		
Total	11	6102.9090		
		Siren mass		
Contrast:	df	SS	F	p›F
(1)	1	6.8987	6.43	0.04
(2)	1	6.4795	6.04	0.05
(3)	1	0.0065	0.01	0.94
Source				
Block	3	5.8659	1.82	0.24
Treatment	2	8.9232		
Error	6	6.4367		
Total	11	22.2259		

5.04–5.37 cm range of annual means reported by Harris et al. (1988) for efts in a North Carolina population.

Larval *Siren* survival was high, averaging 72.9% across all treatments (Fig. 1). Mean growth rates per experimental pond varied from 3.2–28.0 mg d^{-1} ($\bar{x}$ = 14.3); individuals attained final masses ranging from 0.56–5.01 g ($\bar{x}$ = 2.48) and final lengths of 4.4–14.7 cm SVL ($\bar{x}$ = 10.9). Mean *Siren* mass and survival were not significantly correlated ($r = 0.37$, $p < 0.23$). Final *Siren* densities and sizes were within the range of those observed for yearling *Siren* in natural ponds (Davis and Knapp 1953, Bennett and Taylor 1968, Gehlbach et al. 1973, Gehlbach and Kennedy 1978, Fauth, unpubl. data). The larval salamanders in our artificial ponds appear to have experienced natural densities throughout the experiment and to have achieved growth rates within the range observed in natural populations.

Behavioral observations

During weekly searches for metamorphosing *Notophthalmus*, larval *Notophthalmus* were much more frequently observed than larval *Siren*, especially at night. The results of the behavioral census confirmed this impression (Fig. 2). Both species were more active at night (2100-0500 hours) than during the day (0600-2000 hours). Only *Notophthalmus* utilized the open water habitat. The two species overlapped little in microhabitat use during their nocturnal foraging bouts. Larval *Notophthalmus* exhibited a decided tendency to leave the litter at night to forage along the bottom or sides of the pools. Larval *Siren*, on the other hand, spent the majority of their time concealed in the litter, and when outside this refuge, could invariably be found entwined amongst the filamentous algae lining the sides and bottom of the ponds (Fig. 2).

Tab. 2. ANOVA of newt responses. A priori contrasts test the null hypotheses: (1) no newt density effect, (2) no competition between larval newts and larval sirens, and (3) larval newts and larval sirens are equal competitors.

		Newt survival		
Contrast:	df	SS	F	p›F
(1)	1	1130.7865	7.94	0.03
(2)	1	2078.2678	14.59	0.009
(3)	1	143.0620	1.00	0.35
Source				
Block	3	1857.5328	4.35	0.06
Treatment	2	2234.7443		
Error	6	854.5277		
Total	11	4946.8047		
		Newt mass		
Contrast:	df	SS	F	p›F
(1)	1	0.0338	0.59	0.48
(2)	1	0.1122	1.97	0.22
(3)	1	0.0291	0.51	0.51
Source				
Block	3	0.2910	1.70	0.28
Treatment	2	0.1137		
Error	5	0.2851		
Total	10	0.6649		

Spatial variation

The experimental blocks were designed to account for spatial variation at the field site. Differences attributable to blocks accounted for a nonsignificant fraction of the variation in larval salamander performance (Tabs 1, 2). Failure of any *Notophthalmus* to survive in one Block II pool resulted in a nearly significant block effect ($p < 0.06$) in the ANOVA of newt survival (Tab. 2).

Intraspecific competition

All responses of the two species changed in the direction expected if each species was limited by its food supply. Both survival and growth declined at high densities and larval periods of *Notophthalmus* increased (Fig. 2). The modest statistical power of this experiment (only 4 replicates per treatment) and low larval densities employed resulted in only 2 of the 5 tests for density-dependence being significant in an ANOVA; mass of *Siren* and survival of *Notophthalmus*.

Mean *Siren* mass was significantly reduced at high *Siren* density, with individuals attaining only one-half the mass of larvae raised at low density (Fig. 1). *Siren* survival declined 32% at high density, but the reduction was not significant in an ANOVA (Tab. 1). However, a nonparametric G-test indicated that mortality was nonrandomly distributed ($\chi^2 = 3.902$. $P < 0.048$). *Notophthalmus* survival was reduced significantly at high density; doubling their initial density caused a 50% reduction in mean survival (Fig. 1, Tab. 2). Mean mass of *Notophthalmus* declined at high density, but the differences were not significant (Fig. 2, Tab. 2). There was no difference in the mean larval periods of newts raised at different densities (Friedman's Method $\chi^2 = 1.00$, 1 df, $p = 0.430$), although the larval period tended to be prolonged at high density (Fig. 1). A single larva from each initial *Notophthalmus* density became paedomorphic; the only larva which bypassed the eft stage and transformed directly into an aquatic adult was from a low density pond.

