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Timing of large movement events of pond-breeding amphibians in Western Massachusetts, USA

Brad C. Timm*, Kevin McGarigal, Bradley W. Compton

Department of Natural Resources Conservation, Holdsworth Natural Resources Center, University of Massachusetts, Amherst, MA 01003, USA

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ABSTRACT

Understanding the factors influencing the timing of large movement events in pond-breeding amphibians has important conservation implications, especially with regard to establishing road closures aimed at minimizing road mortality. We examined the timing of juvenile emigration and adult immigration in four species of pond-breeding amphibians (*Ambystoma maculatum*, *Ambystoma opacum*, *Notophthalmus viridescens*, and *Rana sylvatica*) at 14 seasonal ponds in western Massachusetts from 1999 to 2003. Regression trees were variously successful in producing an effective and parsimonious description and robust prediction of large movement events based on a suite of temporal and meteorological variables. Julian date, degree-days, temperature, precipitation and droughtiness were all important correlates of movement for one or more species and age class. The amount of rainfall during the previous 24 h period was an important variable in four of the five trees built, and degree-days was an important variable in two of the three trees built describing juvenile emigration. In four of six cases, regression trees identified a few days each year that accounted for a large percentage of the total annual movement, and thus offered a practical means to determine when road-closure events designed to minimize road mortality of pond-breeding amphibians during migratory events would be most effectively employed.

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1. Introduction

The timing of annual migrations to and from breeding sites in pond-breeding amphibians is a topic that has received increasing attention in the scientific literature during recent years (Paton et al., 2000; Paton and Crouch, 2002; Greenberg and Tanner, 2004, 2005; Todd and Winne, 2006). Several authors have attempted to correlate the timing and magnitude of migratory movements with selected environmental variables (e.g., date, temperature, precipitation) and have been met with varied success based on the fit of final explanatory models (Semlitsch, 1985; Beneski et al., 1986; Sexton et al., 1990; Reading, 1998; Greenberg and Tanner, 2004,

2005; Todd and Winne, 2006). In addition, a number of these studies have been conducted at limited spatial (i.e., a single wetland) and/or temporal (i.e., a single year) scales, and as such, the applicability of results obtained from these studies as part of a conservation strategy is suspect.

Understanding factors influencing the phenology of large movement events in pond-breeding amphibians has important conservation implications, especially with regard to establishing road closures aimed at minimizing road mortality (Hels and Buchwald, 2001; Mazerolle, 2004; Gibbs and Shriver, 2005). Several studies have documented road mortality of hundreds of individual amphibians on single road segments (e.g., Wyman, 1991; Ashley and Robinson, 1996; Mazerolle,

* Corresponding author. Tel.: +1 401 595 9934; fax: +1 413 545 4358.

E-mail addresses: timmm@forwild.umass.edu (B.C. Timm), mccgarigalk@forwild.umass.edu (K. McGarigal), bcompton@forwild.umass.edu (B.W. Compton).

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2004; Aresco, 2005). In addition, theoretical models incorporating movement rates across roads in relation to traffic intensities have estimated annual road mortality rates potentially exceeding 20% of the total adult population for several species (Hels and Buchwald, 2001; Gibbs and Shriver, 2005). Given the demographically significant population consequences of road mortality, especially for long-lived species such as ambystomatid salamanders, the ability to reliably predict large movement events is critical in developing effective conservation strategies for pond-breeding amphibians in landscapes where roads are present.

Our study uses regression tree analysis to quantify and predict large movement events of pond-breeding amphibians. Specifically, using data collected at 14 seasonal ponds between 1999 and 2003 in western Massachusetts, USA, we examined the relationship between selected independent variables and (1) the timing of emigrations of newly metamorphosed juveniles of four species of pond-breeding amphibians (marbled salamander, *Ambystoma opacum*; spotted salamander, *Ambystoma maculatum*; wood frog, *Rana sylvatica*; and red-spotted newt, *Notophthalmus viridescens*) and (2) the late summer and early fall immigrations of adults of two species (*A. opacum* and *A. maculatum*). Because this study was part of a larger investigation examining the metapopulation dynamics of *A. opacum*, arrays were not opened early enough in each year to capture all adult adults of all pond-breeding amphibians during spring breeding migrations, and therefore we were unable to conduct analyses for these movement events. The objectives of this paper are to: (1) assess the effectiveness of regression tree analysis in predicting movement events for the study species; (2) identify the role of selected independent variables on the timing of movement events for the study species; (3) establish a methodological framework for collecting and analyzing movement data as the basis for establishing road closures as part of a conservation strategy.

2. Materials and methods

2.1. Study area

The study area encompasses 14 seasonal ponds within a 1-km circular area (approx. 314 ha) of contiguous mixed-deciduous hardwood forests in the southern portion of Hampshire County in western Massachusetts. Elevations range from approximately 60 m to 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) and is dominated by a mixture of oak (*Quercus* spp.), maple (*Acer* spp.), birch (*Betula* spp.), hickory (*Carya* spp.) and two conifer species (*Tsuga canadensis* and *Pinus strobus*), and has an estimated modal stand age of 70 years. The understory is highly variable and consists of sparse to dense patches of shrubs, including blueberries (*Vaccinium* sp.), huckleberries (*Gaylussacia* sp.), maple-leaved viburnum (*Viburnum acerifolium*), mountain-laurel (*Kalmia latifolia*) and witch hazel (*Hamaemelis virginiana*). The closest paved road to any of the study ponds was ~300 m, although the majority of sites were in excess of 600 m from any paved road.

The 14 study ponds range in size at high water from 0.03 ha to 0.35 ha and vary considerably in structure, including scrub/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.

2.2. Amphibian data collection

To monitor amphibian movements, we completely encircled all seasonal ponds with continuous drift fences and pitfall traps. Drift fences were constructed from medium gauge, 35 cm aluminum flashing and placed in a pre-dug trench roughly 12 cm deep approximately 3 m beyond the estimated high-water line of each pond (see Jenkins et al., 2003 for details on fence construction). We buried pitfall traps (#10 tin can) flush to the ground surface on both sides of the fence at 10 m intervals. Each trap contained a wetted sponge and was covered by a board angled above the trap to provide shade and prevent desiccation. During times of high water, when individual traps became flooded, pitfalls were temporarily replaced with terrestrial funnel traps (Enge, 1997).

