

Emigration Timing of Juvenile Pond-Breeding Amphibians in Western Massachusetts

BRAD C. TIMM,¹ KEVIN MCGARIGAL, AND LLOYD R. GAMBLE

Department of Natural Resources Conservation, University of Massachusetts, Amherst, Massachusetts 01003, USA

ABSTRACT.—Understanding the timing of movement events of pond-breeding amphibians to and from breeding and natal ponds, respectively, is essential to implementing effective conservation and monitoring strategies for this group of vertebrates. In this study, we assessed the emigration timing of newly metamorphosed juveniles of four species of pond-breeding amphibians (*Ambystoma maculatum*, *Ambystoma opacum*, *Notophthalmus viridescens*, and *Rana sylvatica*) in western Massachusetts from data collected at 14 seasonal ponds during four consecutive years (2000–2003). Results identified emigration “windows” for juveniles of each species during each year and for all years pooled. Additionally, analyses identified considerable intraspecific variation in the timing of emigration among ponds and years for at least three of the four study species. Our results are directly applicable to management strategies (e.g., road-closures) aimed at minimizing human-related impacts (e.g., road mortality) on populations of pond-breeding amphibians, as well as to mitigation strategies (e.g., maintaining engineered wetlands with an appropriate hydroperiod length) employed in cases of direct habitat loss.

The timing of emigration away from natal ponds by newly-metamorphosed pond-breeding amphibians has received surprisingly limited attention in the scientific literature (but see Shoop, 1974; Paton et al., 2000; Paton and Crouch, 2002). The majority of quantitative studies to date have been conducted at limited spatial (single pond) and temporal (single year) scales (e.g., Loredó and Van Vuren, 1996; Paton et al., 2000). Given the often dramatic biophysical differences among ponds, even those in close proximity (e.g., Jackson and Griffin, 1991), and the pronounced annual variability in conditions likely affecting juvenile emigration (e.g., air temperature, precipitation), studies examining the phenology of emigration must be conducted at adequate spatial and temporal scales (i.e., multiple ponds and years) before robust inferences can be made.

Understanding the timing of juvenile emigration has important conservation and management implications. For example, the implementation of road closures during nights of mass amphibian movements is gaining popularity as a conservation strategy, especially in response to recent evidence suggesting road mortality can have a significant, negative impact on local population persistence (Gibbs and Shriver, 2005). Currently, however, road closures are typically only employed during adult migration periods (P. W. C. Paton, pers. comm.). Extending road closures to include mass juvenile emigration events requires a better understand-

ing of juvenile emigration. With regard to land management, understanding the timing of juvenile emigration is prerequisite to the design of effective mitigation wetlands. In particular, engineering seasonal ponds with appropriate hydroperiods for larval development to metamorphosis and emergence of target species requires an understanding of juvenile emigration timing at natural wetlands (Rowe and Dunson, 1995; Snodgrass et al., 2000; Paton and Crouch, 2002). A better understanding of emigration timing of juveniles may also help to explain year-to-year variability in larval success, especially when paired with hydrology data (e.g., in years when rainfall levels are low, ponds may dry up relatively early, and species that typically do not complete metamorphosis until later in the year may experience partial or complete reproductive failure; Pechmann et al., 1989). This may be particularly relevant given some climate change models, which predict that weather patterns may exhibit much greater variability than has occurred in recent history (Houghton et al., 2001; Hulme et al., 2002).

Our study examines emigration timing of newly metamorphosed individuals of four species of pond-breeding amphibians (Spotted Salamander, *Ambystoma maculatum*; Marbled Salamander, *Ambystoma opacum*; Red-Spotted Newt, *Notophthalmus viridescens viridescens*; and Wood Frog, *Rana sylvatica*) at 14 seasonal ponds between 2000 and 2003 in western Massachusetts. The objectives of this study were to (1) evaluate the timing of juvenile emigration from natal ponds, and (2) compare the timing of emigration across ponds, years and species.

