

Movement Patterns of Adult and Juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in Three Restored Seasonal Pools in Maine

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ABSTRACT.—Research on amphibian movement patterns can aid in strengthening amphibian conservation strategies. Yet for many species, there remain substantial gaps in our knowledge of such movement patterns. From 1999–2002, we documented movement patterns to and from breeding pools of both adult and juvenile *Rana sylvatica* LeConte (Wood Frog) and *Ambystoma maculatum* Shaw (Spotted Salamander) by using drift fence arrays at three restored vernal pools in Maine to lend insight into conservation strategies for these two species. Adults and juveniles of both species exhibited nonrandom movement at breeding pools directed preferentially from and toward closed-canopy forested habitat. Marked male, female, and juvenile *R. sylvatica* were recaptured at 30 m, 150 m, and 300 m from the pool in the surrounding terrestrial environment. Most terrestrial recaptures occurred within the forested wetland habitat to the north of the pool. Median snout–vent lengths (SVL) of recaptured juvenile *R. sylvatica* were progressively larger at greater distances from the pool. Number of juveniles emerging from the pool was positively correlated with number of juveniles recaptured two days later at 30 m, four days later at 150 m, and six days later at 300 m. Male *R. sylvatica* were 98% faithful to their breeding pools from 2001–2002, whereas female *R. sylvatica* were 88% faithful. Male and female *A. maculatum* were 100% faithful to their breeding pools during the same period. Both species' (adult and juvenile) nonrandom movement toward forest upon leaving breeding pools suggests that quality of adjacent terrestrial habitat is relevant to both juvenile and adult pool-breeding amphibians. High levels of pool fidelity observed in these two species emphasize the importance of conserving vernal pools and mitigating for pool-losses on-site if the nonbreeding habitat is still available. Correlations between amphibian migrations and weather variables varied between years and species, suggesting emigration, immigration, and dispersal may be associated other environmental variables in conjunction with temperature and precipitation. However, heightened activity of both species (adults and juveniles) in response to temperature and precipitation can inform the timing of monitoring efforts and conservation strategies aimed at protecting migration routes.

Research on amphibian movement patterns, including orientation during migration, terrestrial travel distances, breeding pool fidelity, and migratory response to weather variables, can aid in strengthening amphibian conservation strategies in several ways. Recent research has shown that conserving landscapes with small, isolated wetlands is necessary for maintaining pool-breeding amphibian populations (Gibbs, 1993, 2000; Semlitsch and Bodie, 1998). Empirical evidence is emerging on importance of quality of terrestrial habitats adjacent to breeding pools (Semlitsch, 2002; Regosin et al., 2003a, Calhoun et al., in press). Documentation of amphibian terrestrial movement to and from breeding pools provides information on the quality and extent of terrestrial habitat used by different species of

pool-breeding amphibians. Last, breeding amphibians are potentially easiest to monitor and most vulnerable to vehicular traffic during peak migration events. Studies of effects of weather cues on amphibians may help predict peak events when monitoring and conservation efforts would be most effective.

Rana sylvatica and *Ambystoma maculatum* have been the focus of a number of amphibian movement studies. For *R. sylvatica*, studies have examined orientation of dispersing juveniles (deMaynadier and Hunter, 1999), terrestrial travel distances of adults (Bellis, 1965), and juveniles (Berven and Grudzien, 1990), breeding pool fidelity (Berven and Grudzien, 1990), wintering habitat (Regosin et al., 2003a), and response to weather variables during the non-breeding season (Heatwole, 1961; Bellis, 1962, 1965). Studies on *A. maculatum* have examined orientation of adults at breeding pools (Shoop, 1965; Douglas and Monroe, 1981; Kleeberger and Werner, 1983; Stenhouse, 1985; Phillips and

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Sexton, 1989) and dispersing juveniles (Rothermel and Semlitsch, 2002), terrestrial travel distances of adults (Douglas and Monroe, 1981; Kleeberger and Werner, 1983; Madison, 1997), and juveniles (Rothermel and Semlitsch, 2002), use of small mammal burrows by adults in terrestrial habitats (Regosin et al., 2003b), breeding pool fidelity (Whitford and Vinegar, 1966) and migratory response of breeding adults to weather variables (Blanchard, 1930; Baldauf, 1952; Sexton et al., 1990). However, we are unaware of any published studies that have specifically examined orientation of adult *R. sylvatica* entering and exiting breeding pools. We are also unaware of any published studies on weather cues associated with breeding migration of adult *R. sylvatica*, emigration of adult *R. sylvatica* and *A. maculatum* from pools postbreeding or emergence of juvenile *R. sylvatica* and *A. maculatum* from their natal pools.

We studied movement patterns of adult and juvenile *R. sylvatica* and *A. maculatum* in three restored vernal pools on Sears Island, Maine, from 1999 to 2002. Our objectives were to (1) document directional orientation of adults and juveniles of each species entering and exiting breeding pools; (2) determine abundance of individuals at three distances from breeding pools; (3) quantify adult breeding pool fidelity; and (4) explore relationship between temperature and moisture to movement of adults and juveniles during migration to and from breeding pools and in the terrestrial environment.