We checked traps daily from May through November of each year from 2000 to 2003, fully encompassing the juvenile emergence period of all four study species and the fall adult migration period of the two adult species. Additionally, similar data collected from August to November 1999 are included in the analyses for the fall migration period of adults because drift-fence arrays around most of the study ponds were completed by this period. Immigration movements by adult *A. opacum* in the late summer and early fall represented breeding movements to dry pond basins. However, the purpose of adult *A. maculatum* movements to the pond basins in the fall is unclear, since this species breeds only in the spring, although this behavior has been observed in other species (e.g., *R. sylvatica* males) and is hypothesized that males may gain a fitness advantage by hibernating close to the breeding pond (Zweifel, 1989). For each individual captured, we recorded the capture date, species, and age class (juvenile, sub-adult, and adult) and then released animals on the opposite side of the fence. Adult *A. opacum* were individually identified using photographs of dorsal patterns and juvenile *A. opacum* were marked using pond-specific toe-clips; juveniles of the other species were not marked, however upon examination of the data, we found very few juveniles were captured on the outside of fences (and subsequently released on the inside of fences) and therefore likely had very little to no impact on results. From December through April, we closed all traps and removed short sections of fence at 10–15 m intervals to allow animals to enter and depart the pond basins.

2.3. Independent variables

Based in part on previous work (e.g., Semlitsch, 1985; Sexton et al., 1990), we identified five regional factors (i.e., operating at the scale of the entire study area, not the individual pond) that may explain the timing of movement events in the four

study species. Each factor was represented by one or more independent variables in the analyses, as described below:

(1) Date – We included a single variable, Julian date (JULIAN), for this factor. For both juvenile and adult movements, we hypothesized that Julian date would function as a constraint on the timing of movement events. For juvenile emigrations from ponds in the summer, we hypothesized that there would be a minimum number of days required for completion of larval development and emergence of metamorphs from the ponds (Paton and Crouch, 2002). Thus, we expected to observe a minimum Julian date before any movement events occurred. Conversely, we hypothesized that after a certain number of days in the pond there would be an increasing propensity to emigrate from ponds to ensure sufficient time to seek terrestrial refugia. Thus, we expected to observe an increasing likelihood of movement events as Julian date increased, until either the pool of potential emigrants was depleted or the pond basin dried up completely. For adult immigrations to ponds in the fall, we hypothesized that Julian date would represent the evolutionarily determined optimal timing of migration. Thus, we expected to observe a time period in which the likelihood of movements first increased and then decreased.

(2) Degree days – We hypothesized that degree-days would provide a more relevant predictor of the timing of larval development and juvenile emergence (Camp and Marshall, 2000; Zou et al., 2004) than Julian date. Specifically, we hypothesized that a minimum number of degree-days would be required before larvae of each species would be ready to metamorphose and emigrate, based on the general understanding that larval developmental rate in aquatic amphibians is positively associated with water temperature (Newman, 1989; Hayes et al., 1993). We did not expect degree-days to be an important predictor of adult immigration to the dry pond basins in the fall. We calculated degree-days as the number of degrees Celsius that the daily mean temperature exceeded a pre-specified developmental threshold of 10 °C (see Charnov and Gillooly, 2003), summed over all days after a fixed starting date. Any day where the mean daily temperature was ≤ 10 °C was given a degree-day value of zero. We calculated degree-days for several starting dates that we hypothesized would be pertinent to the species we examined including 15 April (DDAPR15), 1 May (DDMAY1), 15 May (DDMAY15), 1 June (DDJUN1), and 15 June (DDJUN15).

(3) Temperature – We included a single variable, daily mean air temperature (MEANTEMP) calculated as: $\{(daily\ maximum\ temperature + daily\ minimum\ temperature)/2\}$, for this factor. We hypothesized that both juveniles and adults would show greater propensity for movement on warm days/nights, especially on nights with precipitation (Semlitsch, 1985; Sexton et al., 1990; Vasconcelos and Calhoun, 2004). Since pond-breeding amphibians are ectothermic, activity levels are likely to be strongly driven by ambient temperatures (e.g., Sexton et al., 1990). We recognized that daily mean temperature was confounded with both Julian date and degree-days, and that any one of these variables might obscure the importance of the others.

(4) Precipitation – We hypothesized that both juveniles and adults would show greater propensity for movement following or during precipitation, especially when accompanied by

warm temperatures (Semlitsch, 1985; Sexton et al., 1990; Vasconcelos and Calhoun, 2004). Since many amphibians are prone to desiccation due to skin that is highly permeable to water, activity levels are likely to be strongly driven by precipitation. Considering that surface or sub-surface soil moisture could serve as a more important trigger for movements (Seebacher and Alford, 1999), we included several variables for this factor to account for the possibility of a time lag in soil moisture increase following precipitation events. Precipitation variables included the amount of rain (cm) that fell during the previous 24-, 48-, and 72-h periods (RAINAMOUNT24, RAINAMOUNT48, and RAINAMOUNT72, respectively) measured from midnight to midnight. In addition, we treated precipitation as a binary measure (any precipitation versus no precipitation) and measured whether there was any precipitation during the previous 24-, 48-, and 72-h periods (RAIN24, RAIN48, and RAIN72, respectively).

(5) Drought length – We hypothesized that the propensity for movement during or following a warm, precipitation event would increase as the period without precipitation prior to that event increased (Todd and Winne, 2006). In other words, we expected long periods without precipitation to increase the “staging” of individuals otherwise prepared to migrate, and thereby increase the likelihood of large movement events when suitable proximate conditions occurred. Accordingly, we measured the number of days since the last rainfall event for this factor (RAINDROUGHT).

All weather data was collected from the Amherst College weather station located approximately 8.0 km north-northeast of the study sites which recorded daily maximum and minimum air temperatures and daily precipitation totals.

2.4. Analyses

We used regression tree analysis in the statistical package R (using the “rpart” package) version 2.2.0 (Free Software Foundation, Inc., Boston, MA) to examine the relationship between the independent variables and the timing of juvenile emigration in each of four species (*A. maculatum*, *A. opacum*, *R. sylvatica*, and *N. viridescens*) between 2000 and 2003, and the timing of adult fall immigration in each of two species (*A. opacum* and *A. maculatum*) between 1999 and 2003. A separate analysis was conducted for each species and age class. Because the independent variables considered here were all regional variables (expected to affect all ponds similarly) and because analyses conducted for one species (*A. opacum*) indicated no significant differences in capture probabilities among ponds (Gamble et al., 2006), we pooled the amphibian capture data for each species and age class across all ponds for each observation day. To account for substantial annual variation in total numbers of captures of each species and age-class, the daily number of captures was divided by the total annual number of captures of the respective species and age-class and converted to a percentage. In addition, preliminary analyses revealed highly skewed residuals; therefore, we log-transformed all dependent variables representing daily percent of total annual captures. Lastly, we restricted our analyses to a “potential movement window” in order to eliminate a potentially large number of days with zero movements. For each species and age-class, this movement

window was defined by the earliest Julian date of capture (across all years) and the Julian date at which 95% of total annual captures were observed across all years (Table 1). Therefore, the number of samples (rows) used in the analysis for each species was equal to the number of days included in that species' "potential movement window" (Table 1) multiplied by the number of years of data included for that species (e.g., the number of samples for *A. maculatum* juveniles = 145 days * 4 years = 580).

