

## Emigration Orientation of Juvenile Pond-Breeding Amphibians in Western Massachusetts

BRAD C. TIMM, KEVIN MCGARIGAL, AND CHRISTOPHER L. JENKINS

We studied the emigration of juvenile age-class individuals of four species of pond-breeding amphibians at 14 seasonal ponds over four consecutive years in western Massachusetts. Emigration orientation of each species was non-uniform for the majority of pond-years examined. While orientation was decidedly non-uniform in most individual pond-years, combining data from successive years led to a more uniform distribution for each of the study species, although in no case did it actually become statistically uniform. Additionally, while the exact orientation of each species at each pond differed among years in almost all cases, there were some directions with consistently greater than or less than expected use across years for all ponds. Similarly, despite overall differences in orientation of individuals among ponds for a particular species, or among species at a particular pond, there were some consistent directional biases (positive and negative) across ponds and across species. Overall, our results suggest that while there are some consistent patterns in emigration among years, species, and ponds, variability in orientation over time and space is the norm. Thus, there is a need to acquire data over several years and several ponds before reaching conclusions regarding orientation patterns and making informed conservation decisions.

THE homing and orientation abilities of amphibians have been well documented in the scientific literature over the years. Several studies have documented individuals returning to “home” areas after translocation up to several hundred meters away (Whitford and Vinegar, 1966; Shoop, 1968). In addition, a variety of studies have shown an apparent directional component (i.e., orientation) in the movement towards and/or away from breeding sites by individuals of several species and/or age classes (Sinsch, 1990; Dodd and Cade, 1998; Johnson, 2003). Investigators have proposed a number of possible mechanisms for these behaviors, including magnetic orientation (Phillips, 1986), sun-compass orientation (Landreth and Ferguson, 1967), celestial orientation (Ferguson and Landreth, 1966), olfactory recognition (Grant et al., 1968; Madison, 1969; McGregor and Teska, 1989), orientation via plane-polarized light (Taylor and Adler, 1973), and upland habitat recognition (Rosenberg et al., 1998; deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002).

Evidence suggests that newly metamorphosed juveniles (metamorphs) and sub-adults are responsible for the majority of dispersal in some species of pond-breeding amphibians (Gill, 1978; Berven and Grudzien, 1990; Sjogren-Gulve, 1994). If juveniles, in particular, emigrate from natal ponds in a non-random fashion, as has been documented in a number of cases (Dodd and Cade, 1998; Malmgren, 2002; Johnson,

2003), then the orientation of these movements could have significant implications for metapopulation structure and dynamics (Rothermel, 2004). For example, if juveniles are emigrating primarily in one direction then the likelihood of some individuals encountering neighboring wetlands (and potentially colonizing these) may be reduced in comparison to a more uniform pattern of juvenile emigration from natal ponds. Moreover, if there is pronounced orientation during emigration, and if these patterns are consistent across years, then these movement pathways can be identified and targeted for conservation protection. Identifying these movement pathways may be critical to the conservation of these species since existing regulatory frameworks alone are inadequate to meet the long-term conservation needs of many pond-breeding amphibians (Calhoun and Klemens, 2002; Burne and Griffin, 2005; Gamble et al., 2006).

Most studies that have quantified orientation of emigrating juveniles in pond-breeding amphibians have considered only a single local population (or breeding pond) over one or more years, or multiple populations over a single year (Stenhouse, 1985; Dodd and Cade, 1998; Johnson, 2003). Results from such studies may be limited given the complex spatial and temporal dynamics of amphibian populations and the potential that many species, especially pond-breeding amphibians, may persist in constantly changing metapopulations (Gill, 1978; Trenham

et al., 2001; Gamble, 2004). While there has been debate whether populations of pond-breeding amphibians operate in a metapopulation context in real landscapes (Marsh and Trenham, 2001), results from a larger study suggest that metapopulation theory is supported for at least one species, *A. opacum*, in the study area (Gamble, 2004).

As part of a larger investigation into the spatial dynamics of the Marbled Salamander (*Ambystoma opacum*), we measured the emigration orientation of newly metamorphosed juveniles of four species of pond-breeding amphibians (Marbled Salamander; Spotted Salamander, *Ambystoma maculatum*; Red-spotted Newt, *Notophthalmus v. viridescens*; and Wood Frog, *Rana sylvatica*) at 14 breeding ponds in western Massachusetts, USA, each year from 2000 to 2003. We focused solely on juvenile age-class individuals because our arrays were not opened early enough in each year to capture all adults of the four study species during their breeding migrations. In this study, we address three principal questions: At the scale of the local pond, are there consistent directional preferences in emigration orientation over time for each species? If so, are the local directional preferences over time consistent among species? At a landscape scale, are there consistent directional biases in emigration orientation over time among ponds?

#### MATERIALS AND METHODS

*Study area.*—The study area encompassed 14 seasonal ponds within a 1-km radius circular area (approx. 314 ha) of contiguous mixed-deciduous hardwood forests in the southern portion of Hampshire County in western Massachusetts. Elevation ranged from approximately 60 m to 200 m. The terrain was highly variable with numerous ridges and depressions in which several seasonal wetlands have formed. The vegetation was classified as “transition hardwoods–White Pine–Hemlock forest” (Westveld, 1956) and was dominated by a mixture of oak (*Quercus*), maple (*Acer*), birch (*Betula*), hickory (*Carya*), and two conifer species (*Tsuga canadensis* and *Pinus strobus*); it had an estimated modal stand age of 70 years. The understory was highly variable and consisted of sparse to dense patches of shrubs, including blueberries (*Vaccinium*), huckleberries (*Gaylussacia*), Maple-leaved Viburnum (*Viburnum acerifolium*), Mountain Laurel (*Kalmia latifolia*), and Witch Hazel (*Hamaemelis virginiana*).