MATERIALS AND METHODS

Physical Setting.—The study took place on Sears Island, Searsport, Maine (44°27'N, 68°53'W). Sears Island is a 380 ha, uninhabited, predominantly forested island located in northern Penobscot Bay in midcoast Maine, with approximately 97 ha of freshwater wetlands, the majority of which are seasonally saturated/flooded mixed forests (Normandeau Associate, 1995, unpubl.). Three vernal pools (hereafter referred to as VP1, VP2, and VP3) were constructed on the western side of the island in 1997 as mitigation for the clear-cutting and filling of a forested wetland at the same site in 1984 (VP1, median depth at spring high water = 56.5 cm, maximum area at spring high water = 350 m²; VP2, depth = 62.0 cm, area = 600 m²; VP3, depth = 65.8 cm, area = 950 m²). The three pools were constructed in close proximity to one another (maximum distance between pools = 200 m) within a restored portion of the clearing that has become a seasonally saturated wet meadow (Duke Engineering and Services, 1997, unpubl.). A closed-canopy forest characterized by red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), northern white cedar (*Thuja occi-*

dentalis), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis*) was located 15 m northwest of VP1 and 15 m north of VP2 and VP3. A wet meadow (with potholes) characterized by broad-leaved cattail (*Typha latifolia*), soft rush (*Juncus effusus*), wool grass (*Scirpus cyperinus*), and common horsetail (*Equisetum arvense*) immediately bordered VP1 to the east and west, VP2 to the east and south, and VP3 to the east and southeast. A dry clearing with low herbaceous plants characterized by birdsfoot trefoil (*Lotus corniculatus*), hop clover (*Trifolium agrarium*), dandelion (*Taraxacum officinale*), grasses (Poaceae), cow vetch (*Vicia cracca*), and several species of hawkweed (*Hieracium* spp.) was located 30 m south of VP2 and VP3, and additional forested areas are located 60 m east and south of VP1 and 100 m south of VP2 and VP3 beyond the clearing.

Movement Patterns to and from Breeding Pools.—Amphibians entering and exiting pools were captured using 100% enclosure drift fences from 1999 to 2002. Drift fences were constructed of black silt fence supported by wooden stakes, and were installed 1–10 m out from the average high water mark of each pool. The fences were 60 cm high with the lower edge buried 15 cm below the ground. Pitfall traps were constructed of 15 liters (30 cm deep) plastic buckets buried flush with the level of the ground and placed in pairs every 10 m along the fences, with one trap placed along the fence interior and one along the exterior (for a total of nine trap pairs at VP1, 10 at VP2, and 18 at VP3). Approximately 2 cm of water was added to each trap to prevent amphibian desiccation, rocks were provided to act as cover for trapped amphibians, and small sticks were installed to allow small mammals to escape (Perkins and Hunter, 2002). Traps were checked daily at 0700 h from the onset of adult immigration (late March through early April) until the end of juvenile emergence (late September through early October). All amphibians trapped were identified, sexed (if adult), and released on the opposite side of the fence, approximately 5 m from the point of capture. Trap number was also recorded for each animal.

Terrestrial Movement.—Drift fences were installed in the terrestrial habitat surrounding VP3 in 2001 to recapture marked individuals dispersing from the pool. Trapping effort was focused on VP3 because data from 1999 and 2000 indicated this was the most productive pool (Vasconcelos, 2003). Fences were constructed of the same materials used at the breeding pools and were oriented perpendicular to the presumed direction of travel. Pitfall traps were constructed of two number-10 tin cans connected with duct tape (Corn and Bury, 1990), and funnels (constructed of 1-lb. plastic margarine tubs with the bottoms

removed) were placed in each trap to prevent juvenile amphibians from climbing out. Each fence was 20 m in length and had one pitfall trap installed at each end and one in the middle, resulting in 10-m gaps between traps.

Fences were installed in the forest to the north at 30 m, 150 m, and 300 m from the pool edge, in the clearing to the south at 30 m, and in the forest to the south at 150 m (fences could not be installed to the south at 300 m because of the size and shape of the island). These distances were chosen to encompass published recommendations for terrestrial zones adjacent to wetlands for maintaining amphibian populations in New England of approximately 160–290 m (Semlitsch, 2003). Specific recommendations published for vernal pools range from 15–230 m (D. B. Kittredge Jr. and M. Parker, 1997, unpubl.; Calhoun and Klemens, 2002). Three fences separated by 20-m gaps were installed at each distance in 2001. Two additional fences, one at 150 m and one at 300 m, were added to the northeast of the pool in 2002 to increase capture success, after initial data from 2001 suggested that amphibians were traveling in this direction. This resulted in our trapping over different proportions of the total possible circumference at different distances and between years (64% at 30 m, 13% at 150 m, and 3% at 300 m in 2001, and 64% at 30 m, 15% at 150 m, and 4% at 300 m in 2002).