Interspecific competition

The null hypothesis of no interspecific competition was also rejected for 2 of the 5 responses, *Siren* mass and *Notophthalmus* survival. In all responses the direction of differences was as expected from a competitive effect; each species depressed the growth and survival of the other (Fig. 1).

Competition with larval *Notophthalmus* caused a significant decrease in mean *Siren* mass (Tab. 1). *Siren* raised in the presence of *Notophthalmus* grew to only slightly more than one-half the mass of larval *Siren* raised alone at low density (Fig. 1). In the presence of *Notophthalmus*, *Siren* mortality was 17% higher than when raised alone, although the difference was not significant (Tab. 1). *Notophthalmus* likewise experienced negative effects from competition with *Siren*; larval *Notophthalmus* had significantly higher mortality in the presence of *Siren* than alone at low density (Tab. 2). In pools with *Siren*, the mean mass of *Notophthalmus* declined, but the difference was not statistically significant (Tab. 2, Fig. 1). Mean larval periods also declined, but again the difference was not statistically significant (Friedman's Method $\chi^2 = 0.33$, 1 df, $p < 0.386$).

Equal competitors

Siren larvae responded to *Notophthalmus* larvae as if they were additional conspecifics, and vice versa. Responses of *Siren* and *Notophthalmus* were virtually identical at total larval densities of 6 salamanders per pool, regardless of the species composition (Fig. 1). There was no difference in the duration of the larval period of *Notophthalmus* (Friedman's Method $\chi^2 = 0.33$, 1 df, $p < 0.386$). F-ratios < 1.0 in the ANOVAS for the responses of each species suggested that our failure to detect differences in competitive ability was not due to a lack of statistical power (Tabs 1, 2). Based on these results, *Siren* larvae and *Notophthalmus* larvae are best considered equal competitors under the conditions of this experiment.

Discussion

How prevalent is competition in nature? The answer depends not only upon which ecologist is asked, but also upon the trophic level, habitat, and group of organisms considered (Connell 1983, Schoener 1983). Every experiment explicitly designed to detect competition among temporary pond amphibians has concluded that it occurs. Density-dependent intraspecific competition has been documented several times in anuran tadpoles (Licht 1967, Wilbur 1977a, b, Smith-Gill and Gill 1978, Semlitsch and Caldwell 1982, Smith 1983) including Brockelman (1969) which is sometimes cited as a null example. Similarly, interspecific competition between tadpoles has been demonstrated repeatedly (Wilbur 1977a, 1982, Wilbur et al. 1983, Morin 1983, 1986, 1987, Alford and Wilbur 1985, Morin et al. 1988, Wilbur and Fauth in press). Field studies of salamanders have also demonstrated the effects of both intra- and interspecific competition (Wilbur 1972, Morin 1983, Hairston 1987, Harris 1987b, Semlitsch 1987a, b, Fauth and Resetarits, unpubl.). Competition appears to be commonly experienced by larval temporary pond amphibians, although it may interact with predation, disturbance, and the terrestrial stage of the complex life cycle to determine community structure (Wilbur et al. 1983, Werner 1986, 1988, Wilbur 1987, 1988). However, nearly all of the studies that investigated interspecific competition documented interactions between closely related and morphologically very similar species (e.g. ambystomatid salamanders, Wilbur 1972). We have extended the range of ecological inference by investigating the effects of intraand interspecific competition on two dissimilar species, including an obligately paedomorphic salamander.

At high density, *Notophthalmus* larvae in our experimental ponds experienced much higher mortality than when raised at low density. Harris (1987b), in an experimental study of population regulation in *Notophthalmus*, found density-dependent growth, but not survival. However, the lowest larval density (5.5 m^{-2}) established by Harris (1987b) was higher than the high density we used (3.90 m^{-2}). If larval growth rate is positively correlated with terrestrial survival, age at first reproduction and adult fecundity, then density-dependent larval growth could regulate *Notophthalmus* populations (Harris 1987b). The occurrence of negative density-dependent mortality such as we observed would be a more direct means of population regulation.

