

2000

Density-Dependent Effects on Microhabitat Selection and Activity of Two Species of Larval *Ambystoma* Salamanders


Jeanette M. Jaskula
Saint Joseph's College

Robert Brodman
Saint Joseph's College

Let us know how access to this document benefits you

Copyright © Copyright 2000 by the Iowa Academy of Science, Inc.

Follow this and additional works at: <https://scholarworks.uni.edu/jias>

 Part of the [Anthropology Commons](#), [Life Sciences Commons](#), [Physical Sciences and Mathematics Commons](#), and the [Science and Mathematics Education Commons](#)

Recommended Citation

Jaskula, Jeanette M. and Brodman, Robert (2000) "Density-Dependent Effects on Microhabitat Selection and Activity of Two Species of Larval *Ambystoma* Salamanders," *Journal of the Iowa Academy of Science: JIAS*, 107(3-4), 146-150.

Available at: <https://scholarworks.uni.edu/jias/vol107/iss3/17>

This Research is brought to you for free and open access by the IAS Journals & Newsletters at UNI ScholarWorks. It has been accepted for inclusion in Journal of the Iowa Academy of Science: JIAS by an authorized editor of UNI ScholarWorks. For more information, please contact scholarworks@uni.edu.

Offensive Materials Statement: Materials located in UNI ScholarWorks come from a broad range of sources and time periods. Some of these materials may contain offensive stereotypes, ideas, visuals, or language.

Density-Dependent Effects on Microhabitat Selection and Activity of Two Species of Larval *Ambystoma* Salamanders

JEANETTE M. JASKULA and ROBERT BRODMAN¹

Biology Department, Saint Joseph's College, Rensselaer, Indiana 47978

To be able to distinguish unnatural amphibian declines from natural population fluctuations we need a better understanding of the mechanisms that affect amphibian community structure. Larval pond-breeding salamanders exhibit density-dependent effects on population parameters, but little is known of the effect of density on behaviors that mediate interactions. Two species, *Ambystoma tigrinum* (tiger salamander) and *A. laterale* (blue-spotted salamander), were evaluated in laboratory aquaria for intraspecific and interspecific interactions that affect microhabitat selection and activity. Microhabitat selection was studied by partitioning containers into microhabitats that either contained or lacked refuges, and movement was recorded over a hexagonal grid to determine activity during periods of observation. Both species altered microhabitat preferences and activity levels when they shared tanks with con- or heterospecifics. These density-dependent behavioral changes may indicate that fluctuations in population densities result in behavioral responses that may contribute to coexistence.

INDEX DESCRIPTORS: coexistence, density-dependent, microhabitat, activity, *ambystoma* salamanders, behavioral ecology

Determining whether proposed amphibian declines are natural population fluctuations are difficult to decipher unless there is a better understanding of the mechanisms that determine community structure and stable biodiversity (Pechmann et al. 1991). Ecologists have long debated whether the coexistence of species in a community is in large part due to the interactions of interspecific competition and predation or the consequence of density-independent mortality (Schoener 1983, Strong 1983). Amphibians have become a focus in determining how these regulatory factors contribute to a stable coexistence. Pond-breeding salamander communities are shaped by density-dependent interactions among larvae (Wilbur 1972, Cortwright 1988, Brodman 1996). However, many larval salamanders are intraguild predators of potential intra- and interspecific competitors (Stenhouse et al. 1983, Cortwright 1988, Brodman 1996), complicating the roles of competition and predation in community dynamics (Polis et al. 1989, Werner and Anholt 1993).

Shifts in microhabitat use that result in predator avoidance by larval salamanders are documented. Holomuzki (1986) showed that change in predation risk from predaceous diving beetles caused shifts in microhabitat use by larval *Ambystoma tigrinum*. Larval *A. barbouri* were more common in patches of green algae when in the presence of crayfish and sunfish predators (Holomuzki 1989), and the addition of sunfish reduced the population outside the refuge (Sih et al. 1988). Brodman (1996) found that *A. maculatum* larvae shifted microhabitat use to refuge in the presence of larger *A. jeffersonianum*. Movement of larval salamanders at dusk has been associated with prey availability (Anderson and Graham 1967, Branch and Altig 1981, Holomuzki and Collins 1983), but might also reflect niche partitioning and predator avoidance (Holomuzki 1989, Walls 1995, Brodman 1996).