The 14 study ponds ranged in size at high water from 0.03 ha to 0.35 ha and varied considerably in structure, including shrub-dom-

inated, open-deep water, and shallow (open and/or vegetated) ponds. Two of the ponds contained an abundance of *Sphagnum* and one appeared to be human-made. Hydroperiods and water-level fluctuations varied significantly among ponds and years (Gamble, 2004), with most ponds typically drying between July and September; some ponds do not dry in very wet years.

*Field methods.*—We completely encircled all seasonal ponds with continuous drift fences and pitfall traps between 1998 and 2000 to monitor amphibian movements. Drift fences were constructed of 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 cans) flush to the ground surface on both sides of the fence at 10-m intervals. Each trap contained a moist 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 emergence periods of the four focal species. For each individual we recorded species, age class (juvenile, sub-adult, and adult), and trap number (among other attributes) and then released it on the opposite side of the fence. During the off-season, we closed all traps by inverting pitfall cans and removing any remaining funnel traps. We also removed sections of fence at regular intervals to allow for relatively unencumbered passage of organisms.

*Data analysis.*—We tallied the number of captures of emigrating juvenile age-class individuals of each species ( $n = 4$ ) at each inside trap (i.e., pond side of the fence;  $n = 9\text{--}37$ ) at each pond ( $n = 14$ ) in each year ( $n = 4$ ). At each pond, we assigned each trap to one of eight directional bins (45-degree intervals centered around N, NE, E, SE, S, SW, W, and NW). At each pond, each bin had the same (or nearly the same) number of traps. We used nonparametric analyses instead of circular statistical techniques because our analyses consistently violated assumptions of the parametric circular tests (Batschelet, 1981). In particular, orientation was often bi- or multi-modal, which violated the assumption of a Von Mises distribution (the normal equivalent for circular data) upon which the parametric tests are based.

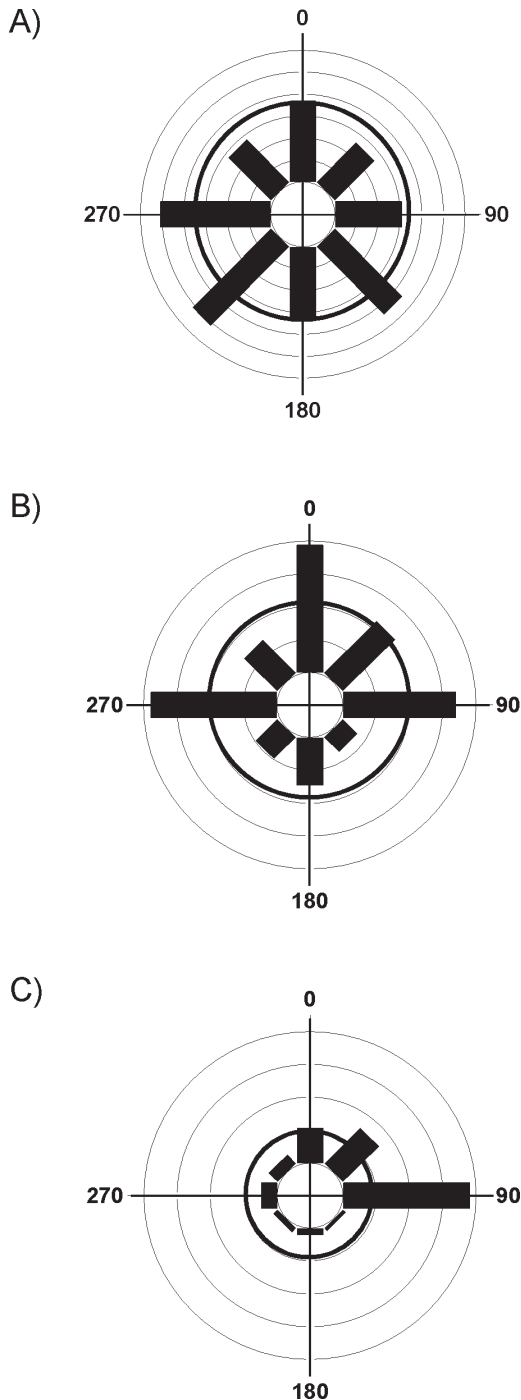


Fig. 1. Circular histograms depicting an example of (A) low (*Ambystoma maculatum*, pond 1), (B) moderate (*A. maculatum*, pond 9), and (C) high (*Notophthalmus viridescens*, pond 9) departure from a uniform distribution for emigrating juvenile amphibians leaving natal ponds in western Massachusetts based on eight directional bins. The cases shown correspond to a low (2.82), moderate (6.29),

In addition, in all analyses we included only pond-years in which a minimum number of 50 individuals of the corresponding species were captured.

To evaluate whether emigration movements were non-uniform, we conducted a separate chi-square goodness-of-fit test of (equal) expected frequency of individuals among the directional bins for each species at each pond and year (species-by-pond-by-year). We interpreted rejection of the null hypothesis as evidence of significant orientation (i.e., concentration of movement) in one or more directions.

To evaluate whether emigration movements were non-uniform when considered over a several-year period (instead of a single year), we pooled captures across years and otherwise conducted the same series of tests as above. To investigate this relationship further, we computed a relative "index of non-uniformity" as the mean across bins of the absolute difference between observed and expected percentage of captures. This index provides a relative measure of the magnitude of non-uniformity in capture distribution, with larger values indicating greater departure from a uniform distribution among directional bins (Fig. 1). This index is a relative measure because it does not vary with the total number of captures at a pond-year. Moreover, it has a straightforward intuitive interpretation as the mean percentage deviation from a uniform expected distribution in any particular direction. We computed this index for each unique species-by-pond-by-year combination in which a minimum number of 50 individuals of the corresponding species were captured. We then computed the mean index of non-uniformity (and standard error) for each species across observations, where each observation represented a specific pond-year combination. For example, a species with sufficient sample sizes at all 14 ponds in each of four years would have a total of 56 observations. We then pooled the data for each species at each pond across all possible combinations of two years (six possibilities), three years (four possibilities), and across all four years, and computed the means and standard errors for

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and high (11.32) index of non-uniformity, which represents the mean across bins of the absolute difference between observed and expected percentage of captures. Each arm depicts one of the eight directional bins, concentric circles represent a given raw number of individuals, and the bold circle delineates the expected bin value given a uniform distribution.

each pooling in a similar fashion. In this manner, we summarized the average magnitude of non-uniformity for each species at each pond in relation to the number of years in which data were pooled. Because the observations used to compute the index of non-uniformity were not independent, we did not use the index to conduct formal hypothesis tests.

