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Orientation of Movements and Habitat Selection in a Spatially Structured Population of Marbled Salamanders (*Ambystoma opacum*)

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ABSTRACT.—Most studies on orientation of movements of pond-breeding salamanders have considered only a single local population (or breeding pond) during ≥ 1 yr, or multiple populations during a single year. We quantified migratory patterns of Marbled Salamanders at nine breeding ponds during 5 yr in western Massachusetts. Based on captures at drift fences, movements were nonuniform at all breeding ponds. In addition, the direction of orientation differed among breeding ponds and changed slightly across years. Within ponds, orientation of adults and juveniles differed significantly in 52% of comparisons, and adult movements were more directionally concentrated than those of juveniles. In addition, migrating salamanders shifted slightly the orientation of their movements as they traveled into uplands, suggesting that migration routes are spatially complex and that determination of migration “corridors” based on concentrated captures at the pond periphery may be misleading. Although salamanders used migration routes with higher canopy cover, our models did not explain a large portion of the variation in orientation, and protecting areas of high canopy cover alone may not be sufficient as a protection strategy. Our results suggest that movement routes, though perhaps concentrated in the short term, are unpredictable in the long term. Thus, we can offer little evidence that distinct corridors can be identified and protected that would be used consistently over time by migrating or dispersing Marbled Salamanders. Consequently, until we better understand mechanisms governing movements in this species, a conservative conservation strategy would require protecting broad terrestrial areas around breeding sites.

The scientific and conservation communities increasingly recognize the significance of upland areas in proximity to wetlands—both as terrestrial habitats for pond-breeding amphibians and as potential corridors for movement between wetlands (Semlitsch, 2000). A better understanding of movements between uplands and breeding sites is therefore critical to conservation of pond-breeding amphibians, especially as habitat loss and fragmentation increase. Movements among breeding sites may be especially important given complex spatial and temporal dynamics of amphibian populations and the likelihood that many species persist in constantly changing spatially structured populations (e.g., Skelly et al., 1999). Despite being such an important component of population structure and dynamics, little is known about the factors affecting such movements in pond-breeding amphibian populations (Pough et al., 2004).

Previous studies on movements in pond-breeding amphibians suggest that individuals may use “corridors” (i.e., areas of concentrated

use) as they migrate to and from breeding sites (Dodd and Cade, 1998; Johnson, 2003). In particular, a number of studies have documented nonuniform orientation of movements for mole salamanders (*Ambystoma*; Shoop and Doty, 1972; Douglas and Munroe, 1981; Stenhouse, 1985; Phillips and Sexton, 1989). Nonuniform orientation of movements during migration may indicate selection for certain habitats in the uplands surrounding breeding ponds (Stenhouse, 1985). Indeed, individuals of some species emigrate along relatively straight paths to upland areas containing small mammal burrows, which are utilized as terrestrial refuges (Madison, 1997; Jehle and Arntzen, 2000). In addition, there may be selection against movement in or toward disturbed or open-canopy areas (DeMaynadier and Hunter, 1998). Regardless of the mechanisms underlying nonuniform orientation of movements, the conservation implications are clear. If salamanders exhibit nonuniform orientation during migration, then these movement corridors can be targeted for protection. The majority of salamander orientation studies have considered only a single local population (or breeding pond) during ≥ 1 yr, or multiple populations during a single year (e.g., Shoop and Doty, 1972; Douglas and Munroe, 1981; Stenhouse, 1985; Phillips and Sexton, 1989; Dodd and Cade, 1998;

