Copeia, 2002(2), pp. 511–517

Effects of Hatching Time for Larval Ambystomatid Salamanders

MICHELLE D. BOONE, DAVID E. SCOTT, AND PETER H. NIEWIAROWSKI

In aquatic communities, the phenology of breeding may influence species interactions. In the early-breeding marbled salamander, *Ambystoma opacum*, timing of pond filling may determine whether interactions among larvae are competitive or predatory. The objectives of our studies were to determine how time of egg hatching affected size, larval period, and survival to metamorphosis in *A. opacum*, and if early-hatching in *A. opacum* influenced the competitive and predator-prey relationships with smaller larvae of the mole salamander, *Ambystoma talpoideum*. Salamander larvae were reared from hatching through metamorphosis in large, outdoor enclosures located in a natural temporary pond in Aiken County, South Carolina, in two experiments. In study 1, we reared early- and late-hatching *A. opacum* larvae separately from hatching through metamorphosis. In study 2, we examined how early- versus late-hatching *A. opacum* affected a syntopic species, *A. talpoideum*. In general, early-hatching *A. opacum* were larger and older at metamorphosis, had greater survival, and left the pond earlier than late-hatching larvae. *Ambystoma talpoideum* reared in the presence of early-hatching *A. opacum* had lower survival than in controls, suggesting that *A. opacum* may predate upon *A. talpoideum* when they gain a growth advantage over later-hatching larvae. Our studies demonstrate that time of pond filling and phenology of breeding may influence population dynamics and alter the nature of relationships that develop among species.

PRIORITY effects influence the outcome of competition (Alford and Wilbur, 1985; Morin, 1987; Lawler and Morin, 1993) and predation (Sredl and Collins, 1991). Typically, species that arrive early are dominant over those that arrive later (Harper, 1961; Wilbur, 1997). For pond-breeding amphibians, the order of arrival at breeding grounds and the abiotic conditions that affect time of breeding both shape the biotic relationships that develop and may influence population abundance through time.

Female *Ambystoma opacum* (the marbled salamander) lay eggs in dry pond basins in the autumn and rely on inundation of eggs later in the season to stimulate hatching (Petranka et al., 1982). Because elevation of nest sites varies within ponds (Petranka and Petranka, 1981; Jackson et al., 1989), hatching may occur at different times (Worthington, 1968) depending on the timing and extent of pond flooding. Other species that coexist with *A. opacum*, such as *Ambystoma talpoideum* (the mole salamander), breed after pond beds have filled and may be vulnerable to both competitive and predatory pressures from early breeding *A. opacum* larvae (Wilbur, 1984). The objectives of our studies were to determine the effects that early- and late-hatching had on body size, larval period, and survival to metamorphosis of *A. opacum*. Additionally, we studied the effect that larger, early-hatching *A. opacum* larvae had on smaller late-hatching larvae of *A. talpoideum*.

MATERIALS AND METHODS

Our studies were conducted at Ginger's Bay, a 0.8-ha temporary pond (a Carolina bay; Sharitz and Gibbons, 1982), in Aiken County, South Carolina. Pond vegetation consisted primarily of sedge (*Scirpus cyperinus*), knotweed (*Polygonum* spp.), black willow (*Salix nigra*), buttonbush (*Cephalanthus occidentalis*), and sweet gum (*Liquidambar styraciflua*). The pond was surrounded by red maple (*Acer rubrum*), oaks (*Quercus* spp.), and slash pine (*Pinus elliottii*) (Scott, 1990). We used 12 field enclosures located in the pond that were previously constructed to rear recently hatched salamander larvae through metamorphosis. Enclosures were located in three blocks within the pond and varied in size: six 41 m^2, three 31 m^2, and three 27 m^2 (for details, see Scott, 1990). Each enclosure encompassed deeper pools and pond edges to include a range of pond microhabitats used by larvae. Additional food resources were not provided because the large size of the field enclosures assured inclusion of indigenous prey populations (Taylor et al., 1988; Scott, 1990).