¹Corresponding Author. E-mail: timm@forwild.umass.edu

MATERIALS AND METHODS

Study area.—The study area encompasses 14 seasonal ponds within a 1-km circular area (approximately 314 ha) of contiguous mixed-deciduous hardwood forests in the southern portion of Hampshire County in western Massachusetts. Elevations range from approximately 60–200 m a.s.l. The terrain is highly varied with numerous ridges and depressions in which several seasonal wetlands have formed. The vegetation is classified as “transition hardwoods-white pine-hemlock forest” (Westveld, 1956).

The 14 study ponds range in size at high water from 0.03–0.35 ha and vary considerably in structure, including shrub-dominated, open-deep water, and shallow (open and/or vegetated) ponds. Two of the ponds contain an abundance of *Sphagnum*, and one appears to be human-made. Hydroperiods and water-level fluctuations vary significantly among ponds and years (Gamble, 2004), with most ponds typically drying between July and September (however, some ponds do not dry in very wet years), and no ponds contained fish at any time during the study.

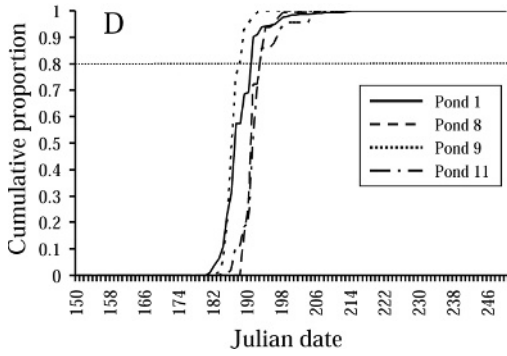
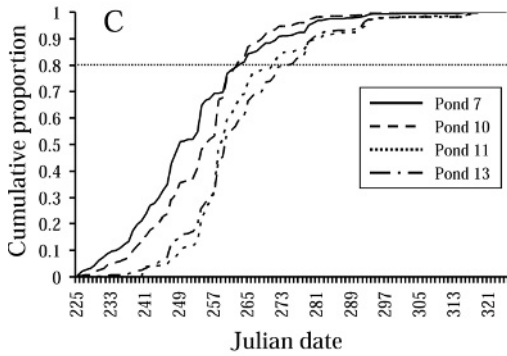
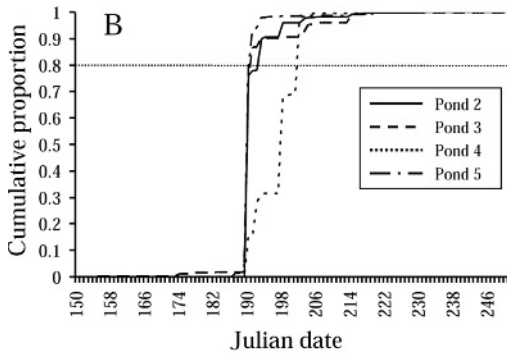
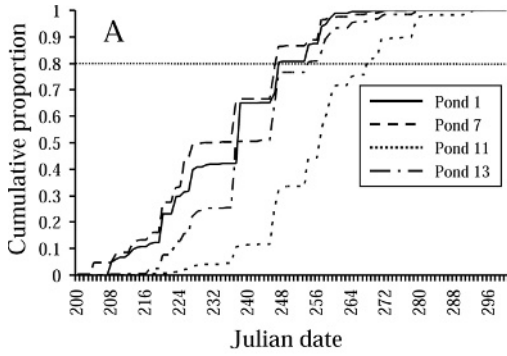
Field methods.—To monitor amphibian movements, we completely encircled all seasonal ponds with continuous drift fences and pitfall traps between 1998 and 2000. Drift fences were constructed from medium gauge, 35-cm aluminum flashing and placed in a predug trench roughly 12 cm deep approximately 3 m beyond the estimated high-water line of each pond (for details on fence construction, see Jenkins et al., 2003). We buried pitfall traps (#10 tin cans) flush to the ground surface on both sides of the fence at 10-m intervals. We checked traps daily from May through November of each year from 2000 to 2003, fully encompassing the emergence periods of juveniles of the four focal species. For each individual, we recorded capture date, species, age class (juvenile, subadult, and adult), and trap number and released animals on the opposite sides of the fence (for further details on array design, see Jenkins et al., 2006).