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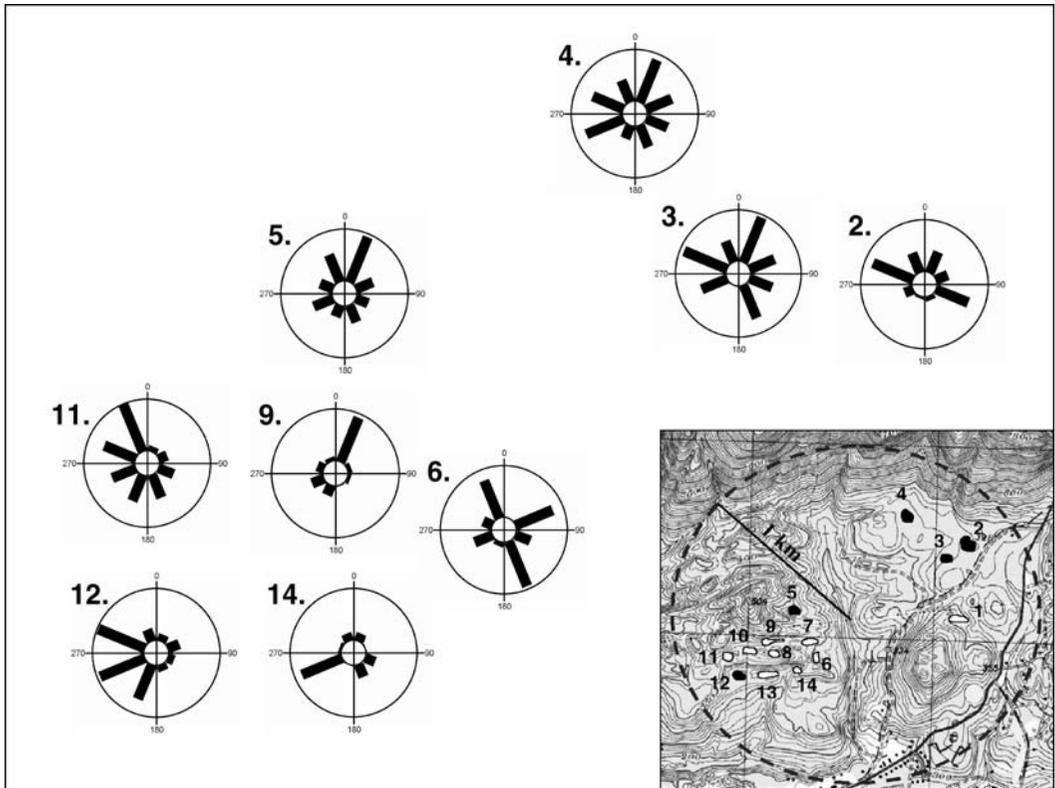


FIG. 1. Diagram showing the orientation of Marbled Salamander movements and the relative spatial distribution of breeding ponds under investigation in South Hadley, Massachusetts. Inset is a map showing the actual distribution of breeding ponds in the study area. Vector plots depict the proportion of total Marbled Salamander captures (pooled across year [1998–2002], age class [juvenile versus adult], and migration period [migration versus immigration] at the 3 m [i.e., shoreline] fence) in each of eight directional bins.

Johnson, 2003). However, studies that address clusters of breeding ponds during multiple years may be critical to understanding orientation because pond-breeding amphibians have complex and dynamic population structures often including multiple interdependent breeding populations (Gill, 1978; Skelly et al., 1999; Marsh and Trenham, 2001; Trenham et al., 2001).

As part of a larger investigation into the spatial structure and dynamics of Marbled Salamander populations, we quantified spatial variation in movement patterns of juvenile and adult salamanders at nine seasonal ponds during 5 yr in western Massachusetts. Our specific objectives were to determine (1) if Marbled Salamanders have clumped (i.e., nonuniform) orientation of movements during breeding migrations, (2) if orientation of movement varies among ponds within a complex of local populations, (3) if orientation of movement varies among years at individual breeding ponds, (4) if orientation varies between adult breeding migrations and juvenile emergence, (5) if orientation of

movement is maintained as salamanders move into upland areas, and (6) if movement routes are associated with particular habitat characteristics.