We sought to minimize the number of independent variables considered by limiting these to one for each of the five independent factors (above). This was motivated by three concerns. First, we sought to minimize the risk of spurious relationships caused by an excessive number of independent variables. Second, we sought to give equal weight to each factor by avoiding the inherent bias associated with having different numbers of variables representing each factor. Lastly, for each of the two factors with multiple variables (precipitation and degree-days), we assumed that the postulated mechanistic relationship was in fact univariate, and that our inclusion of more than one variable merely reflected our inability to distinguish *a priori* the best way of measuring that univariate relationship. Therefore, to select the single "best" explanatory variable within each of these factors we calculated variable importance values (see Breiman et al., 1984) and retained the variable with the greatest importance value in each factor for all analyses. For all species and age classes, RAINAMOUNT24 was the most important precipitation variable. Similarly, for all four species for which we evaluated juvenile emigration, DDMAY1 was the most important degree-day variable. Consequently, the final regression tree analyses included the following independent variables: MEANTEMP, JULIAN, RAINDROUGHT, RAINAMOUNT24 and DDMAY1, although the last variable was only included in the juvenile emigration models because we could not postulate any specific mechanistic relationship with the timing of adult immigrations to the breeding sites in the fall.

2.5. Regression trees

In all analyses, the final regression tree was selected by pruning based on a 10-fold cross-validation and the 1-S.E. rule (De'ath and Fabricius, 2000). Statistical significance of each tree was based on a Monte Carlo permutation test using 100

permutations. The performance of regression trees is typically assessed by the strength of the fit of the final tree, as measured by the coefficient of determination (i.e., model r^2) which ranges from 0 to 1, with larger values indicating a better fit (De'ath and Fabricius, 2000). In our particular case, however, the absolute value of the r^2 did not provide a meaningful measure of model performance, or at least required unique interpretation. This "problem" of interpretation stemmed in part from the large percentage of zeros (i.e., non-movement nights) in the data sets (48.7–75.4% of observations, depending on species and age class) which functioned to deflate the model r^2 which is a common problem in regression analyses using ecological data. Regression trees recursively partition observations (in our case, days) into an increasing number of branches (or leaves) based on splits in independent variable values that minimize the residual variation in the resulting leaves (De'ath and Fabricius, 2000). If, for example, a leaf in the final tree contained a mixture of several zeros and all the large non-zero values (i.e., large movement events), then the residual variation was likely to be quite large – resulting in a low overall r^2 – even though the model effectively predicted the potential for large movement events.

2.6. Model performance

We instead evaluated model performance in three different ways based on how well the model described and/or predicted the probability of a large movement event, defined as an event accounting for $\geq 10\%$ of total annual captures for the corresponding species and age class. First, for observations falling into each leaf, we calculated the probability of observing a movement event of any given magnitude or greater (i.e., $\geq x\%$ of total annual capture for the corresponding species and age-class) and displayed it as a cumulative probability plot. We judged the model effective if the leaves differed substantially in the probability of a large movement event, such that there was a clearly defined set of conditions leading to a high probability of a large movement event and that also accounted for a large percentage of the total annual movement for a given species and age class.

Second, we examined the temporal concentration of movements for each species and age class. Specifically, for each day we calculated the percent of the total annual captures of the corresponding species and age class. We sorted

Table 1 – Time periods associated with juvenile emigration from natal ponds and adult fall immigration to breeding ponds in four species of pond-breeding amphibians in western Massachusetts between 1999 and 2003

Species	Age-class	Analysis window	Number of days
<i>A. maculatum</i>	Juvenile	6 May (JD127)–27 Sept (JD271)	145
<i>A. opacum</i>	Juvenile	26 May (JD147)–21 July (JD203)	57
<i>R. sylvatica</i>	Juvenile	6 May (JD127)–18 July (JD200)	74
<i>N. viridescens</i>	Juvenile	18 July (JD200)–10 Oct (JD284)	85
<i>A. opacum</i>	Adult	2 Aug (JD215)–15 Sept (JD259)	45
<i>A. maculatum</i>	Adult	1 Sept (JD245)–30 Nov (JD335)	91

The starting date for each species and age-class was the earliest date during the study period that an individual of that species and age class was captured; the end date for each species and age class was the date at which 95% of the individuals had completed movement over that same period.

these values in descending order by year and plotted an accumulation curve based on the mean and standard error across years ($n = 4$ years for juveniles; $n = 5$ years for adults). This accumulation curve depicts the average number of movement events (days) in a year required to capture any specified percentage of the population. We interpreted this curve as representing the maximum efficiency possible with any model. In other words, if we could perfectly predict every movement event, our model could do no better in terms of accounting for a given percentage of the total annual movement in the corresponding number of days. By comparing the model accumulation curve to the maximum accumulation curve (based on a perfect model), we were able to judge the relative efficiency of the model.

Lastly, because we were interested in the potential for the final regression trees to be used for predictive purposes, i.e., to predict the occurrence of large movement events on any given day/night for the purpose of establishing road closures, it was also necessary to validate our model predictions. To accomplish this, we conducted a four- or five-fold (for juveniles and adults, respectively) cross-validation by building a predictive model on three or four years of data, respectively, and then testing each model with the holdout year. For this purpose, we focused on the single leaf in each tree that predicted the highest probability of a large movement event, since in practice it is likely that a road closure policy, for example, would only be implemented if it could be done sparingly and under conditions of high likelihood of effectiveness (i.e., the fewest possible days required to protect a large percentage of the population). For each predictive model we computed the percent of total annual captures for the corresponding species and age-class that was accounted for by the “best” leaf. We then used the model to predict movement events for the holdout year and computed the same measure for the holdout observations. We interpreted the ratio of the percent actually accounted for in the holdout year relative to the prediction as a measure of model performance. Specifically, a ratio >1 means that the model performed better than predicted (i.e., accounted for a greater percentage of the population than we predicted), whereas a ratio <1 means that the model did not do as well as predicted. We computed the average predictive performance ratio across the four- or fivefold cross-validations and interpreted this as a practical measure of predictive performance. It is important to note that we evaluated the general predictive performance of our regression trees in this manner, but that the final regression trees that we described and evaluated with the previous two performance measures (above) were based on the full four- or five-year models, respectively.

3. Results

We recorded 95,281 captures of emigrating juvenile age-class individuals of the four study species between 2000 and 2003, including: 15,084 *A. maculatum*, 8603 *A. opacum*, 51,608 *R. sylvatica*, and 19,986 *N. viridescens*. Additionally, we captured 2677 and 1346 immigrating adult *A. opacum* and *A. maculatum*, respectively, during the late summer and early fall seasons from 1999 to 2003.

