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Population Trends of Three Congeners of Mole Salamanders (*Ambystoma*) at an Isolated Pond in Northeast Ohio

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Abstract: Long-term trends and Jolly-Seber estimates were used to study populations of the Spotted Salamander (*Ambystoma maculatum*), Marbled Salamander (*Ambystoma opacum*), and the Jefferson Salamander complex (*Ambystoma jeffersonianum*) at an isolated breeding pond in northeastern Ohio from 1993–2002. Population size of *A. jeffersonianum* complex declined significantly whereas that of *A. maculatum* declined but the decrease was not significant. The population of *A. opacum* fluctuated and exhibited no trend. Average annual adult survivorship was 73% for *A. maculatum* and 56% for both the *A. jeffersonianum* complex and *A. opacum*. Only 16 *A. maculatum* metamorphs were found during the nine year study compared to 56 *A. jeffersonianum* complex and 867 *A. opacum*. Declines were attributed to predation by *A. opacum* larvae and to insufficient hydroperiod. Toxic levels of copper may have contributed directly or indirectly to larval mortality.

Key Words: *Ambystoma*, drift-fence, amphibian decline, population estimation.

Introduction

Herpetologists have expressed concern over declines in many amphibian populations in the United States and elsewhere since the early 1980s (Mossman and Hine 1984; Blaustein and Wake 1990; Barinaga 1990; Stuart et al. 2004). Houlahan et al. (2000) reported that an analysis of nearly 250 data sets of North American amphibian populations showed that population sizes have declined at a rate of two percent annually since 1966. Call monitoring efforts (Mossman and Hine 1984; Moriarty 1996; Johnson 1998), population dynamics studies (Berven 1995; Pellet et al. 2006; Petranka et al. 2007) and temporal survey comparisons of anurans and caudates (Skelly et al. 1999) have provided valuable information regarding the distribution, abundance, and trends of many anuran species. Some long-term studies of salamanders monitored egg mass counts (Brodman 2002), larvae (Petranka et al. 2007) or drift-fence captured juveniles and adults (Gibbons and Semlitsch 1981; Pechmann et al. 1989). However, the local status of most salamander species remains largely unknown and few studies have applied mark/recapture population estimate models. Differentiating between fluctuations and declines of local amphibian populations is difficult and usually requires long-term study.

The number of reports and published papers concerning the effects of metals upon amphibians continues to grow (Freda 1991; Horne and Dunson 1994; Horne and Dunson 1995a, 1995b; Diana and Beasley 1998; Blaustein et al. 2003; Wind 2003). Metal toxicity to most species of amphibians and the toxicity relative to their various ontogenetic life stages have not been determined (Clark and LaZerte, 1987).

The purpose of our study was to investigate persistence stability of an *Ambystoma* community by examining trends and temporal changes in population sizes of the Spotted Salamander (*Ambystoma maculatum* Shaw), Marbled Salamander (*Ambystoma opacum* Gravenhorst), and the Jefferson Salamander complex, *Ambystoma jeffersonianum* (Green) at an isolated pond in a rural metropark. We also examined pH, hydroperiod, and metals as stressors potentially contributing to observed changes in population status. *A. maculatum* and *A. jeffersonianum* are common and widely distributed in Ohio whereas *A. opacum* is common and widespread in southern Ohio but rare and restricted to disjunct populations in the northeast portion of the state where the study took place (Seibert 1989; Pfingsten and Matson 2003). Naturally occurring communities including all three congeners and three ploidy levels of the *A. jeffersonianum* complex are rare in northeastern Ohio.

Methods

The study area was located in the Grand River drainage system of northeastern Ohio. It was within the 108 ha Indian Point Park, part of the Lake Metroparks system, and included an isolated seasonal pond positioned on a 9.2 ha floodplain terrace. The terrace supported a mature, species-rich, mixed floodplain forest community of nearly 20 arboreal species. Dominant tree species included: Tuliptree (*Liriodendron tulipfera* L.), American Elm (*Ulmus americana* L.), Sycamore (*Platanus occidentalis* L.) and Northern Red Oak (*Quercus rubra* L.). The most common understory shrub was Spicebush (*Lindera benzoin* L.). A variety of other spring ephemerals, including Virginia Bluebells (*Mertensia virginiana* L.), carpeted the forest floor around the pond (Bissell 1989). Surface area of the linear pond was 200 m^2; maximum depth was 59 cm (Quinn 2004). The canopy was nearly closed, and the pond did not support aquatic macrophytes, but algae, purple sulfur bacteria, fallen trees, siltstone slabs and accumulated leaf fall were present. Hydroperiod of the pond varied considerably from year to year; it never held water continuously through a calendar year. Although the pond was adjacent to Paine Creek, it did not receive floodwaters nor was it inhabited by ichthyofauna during our study.