To evaluate whether emigration orientation differed among ponds, we conducted a chi-square test of heterogeneity among ponds for each species and year (species-by-year). Specifically, this test compared the overall deviation of observed captures from expected captures in each of the eight directional bins among all ponds for each species and year using an  $n \times 8$  contingency table (where  $n$  = the number of ponds during that year that met the minimum sample size requirement of 50 individuals captured emigrating for the corresponding species, and 8 = the number of directional bins). To determine whether among-pond differences remained the same or changed when considered over a longer time scale, we repeated these analyses with the data pooled across all years. These tests indicate whether there are overall differences among ponds, although they do not elucidate the exact nature of those differences. For example, a significant overall difference does not indicate whether a single pond deviates from the rest of the ponds or whether the differences are ubiquitous among ponds, nor does it distinguish the nature of the differences at the level of individual directional bins. To elucidate the directional nature of differences (or similarities) among ponds, we computed the mean (and standard error) across ponds in the deviation from expected use in each directional bin. Specifically, for each directional bin we computed the difference between observed and expected use at each pond and then calculated the mean (and standard error) across ponds. We did this for each year separately and for the data pooled across all years. We interpreted a mean deviation greater than two standard errors from zero as evidence of significantly greater (positive deviation) or less (negative deviation) than expected use.

To evaluate whether emigration orientation varied among years, we conducted a chi-square test of heterogeneity among years for each pond and species (pond-by-species). Specifically, this test compared the overall deviation of observed captures from expected captures in each of the eight directional bins among all years for each species at each pond using an  $n \times 8$  contingency table (where  $n$  = the number of years at that pond that met the minimum sample size requirement of

50 individuals captured emigrating for the corresponding species, and 8 = the number of directional bins). In addition, we conducted similar tests for each pairwise comparison of years meeting minimum sample size requirements. To elucidate the directional nature among years, we computed the mean (and standard error) across years in the deviation from expected use in each directional bin, as discussed previously.

To evaluate whether there was similar orientation in patterns of emigration among species, we conducted a separate chi-square test of heterogeneity among species for each pond and year (pond-by-year). Specifically, this test compared the overall deviation of observed captures from expected captures in each of the eight directional bins among all species for each year at each pond using an  $n \times 8$  contingency table (where  $n$  = the number of species at that pond that met the minimum sample size requirement of 50 individuals captured emigrating for the corresponding year, and 8 = the number of directional bins). In addition, we conducted similar tests for each pairwise comparison of species meeting the minimum sample size requirements. To examine whether the pattern of orientation emigration among species was similar over a longer time scale, we conducted the same analyses as above but with the data pooled across all years. To determine a directional nature among species we computed the mean (and standard error) across species in the deviation from expected use in each directional bin, similar to above.

To minimize the probability of making Type I errors among all previously described chi-square tests, we employed a sequential Bonferroni procedure for each family of tests conducted. Specifically, following the procedure developed by Hochberg (1988), in each of the four families of chi-square tests we ranked the  $P$ -values from largest to smallest and tested the largest at  $\alpha$  (0.05), the second largest at  $\alpha/2$ , and so on until we reached a significant result. Once a significant result was obtained, that and all remaining tests within that family were deemed significant.

## RESULTS

We recorded 95,281 captures of emigrating juvenile age-class individuals of the four study species over the four-year study period. This total was comprised of 15,084 *A. maculatum*, 8,603 *A. opacum*, 19,986 *N. viridescens*, and 51,608 *R. sylvatica*.

*Orientation of movements.*—Emigration movements were almost universally non-uniform across spe-

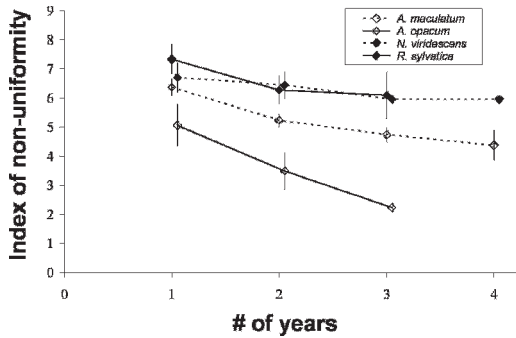


Fig. 2. Mean ( $\pm 1$  SE) index of non-uniformity for emigrating juvenile amphibians leaving natal ponds in western Massachusetts based on eight directional bins, in relation to the number of pooled years of data for each of the four study species. The index of non-uniformity represents the average across bins of the absolute difference between observed and expected percentage of captures. The mean (and SE) was calculated across all ponds and years in which a minimum number of 50 individuals were captured. See text for details on pooling data across years.

cies, ponds, and years. Specifically, there were a total of 99 unique species-by-ponds-by-year combinations, of which 94 had non-uniform emigration distributions, including 39/41 for *A. maculatum*, 10/11 for *A. opacum*, 18/19 for *N. viridescens*, and 27/28 for *R. sylvatica*. Emigration movements were also consistently non-uniform when pooling the data over several years. Specifically, there were a total of 44 unique combinations of species and ponds (pooled across years), of which 43 had non-uniform emigration distributions.

Index of non-uniformity values varied among species and decreased gradually with an increase in the number of years pooled for each species (Fig. 2). Overall, *N. viridescens* and *R. sylvatica* had the most non-uniform distributions, *A. maculatum* was intermediate, and *A. opacum* had the least non-uniform distribution (Fig. 2).