Study 1. Effects of early- and late-hatching of Ambystoma opacum.—We considered the effects that early- versus late-hatching had on *A. opacum* body size, age, date, and survival to metamorphosis. In 1989, the pond held water from early January to late June; the water level became low (2–3 cm deep) in 50% of the enclosures (in one of three blocks) in February. From 4–27 October 1988, 120 male and 120 female *A. opacum* were collected at Ginger's Bay during breeding migrations. Salamanders were placed in cattle tanks containing soil, sod, sedge, and leaf litter, and tanks were situated adjacent to the pond. Females bred and laid eggs in these tanks, and we collected eggs from the same nests across a six-week time period. Once collected, the eggs were stimulated to hatch at two different times by submerging them in water in shallow wading pools. Early and late groups were flooded on 7 January and 19 February 1989, respectively, with a total of 46 days separating the hatching groups. Larvae were placed in enclosures in the pond at realistic densities (Scott, 1990; Petranka and Petranka, 1980) one week after submergence. Two experimental treatments were replicated four times in a randomized block design: early-hatching (4 larvae/m^2) or late-hatching (4 larvae/m^2). Individuals were collected at metamorphosis using minnow traps suspended at the water's surface. Mass, age, date, and survival to metamorphosis were determined.

Study 2. Effects of early- and late-hatching of Ambystoma opacum on Ambystoma talpoideum.—Our objective was to examine whether *A. talpoideum* body size, age, date, and survival to metamorphosis were differentially affected by early- versus late-hatching larvae of *A. opacum.* The pond held water from mid-October 1994 through the summer of 1995. Adult *A. talpoideum* and *A. opacum* are often syntopic and were captured during breeding migrations at a 1.0 ha Carolina bay (Okie Bay) approximately 400 m south of Ginger's Bay. From 2–23 October 1994, 400 male and 337 female *A. opacum* were captured and maintained as described above. Hatching was induced at two different times. Early and late groups were created by flooding on 25 November 1994 and 17 February 1995 with a total of 84 days separating the hatching groups. The larvae of *A. opacum* were added to the enclosures in the pond seven days after inundation of the eggs.

From 1–30 November 1994, 125 male and 144 female *A. talpoideum* were captured and placed separately by sex in aquatic cattle tanks containing leaf litter and 900 liters of well water. Males and females were commingled on 27 December 1994. Eggs were first seen on 3 January and hatched from 13 February to 10 March 1995. Recently hatched *A. talpoideum* were placed in all enclosures from 21 February to 10 March 1995.

Larval *A. talpoideum* were assigned to one of three treatments in a randomized block design with four replicates: (1) a control with no *A. opacum* (total density: 6 *A. talpoideum* larvae/m^2); (2) an equal number of early-hatching *A. opacum* larvae (6 larvae/m^2 of each species; total density: 12 larvae/m^2); or (3) an equal number of late-hatching *A. opacum* larvae (6 larvae/m^2 of each species; total density: 12 larvae/m^2). Densities of both species reflect realistic environmental levels (Scott, 1990; Petranka and Petranka, 1980) and phenology of breeding. Individuals were collected at metamorphosis with minnow traps. Mass, age, date, and survival to metamorphosis were determined.

Our design was constrained by the number of field enclosures available. Because a full reciprocal density design was not possible, we chose a design that was biologically meaningful. Treatments represent different community types: a community with both *A. talpoideum* and *A. opacum* at different hatching times and a community with only *A. talpoideum.* The number of *A. talpoideum* introduced in all enclosures was constant and independent of the presence of *A. opacum.* However, direct comparisons among *A. talpoideum* in controls or mixed-species treatments must be made in light of density effects, because the differences in density used in our study affect size, age, and survival to metamorphosis for both species (Semlitsch, 1987; Scott, 1990; Semlitsch and Walls, 1993). Although the design limits the conclusions we can draw concerning intraspecific effects in *A. talpoideum,* it allows us to examine the interspecific effects of *A. opacum* on *A. talpoideum.*

Statistical methods.—Mass, age, date, and survival to metamorphosis were tested by species for differences among hatching treatments using analyses of variance (ANOVA; SAS/STAT User's Guide, rele. 6.03 ed., SAS Institute, Cary, NC, 1988, unpubl.). Mass, age, and date at metamorphosis were log-transformed, and survival was angularly transformed to normalize the data and stabilize variances (Snedecor and Cochran, 1980). Enclosure block was not included as a source of variation because it was not significant in preliminary analyses. In study 2, analyses were done separately by species and survival was used as a covariate because significant differences in survival can influence mass, date, and age at metamorphosis. Significant pairwise differences among treatments were determined using Scheffe's multiple comparison tests for significant treatment effects. A regression analysis was used to determine the relationship between *A. opacum* and *A. talpoideum* survival.