MATERIALS AND METHODS

Study Area.—The study area encompassed 14 seasonal ponds within a 1 km radius circular area (approximately 314 ha; Fig. 1 inset) on the Holyoke Range in the southern portion of Hampshire County in western Massachusetts. The study area was continuously forested with the exception of a utility corridor (approximately 30 m wide) that bisects the area. The forests, classified as “transition hardwoods-white pine-hemlock” (Westveld, 1956), were dominated by a mixture of deciduous trees, primarily oak (*Quercus* spp.), maple (*Acer* spp.), birch (*Betula* spp.), hickory (*Carya* spp.), and two conifers (*Tsuga canadensis* and *Pinus strobus*). Topography was variable with many ridges and valleys that have allowed nu-

merous seasonal wetlands to form. Elevation varied from approximately 125 to 225 m above sea level.

The Marbled Salamander is one of the rarest pond-breeding amphibians in southern New England (DeGraaf and Rudis, 1983) and is listed as "threatened" under the Massachusetts Endangered Species Act. In our study area, breeding adults immigrate to the ponds primarily in late summer (range, 10 May–15 November; average, 30 August). After breeding, males emigrate back into the surrounding uplands, whereas females create terrestrial nests in the basin substrate and typically brood their eggs until pond inundation. In our study area, adults emigrate from the ponds in the fall (range, 19 August–26 November; average, 28 September). Eggs hatch in the fall shortly after the ponds fill and the larvae overwinter in the ice-covered ponds. Metamorphs emerge from the ponds during the summer (range, 27 May–13 November; average, 21 June).

Study Design and Sampling Layout.—In summer 1998, we installed drift fences using standard protocols (Jenkins et al., 2003) around the perimeters of each of five ponds containing breeding populations of Marbled Salamanders (Fig. 1; ponds 2, 3, 4, 12, and 14). Drift fences were installed approximately 3 m from the shore of the ponds at high water. During the fall of 1998, we placed pitfall traps (Dodd and Scott, 1994) and funnel traps (Enge, 1997) alternately every 10 m along the fences. A single trap was placed at each location on both sides of the fence. Each trap contained a wetted sponge and was covered by a board angled against the fence to provide shade and prevent desiccation. Based on results from 1998 (Jenkins et al., 2003), we replaced all funnel traps with pitfalls in 1999. During periods of excessive high water some pitfalls flooded and we temporarily replaced them with funnel traps. However, this happened so infrequently that it had little effect on salamander captures. During 1999, we installed fences around an additional four ponds (Fig. 1; ponds 5, 6, 9, and 11) and established a second concentric drift fence 30 m from the shoreline fence at three ponds (ponds 4, 5, and 12). These 30 m fences were constructed of 96.5 cm wide silt fence with pitfall traps identical to those at 3 m fences. We removed the 30 m fences in 2000.

We checked all traps daily between 20 August and 30 November in 1998 and between 1 May and 30 November in 1999–2002. For each Marbled Salamander captured, we recorded the trap number and age class (juvenile or adult) based on dorsal patterning and size (Petranka, 1998). We released all animals approximately 2 m away from the point of capture on the opposite side of the fence, given the directional nature of

migration and emergence movements. During the off-season, all traps were closed and "doorways" were opened at approximately 15 m intervals in all fence lines. To measure the orientation of salamander movement at 3 m fences, we measured the azimuth of each trap in relation to both pond geometric center and nearest pond edge at high water. The results were largely consistent between approaches; the results reported here are based on the nearest pond edge approach.

To evaluate habitat use during movements, we measured a suite of habitat variables at all trap locations at the 3 and 30 m fences at ponds 4, 5, and 12 during July 1999, when water levels were relatively low at all ponds. At each location we measured canopy cover, basal area, soil moisture, ground cover, deciduous cover, and coniferous cover. We measured canopy cover directly over each trap using a densiometer. We measured basal area (square meters per hectare) at each trap using a #10 prism. We estimated surface soil moisture by touching the substrate and categorizing the wetness on a scale of 1 to 10 (10 being inundated). To reduce observer bias and temporal variation, all soil moisture estimates were made by the same individual and ponds were sampled in a random order on the same day (10 July 1999). Soil moisture was estimated at two locations 2.5 m on either side of the fence at each trap location and then averaged for each trap. We estimated ground cover by placing two 1 m² plots on each side of the fence 2 m apart and 2.5 m from the fence and trap location. In each plot we visually estimated percent cover of ferns, forbs, grasses, mosses, coniferous litter, coarse woody debris, deciduous litter, mineral soil, and rock, and then averaged these estimates to provide a single value for each trap location.