3.1. Juvenile emigration

A. maculatum – During the comparatively long 145-day emigration period each year for juvenile *A. maculatum* (Table 1), movements were considerably less concentrated than in *A. opacum*, with an average of three large movement events each year and an average of 11 movement events required each year to account for 80% of the total annual emigration (Table 2, Fig. 1a). The final regression tree ($r^2 = 0.35$, $P < 0.01$) included three leaves corresponding to a low, moderate and high probability of a large movement event (Fig. 2a). The probability of large movement events was greatest (10%) when DDMAY1 was ≥ 659 and RAINAMOUNT24 was ≥ 0.22 cm (0.09 in.; Fig. 3a). Collectively, this final leaf included 10% (59/580) of the days (or an average of less than 15 days per year) and accounted for 58% of the total annual movement (Fig. 2a). With a perfect model, the same number of days would have accounted for 87% of the annual total (Fig. 1a). In addition, this single “best” leaf had a predictive performance ratio of 0.92 (Table 3), indicating that the model was quite robust.

A. opacum – Relative to the other species considered, *A. opacum* was characterized by a short (57-day) juvenile emigration period (Table 1). Movements during this period were highly concentrated, with an average of approximately three large movement events ($\geq 10\%$ annual capture) each year (Table 2). On average, four of the largest movement events each year accounted for 80% of the total annual emigration (Fig. 1b). We were unable to build a regression tree for the emigration of juvenile *A. opacum* that was successfully cross-validated. Thus, we could not identify the conditions under which the probability of a large movement event was relatively high.

R. sylvatica – During the 74-day emigration period each year for juvenile *R. sylvatica* (Table 1), movements were considerably less concentrated than in *A. opacum*, with an average of 2.5 large movement events each year and 10 movement events required each year to account for 80% of the total annual emigration (Table 2, Fig. 1c). The final regression tree ($r^2 = 0.76$, $P < 0.01$) included six leaves corresponding to a gradient in the probability of a large movement event (Fig. 2b). When degree-days were between 330 and 502, the probability of a large movement event increased as expected in relation to RAINAMOUNT24 and RAINDROUGHT. In particular, when RAINAMOUNT24 exceeded 0.05 cm (0.02 in.) and RAINDROUGHT exceeded 4.5 days, which accounted for less than 2% (5/296) of the days, there was always a large movement event. If RAINAMOUNT24 was <0.05 cm, there was still a high probability (57%) of a large movement event, but only if RAINDROUGHT exceeded 8.5 days. Collectively, these two “best” leaves (#4 and #6 in Fig. 2b) accounted for less than 4% (12/296) of the days (or an average of 3 days per year), yet accounted for 40% of the total annual movement (Fig. 2b). With a perfect model, the same number of days would have accounted for 47% of the annual total (Fig. 1c). In addition, these two “best” leaves had a predictive performance ratio of 0.98 (Table 3), indicating that the model was quite robust.

N. viridescens – During the 85-day emigration period each year for juvenile *N. viridescens* (Table 1), movements were the least concentrated of the four species, with an average

Table 2 – Number of large movement events ($\geq 10\%$ of the annual total) of juvenile emigration from natal ponds and adult fall immigration to breeding ponds in four species of pond-breeding amphibians in western Massachusetts between 1999 and 2005

Species – age class	Year	# of large movement events	% large mvmt. events in highest probability leaf
<i>Ambystoma maculatum</i> – juvenile	2000	2	100
	2001	3	33
	2002	4	50
	2003	2	50
	2000–2003	11	55
<i>Ambystoma opacum</i> – juvenile	2000	4	a
	2001	4	
	2002	2	
	2003	3	
	2004	4	
	2005	2	
2000–2005	19		
<i>Rana sylvatica</i> – juvenile ^b	2000	2	50
	2001	1	100
	2002	2	100
	2003	5	100
	2000–2003	10	90
<i>Notophthalmus viridescens</i> – juvenile	2000	1	100
	2001	2	100
	2002	4	100
	2003	4	100
	2000–2003	11	100
<i>Ambystoma opacum</i> – adult	1999	3	33
	2000	3	67
	2001	3	0
	2002	3	67
	2003	3	33
	2004	3	33
	2005	2	100
	1999–2005	20	45
<i>Ambystoma maculatum</i> – adult	1999	3	33
	2000	3	67
	2001	3	67
	2002	2	100
	2003	2	50
1999–2003	13	62	

Also included is the percent of those large movement events that were located in the single “best” leaf in the final regression tree model for each species and age-class.

a Denotes a regression tree could not be built (i.e., tree did not cross-validate).

b The two best leaves are used for juvenile *Rana sylvatica*.

of about three large movement events each year and requiring an average of 16 movement events each year to account for 80% of the total annual emigration (Table 2, Fig. 1d). The final regression tree ($r^2 = 0.11$, $P < 0.01$) included only two leaves based on a split in Julian date (JULIAN; Fig. 2c). All large movement events occurred when Julian date was ≥ 233 (Fig. 2c), although the probability of a large movement event was extremely low (3%; Fig. 3c) because of the large number of days

in this leaf (61%, 208/340). Collectively, this leaf accounted for 96% of the total annual movement, but it required an average of 52 days per year (Fig. 2c). In a perfect model, the same number of days would have accounted for 98% of the annual total (Fig. 1d). In addition, this single “best” leaf (#2 in Fig. 2c) had a predictive performance ratio of 0.7 (Table 3), indicating that the model was less robust than we observed for the other species.

3.2. Adult immigration

A. opacum – During the comparatively short 45-day immigration period each year for adult *A. opacum* (Table 1), movements were highly concentrated, with an average of about three large movement events each year and an average of five movement events required each year to account for 80% of the total annual immigration (Table 2, Fig. 1e). The final regression tree ($r^2 = 0.38$, $P < 0.01$) included four leaves corresponding to a gradient in the probability of a large movement event (Fig. 2d). The probability of a large movement event was greatest (90%; Fig. 3d) when RAIN-AMOUNT24 ≥ 0.55 cm and JULIAN was between 234 and 246 (August 22–September 3). Collectively, this final leaf accounted for only 3% (10/315) of the days (or an average of less than 2 days per year), yet accounted for 39% of the total annual movement (Fig. 2d). In a perfect model, the same number of days would have accounted for 60% of the annual total (Fig. 1e). In addition, this single “best” leaf had a predictive performance ratio of 1.02 (Table 3), indicating that the model was quite robust.