*Differences among years.*—Orientation of emigration movements differed among years in almost all cases, although the magnitude and nature of the differences varied somewhat among species, as demonstrated by the orientation patterns at the respective pond supporting the largest cumulative (over time) emergence of each species (Fig. 3). Specifically, there were a total of 29 unique combinations of species and ponds, of which 27 had differences among years, including 12/12 for *A. maculatum*, 4/4 for *A. opacum*, 3/4 for *N. viridescens*, and 8/9 for *R. sylvatica*. Similarly, there were a total of 87

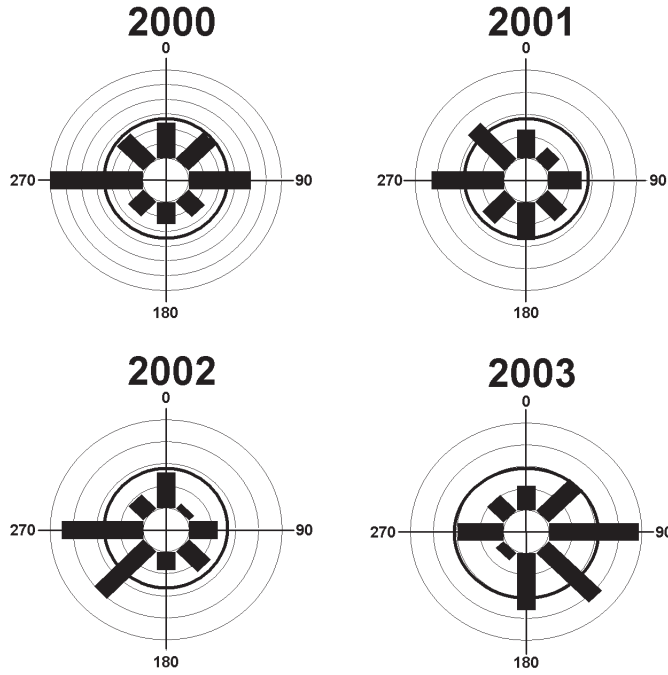
pairwise comparisons between years with unique combinations of species and ponds, of which 77 had differences, including 44/49 for *A. maculatum*, 6/6 for *A. opacum*, 9/13 for *N. viridescens*, and 18/19 for *R. sylvatica*.

Despite the pronounced overall differences among years, there were consistent among-year directional biases (at the level of the individual bin) in emigration movements for each species at every pond. In particular, in every case (species-by-pond) there were typically 1–2 directional bins with consistently greater than expected use and 2–3 directional bins with consistently less than expected use. Thus, for a particular species and pond there were consistent (over time) directional biases to emigration movements, although the level of consistency varied somewhat among species (Fig. 3). Overall (across species and ponds) there were more than twice as many cases with consistently less than expected use of a direction than greater than expected use, and there was some tendency for southern directions (SE, S, and SW) to be used less than expected.

*Differences among ponds.*—Orientation of emigration movements differed among ponds, and this finding was universal among species regardless of whether each year was considered separately or pooled. Specifically, there was a total of 13 unique combinations of species and years meeting minimum sample size requirements, of which all 13 had differences among ponds. Similarly, after pooling data across years, all four species had differences among ponds.

Despite the pronounced overall differences among ponds, there were a number of cases of consistent directional biases among ponds (i.e., greater than or less than expected use of a particular directional bin) involving a particular species either in a particular year or after pooling data across years. There did not appear to be any strong and consistent directional biases to emigration movements across combinations of species and years, although there were a few subtle but noteworthy patterns. First, even though no species had a significant and consistent directional bias (either positive or negative) in all years, there were several cases of consistent (but not always significant) trends. For example, *A. maculatum* had consistently lower than expected emigration to the south and southwest and greater than expected emigration to the west, regardless of the whether the data were pooled across years or not. Second, across species and years, there were almost three times as many cases of consistently less than expected emigration in a specific direction than greater than expected use. Lastly, there was a tendency for

A)



B)

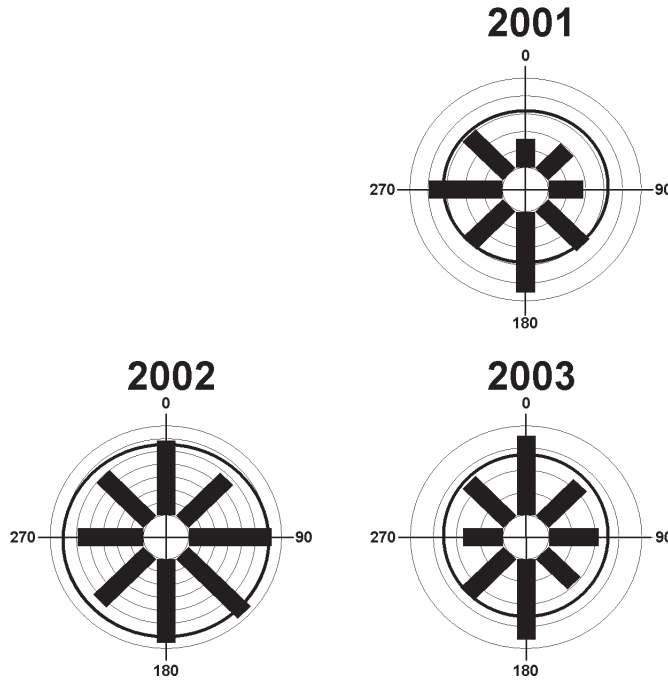
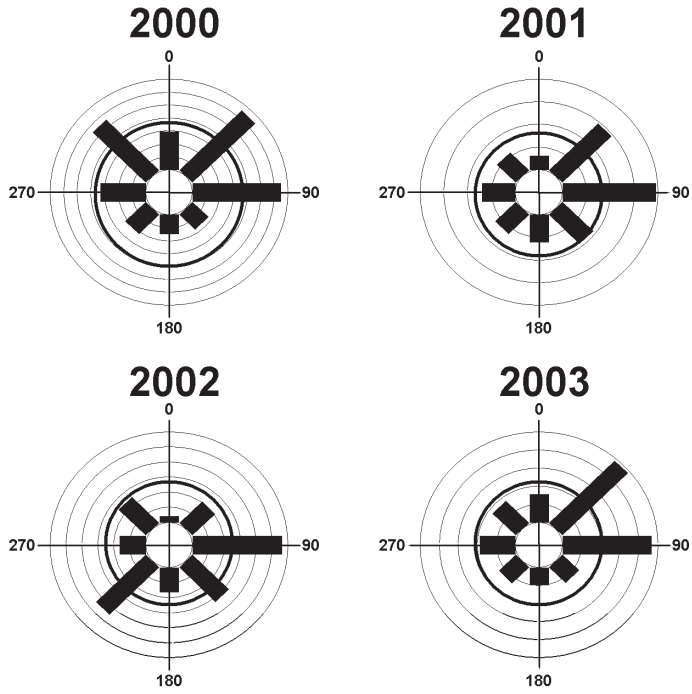