Data Analysis.—To evaluate orientation of movement to and from ponds in relation to pond (nine ponds), year (1998–2002), migration period (immigration versus emigration), age class (adult versus juvenile), and fence location (3 versus 30 m), we used a series of chi-square tests. Captures at the 30 m fences in 1999 were only used in the 3 versus 30 m fence comparison (three ponds). All other tests involved captures at the 3 m fences only. Preliminary analyses indicated that differences between migration periods for adults were trivial (only three of 32 comparisons were significantly different); therefore, we pooled across migration periods for all tests. We used nonparametric analyses instead of circular statistical techniques because our analyses consistently violated assumptions of the parametric circular tests (Batschelet, 1981). In particular, salamander orientation was often bi- or multimodal, which violated the assump-

tion of a Von Mises distribution (the normal equivalent for circular data) upon which the parametric tests are based. In the chi-square tests, we divided the possible azimuths (0–359 degrees) of salamander movement into eight equal-interval categories (i.e., 0–44, 45–89 degrees, and so on), and reduced the number of categories to six or four when necessary to achieve expected cell values of at least five.

We tested the null hypothesis that salamander distributions were uniform using chi-square tests of homogeneity of proportions. The proportions of observed captures were compared to equal expected values across azimuth categories. For this analysis, we combined all salamanders at a given pond (i.e., pooled across all factors) and conducted one test for each pond. Rejection of the null hypothesis was interpreted as evidence of significant nonuniform orientation in movement in one or more directions. Second, we tested the null hypothesis that orientation did not differ between classes of each independent factor (listed above) using chi-square tests of homogeneity of proportions. Notably, these are tests for overall differences and do not indicate the exact nature of the differences (specific directional bins that differ in proportional use). For comparisons among ponds, we pooled all adults and juveniles separately across years and ran two chi-square tests. For this analysis, we used a nine (ponds) by eight (azimuth categories) contingency table for each age class. For comparisons among years, we separately pooled adults and juveniles at each pond and ran two chi-square tests. In these analyses, the size of contingency tables varied based on the number of years during which adequate numbers (at least 10 individuals/yr) of salamanders were captured (2–5 yr) and the number of azimuth categories (four–eight categories) needed to ensure adequate expected cell values. For comparisons between age classes, we used a two (age classes) by four–eight (azimuth categories) contingency table for each year at each pond. Again, we only included years and ponds in which at least 10 individuals were captured. For comparisons between 3 and 30 m fences, we treated adults and juveniles separately and ran two chi-squared tests at each of the three ponds with a 30 m fence in 1999. In these analyses, we used a two (fence location) by eight (azimuth categories) contingency table for each age class. We interpreted rejection of the null hypothesis as evidence that salamander movement routes shifted as animals moved into upland areas.

To assess habitat use during movements of juveniles and adults, we used multiple regression analysis. Selecting the individual model for each dependent variable involved multiple steps. Relative capture rates (number of salamander

captures per trap relative to the total number of salamander captures at a pond) for juveniles and adults were considered dependant variables in separate analyses. Independent variables were selected in a stepwise fashion as follows. First, all habitat variables were examined for colinearity using Pearson product-moment correlations. When two variables had a correlation of ≥ 0.7 , the variable with the largest F-statistic in a univariate regression was retained. Second, of the remaining habitat variables, any variables with zeros (i.e., absence of that habitat characteristic) recorded for $>20\%$ of the trap locations were removed. Remaining habitat variables plus two discrete variables (pond [4, 5, and 12] and fence [3 and 30 m]) were used in a stepwise regression analysis. Independent variables chosen in each stepwise procedure were then used in multiple regression models. Residuals from each model were examined for normality and homoscedasticity, and transformations were made when necessary.