The pond breeding amphibian community included: *A. maculatum*, *A. opacum*, and the *A. jeffersonianum* complex. *A. maculatum* bred in distant ponds within the park but barriers (wide streams, steep cliffs, etc) prevented exchange of individuals with those in the study pond population in all cases but one (Matson 1990a). Several *A. jeffersonianum* complex individuals were located within 1 km of the breeding pond, but they were on the opposite side of Paine Creek which we considered an effective isolating barrier. Additional occurrences of *A. opacum* within the Grand River drainage are known, but none occur within the park or within several kilometers of park boundries. Small breeding aggregations of Spring Peepers (*Pseudacris crucifer* Wied-Neuwied) were occasionally present in the spring but tadpoles were never located. Several other anurans, including Green Frogs (*Lithobates clamitans* (Latreille)) and American Toads (*Anaxyrus americanus* (Holrook)) were captured in the traps but never called while in the pond and no eggs or tadpoles were noted. Gray Treefrogs (*Hyla versicolor* LeConte) called from trees on the terrace but no evidence of breeding success was evident in the pond.

Ambystoma were captured entering and exiting the breeding pond using a drift fence and pitfall array similar to that described by Gibbons and Semlitsch (1981). This method is one of the most effective for conducting long-term population studies of pond breeding terrestrial species (Dodd and Scott 1994). Brown aluminum flashing 61 cm high was installed at a depth of ~13 cm along the rim of the pond depression. Twenty-two pitfall traps (18.9 L plastic buckets) spaced approximately 4.6 m distant were permanently positioned on each side of the fence (44 traps total).

Adult salamanders were marked by toe-clipping. Toe clipping is the most practical method for marking pond breeding salamanders and has no effect on growth or survival (Ott and Scott 1999). In 1993 a cohort mark was used; thereafter individuals were uniquely marked using a system similar to those of Martof (1953) and Twitty (1966). Four of the five toes on each rear foot were used in numbering; the fourth toe from the median was considered to have great importance in locomotion and was not clipped (Scott pers. communication). Levels of ploidy of individuals within the *A. jeffersonianum* complex included diploids, triploids, and tetraploids based upon erythrocyte size as described by Uzzell (1964) and methodology by Matson (1990b).

A rain gauge was used at the site to collect precipitation data on each visit. Pond water depth was also measured during each visit. pH was measured in the field during the a.m. over all seasons. An aliquot of pond water was collected for toxic metal study once at the end of the project; it was collected 10 cm below the surface in a plastic bottle containing nitric acid as preservative in April 2003. Cations tested included aluminum, copper, and total hardness. Chemical testing was conducted by BioSolutions Inc., an independent chemical laboratory.

Pond hydroperiod was calculated from the date at which standing water could be measured in the depression to the date at which no standing water remained in the pond, and it remained dry for an extended period. Spearman's Rank Correlation Coefficient was used to test for significance of the trend in annual pond hydroperiods and in pH samples from 1993–2000.

Annual adult population estimates were calculated using the Jolly-Seber model (Sutherland 1996) which was designed for the analysis of capture-recapture data obtained from open populations and which allows for variable survival rates. The model provides a relatively unbiased estimate of populations (Boulanger and Krebs 1994; Weinstein et al. 1995; Urban et al. 1999). Assumptions of the Jolly-Seber model are: (1) all individuals have equal probabilities of capture in a given year, (2) all marked individuals have the same probability of survival, (3) marks are not overlooked or lost and (4) sampling time is negligible compared to time between sampling periods (Krebs 1998). The most critical of these is the assumption of equal capture probabilities. We examined this assumption using Leslie's Test of Equal Catchability (Krebs 1998). Confidence intervals for population estimates were calculated using the method developed by Manly (1984) because the Jolly-Seber method has been shown to generate artificially small confidence interval estimates. Permutation tests using Spearman's Rank Correlation Coefficient were used to test for significance of population trends.

The method used to calculate annual adult survivorship was similar to that described by Husting (1965). The total number of all adults known to be alive in both year i and year i + 1 was divided by the total number of adults known to be alive in year i. Since it was important to know the capture history of individuals before and after year i and i + 1 respectively, estimates were only made for the years 1995-2000.

Results

During the months of February through May, the pond held standing water every day of each month throughout the 10 years of the study. The longest hydroperiod occurred in 1996 when the pond contained some standing water each month of the year. The shortest occurred in 2002 when the pond dried in early July and did not re-fill that year. During seven of the years, pond hydroperiod ended before August first. In the remaining two years, it extended into mid-August one year and to early September the other. Hydroperiod length declined significantly ($p = 0.02$) over the course of the study. Mean pH of the pond water was 7.0 ($n = 35$; range 6.4–7.9) and declined significantly ($p = 0.001$), but the decline was slight and not considered ecologically significant. Laboratory and in-situ studies have shown that breeding ponds with a pH above 5.5 do not negatively impact pre-metamorphic salamanders either through delayed growth or development or increased mortality (Pough 1976; Sadinski and Dunson 1992; Rowe and Dunson 1993; Petranka 1998).