In contrast to the effect of density on *Notophthalmus*, intraspecific competition reduced both growth and survival of *Siren*. Reduced growth rates may increase the cumulative risk of predation by size-limited predators, which are abundant in temporary ponds. Reduced mass would also increase the risk of mortality by desiccation, because sirenids rely upon accumulated fat reserves in the tail and along the vertebral column to survive droughts (Martof 1969). Smaller *Siren* may suffer higher mortality at these times due to an inability to store fat and their higher metabolic rates and greater rate of water loss than larger *Siren* (Gehlbach et al. 1973). Reduced growth rates may also diminish lifetime fitness if smaller individuals are less fecund or reproduce later than larger ones.

Interspecific competition had the same qualitative effects as intraspecific competition. Interspecific competition primarily acted to retard *Siren* growth and increase *Notophthalmus* mortality. The larvae of both species responded to additional heterospecifics as if they were additional conspecifics. Behavioral observations suggested that the two species overlapped little in microhabitat use during their nocturnal foraging bouts, but both species were feeding on the same pool of microcrustaceans and chironomid larvae. Larval *Siren* were rarely observed, even at night, indicating that much of their time was spent in the bottom litter of the experimental ponds. Larval *Notophthalmus*, on the other hand, were frequently seen feeding in the water column. If competitive interactions between these two species were principally exploitative, one might expect the faster-growing *Siren* to be competitively superior, especially since they enjoyed a one month advantage in hatching date (Alford and Wilbur 1985, Wilbur and Alford 1985) and were larger than *Notophthalmus* at the end of the experiment (Morin and Johnson 1988). However, we found no evidence to indicate that *Siren* was a superior competitor. Coexistence of *Siren* and *Notophthalmus* probably results from environmental instability (i.e. pond drying) and differences in the life histories of the salamanders. In an experimental study of three species of ambystomatid salamander larvae, Wilbur (1972) also found that competition was a function of total larval density, rather than species' identity, indicating the species were equal competitors. He suggested coexistence was a consequence of environmental instability and long adult lifespans.

Few studies have assessed the relative intensity of intra- versus interspecific competition. Despite obvious differences in life history, morphology, and phylogeny, we detected interspecific competition between two important temporary pond predators at realistic densities. We found the intensity of competition between the larvae of these two salamanders to be comparable to that of intraspecific competition within each species. Fauth and Resetarits (unpubl.) found the two species continued to compete as adults, but *Siren* was competitively superior. Competition between these predators may be especially important in natural ponds, because interactions at higher tropic levels may largely determine community structure via cascading direct and indirect effects (Zaret 1980, Kerfoot and Sih 1987, Fauth and Resetarits, unpubl.).

The larval salamanders we studied are typical of species which heretofore have been largely overlooked as potential competitors; distantly related species with divergent life histories and morphologies. Only a handful of experiments have investigated competition between such disparate species (Brown and Davidson 1977, Eadie and Keast 1982, Schluter 1986, Morin et al. 1988). Future ecological studies should investigate competitive interactions amongst members of guilds, as originally defined, as a group of species, without regard to taxonomic boundaries, that exploit the same resource (Root 1967). Within such non-taxonomically circumscribed sets of species, competition should be an important interaction.

Acknowledgements - We gratefully acknowledge the advice and encouragement provided by R. N. Harris, R. D. Semlitsch and J. Van Buskirk at the Zoology Field Station. Previous versions of this paper benefitted from the criticisms of J. Bernardo, R. N. Harris, J. D. Leimberger, A. McCollum and J. Van Buskirk. Special thanks are due to P. J. Morin and L. Persson for their comments. This research was supported by NSF grant BSR-82-06855 to H. M. Wilbur.

References

Alford, R. A. and Wilbur, H. M. 1985. Priority effects in experimental pond communities: competition between *Bufo* and *Rana*. - Ecology 66: 1097–1105.

Bennett, C., and Taylor, R. J. 1968. Notes on the lesser siren, *Siren intermedia* (Urodela). - Southwest. Nat. 13: 455–457.

Bishop, S. C. 1941. The salamanders of New York. - New York State Mus. Bull. 324: 54–81.

Brockelman, W. Y. 1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. - Ecology 50: 632–644.

Brown, J. H. and Davidson, D. W. 1977. Competition between seed-eating rodents and ants in desert ecosystems. - Science 196: 880–882.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. - Am. Nat. 122: 661–696.