RESULTS

Overall, we recorded 9,543 Marbled Salamander captures at 3 m fences from 1998 to 2002. However, the majority (87%) of captures occurred at four ponds (Fig. 1; pond 2 = 1,147, pond 4 = 4,442, pond 5 = 1,001, and pond 12 = 1,726). Salamander captures pooled across years and age classes were nonuniform at all ponds ($df = 7$, $P < 0.001$ for all ponds), suggesting that distinct migration routes were being used at all ponds. Orientation patterns, however, differed among ponds (adult: $df = 56$, $P < 0.001$; juvenile: $df = 56$, $P < 0.001$). With the exception of three ponds, each with low sample sizes (ponds 9, 11, 14), there were numerous cases in which orientation patterns differed significantly among years (Table 1), although generally these differences were not dramatic. For example, at pond 5, captures were concentrated to the north-northeast in 1999 and to the north-northwest in 2000. Orientation patterns differed between age classes in 52% of the comparisons, and adult movements tended to be more concentrated than juvenile movements (Table 2). For example, adult movements were highly concentrated to the north (northeast-northwest) at pond 5, whereas juvenile movements, although still significantly concentrated to the north, were more equitably distributed among all directions (Fig. 2). Last, orientation patterns of both adult and juvenile salamanders consistently differed between 3 and 30 m fences (Fig. 3), suggesting that animals reoriented their movements as they migrated into the uplands.

We observed a significant positive relationship between canopy cover and adult capture rates, and significant positive relationships between

TABLE 1. Summary statistics from chi-square tests of homogeneity of proportions assessing variation in orientation of movements among years for adults and juveniles by pond. Tests were based on data collected from 1998 to 2002 at nine breeding ponds in western Massachusetts. The size of contingency tables varied based on the number of years during which adequate numbers (at least 10 individuals) of salamanders were captured (2–5 yr) and the number of azimuth categories (four–eight categories) needed to ensure adequate expected cell values. Missing values indicate insufficient sample sizes.

Pond	Adults		Juveniles	
	df	P value	df	P value
P2	28	0.006	6	0.017
P3	24	0.024	9	< 0.001
P4	28	< 0.001	9	< 0.001
P5	21	0.066	9	< 0.001
P6	21	< 0.001	—	—
P9	9	0.588	3	0.133
P11	9	0.377	3	0.349
P12	28	< 0.001	6	0.072
P14	6	0.571	—	—

canopy cover, basal area, and soil moisture and juvenile capture rates (Table 3), suggesting that Marbled Salamanders were selecting areas with relatively greater canopy cover and wetter substrates during movement.

DISCUSSION

Orientation of Salamander Movements.—We documented spatial and temporal patterns in the orientation of Marbled Salamander movements to and from nine seasonal ponds during a period of 5 yr in western Massachusetts. The direction of orientation either within a single year or pooled across years differed among ponds, suggesting that there is no hard-wired, compass-based bias to *Ambystoma opacum* movements that has been suggested for other species (Phillips, 1977, 1986).

The direction of orientation within a pond often changed somewhat over time (Table 1), suggesting that there are not strong physical associations with specific movement routes. However, we noted significant selection for routes with higher canopy cover and soil moisture (Table 3). Therefore, it is possible that changes in orientation over time could be attributed to physical changes in the environment. For example, in 1999, Hurricane Floyd caused flooding throughout the study area and, as a result, the physical environment (e.g., soil moisture) along potential migration routes was different in 1999 from other years. In addition, we noted several cases of changes in tree canopy cover at a particular location following tree-falls, which occur regularly in the forest and are particularly prevalent at the edge of wetlands where soil moisture conditions can make trees especially vulnerable to wind-throw and other disturbances. Thus, it is possible that orientation could simply be the direct result of selection for favorable microenvironments. Routes with higher canopy cover and soil moisture presumably are environments where salamanders have a lower likelihood of desiccation (Bartelt et al., 2004). Previous studies that placed forest pond-breeding amphibians in environments where they had the choice of moving into an open or forested area found that amphibians moved disproportionately into forested areas (DeMaynadier and Hunter, 1998; Rothermel and Semlitsch, 2002). Alternatively, Marbled Salamanders breed biennially (Petranka, 1998) and differences in orientation among years could represent different routes being used by different breeding cohorts. It is also possible that salamander movements are influenced by environmental characteristics that were not measured as part of this study, such as slope and aspect. Future studies should focus more extensive efforts on determining the environmental factors that influence salamander movements in relatively undisturbed landscapes, possibly including

TABLE 2. Summary statistics from chi-square tests of homogeneity of proportions assessing variation in orientation between adult and juvenile Marbled Salamanders by year and pond. Data were collected from 1998 to 2002 at nine breeding ponds in western Massachusetts. Tests include only years and ponds in which at least 10 individuals were captured. Missing values indicate insufficient sample sizes.