Total concentrations (µg/L) of cations present in the April 2003 aliquot of pond water were as follows: Al (< 100), Cu (20), and total hardness (300,000). Aluminum concentrations were low and below our level of detection and similar to those found in ponds supporting amphibian populations in central Pennsylvania (Horne and Dunson 1995a) an in Virginia (Blem and Blem 1989, 1991). Copper on the other hand, although low in concentration, was higher than those reported in central Pennsylvaia where *A. jeffersonianum* suffered high mortality (Horne and Dunson 1995a, 1995b). The level was similar to those reported in Virginia contributing to high embryonic mortality in *A. maculatum* (Blem and Blem 1991). Seasonal ponds in eastern states characteristically have low total hardness (Horne and Dunson 1994). Total hardness in our pond was several orders of magnitude greater (hard water, USGS water hardness scale).

The null hypothesis of equal catchability was accepted for *A. opacum* and the *A. jeffersonianum* complex but not for *A. maculatum*. In long-term mark-recapture studies of species with long life spans, low recruitment, and little to no immigration, it is expected that a high percentage of individuals in the population will eventually be marked. Dispersal of juvenile and/or adult *A. maculatum* from the nearest pond ~350 m distant probably explains unequal catchability. Dispersal distances of 249 m for *A. maculatum* were reported by Kleeberger and Werner (1983), and Petranka et al. (2007) placed the average dispersal distance of eastern amphibians as < 1–2 km. Immigration was probable because only 16 metamorphs were recruited from the study pond while unmarked adults were captured each year, including the final years of the project. Immigration would result in an overestimation of population size.

The number of breeding *A. maculatum* captured annually declined 58% from a high of 182 in 1995 to 77 in 2001 and then rose slightly to 93 in 2002 (Figure 1). Sex ratios of breeding adults favored males approximately 2:1 in the early years of the study but shifted to 1:1 by 2002. Recruitment was limited, 16 larvae transformed from 1994–2002, a mean of 1.8 metamorphs annually (Table 1).

The breeding population of *A. jeffersonianum* complex decreased 88%, from 154 in 1994 to 19 in 2002 (Figure 1). The ratio of diploid individuals to polyploidy unisexuals and those of unknown ploidy captured each year was approximately 1:1 through 1999. In the last three years of study, the number of unisexuals and unknowns exceeded that of diploids nearly 2:1. The overall sex ratio of breeding adults was highly skewed toward females, attributable to the high numbers of polyploid unisexuals. In 1994 the ratio of males to females was 1:6.6; it declined to 1:11 by 2001. Only two males were captured in 2001 and one in 2002. From 1994–2002 56 metamorphs were found, a mean of 6.2 annually (Table 1); however, only one metamorph was recruited after 1998.