Analysis.—To describe the timing of juvenile emigration among ponds and years for each species, we constructed accumulation curves displaying the cumulative proportion of individuals having emigrated against Julian date. To compare the timing of emigration among species, we constructed similar accumulation curves using data pooled over all ponds and years. For all analyses, to eliminate potential spurious results from specific pond-years with low sample sizes, we only included pond-years where a minimum number of 10 individuals of the corresponding species emerged. To facilitate

comparisons, we used an accumulation threshold of 80% (cumulative proportion of individuals having emigrated = 0.8). Although somewhat arbitrary, we decided to use 80% as our threshold value because we wanted to describe emigration patterns at a level when the large majority of individuals had emigrated; however, we did not want extreme observations (i.e., “late” emigrants; those located at the far right end of accumulation curves) to bias comparisons mainly because these could represent individuals that emigrated earlier in the year but did not intersect our fences until a later date (i.e., individuals that used terrestrial habitats intervening the wetland edge and fences). In preliminary analyses, we also used a threshold of 90% and found no qualitative change from those obtained with the 80% threshold.

Among-ponds comparison.—We hypothesized that there would be differences among ponds in the timing of emigration for each species because of variation in local (pond-specific) variables known to influence larval development rates (e.g., con- and heterospecific larval densities, food availability, hydroperiod; Scott, 1990; Skelly, 1992; Leips and Travis, 1994; Denver et al., 1998). To examine this hypothesis for each species, we plotted accumulation curves from four ponds in a single year against each other. For this purpose, we selected the year with the greatest total number of juvenile emigrants pooled over all study ponds and the four ponds with the greatest number of emigrants during that year for the corresponding species. We decided to use the four ponds with the greatest number of emigrants because (1) figures constructed using all ponds meeting minimum sample size requirements (i.e., number of emigrants of the corresponding species \geq 10 individuals) for each species were too cluttered; and (2) the patterns and relationships among the four selected ponds were similar to those of the entire set of ponds for each species that met minimum sample size requirements.

Among-years comparison.—We hypothesized that there would be differences among years in the timing of emigration for each species because of variation in climatic factors likely to influence larval development rates (e.g., ambient temperature and hydroperiod) in addition to the uncertainty associated with the proximate conditions (e.g., precipitation) associated with movement events (Sexton et al., 1990; Vasconcelos and Calhoun, 2004). To examine this for each species, we plotted accumulation curves for each year. For this purpose, we pooled capture data across all ponds meeting minimum sample-size requirements; therefore, each day represented the cumulative proportion having



emigrated across the entire set of local populations (i.e., ponds) in a given year. In addition, to compare results to a similar study conducted in Rhode Island from 1997–1999 (Paton and Crouch, 2002), we determined the Julian date at 5%, 50%, and 95% cumulative emigration for each species and year and, for data pooled over all years, using only pond-years meeting minimum sample-size requirements.

Among-species comparison.—We hypothesized that there would be differences among species in the timing of emigration because of variation in life-history traits (e.g., timing of adult breeding, larval life-history strategies). To examine this, we plotted accumulation curves against each other for each possible pair of species. For this purpose, we pooled capture data across all ponds and years meeting minimum sample-size requirements; therefore, each day represented the cumulative proportion having emigrated across the entire set of pond-years.

RESULTS

We recorded 95,281 captures of emigrating juvenile age-class individuals of the four study species between 2000 and 2003, including: 8,603 *A. opacum*, 15,084 *A. maculatum*, 51,608 *R. sylvatica*, and 19,986 *N. viridescens*. Numbers of juveniles of each species emigrating from a single pond during a single year varied considerably, with a range of 0–4,042 for *A. opacum* (mean = 154), 0–1,551 for *A. maculatum* (mean = 269), 0–13,122 for *R. sylvatica* (mean = 922), and 0–7,420 for *N. viridescens* (mean = 357).