Pond	1999		2000		2001		2002	
	df	P value						
P2	7	0.009	—	—	7	0.158	7	0.113
P3	6	0.284	6	0.202	6	0.217	6	0.030
P4	7	< 0.001	7	0.357	7	< 0.001	7	< 0.001
P5	7	0.004	7	0.005	7	0.121	7	< 0.001
P6	3	0.110	—	—	—	—	—	—
P9	3	0.128	—	—	—	—	3	0.038
P11	3	0.077	—	—	—	—	3	0.250
P12	7	< 0.001	7	0.001	—	—	7	< 0.001

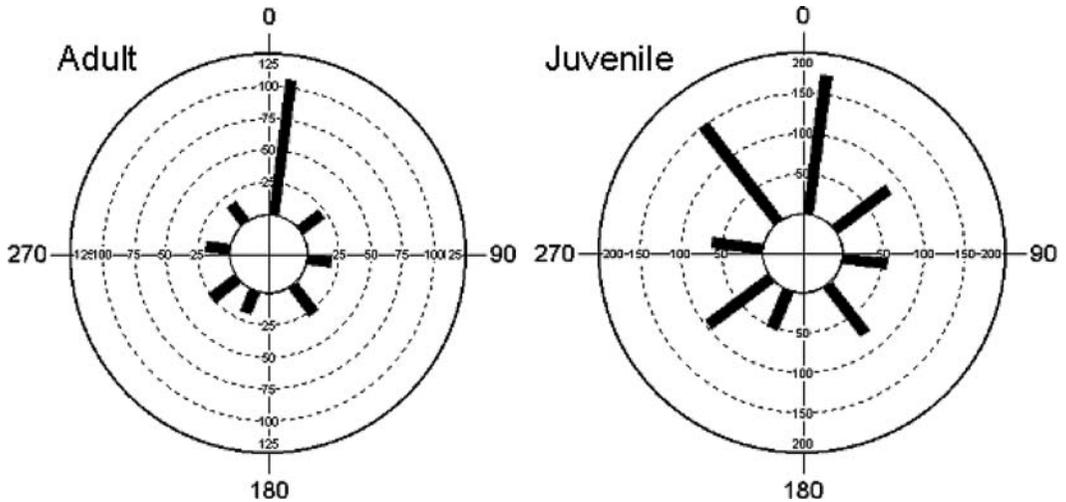


FIG. 2. Vector plots depicting the number of adult and juvenile Marbled Salamander captures (pooled across years [1998–2002] and migration period [emigration versus immigration] for adults at the 3 m [i.e., shoreline] fence) in each of eight directional bins at one breeding pond (Fig. 1; pond 5) in South Hadley, Massachusetts.

broad-scale habitat analyses and microhabitat analyses. Overall, it is important to note that although we documented statistically significant differences in orientation among years, orientation was still generally in the same direction among years (i.e., there were no instances where orientation changed dramatically from a north to a south direction, for example).

Emerging metamorphs as often as not (52% of the time) oriented differently from adults during emigration from their natal ponds (Table 2). Moreover, in contrast to Stenhouse (1985), juvenile movements were more widely dispersed than adults in general (Fig. 2), although there was considerable variability among ponds and years. The more random movements by juveniles suggest that there are no innate mechanisms determining orientation. Unfortunately, the implications of these movement patterns are unclear, given that the fate of those juveniles leaving in more random directions is unknown. They could be adjusting their movements in the uplands and eventually following similar routes as adults, in which case their initial orientation at emergence from the pond basin ultimately may be irrelevant. Alternatively, they could be dispersing to breed as adults at other ponds, as has been shown for other pond-breeding amphibians (Berven and Grudzien, 1990), in which case their movements may not be governed by the same mechanisms as those of adults. Finally, they could be moving to upland areas of varying habitat quality, resulting in differential survival, which ultimately is expressed as concentrated immigration movements

as adults when they return to breed. Determining the fate of juveniles is a focus of the larger investigation.