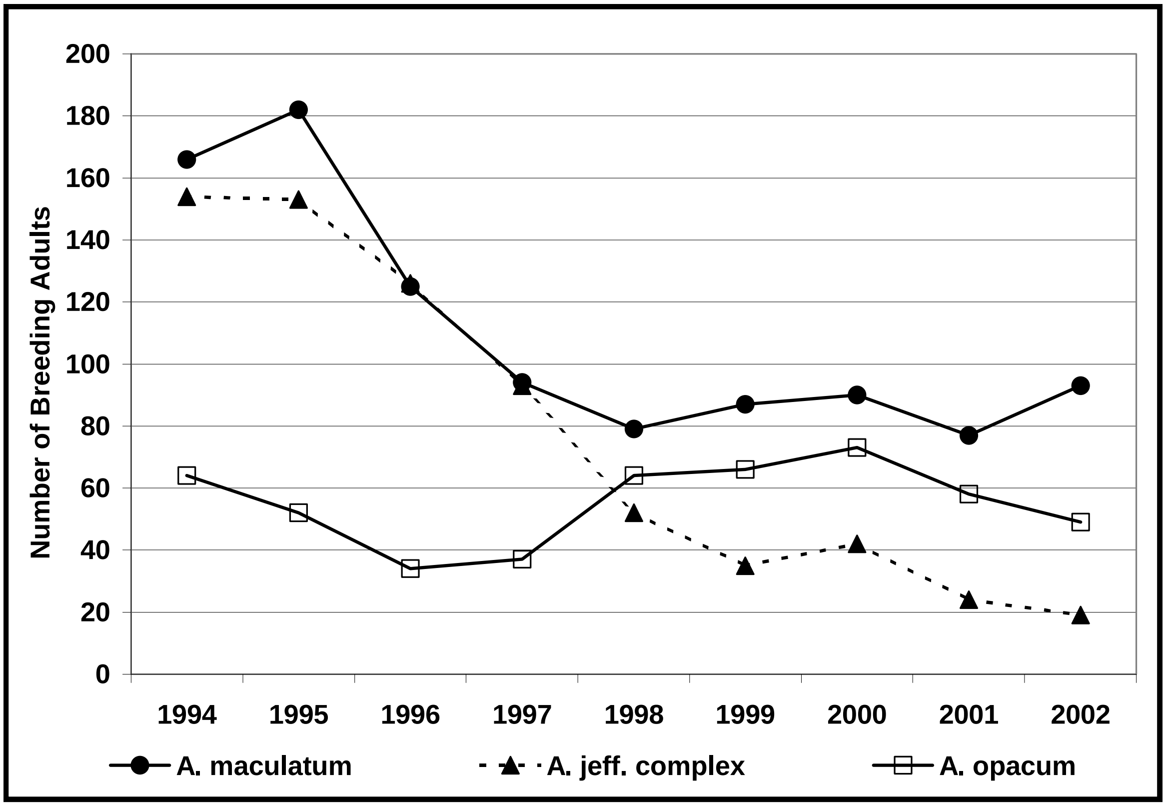

Figure 1. Number of adult salamanders of each taxon captured at the drift-fence moving toward the breeding pond from 1994–2002.

No trend was apparent in the annual breeding counts of *A. opacum* (Figure 1). Ratios of males to females varied from 1:1 to nearly 3:1, although in two years, females outnumbered males approximately 2:1. From 1994–2002, 867 juveniles were captured, a mean of 96.3 annually (Table 1). Mean annual adult survivorship for *A. maculatum* was 73% (range 66–81%) whereas that of both the *A. jeffersonianum* complex and *A. opacum* was 56% (ranges 49–66 % and 49–65%, respectively).

Table 1. Juvenile recruitment of taxa captured at the drift-fence moving outward from the breeding pond from 1994–2002.

Year	***A. maculatum***	***A. jeffersonianum* complex**	***A. opacum***
1994	4	4	99
1995	0	3	29
1996	2	1	237
1997	1	36	3
1998	7	11	22
1999	0	0	70
2000	2	1	150
2001	0	0	235
2002	0	0	22
Total	**16**	**56**	**867**