Because activity is a component of salamander behavior that contributes to the process of prey detection and encounter by predators, selective pressures should moderate activity (Werner 1991, Werner

and Anholt 1993). Werner (1991) showed that at lower activity levels with predators present, tadpoles took more time to deplete food resources resulting in reduced net growth and longer larval periods. Consequently, this relation outlines the fundamental trade-off between activity level and prey vulnerability. Holomuzki (1986) reports a similar trade-off between the demands of resource acquisition and predator avoidance. In his laboratory studies he shows that *A. tigrinum* used safer microhabitats with lower food density only during periods when the predaceous diving beetles are active in areas with higher food density.

Changes in larval activity influence foraging success (McWilliams and Bachmann 1989, Werner 1991, Werner and Anholt 1993) and predator avoidance (Skelly and Werner 1990, Kutka 1994, Skelly 1994). Tadpoles of *Bufo americanus* respond to the presence of larval dragonfly predators by reducing activity, thereby reducing mortality (Skelly and Werner 1990). However, this reduction in activity occurred at the expense of decreased growth. In a similar study, Werner (1991) showed that lower activity levels with a predator present led to a decreased foraging rate in tadpoles. Adjusting such activities may influence growth and survivorship by decreasing the effects of interspecific interactions. Laboratory experiments revealed that the differences in foraging behavior of *A. maculatum* and *A. talpoideum* might provide a mechanism by which these species coexist (Walls 1996).

Aquatic larvae of the eastern tiger salamander, *Ambystoma tigrinum*, and the blue-spotted salamander, *A. laterale*, coexist in areas of the Midwest. *Ambystoma tigrinum* typically breeds earlier and grows faster during the larval period than *A. laterale* (Minton 1972) and can attain sizes that allow them to prey upon smaller congeners (Wilbur 1972). While these species coexist in a number of ponds in northwest Indiana, their relative abundance varies considerably and they differ in the way that they are distributed spatially (Brodman 1999).

Wilbur (1972) found that *A. tigrinum* acts principally as a predator in temporary pond food webs, reducing the survivorship of *A. laterale*. Anderson and Graham (1967) found that stratification of *A.*

¹ Email: bobb@saintjoe.edu

laterale-complex and *A. tigrinum* larvae is important in facilitating coexistence of these species by decreasing interactions. However, there is little information on how behavioral interactions of these larvae affect community structure.

Several hypotheses have been developed to explain coexistence among larval salamanders. While it has been hypothesized that interspecific differences in breeding phenology and rate of development minimize competition for food or offer advantages among years in which the ponds dry at differing rates (Anderson and Graham 1967, Keen 1975, Wilson 1976, Smith 1990, Talentino and Landre 1991), this pattern also leads to intraguild predation (Brodman 1996) and interference competition (Walls and Jaeger 1987, Smith 1990). Microhabitat partitioning may minimize interspecific interactions such as intraguild predation or interference competition (Holomuzki 1986, 1989, Walls 1995).

To evaluate the effects of intraguild interactions on the coexistence of *A. tigrinum* and *A. laterale*, we designed three experiments to test the effect of larval density, presence of predators, and availability of refuge on larval survival, growth, activity and microhabitat partitioning.

METHODS

Mesocosm Experiment

We designed a mesocosm experiment to examine density-dependent effects and the predator-prey relationship of *A. tigrinum* and *A. laterale*. Larvae were raised in 85-l plastic tubs (0.16 m²). Leaf litter, zooplankton, and 40 tadpole hatchlings (*Rana pipiens*) were added to each tub that was left open to colonization by aquatic insects. We had five treatments with six replicates each. Two treatments had five or ten *A. laterale* to test for density-dependent effects on growth and survivorship. Similarly, two treatments had three or six *A. tigrinum* to test for density-dependent effects on growth and survivorship. The fifth treatment had five *A. laterale* and three *A. tigrinum* as a mixed-species test for the effect of species on each other. The experimental densities (18–61 larvae/m²) are within the range of *Ambystoma* found in the field (Shoop 1974, Cortwright 1988, Stangel 1988, Van Buskirk and Smith 1991, Brodman 1995). Eggs were collected and randomly assigned to tubs on 3 April 1998. The number of larvae surviving and snout-vent length (SVL) was measured at the conclusion of the experiment on 3 July 1998. The tubs were searched twice a week for dead larvae so that indirect accounts of predation could be determined.

Low density single-species conditions were controls to test the effect of density and heterospecifics on survival and growth over a three month period. Data was analyzed by ANOVA ($\alpha = 0.05$).