Among-ponds comparison.—The timing of emigration varied somewhat among ponds within a single year for each of four species, although the differences were more pronounced for some species than others (Fig. 1). Considering the four ponds with the largest emergence in a single year for each species, the maximum difference among ponds in Julian date (JD) to

FIG. 1. Timing of juvenile emigration (shown as the cumulative proportion of total emigration against Julian date) at different natal ponds in the same year in western Massachusetts for (A) *Ambystoma maculatum*, (B) *Ambystoma opacum*, (C) *Notophthalmus viridescens*, and (D) *Rana sylvatica*. Cases shown represent emigration during the year containing the greatest total number of emigrants of the corresponding species across all 14 ponds and the four ponds with the greatest number of emigrants of that species in that year. The dotted horizontal line indicates 80% total emigration.

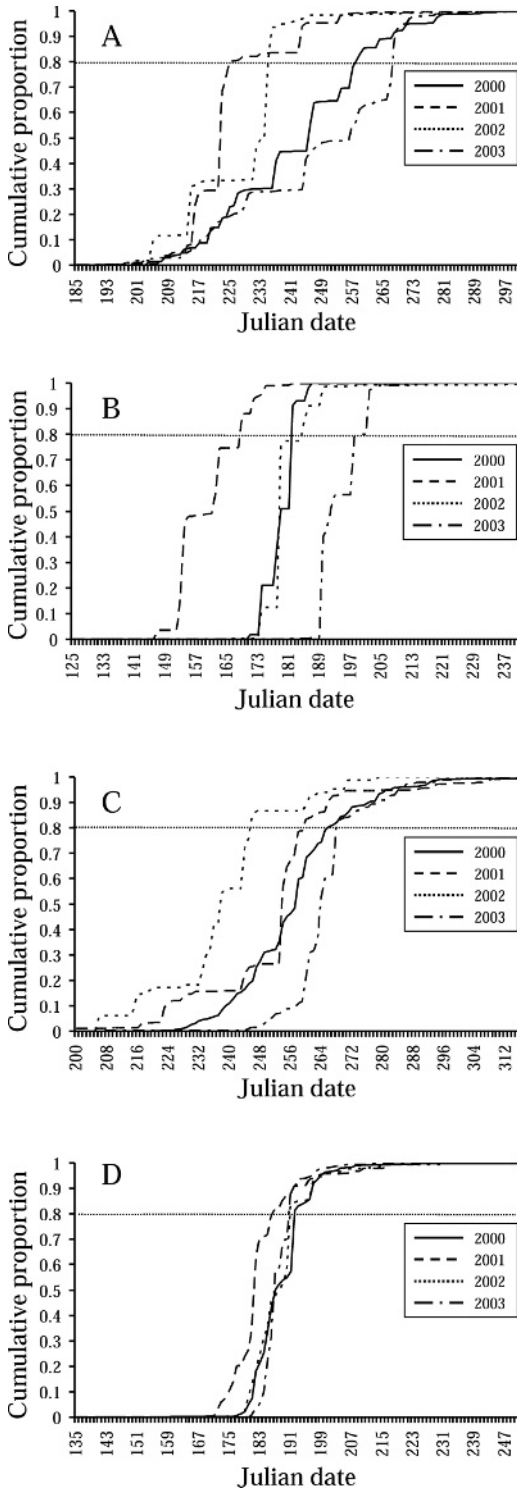


FIG. 2. Timing of juvenile emigration (shown as the cumulative proportion of total emigration against Julian date) from 14 seasonal ponds in each of four years between 2000 and 2003 in western Massachu-

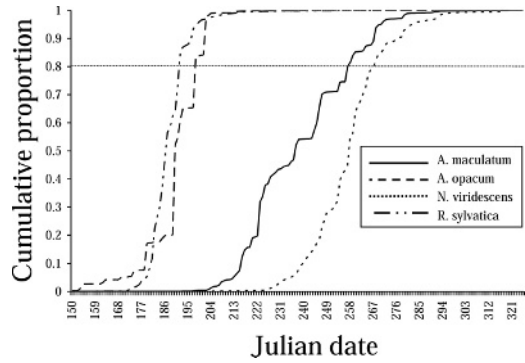


FIG. 3. Timing of juvenile emigration (shown as the cumulative proportion of total emigration against Julian date) from 14 seasonal ponds between 2000 and 2003 in western Massachusetts for four species of pond-breeding amphibians: *Ambystoma maculatum*, *Ambystoma opacum*, *Notophthalmus viridescens*, and *Rana sylvatica*. Only pond-years with ≥ 10 individuals of the corresponding species were included. The dotted horizontal line indicates 80% total emigration.