A

Ambystoma maculatum

B

Ambystoma jeffersonianum
Complex

C

Ambystoma opacum

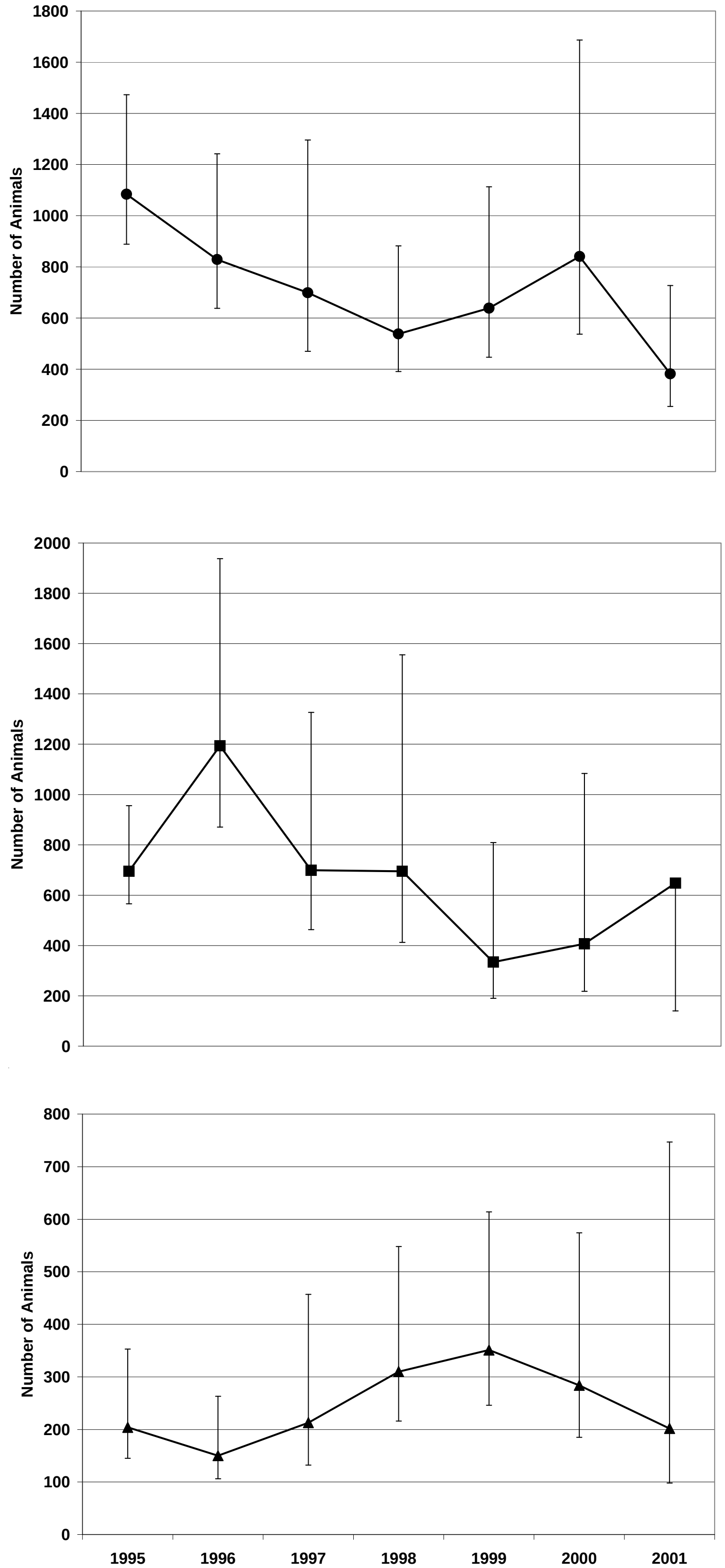

Figure 2. Annual Jolly-Seber population estimates of adult salamanders of each taxon captured at the drift-fence moving toward the breeding pond from 1995–2001. Error bars represent 95% confidence intervals. A. (upper) estimates for *Ambystoma maculatum*; B. estimates for the *A. jeffersonianum* complex; C. (lower) estimates for *A. opacum*.

Comparison of Jolly-Seber population estimates was consistent with count trends of breeding adults for all taxa (Figure 2). Annual population estimates for *A. maculatum* including unknown numbers of immigrating individuals indicate an insignificant decline from 1995–2001 ($p = 0.08$) whereas those for the *A. jeffersonianum* complex population indicate a significant temporal population decline ($p = 0.04$) over the seven year period. A number of researchers (Semlitsch and Brodie 1998; Lehtinen et al. 1999; Marsh and Trenham 2001) have emphasized the importance of metapopulation dynamics in preserving pond-breeding amphibians. Immigration at least partially explains the lack of significance between population estimates for *A. maculatum,* especially when considering the low reproductive recruitment. In contrast, annual population estimates for *A. opacum* varied above and below 1995 levels ($p = 0.56$) and appeared to exhibit the truncated curve of a species near carrying capacity (Smith and Smith 2001).

Discussion

Quantitative evidence indicates that substantial declines in the population size of the *A. jeffersonianum* complex and *A. maculatum* occurred. Predation by larval congeners and limited hydroperiod were probable causal factors with copper toxicity a probable contributing stressor. Annual survivorship indicates that about one-third of *A. maculatum* adults and nearly one half of the adult *A. jeffersonianum* complex died each year. Furthermore, little juvenile recruitment (*A. maculatum*) and no immigration (*A. jeffersonianum* complex) occurred to replace those losses.

There is no direct evidence that predation by larval congeners was a major factor in the decline of *A. jeffersonianum* complex and *A. maculatum* populations. However, *A. opacum* larvae have been cited as causing decreased survivorship of *A. jeffersonianum* larvae in experimental pens (Cortwright 1988), of newly hatched *A. jeffersonianum* larvae in a permanent pond (Williams 1973), and of both eggs and larvae of *A. jeffersonianum* (Walters 1975). Adult female *A. jeffersonianum* arrived at the breeding pond an average of 20 days earlier than those of *A. maculatum*; consequently, *A. jeffersonianum* eggs and larvae were potentially subjected to heavier predation by *A. opacum* than those of *A. maculatum* whose eggs were laid later and require longer developmental periods (Downs 1989; Nyman 1991; Brodman 1995).

High premetamorphic mortality of *A. maculatum* from *A. opacum* has been reported in ponds by Wilbur (1972), Williams (1973), Doty (1978) and Stenhouse (1985). In addition to predation by *A. opacum* larvae, *A. maculatum* larvae were also subject to predation by *A. jeffersonianum* larvae (Walters 1975). In experimental tanks, Walls and Williams (2001) showed that *A. jeffersonianum* larvae depress the biomass of *A. maculatum* by 47.9% and by 74.6% when in combination with *A. opacum*.

A. maculatum larvae surviving in ponds with *A. opacum* larvae have been reported by Doty (1978) and Cortwright (1988). However, mitigating factors including alternative prey, such as tadpoles of the Wood Frog, *Lithobates sylvaticus* (LeConte), and Cope's Gray Treefrog, *Hyla chrysoscelis* Cope, or the presence of suitable refugia were present, or periodic lengthy hydroperiods occurred (Stenhouse 1985; Petranka 1998). At our pond, no alternative anuran tadpole prey existed and hydroperiods were rarely optimal for *A. maculatum*.