Microhabitat Partitioning and Refuge Use

We designed an experiment to examine if use of refuge and microhabitat partitioning shift as a result of increasing density or presence of heterospecifics. The experimental arena for these laboratory experiments was a 9 × 17 × 32 cm plastic aquarium partitioned widthwise into two equal chambers by chickenwire. We placed a 2 cm thick layer of pondweed, leaf litter and algae into one chamber, leaving the second chamber clear. Larval salamanders traveled freely through the openings of the chickenwire between vegetated and un-vegetated chambers. Larvae were also capable of floating in the water column and making swimming lunges at prey. Approximately 1 month old larvae of *A. tigrinum* (mean SVL 28.6 mm) and *A. laterale* (mean SVL 23.6 mm) were collected in late April/early May from several ponds in Jasper County in northwest Indiana and placed into a randomly assigned experimental chamber. The size differences were sufficient that the largest *A. tigrinum* could prey upon *A. laterale* and

the smallest conspecifics (pers. obs. 1998). Microhabitat preferences were measured by observing the percentage of time that individuals spent in refuge.

As a control to evaluate microhabitat preferences for each species, a single individual was placed into each of the experimental chambers. The percentage of time that single individuals spent in refuge was used for comparison to evaluate if increasing density or heterospecifics cause altered patterns of microhabitat use. To test for density effects, treatments with two individuals per chamber and four individuals per chamber were observed. The average amount of time spent in each microhabitat was measured. To test the effect of interspecific interactions on microhabitat use we treated single-species microhabitat preferences as controls to determine whether interspecific interactions alter microhabitat choice. Higher intraspecific densities are also compared to control for densities when species composition is different. Mixed-species treatments were conducted at densities of one, two and four individuals of each species together in one arena. These densities (18.4–147 larvae/m²) are within the range of *Ambystoma* found in the field (Shoop 1974, Cortwright 1988, Stangel 1988, Van Buskirk and Smith 1991, Brodman 1995).

Observations were recorded three times daily for two weeks from 20 May–4 June 1998. Each observation period was a 5 min. interval under ambient light conditions between 0800–1000 h, 1200–1400 h, and 1800–2000 h. Each individual was observed for a total of 200 min. After observations, leaf litter was searched to determine if larvae were dead rather than hiding in refuge. Animals were maintained during the duration of the experiment in the trial chambers and fed zooplankton at the end of the day.

Changes in microhabitat patterns were considered evidence of spatial niche partitioning. There were ten independent replicates for each control and treatment. Microhabitat usage patterns between species and among treatments were compared by using the Mann-Whitney U-test on the amount of time spent using refuge. Because each single species treatment is compared at two densities and to a mixed-species treatment, we use Bonferroni's adjustment to α and consider differences significant at $\alpha = 0.0167$. The sequence that treatments were run was randomized.

Larval Activity

This experiment was designed to test the effect of increasing density or presence of heterospecifics on larval activity. A glass dish (20 × 20 × 5 cm) was placed over a hexagonal grid where the position of each salamander larva was observed every 30 s for 10 min. The mean distance moved during 30-s intervals, the percentage of time moving, and the mean number of prey items eaten were used as measures of larval activity. To establish a control for larval activity the movement of an individual larva was compared to intraspecific and interspecific pairs of larvae. Treatments with the addition of prey items (zooplankton and small larva), increasing density (two conspecifics per chamber) and the addition of a heterospecific were used to determine their effects on larval activity. Experimental densities (25 and 50 larvae/m²) were within the range of *Ambystoma* found in the field (Shoop 1974, Cortwright 1988, Stangel 1988, Van Buskirk and Smith 1991, Brodman 1995). Prey items included 25-ml aliquots of pond water containing zooplankton concentrated by a dip net, and two small amphibian larvae (*A. maculatum* hatchlings or *Pseudacris* tadpoles).

Data were compared and analyzed by one-tailed Dunnett's tests for a priori comparison of control mean to each other group mean. The Dunnett testing procedure (Dunnett 1955) allows powerful independent testing of treatments under the protection of a single probability of sampling error ($\alpha = 0.05$). Individual animals were used in only one trial. Each control was replicated 14 times and each

Table 1. Survival and growth *Ambystoma laterale* and *A. tigrinum* in mesocosms. Values are the mean percent survival and SVL (mm) of 3 mo old larvae. Values with asterisks are significantly different from intraspecific controls (* = $P < 0.05$; ** = $P < 0.005$) by ANOVA ($n = 3, 15$).