achieve 80% total emigration was 21 days for *A. maculatum*, 12 days for *N. viridescens*, 11 days for *A. opacum*, and five days for *R. sylvatica*.

Among-years comparison.—The timing of emigration varied considerably among years for the three salamander species (*A. maculatum*, *A. opacum*, and *N. viridescens*) but was remarkably consistent among years for *R. sylvatica* (Fig. 2). Considering all pools combined within each year for each species, the maximum difference among years in Julian date to achieve 80% total emigration was 43 days for *A. maculatum*, 32 days for *A. opacum*, 22 days for *N. viridescens*, and five days for *R. sylvatica* (Fig. 2). Moreover, the length of the emigration period varied dramatically among years as well. For example, the period encompassing 5–95% total emigration varied from 30 to 62 days among years for *A. maculatum*.

Among-species comparison.—The juvenile emigration period for all four species analyzed extended from late-May through mid-November, although each species generally exhibited a much narrower emigration window, and there appeared to be two distinct emigration patterns (Fig. 3). The emigrations of *A. opacum* and *R. sylvatica* were relatively concentrated in a three- to four-week period during the earlier part of

←

sets for (A) *Ambystoma maculatum*, (B) *Ambystoma opacum*, (C) *Notophthalmus viridescens*, and (D) *Rana sylvatica*. Only pond-years with ≥ 10 individuals of the corresponding species were included. The dotted horizontal line indicates 80% total emigration.

the summer (generally mid-June through mid-July). In contrast, *A. maculatum* and *N. viridescens* emerged later in the season (generally late July through mid-September, and mid-August through late September, respectively) and exhibited a much longer emigration window.

DISCUSSION

Our results demonstrate considerable variation among ponds, years, and species in the timing and concentration of juvenile emigration for four species of pond-breeding amphibians in western Massachusetts. The interspecific differences we documented are consistent with the findings from a similar study in Rhode Island (Paton and Crouch, 2002). However, to our knowledge, this is the first study to document variation in emigration timing and concentration among several years and multiple ponds for juvenile age-class individuals of these species. This added perspective in spatial and temporal scale revealed among-pond differences in emigration timing of some species in a given year as well as considerable interannual variation in emigration timing of three of the four study species (with *R. sylvatica* being the exception) among all 4 years.

We documented considerable variation in emigration timing among ponds within a given year for all three salamander species (Fig. 1). Based on the date to achieve 80% total annual emigration, all salamander species displayed maximum deviances among ponds of >10 days. This was somewhat surprising given the relative proximity of ponds (maximum Euclidean distance between any two ponds was <1.5 km) and our a priori assumption that weather was a principal determinant of emigration timing. Given that all ponds experienced the same regional weather pattern, it is likely, therefore, that local (pond-specific) factors played an important role in determining the timing of emigration and that local weather was important only as a proximate factor. This is consistent with the findings of previous studies regarding factors affecting larval development rates that are likely to vary among ponds, including con- and heterospecific larval densities (Semlitsch and Caldwell, 1982; Scott, 1990; Skelly, 1992), water temperature (Downie et al., 2004), and food availability (Berven and Chandra, 1988; Leips and Travis 1994). The relative consistency among ponds in the Julian date to achieve 80% total annual emigration for *R. sylvatica* suggests that larval development rate in this species was relatively unaffected by pond-level variables or that environmental variables important to this species were relatively consistent among our study ponds.