A. maculatum – During the comparatively long 91-day immigration period each year for adult *A. maculatum* (Table 1), movements were highly concentrated, with an average of about 2.5 large movement events each year and an average of six movement events required each year to account for 80% of the total annual immigration (Table 2, Fig. 1f). The final regression tree ($r^2 = 0.41$, $P < 0.01$) included four leaves corresponding to a gradient in the probability of a large movement event (Fig. 2e). The probability of a large movement event was greatest (39%; Fig. 3e) when RAIN-AMOUNT24 was ≥ 0.69 cm, JULIAN was ≥ 279 , and MEAN-TEMP was ≥ 8.6 °C. Collectively, this final leaf included 5% (23/455) of the days (or an average of less than five days per year) and accounted for 64% of the total annual movement (Fig. 2e). With a perfect model, the same number of days would have accounted for 78% of the annual total (Fig. 1f). In addition, this single “best” leaf had a predictive performance ratio of 0.8 (Table 3), indicating that the model was moderately robust.

4. Discussion

Previous investigators have described movement windows for pond-breeding amphibians (Paton et al., 2000; Paton and Crouch, 2002), and/or the role of specific meteorological variables in the timing of movements in general (Semlitsch, 1985; Sexton et al., 1990; Reading, 1998; Todd and Winne, 2006), but to our knowledge, this is the first study to incorporate temporal and meteorological variables in a regression tree framework to describe and/or predict the timing of movement

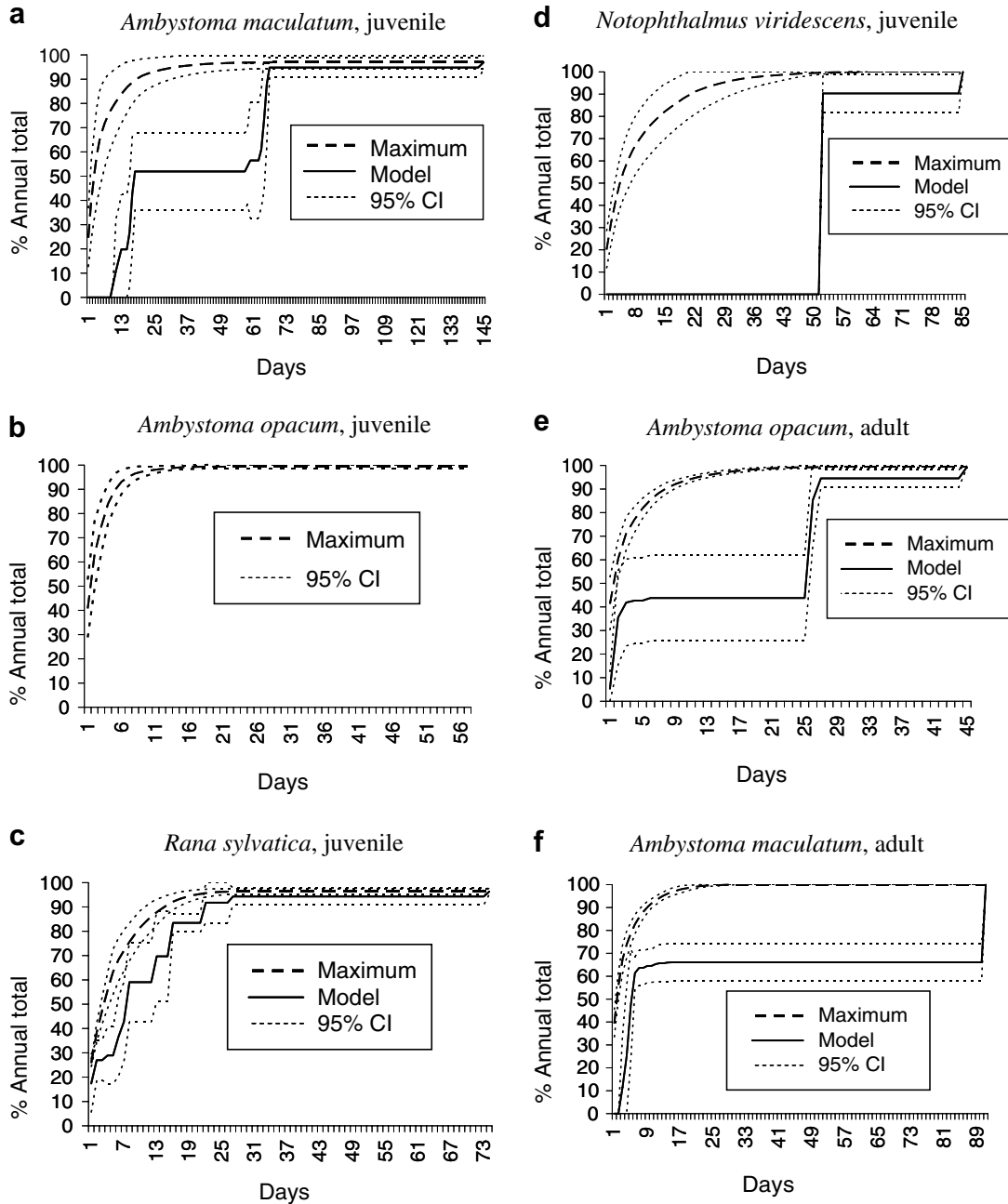


Fig. 1 – Accumulation curves depicting the average (and 95% confidence interval (CI)) number of movement events (days) in a year required to capture any specified percentage of the population (labeled as “maximum”), and similar curves based on the final regression tree (i.e., steps correspond to increments associate with the leaves of the tree) for each study species.

events for these species as the basis for conservation action. Moreover, our findings are particularly robust in comparison to previous work given the considerable spatial (14 ponds) and temporal (4–5 years) scope of the data.

4.1. Migration periods

We documented a more than threefold difference in the total length/duration of the movement window among species and age classes considered (Table 1). These differences may be

partly attributable to differences in life history strategies. For example, among the species where juveniles were considered, *A. opacum* and *R. sylvatica* exhibited the shortest emigration windows (57 and 74 days, respectively) and consistently exhibited the greatest degree of temporal concentration in emigration, requiring an average of four and ten movement nights each year to reach 80% total annual emigration, respectively. Paton and Crouch (2002) suggest that the larval strategy of these two species involves initiating metamorphosis after either a minimum number of days or a minimum size