Treatments	<i>Ambystoma laterale</i>		<i>Ambystoma tigrinum</i>	
	survival (%)	SVL (mm)	survival (%)	SVL (mm)
Low density	60	26.4	67	28.1
High density	49*	22.8*	47*	32.8**
Mixed-species	17**	24.2*	40*	32.3**

Table 2. Microhabitat preferences of larval *Ambystoma laterale* and *A. tigrinum*. Values are the mean amount of time out of 200 minutes of observation that larvae were observed within a given microhabitat. Patterns with asterisks are significantly different from low density controls (* = $P < 0.0125$; ** = $P < 0.001$) by the Mann-Whitney U-test of independence. There were ten replicates for each treatment.

<i>Ambystoma laterale</i>		<i>Ambystoma tigrinum</i>	
Treatments	Vegetated/Clear	Treatments	Vegetated/Clear
Density 1	128/72	Density 1	128/72
Density 2	175/25	Density 2	96/104
Density 4	158/42	Density 4	79/121
Mixed-species (1 + 1)	179/21	Mixed-species (1 + 1)	84/116
Mixed-species (4 + 4)	174/26	Mixed-species (4 + 4)	45/155
Significant Comparisons		Significant Comparisons	
1 vs. 2*		1 vs. 2**	2 vs. 4 + 4*
2 vs. 4**		1 vs. 4**	4 vs. 4 + 4**
1 vs. 1 + 1*		1 vs. 1 + 1**	1+1 vs. 4 + 4**
1 vs. 4 + 4*		1 vs. 4 + 4**	

Table 3. Salamander larvae movements in 30 s intervals, 20 trials, 20 replicates: Mean (\pm SE) distance moved and percentage of time moving between trials per replicate. Differences from the control tested by the Dunnett's testing procedure. * = $P < 0.05$.

	Distance	Movement
<i>A. laterale</i>		
Control	5.43 \pm 0.56	86.1 \pm 3.2%
two <i>A. laterale</i>	4.12 \pm 0.33*	75.4 \pm 3.9%
with food	4.93 \pm 0.43	74.5 \pm 3.4%
with <i>A. tigrinum</i>	3.89 \pm 0.25*	69.9 \pm 4.6%*
<i>A. tigrinum</i>		
Control	5.52 \pm 0.52	74.0 \pm 3.3%
two <i>A. tigrinum</i>	5.78 \pm 0.39	90.1 \pm 2.0%*
with food	3.04 \pm 0.66*	61.4 \pm 8.5%
with <i>A. laterale</i>	2.46 \pm 0.50*	80.1 \pm 4.3%

treatment was independently replicated 20 times because the optimum allocation of plots among the control and the three treatment groups is such that the control has a little less than $(k - 1)^{-1}$ times as many replicate as each treatment (Dunnett 1955).

RESULTS

Mesocosm Experiment

Larvae of both species had significantly reduced survivorship at higher density (Table 1). The SVL of three month old *A. laterale*

were significantly smaller at high density, whereas *A. tigrinum* were significantly larger at high density.

Larvae of both species had significantly reduced survivorship in the presence of heterospecifics (Table 1). The SVL of three month old *A. laterale* were significantly smaller in the presence of *A. tigrinum*, whereas *A. tigrinum* were significantly larger in the presence of heterospecifics.

The larger *A. tigrinum* larvae were occasionally observed to prey upon *A. laterale* as well as smaller conspecifics. Larvae who were missing were presumed to have been eaten by larger larvae. The recovery of dead bodies suggests that up to 76% of the *A. tigrinum* mortality and 81% of the *A. laterale* mortality was due to predation.

Microhabitat Partitioning and Refuge Use

Larvae of both species spent a majority of time in vegetation during the single individual controls (Table 2), however in mixed-species treatments *A. laterale* spent significantly more time in vegetation than *A. tigrinum* ($P < 0.001$). Both species demonstrated density-dependent effects on microhabitat use. Intraspecific increases in larval density of *A. laterale* resulted in significantly more time spent in vegetation, whereas increased density of *A. tigrinum* significantly reduced the amount of time spent in vegetation (Table 2). Similarly, *A. tigrinum* at high density in the mixed-species treatments spent significantly less time in vegetation at low density (Table 2).