We also documented considerable variation in emigration timing among years for each species (Fig. 2). These differences were likely caused by a combination of factors that varied annually, including variation in the timing of adult breeding (Semlitsch, 1985; Reading, 1998), variation in weather patterns including the timing and magnitude of rainfall events (Sexton et al., 1990; Greenberg and Tanner, 2005; Todd and Winne, 2006), number of days since the most recent rainfall event (Greenberg and Tanner, 2005; Todd and Winne, 2006), daily air temperatures (Semlitsch, 1985; Greenberg and Tanner, 2005; Todd and Winne, 2006), and the aforementioned local variables known to affect larval development rates. Again, *R. sylvatica* was the one species exhibiting striking consistency in emigration timing among years, with only a five-day difference among years in the date to achieve 80% total annual emigration.

We noted two distinct windows of juvenile emigration, with *A. opacum* and *R. sylvatica* emerging earlier in the season over the course of one month, and *A. maculatum* and *N. viridescens* emerging later in the season over the course of about three months. These findings are consistent with previous findings for these species in Rhode Island (Paton and Crouch, 2002). Specifically, our dates to 5%, 50%, and 95% total emigration for *A. maculatum*, *A. opacum*, and *R. sylvatica* (pooled across ponds and years) were within 10 days (typically later) of those reported by Paton and Crouch (2002). *Notophthalmus viridescens* was the only exception, with emigration in our study occurring several weeks earlier than in the Rhode Island study. The overall similarity in emigration dates between studies (for three of the four study species) is notable given the distance between study areas (~120 km) and the lack of overlap in years of study (1997–99 vs. 2000–03) and suggests that there is regional consistency and stability in the seasonal timing of emigration for these species. The similarity in seasonal timing of emigration for some species and differences for others may largely be attributed to the breeding phenology of adults. For example, adult *A. opacum* breed in late summer (August and September; Paton and Crouch, 2002), whereas adults of the other two salamander species examined in this study (*A. maculatum* and *N. viridescens*) breed during early spring (March and April; Paton and Crouch, 2002), which may account for the similarity in juvenile emigration timing for the latter two species and the dissimilarity to *A. opacum*. In addition, the duration of the emigration period for each species was notably similar between studies as well. Specifically, in both studies the number of days between the dates to achieve 5% and 95% total emigration for *A. opacum* and

TABLE 1. Dates to achieve 5%, 50%, and 95% total annual emigration of juvenile individuals between 2000 and 2003 for four species of pond-breeding amphibians at 14 seasonal ponds in western Massachusetts, along with the number of days between dates to achieve 5% and 95% total annual emigration. Data includes only pond-years in which ≥ 10 individuals of the corresponding species were captured. Dates in parenthesis are based on a similar study in Rhode Island for comparison (Paton and Crouch, 2002).

Species	Year	5%	50%	95%	5-95% interval
<i>Ambystoma maculatum</i>	2000	31 Jul	2 Sep	1 Oct	62
	2001	3 Aug	11 Aug	2 Sep	30
	2002	24 Jul	23 Aug	29 Aug	36
	2003	2 Aug	14 Sep	29 Sep	58
	2000-03	1 Aug (21 Jul)	25 Aug (18 Aug)	27 Sep (28 Sep)	
<i>Ambystoma opacum</i>	2000	22 Jun	26 Jun	4 Jul	12
	2001	2 Jun	11 Jun	23 Jun	21
	2002	23 Jun	28 Jun	9 Jul	16
	2003	9 Jul	11 Jul	21 Jul	12
	2000-03	21 Jun (14 Jun)	9 Jul (27 Jun)	21 Jul (23 Jul)	
<i>Notophthalmus viridescens</i>	2000	22 Aug	14 Sep	8 Oct	47
	2001	11 Aug	11 Sep	16 Oct	66
	2002	25 Jul	26 Aug	24 Sep	61
	2003	8 Sep	21 Sep	12 Oct	34
	2000-03	24 Aug (13 Sep)	15 Sep (2 Oct)	10 Oct (18 Nov)	
<i>Rana sylvatica</i>	2000	28 Jun	5 Jul	17 Jul	19
	2001	22 Jun	1 Jul	18 Jul	26
	2002	29 Jun	5 Jul	20 Jul	21
	2003	2 Jul	6 Jul	16 Jul	14
	2000-03	28 Jun (18 Jun)	6 Jul (29 Jun)	18 Jul (20 Jul)	