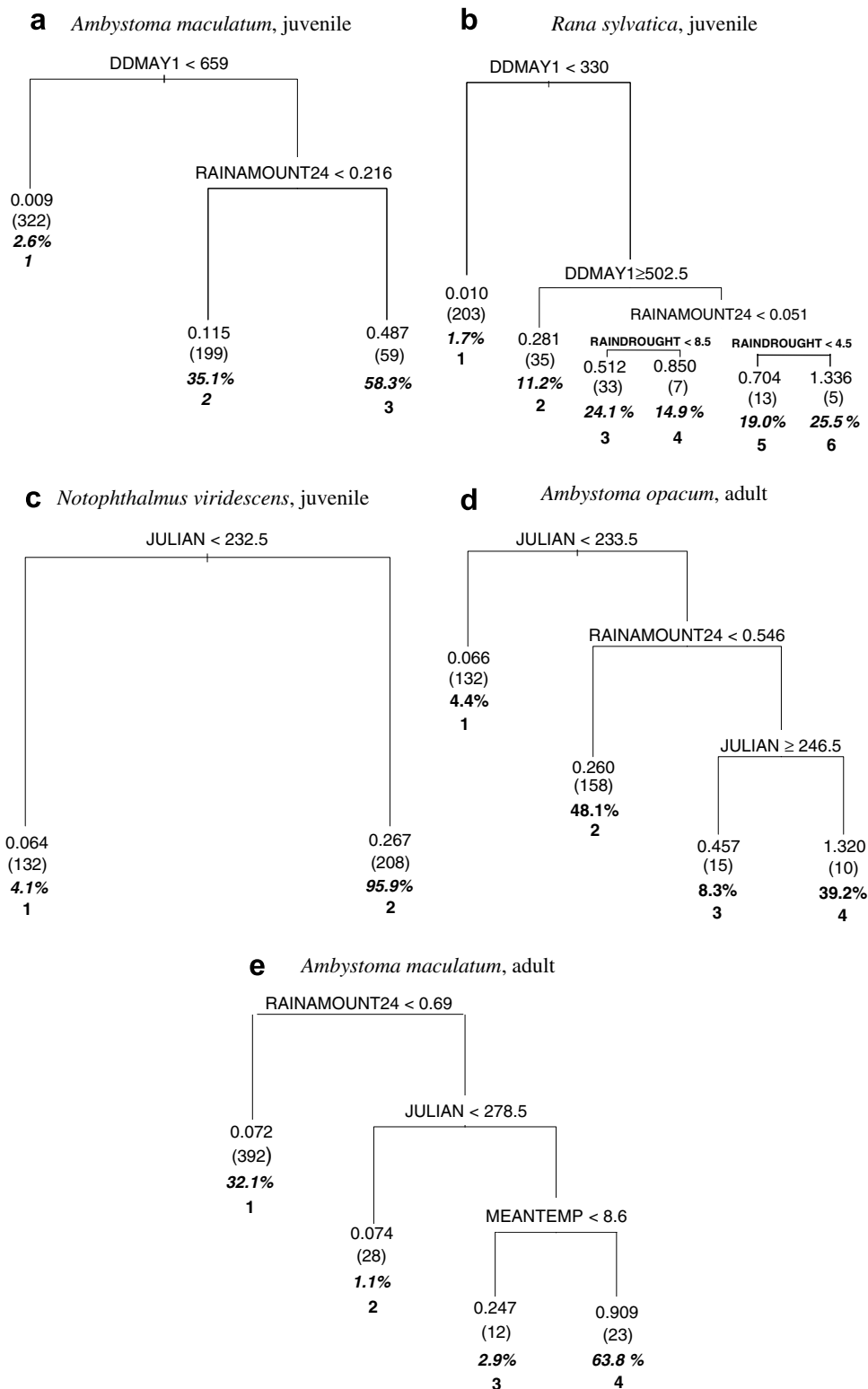


Fig. 2 – Regression trees describing the timing of movement events each study species at 14 ponds in western Massachusetts between 2000 and 2003. The regression trees depicts a recursive partitioning of days (observations) into a set of final leaves based on environmental variables that best explain differences in the magnitude of movement events. Observations that are “true” for the expression go to the left branch; otherwise they go to the right branch. The value at the top of each final leaf corresponds to the mean log(+1)-transformed percent of the total annual capture; the number in parenthesis indicates the number of days in the leaf (pooled across years); the first bold number below represents the percentage of total captures (throughout the entire study period) accounted for by the observations in that leaf; the second bold number represents the leaf number.