Larval Activity

The addition of an intraspecific or interspecific competitor resulted in significantly decreased activity of larval *A. laterale* (Table 3). Foraging for zooplankton did not significantly alter the mean distance

moved or the percentage of time spent moving. The addition of zooplankton or larval *A. laterale* significantly decreased the mean distance moved by foraging larval *A. tigrinum* (Table 3). They would typically stay still in the water column and take swimming lunges at prey. They ate an *A. laterale* larva on during one trials and bit off a limb or part of the tail during two other trials. The addition of a conspecific competitor significantly increased the percentage of time *A. tigrinum* spent moving.

DISCUSSION

Density-dependent effects include altered growth, survival and behavior of *A. tigrinum* and *A. laterale*. These results are consistent with density-dependent effects commonly demonstrated in other populations of *Ambystoma* larvae (Scott 1990, Van Buskirk and Smith 1991, Wilbur 1972). The larvae of *A. tigrinum* prey upon *A. laterale*, however both species have reduced survival and altered growth rates in the presence of the other. This pattern is similar to that of *A. jeffersonianum* and *A. maculatum* that are competitive equals even though *A. jeffersonianum* is an important intraguild predator (Brodman 1996). The mechanism by which the smaller species elicits mortality in the larger species remains unknown.

We present evidence that *A. laterale* and *A. tigrinum* can facilitate their coexistence by microhabitat partitioning and the use of refuge by *A. laterale*. When raised together the larvae of *A. laterale* and *A. tigrinum* use the habitat differently with the smaller larvae spending most of the time in vegetation. The patterns are similar to that of *A. jeffersonianum* and *A. maculatum* where the use of vegetation as refuge allowed coexistence with an intraguild predator (Brodman 1996) suggesting the possibility that this is a general phenomenon in coexisting pond-breeding salamanders with differing developmental rates and breeding phenology. These data indicate that species richness of pond-breeding salamanders can be enhanced in wetlands that have abundant leaf litter and aquatic vegetation.

Ambystoma laterale reduced activity in the presence of competitors and intraguild predators. Decreased activity reduces interference competition and the risk of predation from a sit-and-wait predator (Skelly and Werner 1990) such as *A. tigrinum*. These behaviors can also reduce foraging (Werner 1991) which can explain the smaller body size of *A. laterale* surviving in the presence of *A. tigrinum*.

We hypothesize that microhabitat partitioning and altered activities are factors that minimize both interspecific competition and intraguild predation. One of the mechanisms of coexistence between larval *A. maculatum* and its intraguild predator *A. jeffersonianum* is microhabitat partitioning due to smaller larvae shifting behavior to refuge use and altered activity rates (Stenhouse 1985, Kutka 1994, Brodman 1996). These experiments showed that use of refuge and activity levels were more important than vertical or temporal shifts. So we hypothesize that the use of vegetation as refuge and reduced activity by *A. laterale* larvae decrease the risk of aggressive interactions and predation from *A. tigrinum* larvae and that *A. tigrinum* alters microhabitat use and foraging strategy in the presence of competitors.

Natural fluctuations in the size of pond-breeding salamander populations can be due to changes in habitat characteristics such as hydroperiod and aquatic vegetation. Managers involved with wetland protection and restoration need to understand the impact of refuge on predator-prey interactions and habitat partitioning of amphibians.

ACKNOWLEDGEMENTS

We thank R. Jaeger, M. Nichols, and J. Nichols for commenting on this manuscript. B. Rasmussen assisted with some of the field work and laboratory observations.

LITERATURE CITED

ANDERSON, J. D. and R. E. GRAHAM. 1967. Vertical migration and stratification of larval *Ambystoma*. *Copeia* 1967:371-374.

BRANCH, L. C. and R. ALTIG. 1981. Nocturnal stratification of three species of *Ambystoma* larvae. *Copeia* 1981:870-873.

BRODMAN, R. 1995. Annual variation in breeding success in two syntopic species of *Ambystoma* salamanders. *Journal of Herpetology* 29:111-113.

BRODMAN, R. 1996. Effects of intraguild interactions on fitness and microhabitat use of larval *Ambystoma* salamanders. *Copeia* 1996:372-378

BRODMAN, R. 2000. Differences among the spatial distribution of sympatric amphibians. Proceedings of the Midwest Declining Amphibian Symposium. H. Kaiser and G. Casper, eds. *Journal of the Iowa Academy of Science* 107:200-202.

CORTWRIGHT, S. A. 1988. Intraguild predation and competition: an analysis of net growth shifts in larval amphibian prey. *Canadian Journal of Zoology* 66:1813-1821.