TABLE 1. SUMMARY OF THE ANOVA RESULTS (STUDY 1) FROM THE EFFECTS OF HATCHING TIME ON *A. opacum* MASS, DATE, AGE, AND SURVIVAL TO METAMORPHOSIS.

Response	Source of variation	Degrees of freedom	Mean square	*F*	*P*
Early- versus late-hatching					
Mass at metamorphosis	Hatching treatment	1	0.0581	7.39	0.0300
	Error	6	0.0079		
Date at metamorphosis	Hatching treatment	1	0.0086	9.00	0.0200
	Error	6	0.0010		
Age at metamorphosis	Hatching treatment	1	0.3020	307.92	0.0001
	Error	6	0.0010		
Survival to metamorphosis	Hatching treatment	1	0.0000	0.00	0.9597
	Error	6	0.0141		

RESULTS

Effects of early- and late-hatching of Ambystoma opacum.—In study 1, early-hatching larvae were significantly larger (2.75 ± 0.09 and 2.32 ± 0.12 g for early and late, respectively; mean ± 1 SE) and older (118.1 ± 2.6 and 80.0 ± 0.4 days for early and late, respectively; mean ± 1 SE) at metamorphosis (Table 1). Early-hatching *A. opacum* metamorphosed an average of eight days before those hatching later (118.1 ± 2.6 and 126.0 ± 0.4 for early and late; Table 1). Early- or late-hatching, however, had no effect on survival to metamorphosis (69.9% ± 5.4 and 69.6% ± 5.2 for early and late; mean ± 1 SE) despite a 46-day difference in hatching time. In study 2, early-hatching *A. opacum* larvae metamorphosed at a significantly earlier date (Fig. 1A) and older age (Fig. 1B) with a greater probability of surviving to metamorphosis (Fig. 1C) than late-hatching larvae (Table 2). Early-hatching *A. opacum* also showed a trend of greater mass at metamorphosis than late-hatching larvae (Fig. 1D).

Effects of early- and late-hatching of Ambystoma opacum on Ambystoma talpoideum.—The survival of *A. talpoideum* was significantly affected by the timing of *A. opacum* hatching (Fig. 2). *Ambystoma talpoideum* larvae reared with early-hatching *A. opacum* had lower survival than those reared with late-hatching or no *A. opacum.* Although *A. talpoideum* survival in the early-hatching *A. opacum* treatment was significantly lower than in ponds where *A. talpoideum* were reared alone, survival of *A. talpoideum* in the early-hatching *A. opacum* treatment was not significantly different from the late treatment; however, the coefficient of variation for *A. talpoideum* survival in the early treatment was large (Fig. 2). Additionally, a regression analysis indicated that survival of *A. opacum* was negatively correlated with *A. talpoideum* survival ($F_{1,11} = 6.58$, $r^2 = 0.38$, $P = 0.03$). Exposure to early- versus late-hatching larvae of *A. opacum*, did not have a significant effect on *A. talpoideum* in terms of mass, date, or age at metamorphosis (Table 2).

DISCUSSION

Our studies suggest that time of hatching can influence size at metamorphosis, length of the larval period, and survival to metamorphosis–parameters that can shape population and community processes over time–and that there are a number of advantages to a life-history strategy that favors early breeding in recently filled or filling ponds. Fall and winter rains that fill temporary breeding areas can significantly influence the abundance of early breeders like *A. opacum* that rely on egg submergence to stimulate hatching. In addition to other abiotic factors known to alter population dynamics (e.g., hydroperiod; Semlitsch et al., 1996), time of pond filling can also influence species interactions.

The timing of *A. opacum* hatching was predicted to have several consequences. Early-hatching larvae may gain a growth advantage over late-hatching larvae and prey upon them, while simultaneously reducing their vulnerability to predaceous insect larvae due to larger body size. Predator-prey relationships are known to develop within (Stewart, 1956; Collins and Cheek, 1983; Nyman et al., 1993) and among ambystomatid species (Stewart, 1956; Stenhouse et al., 1983). Therefore, *A. opacum* larvae may also prey upon smaller amphibian larvae when they achieve a growth advantage, and act as competitors with larvae when they do not (Wilbur 1984).