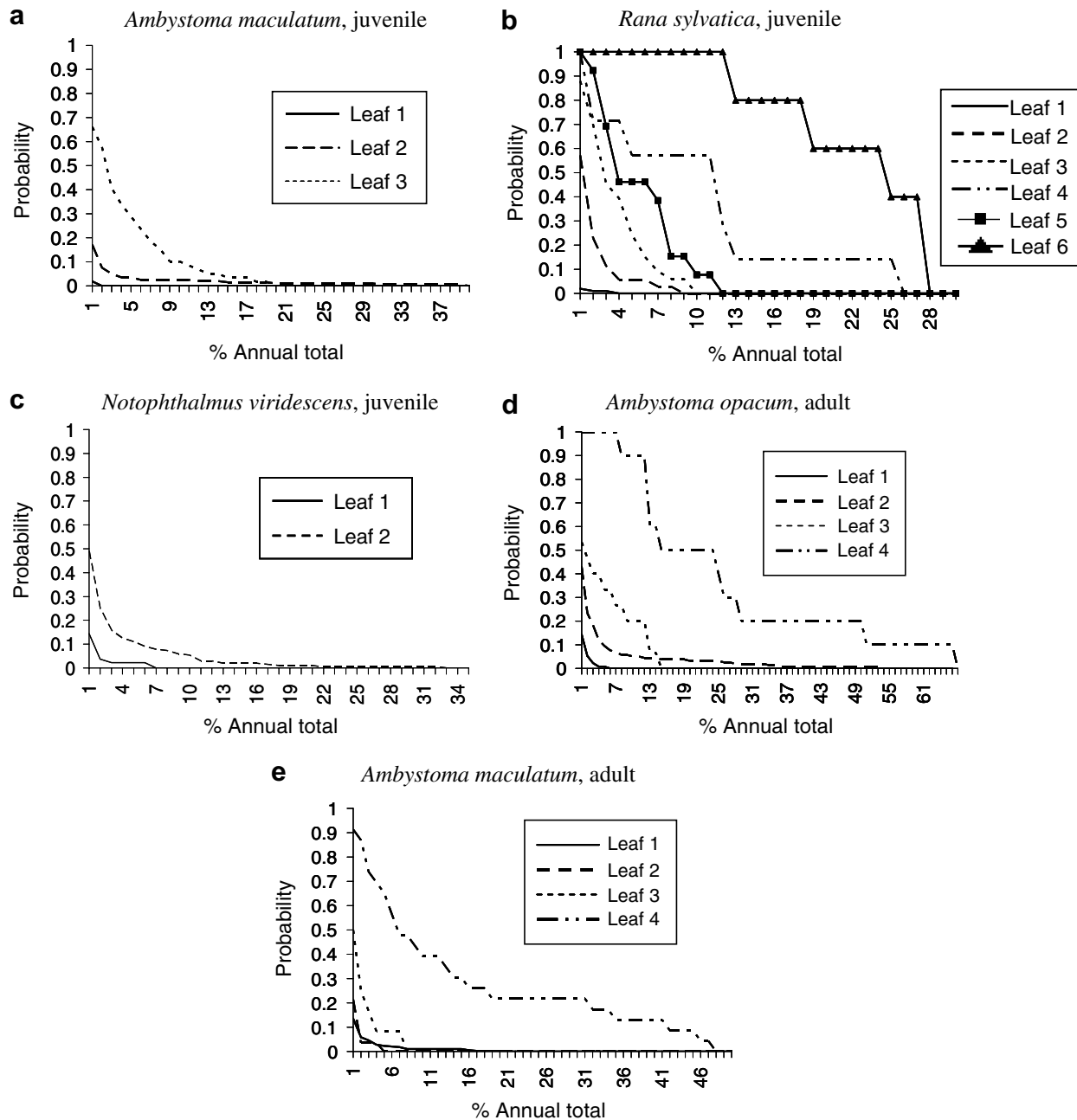


Fig. 3 – Plots depicting the probability that an event of a given percent of the total annual capture will occur for each leaf of the final regression tree for each study species.

(see also Semlitsch and Wilbur, 1988). In either case, given the relatively synchronized breeding of adults (Paton and Crouch, 2002), it is likely that the majority of individuals of each species develop at similar rates and then undergo metamorphosis at about the same time, subsequently emerging within a relatively narrow time window. In contrast, the larval strategy of *A. maculatum* involves maximizing the amount of time spent in the pond (Paton and Crouch, 2002), thereby extending the emigration window as long as possible as governed by the timing of pond drying. *A. maculatum* exhibited the longest emigration window (145 days) and required an average of 11 nights each year to reach 80% total annual emigration.

Similarly, the dramatic differences in the length of the immigration window for the two species examined as adults (45 days for *A. opacum* and 91 days for *A. maculatum*) may be partly attributable to differences in breeding strategies. In contrast to most of their eastern congeners, adult *A. opacum* court in the late summer and early fall and subsequently lay eggs terrestrially in receded or dry pond basins (Noble and Brady, 1933; Bishop, 1941). Eggs are typically brooded by females until rising waters inundate them in the fall, and once inundated, eggs hatch almost immediately into aquatic larvae that overwinter in the ponds (Petranka, 1998). Energetic costs and elevated mortality risks associated with brooding

Table 3 – Performance of regression trees in predicting the timing of juvenile emigration from natal ponds and adult fall immigration to breeding ponds in four species of pond-breeding amphibians in western Massachusetts between 2000 and 2003

Species – age-class	Holdout year	% Total annual capture in “best” leaf		Performance
		Predictive model (3, 4, or 6-year tree)	Validation (holdout year)	
<i>Ambystoma maculatum</i> – juvenile	2000	45.03	56.98	1.27
	2001	54.60	35.86	0.66
	2002	53.75	35.26	0.66
	2003	51.35	56.67	1.10
				Mean = 0.92
<i>Rana sylvatica</i> – juvenile	2000	96.17	96.11	1.00
	2001	95.35	85.49	0.90
	2002	96.51	95.10	0.99
	2003	95.51	98.08	1.03
				Mean = 0.98
<i>Notophthalmus viridescens</i> – juvenile	2001	92.41	84.06	0.91
	2002	89.10	43.90	0.49
				Mean = 0.70
<i>Ambystoma opacum</i> – adult	1999	44.01	14.79	0.34
	2000	a	a	a
	2001	42.40	0.00	0.00
	2002	33.92	49.82	1.47
	2003	42.01	67.12	1.60
	2004	37.52	23.52	0.63
	2005	37.32	77.69	2.08
				Mean = 1.02
<i>Ambystoma maculatum</i> – adult	1999	65.89	50.26	0.76
	2000	a	a	a
	2001	64.08	15.11	0.24
	2002	62.37	72.69	1.17
	2003	85.38	89.36	1.05
				Mean = 0.80

For each holdout year, we developed a regression tree based on the remaining three years and calculated the percent of total annual capture accounted for by the single “best” leaf (labeled “predictive model” in table). Based on this model, we predicted movement for the holdout year and calculated the same metric for the holdout year observations (labeled “validation” in table). A performance index was calculated as the ratio of the percent total annual capture accounted for in the validation year relative to the predictive model. A performance index $\cong 1$ means that the model resulted in perfect prediction.

a Denotes a regression tree could not be built (i.e., tree did not cross-validate).

eggs may exert strong selection for optimal timing of breeding so that females can mate and deposit eggs as close to (but not after) the time of pond filling as possible. Vulnerability to freezing temperatures (at northern latitudes) and/or desiccation may further constrain an optimal window for breeding. Conversely, the relatively protracted movement window observed for *A. maculatum* is not surprising given that the fall immigrations are non-breeding migrations, as this species typically breeds in the spring in the northeastern US (Klomens, 1993). Although the purpose of these fall migrations is unclear, it seems plausible that these are “staging” events by a portion of the adult population in order to establish an overwintering location near the breeding site that will facilitate an early arrival to the breeding pond the following spring (Zweifel, 1989). In a recent telemetry study of spotted salamander adults in Rhode Island, McDonough-Haughey and Paton (in press) found that only male individuals made fall migrations back toward breeding ponds; females tended to remain away from ponds.

4.2. Environmental correlates of large movement events

Our results supported all of our *a priori* hypotheses regarding environmental correlates of large movement events. First, we hypothesized that Julian date would function as a constraint on the timing of both juvenile emigration and adult immigration events, consistent with the findings of other studies (e.g., Paton and Crouch, 2002; Vasconcelos and Calhoun, 2004). In our study, there was a clearly defined migration window for each species and age class (that was relatively consistent from year to year), although the start and end of the window varied considerably among species (Table 1). Julian date was a primary splitting variable in the final regression trees in three of the six cases examined, although it was only truly effective in explaining the timing of large movement events for adult immigration in *A. opacum* and *A. maculatum* (Fig. 2d and e).

Second, we hypothesized that degree-days would provide a more relevant predictor of the larval development period and therefore the timing of juvenile emergence from the ponds,

than Julian date. Indeed, in the two cases in which Julian date was not in the final model (juvenile emigration of *A. maculatum* and *R. sylvatica*), degree-days was the first splitting variable in the tree (Fig. 2a and b). The occurrence of a minimum number of degree-days for emergence of both species is consistent with the general understanding that larval developmental rate in aquatic amphibians is positively associated with water temperature (Newman, 1989; Hayes et al., 1993). The relative importance of degree-days in explaining the timing of juvenile emigration in these species is in fact remarkable given the number of other unrelated factors known to affect larval development rates in these and other pond-breeding amphibians. For example, the duration of the larval period to metamorphosis can fluctuate within a species as a function of different densities of competitors and predators (Wilbur, 1972, 1980; Semlitsch and Wilbur, 1988; Berven, 1990), food levels (Berven and Chadra, 1988; Leips and Travis, 1994) and the timing of pond drying (Semlitsch, 1987; Wilbur, 1987; Semlitsch and Wilbur, 1988; Skelly, 1996; Paton and Crouch, 2002).