R. sylvatica was <30 in all years, whereas the comparable emigration window for *A. maculatum* and *N. viridescens* was >30 . These differences have been attributed to differences in life-history strategies among these species with *R. sylvatica* and *A. opacum* adopting a strategy of initiating metamorphosis after a minimum number of days and variable size, or after a minimum size and variable number of days, thereby leading to a relatively concentrated period of emigration, whereas *A. maculatum* and *N. viridescens* adopt a strategy such that larvae maximize the amount of time in ponds prior to initiating metamorphosis, thereby leading to a relatively protracted period of emigration (Semlitsch and Wilbur, 1988; Paton and Crouch, 2002).

Conservation implications.—Our findings have two important conservation implications. First, for species such as *R. sylvatica*, where the timing of emigration is highly consistent among ponds and years and concentrated into a narrow time period, it may be practical to focus conservation efforts during the emigration period. For example, a strategy that incorporates road closures aimed at protecting individuals from road mortality is most likely to succeed if the emigration period is well defined and predictable.

Second, our results demonstrate that species differ in the length of time that larvae remain in

ponds and that these differences are relatively consistent among ponds and years. Therefore, we can infer that species differ in their pond hydroperiod requirements. For example, *R. sylvatica* and *A. opacum* typically emerge from ponds between 21 June and 12 July in our study area. Therefore, it is reasonable to assume that ponds that dry prior to late-June would not have sufficient hydroperiods to allow successful recruitment. Likewise, it is also reasonable to assume that ponds with a much longer hydroperiod will not confer any advantage to these species and may, in fact, be suboptimal because of ecological interactions with species that excel in these conditions (Wellborn et al., 1996; Snodgrass et al., 2000; Babbitt et al., 2003). *Ambystoma maculatum* and *N. viridescens*, however, apparently require ponds with a much longer hydroperiod. These differences have clear implications for assessing the capability of ponds of varying hydroperiod to support any particular amphibian assemblage, especially in the case of wetlands constructed and maintained for mitigation purposes.

Scope and limitations.—Our study was conducted at a single study site consisting of 14 ponds in relative close proximity (<1.5 km). Thus, all ponds and individuals were subject to the same general weather patterns (e.g., localized thunderstorms common throughout the study area during summer months); therefore,

the applicability of these results to populations beyond the immediate vicinity of our study ponds is unknown. However, the similarity of our results to those obtained from a study in Rhode Island (Paton and Crouch, 2002) suggests that this may not be a major issue. Future studies focused on quantifying the movement phenology of pond-breeding amphibians should collect data from populations separated by larger distances (or even from multiple local populations in close proximity at each of several spatial scales) to allow for a more robust understanding of the timing of movement events throughout a larger geographic area.

Acknowledgments.—We are grateful to C. Jenkins, B. Compton, S. Jackson, S. Melvin, and A. Richmond for valuable input throughout all stages of this project. We also thank the Valley Land Fund and numerous private landowners for permitting access to their properties. This work would not have been possible without the dedication and hard work of many individuals who helped over the years, including K. Berger, N. Bovaird, D. Brennan, M. Contois, R. DeAngelis, C. Eiseman, M. Grgurovic, M. Hey, K. McKenney, K. Montieth, K. Phelan, J. Roberts, E. Weymouth, and many additional volunteers. This work was funded by the Natural Heritage and Endangered Species Program of the Massachusetts Division of Fisheries and Wildlife, Sweet Water Trust (Boston, MA), the U.S. Geological Survey Amphibian Research & Monitoring Initiative (ARMI), the Silvio Conte National Wildlife Refuge (Challenge Grant 50181-1-J045A), and the Massachusetts Environmental Trust (Boston, MA). Handling of animals was conducted under the University of Massachusetts Amherst Institutional Animal Care and Use Protocol (IA-CUC) 22-02-02 and annual collection permits granted by the Massachusetts Division of Fisheries and Wildlife.

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Accepted: 12 December 2006.