Since the pond was nearly always dry by late August, it provided optimal conditions for egg laying and larval development of *A. opacum* which, in turn, would predictably increase predation on the two spring breeding congeners. The typical hydroperiod, which ended in early to mid-July, was too short to allow transformation of most *A. maculatum* larvae, but it was sufficiently long for transformation of some *A. jeffersonianum* complex larvae. The majority of *A. maculatum* metamorphs in ponds at similar latitude and climate to our pond disperse from mid-August through September (Shoop 1974; Wilson 1976; Downs 1989; Paton and Crouch 2002). In some nearby permanent, fishless ponds, metamorphs and gilled larvae can be found at least into mid-September (Matson, pers. observation). Recent metamorphs and some transforming larvae can survive in the wet pond substrate for a period of time after pond drying (Shoop 1974). Therefore, a hydroperiod continuing into at least the first weeks of August was required to allow even moderate *A. maculatum* recruitment, a hydroperiod that occurred twice during the 10 years. In contrast, most *A. jeffersonianum* metamorphs disperse in July and August suggesting that, with low predation, more than the documented 6.2 juveniles per year would be recruited. Some authors (Bishop 1941; Wacasey 1961; Williams 1973) though, report transformation occurring in late August or mid-September indicating that more *A. jeffersonianum* complex larvae may have transformed given a longer hydroperiod.

Copper was found to cause complete mortality in *A. jeffersonianum* larvae at a concentration of 15 µg/L in toxicity tests conducted at pH 4.5 and 5.5 (Horne and Dunson 1995b). The low recruitment and significant decline in population size of the *A. jeffersonianum* complex at our site ([Cu] = 20 µg/L), may in part, be attributable to direct or indirect effects of toxic concentrations of copper, but more study at higher pH and higher hardness levels are required to support this hypothesis. Reduced growth rate of *Lithobates pipiens* (Schreber) tadpoles (Lande and Guttman 1973) and reduced antipredator response by *Rana luteiventris* Thompson tadpoles (Lefcort et al. 1998) subjected to sublethal concentrations of metals have been reported. Similarly, Freda and Dunson (1985) have pointed out that reduced growth rate resulting from low pH can cause gape-limited predators such as *Ambystoma* larvae to be restricted to smaller prey because prey outgrow the size limitations of the predator. Reduced activity levels may contribute to reduced foraging efficiency and reduced growth rate of *Ambystoma* larvae which would extend the larval time to transformation and require a lengthened hydroperiod.

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Literature Cited

Barinaga, M. 1990. Where have all the froggies gone? Science 247: 1033-34.

Berven, K.A. 1995. Population regulation in the wood frog, *Rana sylvatica*, from three diverse geographic localities. Australian Journal of Ecology 20: 385-392.

Bishop, S.C. 1941. Salamanders of New York. New York State Museum Bulletin 324: 1-365.

Bissell, J.K. 1989. Plant survey of Indiana Point, Lake Metroparks. Unpublished report. Cleveland Museum of Natural History. Cleveland, OH USA.

Blem, C.R. and L.B. Blem. 1989. Tolerance of acidity in a Virginia population of the spotted salamander, *Ambystoma maculatum* (Amphibia: Ambystomatidae). Brimleyana 15: 37-45.

Blem, C.R. and L.B. Blem. 1991. Cation concentration and acidity in breeding ponds of the spotted salamander, *Ambystoma maculatum* (Shaw) (Amphibia: Ambystomatidae), in Virginia. Brimleyana 17: 67-76.

Blaustein, A.R. and D.B. Wake. 1990. Declining amphibian populations: a new global phenomenon? Trends in Ecology and Evolution 5: 203-204.

Blaustein, A.R., J.M. Romansic, J.M. Kiesecker, and A.C. Hatch. 2003. Ultraviolet radiation, toxic chemicals and amphibian population declines. Diversity and Distributions 9: 123-140.

Boulanger, J. and C.J. Krebs. 1994. Comparison of capture-recapture estimators of snowshoe hare populations. Canadian Journal of Zoology 72: 1800-1807.

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

Brodman, R. 2002. Twelve year study monitoring two species of pond-breeding salamanders in northeast Ohio. Ohio Journal of Science 102: 123-127.

Clark, K.L. and B.D. LaZerte. 1987. Intraspecific variation in hydrogen ion aluminum toxicity in *Bufo americanus* and *Ambystoma maculatum*. Canadian Journal of Fisheries and Aquatic Science 44: 1622-1628.

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.

Diana, S.G. and V.R Beasley. 1998. Amphibian toxicology. Pp. 266-277 *In* M.J. Lannoo, ed., Status and conservation of midwestern amphibians. University of Iowa Press, Iowa City, IA. USA.