Third, because the study organisms are ectotherms, we hypothesized that both juveniles and adults would show greater propensity for movement on warm days and nights, especially when accompanied by precipitation. We found no direct evidence that temperature was important for the timing of juvenile emigration, perhaps because the temperatures were relatively warm during most of the juvenile emigration period for all species. However, we did observe an important role of temperature in the timing of adult *A. maculatum* emigrations in the fall. Specifically, given adequate rainfall (≥ 0.69 cm) within a 24 h period after Julian date 278 (October 5), there was a minimum mean daily air temperature threshold (8.6 °C) that was always met or exceeded before the majority of large fall immigrations occurred (Fig. 2e).

Fourth, we hypothesized that both juveniles and adults would show greater propensity for movement following or during precipitation, especially when accompanied by warm temperatures, although we were uncertain as to the specific nature of the relationship (i.e., the amount, duration or timing of precipitation needed to trigger a movement event). Our results indicate that the amount of rain during the 24 h period preceding capture was an important variable affecting the probability of a large movement event in four of the six cases (species and age class) examined (Fig. 2a, b, d, and e). For each species and age class there appeared to be a species-specific minimum amount of rain before the majority of large movement events occurred. These results are consistent with the results from other studies (Sexton et al., 1990; Todd and Winne, 2006) and are not surprising given that amphibians are known to be highly prone to desiccation (Feder, 1983). The one exception to this pattern (where a regression tree was built) was juvenile *N. viridescens*, which apparently has a high tolerance to dehydration and rapid rehydration rate compared to other species of amphibians (Walters and Greenwald, 1977).

Lastly, we hypothesized that the propensity for movement during or following a warm, precipitation event would increase as the period without precipitation prior to that event increased (Todd and Winne, 2006). As we suspected, juveniles of at least one species (*R. sylvatica*) exhibited a higher probability of a large movement event when enough precipitation

(the proximate trigger for a movement event) followed a lengthy drought period (Fig. 2b). Moreover, there was some evidence in the case of *R. sylvatica* to suggest that after a long period without rain, less rain was required to trigger a large movement event. It is unclear why the length of the drought period was relatively less important for the other species and age classes examined.

While the environmental variables we considered were sufficient to predict large movement events for most species and age classes, they were not able to reliably predict large movements of juvenile *A. opacum*. We suspect that we failed to include some important regional variables that exclusively affect this species due to its unique fall breeding strategy. In particular, the timing of nest inundation (and concurrent initiation of the larval period) can vary considerably among years due to variation in timing of pond filling (Gamble, 2004). In years when nests flood later, larvae have a shorter period of growth during the fall compared to years in which nests flood earlier. Consequently, the timing of pond filling in the fall may influence larval development and thus the timing of emergence in the spring.

4.3. Scope and limitations

The conservation implications discussed above must be interpreted in the context of the scope and limitations of our study. First, our results pertain to the movement of individuals at the immediate pond periphery (3 m from high water mark). Unfortunately, we do not know how far: (1) adults traveled during the night of immigration, or (2) juveniles would have traveled during the night of emigration. Therefore, we cannot determine with any certainty how many of these individuals would likely cross a road at a given distance from the pond during the night of immigration (adults) or emigration (juveniles).

Second, our study was conducted in a single study site consisting of 14 ponds in relatively close proximity (<1.5 km). Thus, all ponds and individuals were subject to the same general weather patterns. It is unclear whether the movement patterns we observed in response to meteorological conditions hold for other geographic regions.

Third, precipitation data used in these analyses were only available as daily totals (midnight-to-midnight). If precipitation data was available at a finer-scale resolution (e.g., hourly), then regression trees may have been more effective in describing large movement events. Additionally, weather data was collected off-site (at a weather station approximately 8.0 km from the study sites) and it is unknown if collection of weather data at our study sites would have improved our results.

4.4. Future directions

In order to be effective, conservation strategies designed at protecting pond-breeding amphibians must evolve with the increased understanding of these animals' life history patterns and the impacts human activities have in relation to these. For example, research has documented that many pond-breeding amphibian species are primarily terrestrial organisms that migrate to breeding wetlands for reproduction

purposes, after which time they return to surrounding uplands (Semlitsch, 1998; Semlitsch and Bodie, 2003). Due to considerable distances traveled (Semlitsch, 1998) there is a likelihood individuals will encounter roads (and hence, be exposed to potential road mortality) during these migration events, increasingly so in developed areas. Recent research suggests that road mortality rates during these migratory events may be considerable enough to significantly reduce the long-term population persistence of local populations for at least one species (*A. maculatum*) in central and western Massachusetts, USA (Gibbs and Shriver, 2005).

In response to an increased awareness of road-mortality events, local communities throughout Massachusetts have employed specific conservation strategies aimed at minimizing this road mortality of pond-breeding amphibians. One such conservation strategy which holds considerable promise involves closing specific road segments to vehicle traffic during nights when activity of pond-breeding amphibians on roadways is expected to be high (R. Cook, pers. comm.). Unfortunately, at the current time these road closure events are largely employed via a subjective decision-making process (i.e., nights when those implementing closures “think” large number of individuals will be on roadways), primarily due to the lack of an objective means (i.e., scientifically generated predictive models) to guide when road-closures would be most effectively implemented.

Results obtained from our analyses suggest that regression trees analysis may be effective in describing/predicting when large movement events of particular species and age-classes of pond-breeding amphibians occur, which can then be used to guide when road-closures would be most effectively implemented. For example, the largest (on average) movement events of adult *A. opacum* occurred in the leaf where the Julian date (JULIAN) was between 234 and 246 and the amount of rainfall during the previous 24 h period (RAINAMOUNT24) was ≥ 0.546 cm, which included 39% of the total captures of adult *A. opacum* throughout the entire study period during only 1–2 nights annually (Fig. 2d). The likelihood of implementing road closures in this case would be increased because a relatively large percent of individuals were encompassed in a comparatively small number of nights.

We encourage biologists to use existing data in a regression trees framework to examine environmental correlates of large movement events of pond-breeding amphibians. Additionally, we encourage biologists to design similar studies at broad spatial (multiple “ponds”) and temporal (multiple years) scales with the goal of constructing predictive models describing the timing of large migration events, which can then be used to more effectively guide conservation practices (i.e., road closures) aimed at protecting pond-breeding amphibians.

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