Fig. 3. Circular histograms depicting the orientation of emigrating juvenile amphibians leaving natal ponds in western Massachusetts based on eight directional bins for four species: (A) *Ambystoma maculatum*, (B) *A. opacum*, (C) *Notophthalmus viridescens*, and (D) *Rana sylvatica*. Cases shown represent emigration orientation during years in which a minimum number of 50 individuals were captured at the pond with the greatest cumulative number of emerging metamorphs of the corresponding species over the study period. Each arm depicts one of the eight directional bins, and the bold circle delineates the expected bin value given a uniform distribution.

C)



D)

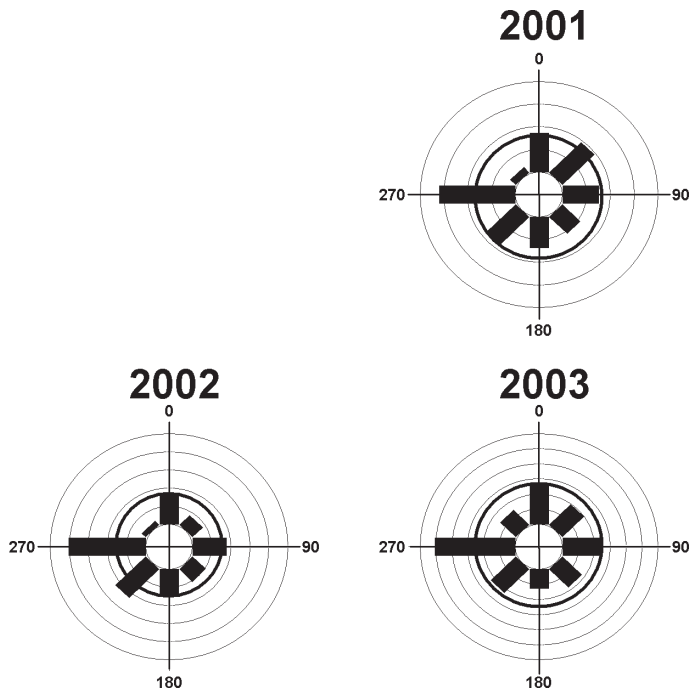
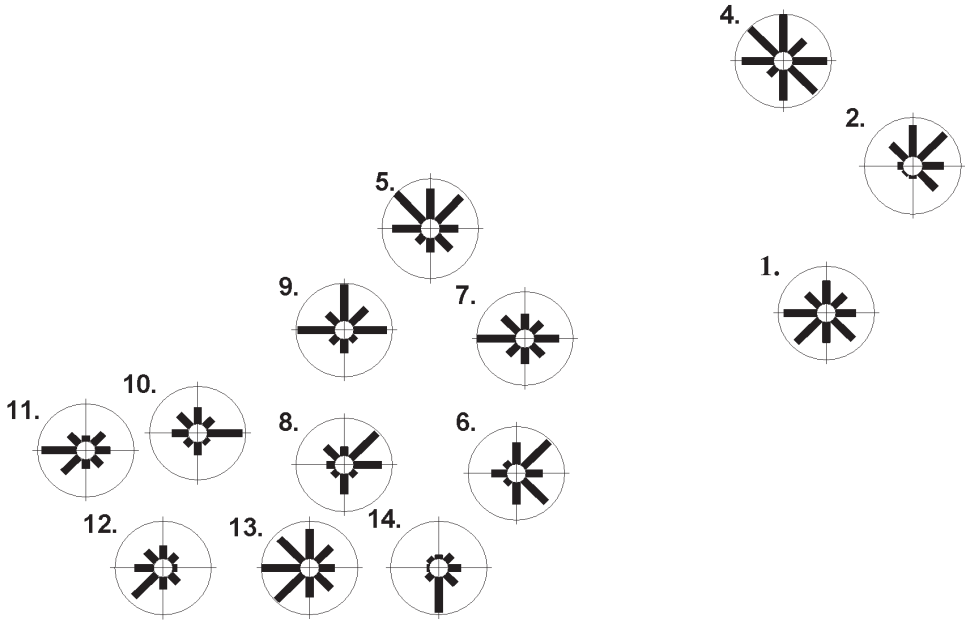


Fig. 3. Continued.