Cope, E. D. 1889. The Batrachia of North America. – United States Nat. Mus. Bull. No. 34, 1889.

Davis, W. B., and Knapp, F. T. 1953. Notes on the salamander *Siren intermedia*. – Copeia 1953: 119–121.

Diamond, J. 1986. Laboratory experiments, field experiments, and natural experiments. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, NY.

Draper, N. R. and Smith, H. 1981. Applied regression analysis. – Wiley, New York.

Eadie, J. M. and Keast, A. 1982. Do goldeneye and perch compete for food? – Oecologia (Berl.) 55: 225–230.

Gause, G. F. 1935. Experimental demonstration of Volterra's periodic oscillation in the numbers of animals. – J. Exp. Biol. 12: 44–48.

Gehlbach, F. R. and Kennedy, S. E. 1978. Population ecology of a highly productive aquatic salamander (*Siren intermedia*). – Southwest. Nat. 23: 423–430.

– , Gordon R. and Neill, J. B. 1973. Aestivation of the salamander, *Siren intermedia*. – Am. Midl. Nat. 89: 455–463.

Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). – Ecol. Monogr. 48: 145–166.

Godley, J. S. 1983. Observations on the courtship, nests and young of *Siren intermedia* in southern Florida. – Am. Midl. Nat. 110: 215–219.

Goin, C. J., Goin, O. B. and Zug, G. R. 1978. Introduction to herpetology. – Freeman, San Francisco.

Hairston, N. G. 1980. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. – Ecology 61: 817–826.

– 1987. Community ecology and salamander guilds. – Cambridge Univ. Press, New York.

Hamilton, W. J., Jr. 1940. The feeding habits of larval newts with reference to availability and predilection of food items. – Ecology 21: 351–356.

Harris, R. N. 1987a. Density-dependent paedomorphosis in the salamander *Notophthalmus viridescens dorsalis*. – Ecology 68: 705–712.

– 1987b. An experimental study of population regulation in the salamander. *Notophthalmus viridescens dorsalis* (Urodela: Salamandridae). – Oecologia (Berl.) 71: 280–285.

– , Alford R. A. and Wilbur, H. M. 1988. Density and phenology of *Notophthalmus viridescens dorsalis* in a natural pond. – Herpetologica 44: 234–242.

Hecht, M. K. and Edwards, J. T. 1977. The methodology of phylogenetic inference above the species level. – In: Hecht, Goody and Hecht (eds.), Major patterns in vertebrate evolution. – NATO Adv. Studies Ser. A. Vol. 14, Plenum Press, pp. 3–31.

Kaplan, R. H. and Salthe, S. N. 1979. The allometry of reproduction: an empirical view in salamanders. – Am. Nat. 113: 671–689.

Kerfoot, W. C. and Sih, A. 1987. Predation: direct and indirect impacts on aquatic communities. – Univ. Press of New England, Hanover, NH.

Levins, R. 1968. Evolution in changing environments. – Princeton Univ. Press, Princeton, NJ.

Licht, L. E. 1967. Growth inhibition in crowded tadpoles: intraspecific and interspecific effects. – Ecology 48: 736–745.

Lotka, A. J. 1932. The growth of mixed populations: two species competing for a common food supply. – J. Wash. Acad. Sci. 22: 461–469.

Mardia, K. V., Kent, J. T. and Bibby, J. M. 1979. Multivariate analysis. – Academic Press, New York.

Martof, B. S. 1969. Prolonged inanation in *Siren lacertina*. – Copeia 1969: 285–289.

– 1973. *Siren intermedia*. – In: Catalogue of American Amphibians and Reptiles. Soc. Study of Amphibians and Reptiles, pp. 127.1–127.3.

May, R. M. 1973. Stability and complexity in model ecosystems. – Princeton Univ. Press, Princeton, NJ.

Morin, P. J. 1981. Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. – Science 212: 1691.

– 1983. Predation, competition, and the composition of larval anuran guilds. – Ecol. Monogr. 53: 119–138.

– 1986. Interactions between intraspecific competition and predation in an amphibian predator-prey system. – Ecology 67: 713–720.

– 1987. Predation, breeding asynchrony, and the outcome of competition among treefrog tadpoles. – Ecology 68: 675–683.

– and Johnson, E. A. 1988. Experimental studies of asymmetric competition among anurans. – Oikos 53: 398–407.

– , Lawler, S. P. and Johnson, E. A. 1988. Competition between aquatic insects and vertebrates: experimental measures of interaction strength and higher order interactions. – Ecology 69: 1401–1409.