Dodd, C.K. Jr., and D.E. Scott. 1994. Drift fences encircling breeding sites. Pp. 125-130 *In* R.W. Heyer, M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster, eds., Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press. Washington D.C., USA.

Doty, T.L. 1978. A study of larval amphibian population dynamics in a Rhode Island vernal pond. Ph.D. Dissertation, University of Rhode Island. Kingston, RI, USA.

Downs, F. 1989. *Ambystoma maculatum* (Shaw) spotted salamander. Pp. 108-125 *In* R.A. Pfingsten and F. Downs, eds., Salamanders of Ohio. Ohio Biol. Surv. Bull. New Series Vol.7 No. 2 xx +315 p. + 29 pls.

Freda, J. 1991. The effects of aluminum and other metals on amphibians. Environmental Pollution 71: 305-328.

Freda, J., and W.A. Dunson. 1985. The effect of acidic precipitation on amphibian breeding in temporary pools in Pennsylvania. U.S. Fish and Wildlife Service, Eastern Energy and Land Use Team, Washington, D.C., USA. Biol. Rep. 80 (40.22).

Gibbons, J.W., and R.D. Semlitsch. 1981. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimleyana 7: 1-16.

Horne, M.T., and W.A. Dunson. 1994. Exclusion of the Jefferson salamander, *Ambystoma jeffersonianum* from some potential breeding ponds in Pennsylvania: effects of pH, temperature and metals on embryonic development. Archives of Environmental Contamination and Toxicology 27: 320-330.

Horne, M.T., and W.A. Dunson. 1995a. Toxicity of metals and low pH to embryos and larvae of the Jefferson salamander, *Ambystoma jeffersonianum*. Archives of Environmental Contamination and Toxicology 29: 1101-1114

Horne, M.T., and W.A. Dunson. 1995b. Effects of low pH, metals and water hardness on larval amphibians. Archives of Environmental Contamination and Toxicology 29: 500-505.

Houlahan, J.E., C.S. Findlay, B.R. Schmidt, A.H. Meyer, and S.L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. Nature 404: 752-755.

Husting, E.L. 1965. Survival and breeding structure in a population of *Ambystoma maculatum*. Copeia 3: 352-362.

Johnson, T.R. 1998. Missouri toad and frog calling survey: the first year. Pp. 357-359 *In* M.J. Lannoo, ed., Status and Conservation of Midwestern Amphibians. University of Iowa Press. Iowa City, IA, USA.

Kleeberger S.R., and J.K. Werner. 1983. Post-breeding migration and summer movement of *Ambystoma maculatum.* Journal of Herpetology 17: 176-177.

Krebs, C.J. 1998. Ecological methodology. Addison-Wesley Educational Publishers. Menlo Park, CA, USA.

Lande, S.P., and S.I. Guttman. 1973. The effects of copper sulfate on the growth and mortality rate of *Rana pipiens* tadpoles. Herpetologica 29: 2-27.

Lefcort, H., L.H. Mcguire, L.H. Wilson, and W.F. Ettinger. 1998. Heavy metals alter survival, growth, metamorphosis and antipredatory behavior of Columbia Spotted Frog (*Rana luteiventris*) tadpoles. Archives of Environmental Contamination and Toxicology 35: 447-456.

Lehtinen, R.M., S.M. Galatowitsch, and J.R. Tester. 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19: 1-12.

Manly, B.F.J. 1984. Obtaining confidence limits on parameters of the Jolly-Seber model for capture-recapture data. Biometrics 40: 749-758.

Marsh, D.M., and P.C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15: 40-49.

Martof, B.S. 1953. Territoriality in the green frog, *Rana clamitans*. Ecology 34: 165-174.

Matson, T.O. 1990a. An inventory of the amphibians and reptiles of Hidden Valley, Indian Point and Riverview Metroparks, Lake County, Ohio. Unpublished report. The Cleveland Museum of Natural History. Cleveland, OH, USA.

Matson, T.O. 1990b. Erythrocyte size as a taxonomic character in the identification of Ohio *Hyla chrysoscelis* and *H. versicolor*. Herpetologica 46: 457-462.

Moriarty, J J. 1996. Minnesota's frog and toad survey: results of a pilot program. Pp. 69-74 *In* J.J. Moriarty, and D. Jones, eds., Minnesota's Amphibians and Reptiles: Conservation and Status, Proceedings of Symposium. Serpent's Tale Press, Excelsior, MN, USA.

Mossman, M.J., and R.L. Hine. 1984. The Wisconsin frog and toad survey: establishing a long-term monitoring program. Endangered Resources Report Number 9, Wisconsin Department of Natural Resources, Madison, WI, USA.

Nyman, S. 1991. Ecological aspects of syntopic larvae of *Ambystoma maculatum* and the *A. laterale-jeffersonianum* complex in two New Jersey ponds. Journal of Herpetology 25: 505-509.