A) *Ambystoma maculatum*



B) *A. opacum*

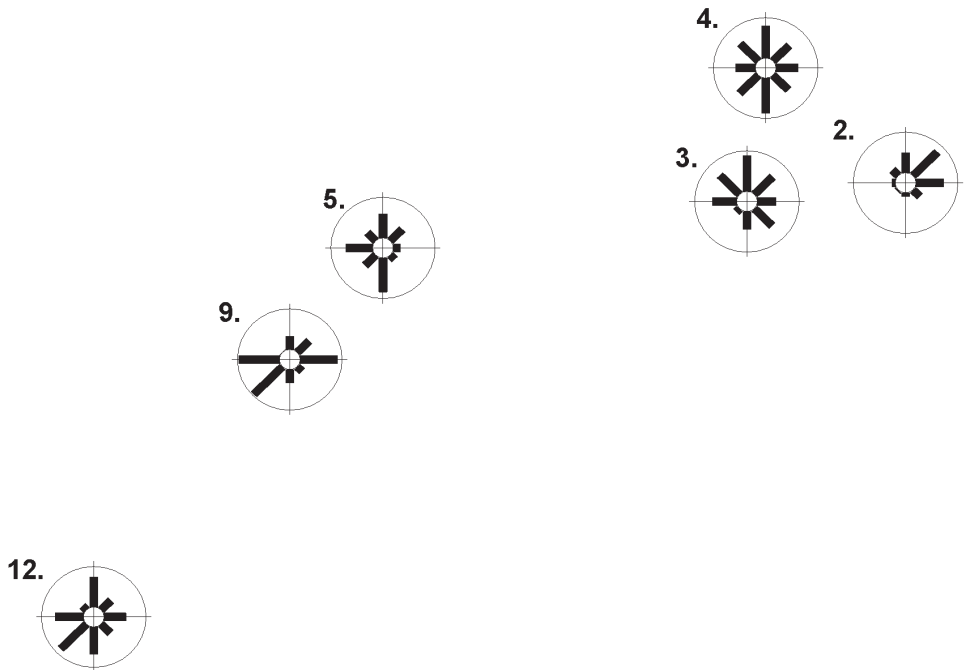
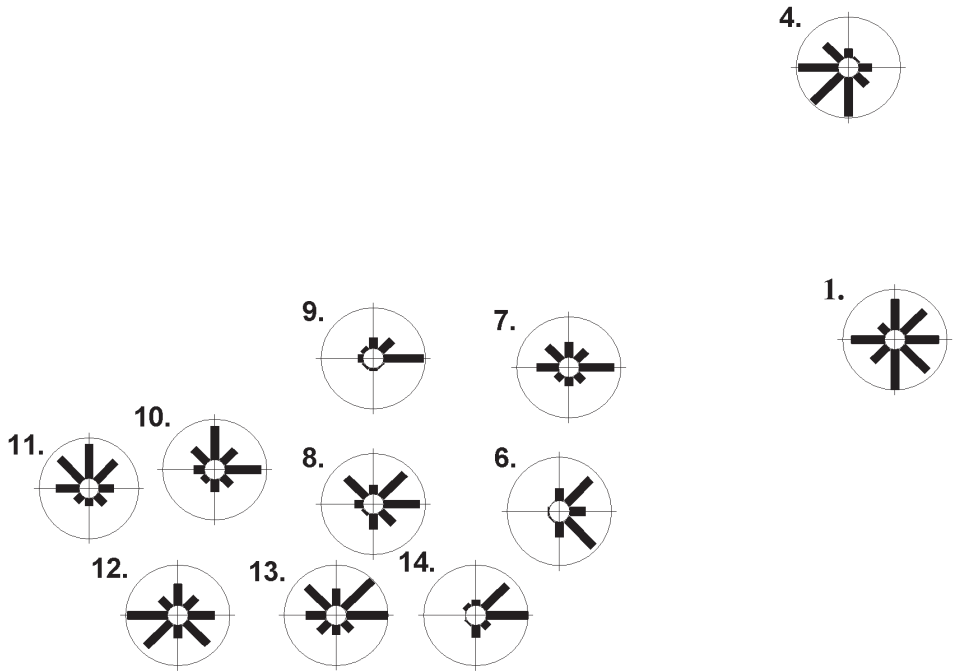


Fig. 4. Diagram showing the orientation of juvenile emigration and the relative spatial distribution (not to scale) of the 14 natal ponds in South Hadley, Massachusetts. Vector plots depict the number of total captures of juveniles of each species (pooled across all years, 2000–2003) in each of eight directional bins at each pond. Numbers adjacent to vector plots are pond identifiers (1–14). Included are only pond-years in which a minimum of 50 individuals of the corresponding species were captured emigrating.



C) *Notophthalmus viridescens*



D) *Rana sylvatica*

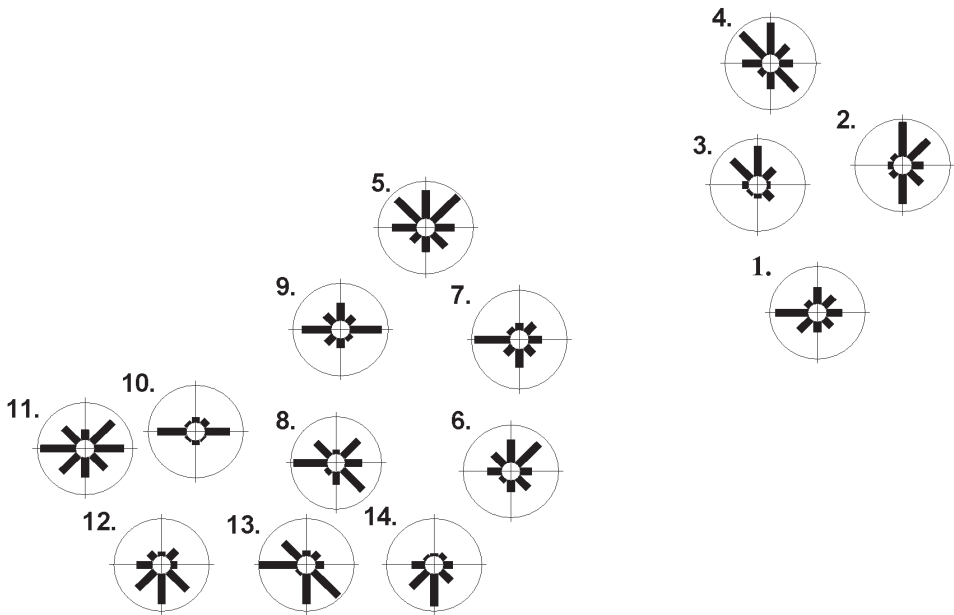


Fig. 4. Continued.

southern directions (SE, S, and SW) to be used consistently less than expected, although this tendency was more pronounced for some species (e.g., *N. viridescens*) than others (e.g., *A. opacum*; Fig. 4).