DUNNETT, C. W. 1955. A multiple comparison procedure for comparing several treatments with a control. *Journal of the American Statistical Association* 75:789-795.

HOLOMUZKI, J. R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. *Ecology* 67:737-748.

HOLOMUZKI, J. R. 1989. Predation risk and macroalga use by the stream dwelling salamander *Ambystoma texanum*. *Copeia* 1989:22-28.

HOLOMUZKI, J. R. and J. P. COLLINS. 1983. Diel movement of larvae of the tiger salamander, *Ambystoma tigrinum nebulosum*. *Journal of Herpetology* 17:276-278.

KEEN, W. H. 1975. Breeding and larval development of three species of *Ambystoma* in central Kentucky (Amphibia: Urodela). *Herpetologica* 31: 18-21.

KUTKA, F. J. 1994. Low pH effects on swimming activity of *Ambystoma* salamander larvae. *Environmental Toxicology and Chemistry* 13:1821-1824.

MCWILLIAMS, S. R. and M. BACHMANN. 1989. Foraging ecology and prey preferences of pond-form larval small-mouthed salamanders, *Ambystoma texanum*. *Copeia* 1989:948-961.

MINTON, S. A. 1972. Amphibians and reptiles of Indiana. *Indiana Academy of Sciences, Indianapolis*.

PECHMANN, J. H. K., D. E. SCOTT, R. D. SEMLITSCH, J. P. CALDWELL, L. J. VITT and J. W. GIBBONS. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253:892-895.

POLIS, G. A., C. A. MEYERS, and R. D. HOLT. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297-330.

SCHOENER, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240-285.

SCOTT, D. E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. *Ecology* 71:296-306.

SHOOP, R. C. 1974. Yearly variation in larval survival of *Ambystoma maculatum*. *Ecology* 55:440-444.

SIH, A., J. W. PETRANKA, and L. B. KATS. 1988. The dynamics of prey refuge use: a model and tests with sunfish and salamander larvae. *American Naturalist* 132:463-483.

SKELLY, D. K. 1994. Activity level and the susceptibility of anuran larvae to predation. *Animal Behavior* 47:465-468.

SKELLY, D. K. and E. E. WERNER. 1990. Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology* 71: 2313-2322.

SMITH, C. K. 1990. Effects of variation in body size on intraspecific competition among larval salamander. *Ecology* 71:1777-1788.

STANGEL, P. W. 1988. Premetamorphic survival of the salamander *Ambystoma maculatum*, in eastern Massachusetts. *Journal of Herpetology* 22: 345-347.

STENHOUSE, S. L. 1985. Interdemic variation in predation on salamander larvae. *Ecology* 66:1706-1717.

STENHOUSE, S. L., N. G. HAIRSTON, and A. E. COBEY. 1983. Predation and competition in *Ambystoma* larvae: field and laboratory experiments. *Journal of Herpetology* 17:210-220.

STRONG, D.R. 1983. Natural variability and the manifold mechanisms of ecology communities. *American Naturalist* 122:636-660.

- TALENTINO, K. A. and E. LANDRE. 1991. Comparative development of two species of sympatric *Ambystoma* salamanders. *Journal of Freshwater Ecology* 6:395–401.
- VAN BUSKIRK, J. and D. C. SMITH. 1991. Density-dependent population regulation in a salamander. *Ecology* 72:1747–1756.
- WALLS, S. C. 1995. Differential vulnerability to predation and refuge use in competing larval salamanders. *Oecologia* 101:86–93.
- WALLS, S. C. 1996. Differences in foraging behaviour explain interspecific growth inhibition in competing salamander. *Animal Behavior* 52:1157–1162.
- WALLS, S. C. and R. G. JAEGER. 1987. Aggression and exploitation as mechanisms of competition in larval salamanders. *Canadian Journal of Zoology* 65:2938–2944.
- WERNER, E. E. 1991. Nonlethal effects of a predator on competitive interactions between two anuran larvae. *Ecology* 72:1709–1720.
- WERNER, E. E. and B. R. ANHOLT. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142:242–272.
- WILBUR, H. M. 1972. Competition, predation, and the structure of the *Ambystoma-Rana sylvatica* community. *Ecology* 53:3–21.
- WILSON, R. E. 1976. An ecological study of *Ambystoma maculatum* and *Ambystoma jeffersonianum*. Unpubl. Ph.D. Thesis, Cornell University, Ithaca, New York, USA.