Ott, J.A. and D. E. Scott. 1999. Effects of toe-clipping and PIT-tagging on growth and survival in metamorphic *Ambystoma opacum*. Journal of Herpetology 33(2): 344-348.

Paton, P. and W.B. Crouch. 2002. Using the phenology of pond-breeding amphibians to develop conservation strategies. Conservation Biology 16(1): 194-204.

Pechmann, J.H.K., D.E. Scott, J.W. Gibbons, and R.D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1: 3-11.

Pellet, J., B.R. Schmidt, F. Fivaz, N. Perrin, and K. Grossenbacher. 2006. Density, climate and varying return points: an analysis of long-term population fluctuations in the threatened European tree frog. Oecologia 149: 65-71.

Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D. C., USA.

Petranka, J.W., E.M. Harp, C.T. Holbrook, and J.A. Hamel. 2007. Long-term persistence of amphibian populations in a restored wetland complex. Biological Conservation 138: 371-380.

Pfingsten, R.A. and F.L. Downs (editors). 1989. Salamanders of Ohio. Ohio Biological Survey Bulletin. New Series Vol. 7 No. 2 xx + 315pp + 29 Pls.

Pfingsten, R.A. and T.O. Matson. 2003. Ohio salamander atlas. Ohio Biological Survey Miscellaneous Contributions Number 9. iv + 32p.

Pough, F.H. 1976. Acid precipitation and embryonic mortality of spotted salamanders, *Ambystoma maculatum*. Science 192: 68-70.

Quinn, E.M. 2004. Population trends of three taxa of mole salamanders (genus *Ambystoma*) at a protected northeast Ohio breeding pond 1994-2002. M.S. Thesis, University of Minnestota.

Rowe, C.L., and W.A. Dunson. 1993. Relationships among abiotic parameters and breeding effort by three amphibians in temporary wetlands of central Pennsylvania. Wetlands 13: 237-246.

Sadinski, W.A., and W.A. Dunson. 1992. A multi-level study of effects of low pH on amphibians of temporary ponds. Journal of Herpetology 26: 413-422.

Seibert, H.C. 1989. *Ambystoma opacum* (Gravehorst) marbled salamander. Pp. 125-131 *In* R.A. Pfingsten and F. Downs, eds., Salamanders of Ohio. Ohio Biol. Surv. Bull. New Series Vol.7 No.2 xx +315 p. + 29 pls.

Semlitsch, R.D., and J.R. Brodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12: 1129-1133.

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

Skelly, D.K., E.E. Werner, and S.A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80: 2326-2337.

Smith, R.L. and T.M. Smith. 2001. Ecology and Field Biology. Sith edition. Benjamin Cummings, San Francisco, USA.

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

Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783-1786.

Sutherland, W.J. 1996. Ecological census techniques – a handbook. Cambridge University Press. New York, NY, USA.

Twitty, V.C. 1966. Of scientists and salamanders. W. H. Freeman, San Francisco, CA, USA.

Urban, J.R., C.F. Alavarez, M.Z. Salinas, J.Jacobsen, K.C. Balcomb, A.L. Jaramillo, P.P. Ladron de Guevara, and A.L. Aguayo. 1999. Population size of humpback whale *Megaptera novaeangliae* in waters of the Pacific coast of Mexico. Fishery Bulletin 97: 1017-1024.

Uzzell, T.M. Jr. 1964. Relationships of the diploid and triploid species of the *Ambystoma jeffersonianum* complex (Amphibia: Caudata). Copeia 1964(2): 257-300.

Wacasey, J.W. 1961. An ecological study of two sympatric species of salamanders, *Ambystoma maculatum* and *Ambystoma jeffersonianum* in southern Michigan. Ph.D. Dissertation, Michigan State University. East Lansing, MI, USA.

Walls, S.C., and M.G. Williams. 2001. The effect of community composition on persistence of prey with their predators in an assemblage of pond-breeding amphibians. Oecologia 128: 134-141.

Walters, B. 1975. Studies of interspecific predation within an amphibian community. Journal of Herpetology (9)3: 267-279.

Weinstein, M., B.D. Leopold, and G.A. Hurst. 1995. Evaluation of wild turkey population estimation methods. 1995 Proc. Annual Conf. SEAFWA

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

Wilson, R.E. 1976. An ecological study of *Ambystoma maculatum* and *Ambystoma jeffersonianum* (Amphibia: Caudata). Ph.D. Dissertation, Cornell University, Ithaca, NY, USA.

Williams, P.K. 1973. Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma*. Ph.D. Dissertation, Indiana University. Bloomington, IN USA.

Wind, E. 2003. Amphibian surveys of Spectacle Lake 203 (Lower Pyrrotite Lake). Report produced for the Pacific Salmon Foundation, Ministry of Water, Land, and Air Protection, and Tiber West, Victoria, BC.