Effects of early- versus late-hatching in Ambystoma opacum.—Both of our studies indicated that there were realized benefits for *A. opacum* that hatch early. Early-hatching larvae of *A. opacum* were larger at metamorphosis than larvae that hatched later. Because overwinter survival and lifetime reproduction are positively correlated with size at metamorphosis (Semlitsch and Wilbur, 1988; Scott, 1994; Scott and Fore, 1995), the benefit of hatching early and attaining a larger metamorph size may have long-lasting effects by increasing population size through time. Larger metamorph size of early-hatching larvae compared to late-hatching was presumably achieved by extending the larval period (Wilbur and Collins 1973), because the variation in the date at metamorphosis between hatching groups was small relative to initial hatching time. Although early-hatching larvae were 38 or 63 days older at metamorphosis on average than late-hatching larvae, they left the pond only eight or 17 days earlier than *A. opacum* larvae that hatched 46 or 84 days later (in studies 1 and 2, respectively). This relatively contracted period of metamorphosis also results when larval density, not hatching time, is manipulated (Scott, 1994). Given the link between body size at metamorphosis, and adult size and survival, it is surprising that larval *A. opacum* do not extend their larval period, at least in wet years such as 1994. This provides further evidence that there appears to be strong selection in this geographic region for *A. opacum* to metamorphose prior to summer months (Scott, 1994).

In study 2, early-hatching *A. opacum* enjoyed greater survival than later-hatching larvae, presumably because of reduced competition for food resources and reduced vulnerability to aquatic insect predators (Petranka and Petranka, 1980). Late-hatching larvae hatch into ponds that typically contain other larvae; therefore they experience a greater larval density throughout much of their larval period. The lower density experienced by larvae that hatch early during pond filling may be partially responsible for the increased probability of survival.

There was no difference in survival to metamorphosis between early- and late-hatching larvae with only 46 days separating hatching groups (in study 1), however. Because the pond filled in early January 1989 and all larvae were added to the pond within two months after filling, all larvae may have been "early-hatching" and reaped the benefits. In study 2, the pond filled in October 1994 and early-hatching larvae were added approximately one month after pond-filling with late-hatching larvae added three months later. Time of hatching in rela-