*Differences among species.*—Emigration movements differed among species, and this finding was nearly universal among ponds regardless of whether each year was considered separately or pooled. Specifically, there was a total of 36 unique combinations of ponds and years, of which 35 had differences among species. After pooling data across years, all 14 ponds had differences among species. Similarly, 63/66 pairwise comparisons between species within unique combinations of pond and year had differences, and 45/47 pairwise comparisons between species had differences after pooling data across years within pond.

Despite the pronounced overall differences among species, there were consistent directional biases among species to emigration movements at each pond in each year (Fig. 5), and in most cases these biases were maintained over time. Overall, there was a tendency for southern directions (SE, S, and SW) to be used consistently less than expected, although this tendency was more pronounced for some ponds than others.

#### DISCUSSION

Our results demonstrate that juvenile age-class cohorts of the four study species consistently had a non-uniform orientation in their emigration away from natal ponds. This finding is consistent with similar studies that have examined amphibian movement patterns in these and other species (Dodds and Cade, 1998; Rothermel and Semlitsch, 2002; Vasconcelos and Calhoun, 2004). In comparison to previous studies, however, our finding is particularly robust, as we observed non-uniform orientation consistently across 14 different ponds, in four different years and for four different species. If these non-uniform orientation patterns are maintained into more distant terrestrial habitats, then our finding has significant implications for metapopulation processes. Specifically, given the particular configuration of breeding sites, non-uniform dispersal may influence the likelihood of individuals encountering other sites and thus affect the dispersal rate between local populations.

For each species, the exact orientation (i.e., proportional use of each direction) at a particular pond varied over time, and this pattern was

nearly universal among species and ponds (Fig. 3). Despite the overall variability, however, there were always some directions with consistently greater than or less than expected use over time. This finding suggests that certain environmental conditions are selected for or against by individuals during emigration. In a related study, Jenkins et al. (2006) reported weak selection by juvenile *A. opacum* for emigration routes with moister substrates and higher canopy cover and basal area, consistent with expectations (deMaynadier and Hunter, 1998; Rothermel and Semlitsch, 2002; Bartelt et al., 2004). Interestingly, *A. opacum* showed the least directional bias during emigration of the four species considered here (Fig. 3B). Thus, we might expect the other species examined to show even stronger environmental determinants. Further elucidating these environmental determinants should be an important focus for future investigation because an understanding of the factors underlying the patterns of emigration orientation would allow managers to identify and target specific areas for conservation. It is important to note that there was no obvious relationship between pond-specific orientation bias and the location and proximity of other ponds, despite the close proximity (e.g., <100 m) of other ponds in several cases. This is not surprising, however, since individuals were emigrating from their natal ponds for the first time and had no prior experience with the surrounding landscape during their search for suitable over-wintering terrestrial habitat.

We documented consistently more cases of negative bias of emigration in specific directions than positive bias, suggesting that individuals may be selecting against certain adverse environmental conditions more so than they may be selecting for favorable conditions. In general, we noted that directions where emigration occurred less than expected were comparatively less variable in proportional use over time, whereas directions where emigration occurred more than expected were often highly variable over time. We interpret this to mean that some directions are actively selected against, perhaps due to unfavorable local environmental conditions, whereas the use of other directions varies somewhat over time, perhaps due to changing environmental conditions (e.g., changes in pond water levels, adjacent upland soil moisture content, and/or vegetation structure) or due to chance alone.

Our results suggest that the magnitude of these pond-specific directional biases diminishes gradually with each additional year of emer-

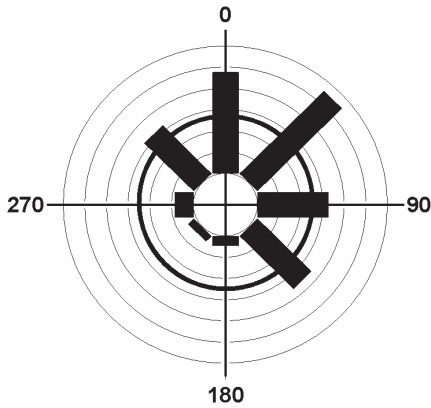
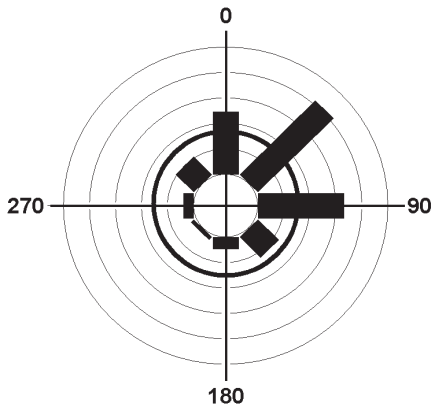
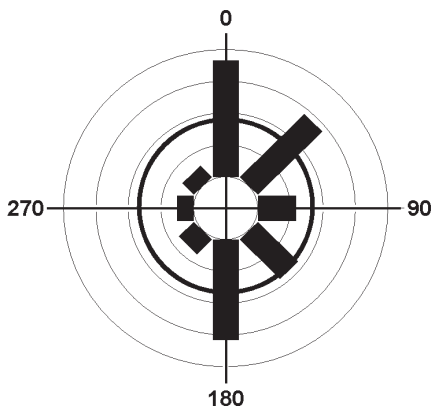
***Ambystoma maculatum******Ambystoma opacum******Rana sylvatica***