Overall, our results indicate that salamander movements were concentrated within ponds and within years, consistent with findings from other studies (Shoop and Doty, 1972; Stenhouse, 1985), but that the direction of orientation varied markedly among ponds and somewhat over time as well. Despite the variation over time, salamander movements when pooled across age class and years were nonetheless nonuniform at all ponds. However, we noted a tendency for this pattern to diminish increasingly with each additional year of data collection and to approach a more uniform pattern. Thus, movement routes, though perhaps concentrated in the short term, were less predictable in the long term.

Conservation Implications.—In rapidly developing regions of the world such as the northeastern United States, large contiguous patches of forest are being fragmented by human development (Noss and Csuti, 1997). At the same time, conservation biologists increasingly are recognizing the importance of terrestrial areas immediately surrounding pond basins as critical staging areas for adult amphibians or temporary refugia for newly metamorphosing individuals, as well as for their values in protecting the integrity of the breeding sites (Semlitsch, 1998). Several studies have suggested that terrestrial areas immediately surrounding breeding ponds may be used unequally by salamanders during movements to and from pond basins (e.g., Shoop and Doty, 1972; Douglas and Munroe, 1981;

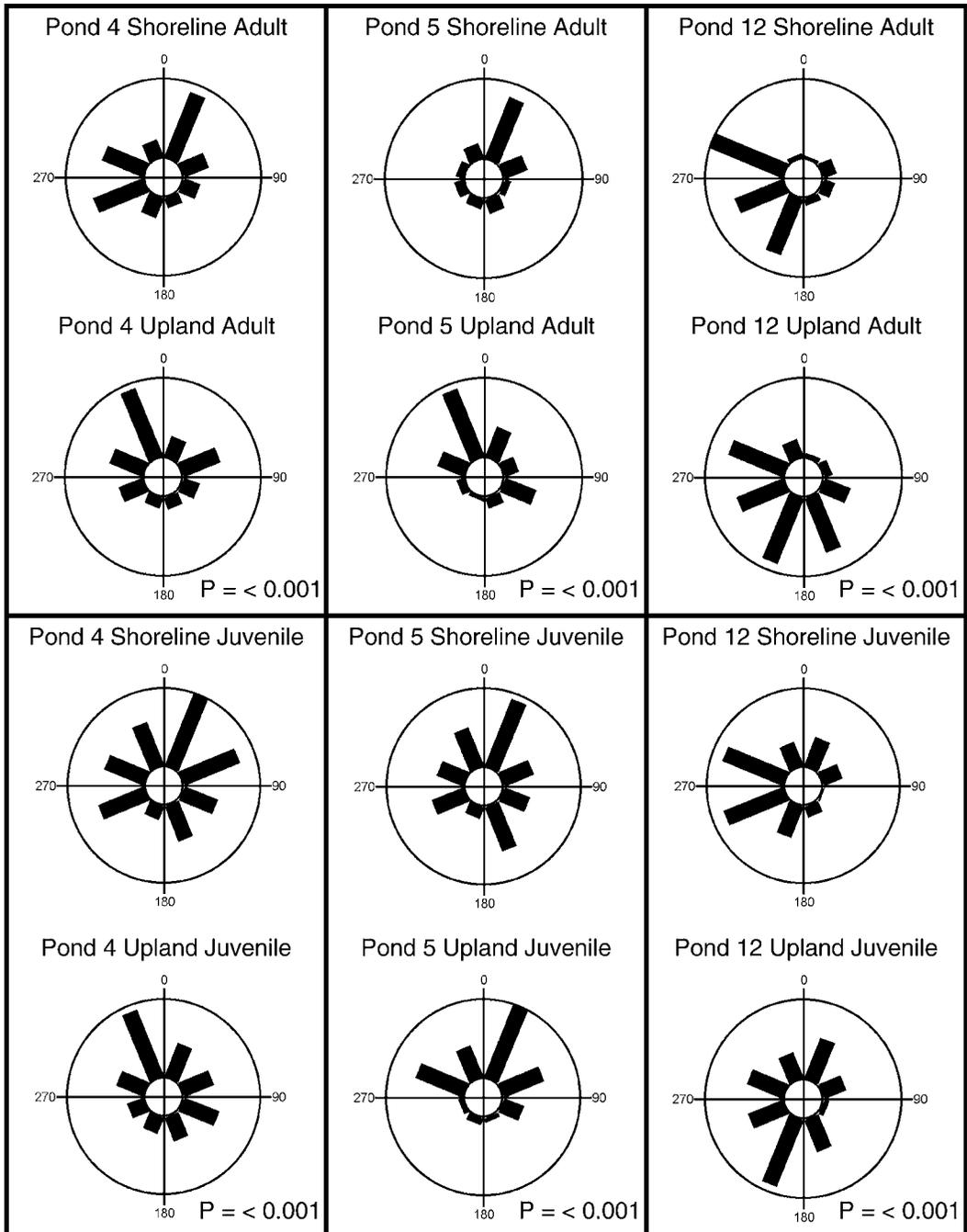


FIG. 3. Vector plots depicting the proportion of adult and juvenile salamanders captures in 1999 at 3 m (i.e., shoreline) versus 30 m (i.e., upland) fences in each of eight directional bins at three ponds (Fig. 1; ponds 4, 5, and 12) in South Hadley, Massachusetts.

Stenhouse, 1985; Phillips and Sexton, 1989; Dodd and Cade, 1998; Johnson, 2003) and, therefore, that these movement corridors could be targeted for protection as a way to protect critical habitat,

while at the same time accommodating development. In our study, we found that breeding ponds in close proximity might be characterized by amphibian migrations in completely different