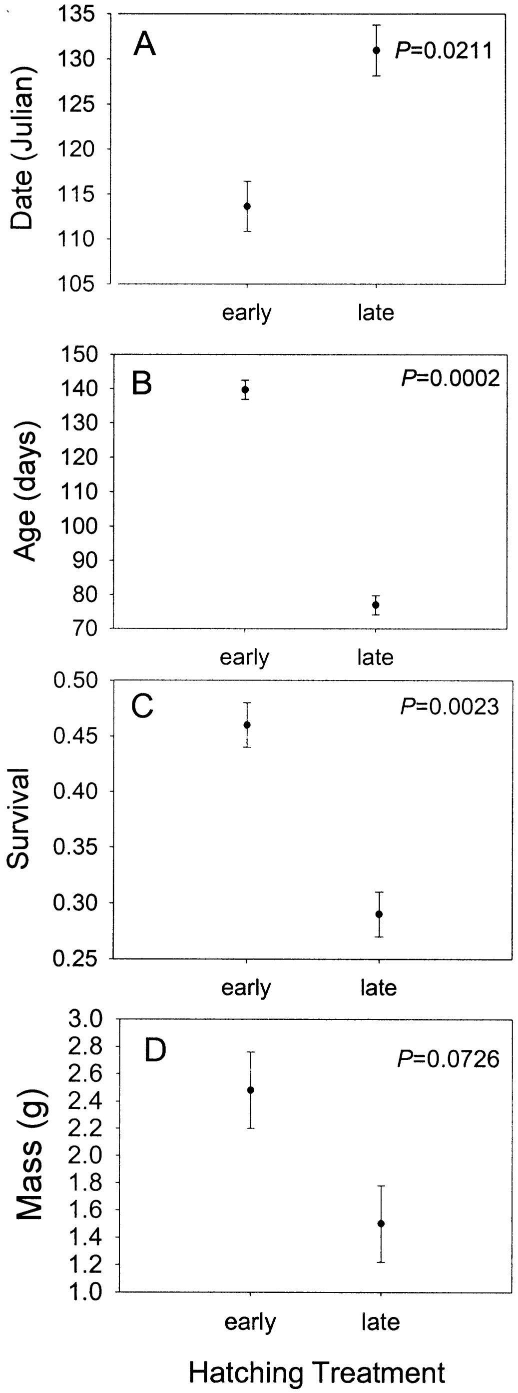

Fig. 1. Mean mass, date, age, and survival to metamorphosis for early- and late-hatching *Ambystoma opacum* (study 2). Plotted values are least-square means. Error bars represent standard errors.

TABLE 2. SUMMARY OF THE ANCOVA RESULTS FOR *A. opacum* AND *A. talpoideum* (STUDY 2) FROM THE EFFECTS OF HATCHING TIME OF *A. opacum* ON MASS, DATE, AGE, AND SURVIVAL TO METAMORPHOSIS.

Response	Source of variation	Degrees of freedom	Mean square	*F*	*P*
Ambystoma opacum					
Mass at metamorphosis	Survival (covariate)	1	0.0072	0.33	0.5893
	Hatching treatment	1	0.1110	5.14	0.0726
	Error	5	0.0216		
Date at metamorphosis	Survival (covariate)	1	0.0003	0.44	0.5348
	Hatching treatment	1	0.0070	10.99	0.0211
	Error	5	0.0006		
Age at metamorphosis	Survival (covariate)	1	0.0000	0.00	0.9792
	Hatching treatment	1	0.1237	94.61	0.0002
	Error	5	0.0013		
Survival to metamorphosis	Hatching treatment	1	0.0648	25.70	0.0023
	Error	6	0.0025		
Ambystoma talpoideum					
Mass at metamorphosis	Survival (covariate)	1	0.2223	2.84	0.1302
	Hatching treatment	2	0.0540	0.69	0.5286
	Error	8	0.0781		
Date at metamorphosis	Survival (covariate)	1	0.0001	0.04	0.8469
	Hatching treatment	2	0.0120	3.55	0.0789
	Error	8	0.0034		
Age at metamorphosis	Survival (covariate)	1	0.0003	0.04	0.8447
	Hatching treatment	2	0.0248	3.50	0.0808
	Error	8	0.0071		
Survival to metamorphosis	Hatching treatment	2	0.0989	4.33	0.0481
	Error	9	0.0228		

tionship to the time the pond fills, therefore, may also be an important factor affecting larval survival and juvenile abundance in *A. opacum.*

Of course, there are likely trade-offs in hatching early versus late. Early-hatching may be favorable in years with high rainfall but unfavorable in years with sporadic rainfall. If hatching is stimulated early in the season and if the pond dries shortly after filling, then early-hatching could be detrimental (Petranka and Petranka, 1981). Late-hatching larvae may face a greater number of predators, but the pond is less likely to dry after larvae hatch. Although there may be benefits to early-hatching in some years, there may be great costs in others.

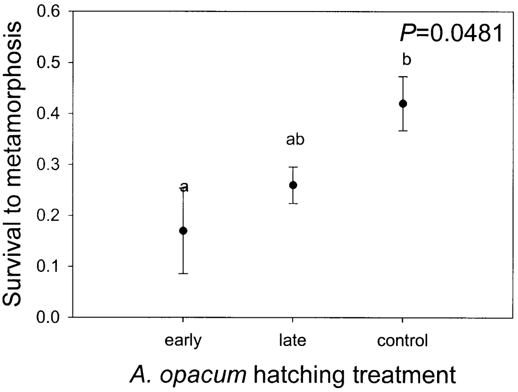

Fig. 2. Survival to metamorphosis for *Ambystoma talpoideum* across *Ambystoma opacum* hatching treatments (study 2). Error bars represent standard errors.