Fig. 5. Circular histograms depicting the orientation of emigrating juvenile amphibians leaving natal ponds in western Massachusetts based on eight directional bins for the three species at pond #2 pooled across all years in which a minimum of 50

gence data we collected (Fig. 2). Specifically, we noted a tendency for the emigration pattern of each species at a particular pond to shift slightly over the years, causing the overall orientation pattern to become slightly more uniform with each successive year. However, in no case during the four-year duration of this study did the orientation pattern reach statistical uniformity. Given the limited duration of our study, we are uncertain as to whether the pattern of diminishing non-uniformity over time will continue at the same rate with additional years of data. If the magnitude of non-uniformity continues to diminish over time, then the distribution will eventually become uniform and the directional biases we observed would ultimately be deemed ephemeral. This scenario would have important conservation implications, as it would mean that habitat conservation of targeted areas around breeding sites based on short-term observations may not be effective in the long term. On the other hand, if the magnitude of non-uniformity fails to diminish over time, then habitat conservation of targeted areas around breeding sites may be part of a viable conservation strategy.

At each pond, despite the fact that the exact orientation (proportional emigration in each direction) varied among species, there were some directions that had consistently greater than or less than expected use over time across species (Fig. 5). This finding suggests that different species may be responding similarly to local within-pond environmental factors (e.g., topography, vegetation structure). In addition, it suggests that habitat conservation of targeted areas around breeding sites may be part of a conservation strategy for pond-breeding amphibians in general.

For each species, there were some directions that had consistently greater than or less than expected use over time despite the fact that the exact orientation (proportional emigration in each direction) varied among ponds (in any given year or for all years combined). In other words, whereas the directional biases varied somewhat among ponds, there was an apparent study area-wide (across ponds) directional bias

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individuals were captured. Each arm depicts one of the eight directional bins, and the bold circle delineates the expected bin value given a uniform distribution. The histograms depict a consistent positive bias (greater than expected use) to the N and NE and negative bias (less than expected use) to the SW and W.

for each species. In general, for *A. maculatum* and *R. sylvatica* there was a positive bias to the west and a negative bias to the south-southwest; *N. viridescens* had a positive bias to the northeast and negative bias to the south-southwest; *A. opacum* had only a negative bias to the southeast. Overall, the only consistent study area-wide directional bias among all species was the tendency for a southern (SE, S, and SW directions) negative bias (Fig. 4). Given the study area setting, in particular the relatively homogeneous upland forest matrix, we have not been able to develop any plausible mechanistic explanations for these study area-wide directional biases.

Our findings pertain to the orientation patterns of newly metamorphosed juveniles emerging from their natal ponds. Based on our sampling scheme we cannot infer movement patterns beyond the pond periphery (3 m from high water mark). There is some evidence from our study site that juvenile *A. opacum* shift their orientation slightly and become more concentrated (i.e., more non-uniform) as they move between the pond periphery and 30 m into the uplands (Jenkins et al., 2006). This may reflect selection after leaving the pond basin for favorable upland habitat. However, this pattern was examined and documented for only three ponds in a single year; it is unclear whether this pattern holds for all ponds, over time, or for the other species. Determining the upland movement patterns of emigrating juveniles should be a high priority for future research.

In contrast to other similar studies (Rothermel and Semlitsch, 2002; Vasconcelos and Calhoun, 2004), our study was conducted in a relatively undisturbed landscape. In our study area the breeding ponds are surrounded by relatively homogeneous, contiguous mixed-deciduous hardwood forest. In this setting, upland habitat selection may not have played a significant role in the emigration orientation of individuals away from natal ponds, as has been documented for adults and juveniles in other cases (deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002). However, we are planning to conduct a future investigation measuring habitat variables (e.g., slope, aspect, vegetation) at each site to see if the emigration patterns we have observed are related to any of these environmental variables.

Our findings clearly demonstrate that emigration orientation of newly metamorphosed juvenile individuals of four species of pond-breeding amphibians was consistently non-uniform across ponds, years, and species. The variability in orientation over space and time highlights the

potential pitfalls of short-term studies conducted at only one or a few sites. We observed substantial variability in orientation among individual ponds and years. Hence, even if long-term orientation biases exist at a particular pond, they may not be recognized in any single year of sampling due to stochastic variation in metamorph production and environmental conditions, among other factors. A single year of data may lead to erroneous conclusions regarding long-term orientation patterns.

Despite the overall trademark of spatial and temporal variability in orientation, we noted several patterns of individual directions being used consistently more or less than expected, suggesting that there may be environmental determinants of orientation. These findings invite the suggestion that habitat conservation of targeted areas around breeding sites may be part of a conservation strategy for pond-breeding amphibians. While we entertain this possibility, we stress that it is premature to reach this conclusion until it can be verified that directional biases do not continue to diminish over time as depicted in Figure 2. In the meantime, until we better understand the mechanisms governing emigration orientation and can verify persistent directional biases, along with gaining a greater understanding of movement patterns into the more distant terrestrial habitat, a conservative conservation strategy would require protecting broad terrestrial areas around breeding sites.

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- (BCT, KM) DEPARTMENT OF NATURAL RESOURCES CONSERVATION, UNIVERSITY OF MASSACHUSETTS—AMHERST, HOLDSWORTH NATURAL RESOURCES CENTER, AMHERST, MASSACHUSETTS 01003; AND (CLJ) GREATER YELLOWSTONE PROGRAM, WILDLIFE CONSERVATION SOCIETY, 1780 1<sup>ST</sup> STREET, IDAHO FALLS, IDAHO 83401. E-mail: (BCT) [timmm@forwild.umass.edu](mailto:timmm@forwild.umass.edu); (KM) [mccgarigalk@forwild.umass.edu](mailto:mccgarigalk@forwild.umass.edu); and (CLJ) [cjenkins@wcs.org](mailto:cjenkins@wcs.org). Send reprint requests to BCT. Submitted: 10 Jan. 2006. Accepted: 16 Jan. 2007. Section editor: S. F. Fox.