TABLE 3. Results of multiple regression models (after stepwise selection of variables) to determine if habitat variables can explain the orientation of movement of adult and juvenile Marbled Salamanders at three breeding ponds in South Hadley, Massachusetts, during 1999. The dependent variable represents the total number of adults or juveniles captured at a trap location in 1999 relative to the total number captured at that pond during that year.

Dependent variable	Independent variables	Coefficient	T value	P value	Model R ²
Adult	Canopy cover	0.00015	2.11	0.037	15%
	Fence location (3 m)	-0.00503	-4.45	< 0.001	
Juvenile	Canopy cover	0.00016	2.07	0.041	11%
	Basal area	0.00003	2.07	0.040	
	Soil moisture	0.00226	2.64	0.009	

directions. In addition, we found that there can be significant differences in the orientation of migration routes between years and age classes, making it difficult to predict any single route for protection based on a single year or age class. Moreover, we also found that migrating salamanders shifted slightly the orientation of their movements as they traveled into upland areas, suggesting that migration routes are spatially complex and that determination of corridors based on concentrated captures at the pond periphery may be misleading. Although we found that salamanders used migration routes with higher canopy cover, our models did not explain a large portion of the variation in orientation. Thus, protecting areas of high canopy cover alone may not be sufficient as a protection strategy. It is important to recognize that we studied salamander movements in a relatively undisturbed area and results from other studies suggest that factors such as canopy cover can be important predictors of movement corridors in more disturbed landscapes (DeMaynadier and Hunter, 1998).

We believe that there is potential for protecting broad movement corridors that encompass temporal variation in salamander movements, but determination of the placement of these corridors requires pond-specific studies examining variation in movements among age classes as well as the deviation of movement as salamanders move further into upland areas. Consequently, until we better understand mechanisms governing movements in this species, a conservative conservation strategy would require protecting broad terrestrial areas around breeding sites that encompass their known movement distances from breeding ponds (Semlitsch 1998).

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