Effects of early-hatching Ambystoma opacum on late-hatching Ambystoma talpoideum.—Both laboratory and mesocosm studies (e.g., artificial ponds) suggest that predation structures larval amphibian communities (Morin, 1981; Wilbur, 1987; Cortwright, 1988). For instance, predation by newts reduces the number of tadpoles of species that normally out-compete and dominate other species in larval anuran communities when newts are absent (Morin, 1981). Predation can also ameliorate competitive effects at high density by removing individuals from the environment, thereby reducing competitive interactions among the survivors (Wilbur, 1987). Increased environmental complexity, however, may reduce the impact that predators have on the community (Stenhouse et al., 1983). Laboratory or mesocosm studies may overemphasize the importance of predation for natural systems; therefore experiments in natural ponds can help resolve the impact of predators in nature.

When early-hatching larvae gain a growth advantage over larvae that hatch later, a predator-prey relationship could develop. Early-hatching *A. opacum* gained a growth advantage over late-hatching *A. talpoideum* and appeared to have reduced their survival. Survival of *A. talpoideum* in controls was significantly greater than survival in early-hatching *A. opacum* treatments. However, density in *A. talpoideum* controls was half that of mixed-species treatments; hence, high survival in controls may be a result of reduced density rather than lack of predation by *A. opacum* larvae. Studies on density in the same pond and enclosures (Scott, 1990) indicated that higher densities resulted in food limitation, delayed metamorphosis, and reduced growth and survival. Although the difference in density (double) between single and mixed-species treatments was not as extreme as Scott (1990), it is possible that the responses we observed were because of density effects rather than predation.

Two lines of evidence, however, support predation by *A. opacum* as the underlying cause of reduced *A. talpoideum* survival in the early-hatching treatment. First, the initial density differences in enclosures containing or not containing *A. opacum* were reduced as *A. opacum* larvae metamorphosed. *Ambystoma talpoideum* in mixed-species treatments were at a density roughly equal to controls during 40–50% of their larval period, for an average of 55 and 72 days in early- and late-hatching treatments, respectively.

Second, neither body size nor larval period of *A. talpoideum* was affected by early-hatching *A. opacum*, but *A. talpoideum* survival was significantly reduced. This response pattern is consistent with predation on *A. talpoideum* larvae early in the larval period by *A. opacum* larvae, because invertebrate predators are not abundant at that time. Regardless of whether observed effects stemmed from competition or predation, factors in the early larval development of *A. talpoideum* (i.e., the presence of *A. opacum* as competitors or as predators) had lasting effects on larval survival.

Overall, *A. talpoideum* survival was reduced in all enclosures where they were reared with *A. opacum*. The relationship between *A. talpoideum* and *A. opacum* was significant with the highest *A. talpoideum* mortality occurring in early *A. opacum* treatments. One replicate, however, had extremely high *A. talpoideum* survival. A number of reasons were considered to explain this anomaly including differences in survival of early-hatching *A. opacum*, the type of pond vegetation, and differences in alternative prey choices (e.g., tadpoles of *Rana* spp.); however, we detected no difference among enclosures. In general, however, the trend of low *A. talpoideum* survival in treatments with early-hatching *A. opacum* suggests that a predator-prey relationship may have developed and warrants further investigation. Our experiments indicate that against the backdrop of pond filling and pond hydroperiod, time of hatching in one species can alter the population dynamics within the season and may impact the community structure for seasons that follow.

Acknowledgments

This manuscript benefited from the thoughtful comments of C. Bridges, J. Krenz, T. Ryan, and R. Semlitsch. We appreciate A. Chazal and W. Hicks for field assistance. This research was supported by Financial Assistance Award DE-FC09–96SR18546 from the U.S. Department of Energy to the University of Georgia Research Foundation.

Literature Cited

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

Collins, J. P., and J. E. Cheek. 1983. Effect of food and density in development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. Am. Zool. 23:77–84.

Cortwright, S. A. 1988. Intraguild predation and competition: an analysis of net growth shifts in larval amphibian prey. Can. J. Zool. 66:1813–1821.

Harper, J. L. 1961. Approaches to the study of plant competition. Symp. Soc. Exp. Biol. 15:1–39.

Jackson, M. E., D. E. Scott, and R. A. Estes. 1989. Determinants of nest success in the marbled salamander (*Ambystoma opacum*). Can. J. Zool. 67:2277–2281.