Park, T. 1948. Experimental studies of interspecific competition. I. Competition between populations of the flour beetles *Tribolium confusum* Duval and *Tribolium confusum* Herbst. – Ecol. Monogr. 18: 267–307.

Petranka, J. W. and Sih, A. 1986. Environmental instability, competition, and density-dependent growth and survivorship of a stream-dwelling salamander. – Ecology 67: 729–736.

Reichman, O. J. 1979. Competition between distantly related taxa: a symposium. – Am. Zool. 19: 1027–1175.

Root, R. B. 1967. The niche exploitation patterns of the blue-gray gnatcatcher. – Ecol. Monogr. 37: 317–350.

SAS Institute Inc. 1982. SAS User's Guide: Statistics. 1982 Edition. – SAS Institute Inc., Cary, NC.

Schluter, D. 1986. Character displacement between distantly related taxa? Finches and bees in the Galapagos. – Am. Nat. 127: 95–102.

Schoener, T. W. 1983. Field experiments on interspecific competition. – Am. Nat. 122: 240–285.

Semlitsch, R. D. 1987a. Paedomorphosis in *Ambystoma talpoideum*: effects of density, food, and pond drying. – Ecology 64: 994–1002.

– 1987b. Density-dependent growth and fecundity in the paedomorphic salamander *Ambystoma talpoideum*. – Ecology 64: 1003–1008.

– and Caldwell, J. P. 1982. Effects of density on growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. – Ecology 63: 905–911.

– , Scott, D. E. and Pechmann, J. H. K. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. – Ecology 69: 184–192.

Smith, D. C. 1983. Factors controlling tadpole populations of the chorus frog *(Pseudacris triseriata)* on Isle Royale, Michigan. – Ecology 64: 501–510.

– 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. – Ecology 68: 344–350.

Smith-Gill, S. J. and Gill, D. E. 1978. Curvilinearities in the competition equations: an experiment with ranid tadpoles. – Am. Nat. 112: 557–570.

Sokal, R. R. and Rohlf, F. J. 1981. Biometry. – Freeman, New York.

Taylor, B. J., Estes R. A., Pechmann J. H. K. and Semlitsch, R. D. 1988. Trophic relationships in a temporary pond: larval salamanders and their macroinvertebrate prey. – Can. J. Zool. 66: 2191–2198.

Vandermeer, J. H. 1969. The competitive structure of communities: an experimental approach with protozoa. – Ecology 50: 362–371.

Verrell, P. A. 1982. Male newts prefer large females as mates. – Anim. Behav. 30: 1254–1255.

– 1986. Wrestling in the red-spotted newt (*Notophthalmus viridescens*): resource value and contestant asymmetry determine contest duration and outcome. – Anim. Behav. 34: 398–402.

Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. – Am. Nat. 128: 319–341.

– 1988. Size, scaling, and the evolution of complex life cycles. – In: Ebenman, B. and Persson, L. (eds), Size-structured populations. Springer, Berlin, pp. 60–84.

Wilbur, H. M. 1972. Competition, predation and the structure of the *Ambystoma-Rana sylvatica* community. – Ecology 53: 3–21.

– 1977a. Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. – Ecology 56: 196–200.

– 1977b. Interaction of food level and population density in *Rana sylvatica*. – Ecology 58: 206–209.

– 1980. Complex life cycles. – Ann. Rev. Ecol. Syst. 11: 67–93.

– 1982. Competition between tadpoles of *Hyla femoralis* and *Hyla gratiosa* in laboratory experiments. – Ecology 63: 278–282.

– 1987. Regulation of structure in complex systems: experimental temporary pond communities. – Ecology 68: 1437–1452.

– 1988. Interactions between growing predators and growing prey. – In: Ebenman, B. and Persson, L. (eds). Size-structured populations. Springer, Berlin, pp. 157–172.

– and Alford, R. A. Priority effects in experimental pond communities: responses of *Hyla* to *Bufo* and *Rana*. – Ecology 66: 1106–1114.

– and Fauth, J. E. 1990. Experimental aquatic food webs: interactions between two predators and two prey. – Am. Nat. in press.

– , Morin, P. J. and Harris, R. N. 1983. Salamander predation and the structure of experimental communities: anuran responses. – Ecology 64: 1423–1429.

Zaret, T. M. 1980. Predation and freshwater communities. – Yale Univ. Press, New Haven, CT.