Lawler, S. P., and P. J. Morin. 1993. Temporal overlap, competition, and priority effects in larval anurans. Ecology 74:174–182.

Morin, P. J. 1981. Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. Science 212:1284–1286.

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

Nyman, S., R. F. Wilkinson, and J. E. Hutcherson. 1993. Cannibalism and size relations in a cohort of larval ringed salamanders (*Ambystoma annulatum*). J. Herpetol. 27:78–84.

Petranka, J. W., and J. G. Petranka. 1980. Selected aspects of the larval ecology of the marbled salamander *Ambystoma opacum* in the Southern portion of its range. Am. Midl. Nat. 104:352–363.

———, AND ———. 1981. On the evolution of nest site selection in the marbled salamander, *Ambystoma opacum.* Copeia 1981:387–391.

———, J. J. JUST, AND E. C. CRAWFORD. 1982. Hatching of amphibian embryos: the physiological trigger. Science 217:257–259.

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

———. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum. Ibid.* 75: 1383–1396.

———, AND M. R. FORE. 1995. The effect of food limitation on lipid levels, growth, and reproduction in the marbled salamander, *Ambystoma opacum.* Herpetologica 51:462–471.

SEMLITSCH, R. D. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum.* Copeia 1987:61–69.

———, AND S. C. WALLS. 1993. Competition in two species of larval salamanders: a test of geographic variation in competitive ability. *Ibid.* 1993:587–595.

———, AND H. M. WILBUR. 1988. Effects of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum. Ibid.* 1988:978–983.

———, D. E. SCOTT, J. H. K. PECHMANN, AND J. W. GIBBONS. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond, p. 217–248. *In*: Long-term studies of vertebrate communities. M. L. Cody and J. A. Smallwood (eds.). Academic Press, San Diego, CA.

SHARITZ, R. R., AND J. W. GIBBONS. 1982. The ecology of southeastern shrub bogs (pocosins) and Carolina bays: a community profile. U.S. Fish and Wildlife Service, Division of Biological Services, Washington, DC.

SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods. Iowa State Univ., Press, Ames.

SREDL, M. J., AND J. P. COLLINS. 1991. The effect of ontogeny on interspecific interactions in larval amphibians. Ecology 72:2232–2239.

STENHOUSE, S. L., N. G. HAIRSTON, AND A. E. COBEY. 1983. Predation and competition in *Ambystoma* larvae: field and laboratory experiments. J. Herpetol. 17:210–220.

STEWART, M. M. 1956. The separate effects of food and temperature differences on development of marbled salamander larvae. J. Elisha Mitchell Sci. Soc. 72:47–56.

TAYLOR, B. E., R. A. ESTES, J. H. K. PECHMANN, AND R. D. SEMLITSCH. 1988. Trophic relations in a temporary pond: larval salamanders and their microinvertebrate prey. Can. J. Zool. 66:2191–2198.

WILBUR, H. M., AND J. P. COLLINS. 1973. Ecological aspects of amphibian metamorphosis. Science 182: 1305–1314.

———. 1984. Complex life cycles and community organization in amphibians. p. 195–224. *In:* A new ecology: novel approaches to interactive systems. P. W. Price, C. N. Slobodchikoff, and W. S. Gaud (eds.). John Wiley and Sons, New York.

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

———. 1997. Experimental ecology of food webs: complex systems in temporary ponds. *Ibid.* 78: 2279–2302.

WORTHINGTON, R. D. 1968. Observations on the relative sizes of three species of salamander larvae in a Maryland pond. Herpetologica 24:242–246.

(MDB) 4200 NEW HAVEN ROAD, USGS COLUMBIA ENVIRONMENTAL RESEARCH CENTER, COLUMBIA, MISSOURI 65201; (DES) SAVANNAH RIVER ECOLOGY LABORATORY, DRAWER E, AIKEN, SOUTH CAROLINA 29802; AND (PHN) DEPARTMENT OF BIOLOGY, UNIVERSITY OF AKRON, AKRON, OHIO 44325-3908. E-mail: (MDB) michelle_boone@usgs.gov; (DES) scott@srel.edu; and (PHN) phn@uakron.edu. Send reprint requests to MDB. Submitted: 16 May 2000. Accepted: 8 Dec. 2001. Section editor: W. L. Montgomery.