All adult and juvenile *R. sylvatica* and *A. maculatum* exiting VP3 were sexed and marked with visible implant fluorescent elastomer (Northwest Marine Technology, Inc.), and SVL was measured to the nearest 0.5 mm for all juveniles. *Rana sylvatica* were marked on the ventral side of the left rear leg, whereas *A. maculatum* were marked on the left side of the body anterior to the rear leg. Terrestrial traps were checked daily following trap checking at the pools. All recaptured amphibians were remarked with a color unique to the distance of capture in the opposite leg (for *R. sylvatica*) or the opposite side of the body (for *A. maculatum*) as the pool mark to ensure that no individuals were counted at the same distance more than once. Recaptured adult *R. sylvatica* and *A. maculatum* were sexed, and the SVL of all recaptured juveniles was measured to the nearest 0.5 mm. Amphibians were then released approximately 5 m from the trap of capture on the opposite side of the fence. Because of the timing of fence construction, adults were only recaptured in 2002, whereas juveniles were recaptured in both 2001 and 2002.

Pool Fidelity.—In 2001, all adult *R. sylvatica* and *A. maculatum* exiting the three pools postbreeding were sexed and marked with a color unique to their pool of origin using visible implant fluorescent elastomer. In 2002, we sexed all

immigrating adults and searched for marks before releasing them into the pools.

Temperature and precipitation data were collected daily in the field in the morning before trap checking in 2001 and 2002. The maximum daily and minimum nightly temperatures for the preceding 24 h were measured to the nearest °C with a maximum-minimum thermometer located on the edge of the forest. Precipitation for the preceding 24 h was measured to the nearest mm with a rain gauge located in an open area between VP1 and VP2.

Analysis.—All statistical analyses were conducted using SYSTAT version 10.2 software ($\alpha = 0.05$; SYSTAT Software, Inc., 2002). We used circular statistical methods to calculate separate mean angles of entry into and departure from each pool for adult male, adult female, and juvenile *R. sylvatica* and *A. maculatum* for each year from 1999 through 2002 (Batschelet, 1965). Circular statistics were deemed appropriate despite the fact that VP3 was irregularly shaped because VP1 and VP2 and the fences at all three pools were roughly circular. We do, however, restrict ourselves to discussing general cardinal directions of movement, as opposed to exact angles, because of these departures from perfect circularity. We multiplied r (length of each movement vector) by a correction term to account for the grouping of data, and used the Rayleigh test to determine whether the direction of movement into and out of pools was significantly directional or randomly distributed around a circle (Batschelet, 1965; Zar, 1999). For all significant angles, we constructed 95% confidence limits and used these limits to check for differences between years and genders (Zar, 1999). Finding nonsignificant differences, we pooled the data across year and gender and calculated mean angles of orientation for adults and juveniles of each species.

We used one-way analysis of variance to test for differences in the mean SVL of *R. sylvatica* juveniles exiting VP3 and recaptured at 30 m, 150 m, and 300 m from the pool in 2001 and 2002. We then used cross-correlation functions to estimate the average number of days spent traveling by dispersing *R. sylvatica* juveniles between VP3 and terrestrial traps at each distance. This method involved the calculation of Spearman rank correlation coefficients (r_s) between the number of juveniles emerging from the pool each day and the number of juveniles recaptured at 30 m, 150 m, and 300 m varying numbers of days later. We used daily counts from 28 June (day of first juvenile emergence) through September 6 (day of final terrestrial recapture) 2002. We only used data from 2002 because trapping success was limited in 2001. Data from all traps at each distance were combined before analysis.

We calculated Spearman rank correlation coefficients (at 95% CI) between daily amphibian counts (adults entering pools to breed and exiting pools postbreeding, and juveniles emerging from pools and recaptured in terrestrial traps) and weather data for the preceding 24-h period (precipitation, maximum temperature, and minimum temperature) to test for associations between weather cues and amphibian movement in 2001 and 2002. For terrestrial recaptures, we only calculated correlation coefficients for *R. sylvatica* juveniles because terrestrial recaptures of adults of each species and juvenile *A. maculatum* were limited. For each year, amphibian counts from all three pools or all terrestrial traps were combined because of their close proximity and exposure to the same weather patterns. We only included data from the day of first capture through the capture of 95% of individuals because the final 5% of each group tended to move sporadically over a period of several weeks, with many days of no captures.

RESULTS

Movement Patterns to and from Breeding Pools.—

The majority of the 95% confidence limits for each mean angle of movement overlapped or were separated by far less than the angular distance between neighboring traps, indicating no true differences in orientation between years or between males and females for either species. Therefore, we pooled the data across year and gender before interpreting movement patterns. Adult and juvenile *R. sylvatica* and *A. maculatum* entered and exited the three pools with pronounced directionality (Figs. 1–2). At VP1, amphibians entered and exited primarily on the eastern side of the pool, which borders the wet meadow and is approximately 60 m from the nearest forest edge. The majority of captures at VP2 and VP3 were on the forested north side of the pools, with movement directed roughly north at VP2 and northeast at VP3 toward an *Alnus incana* (Speckled Alder)/*Symplocarpus foetidus* (Skunk Cabbage) wetland on the edge of a more extensive forested wetland. Movement patterns to and from the pools differed significantly from a random circular distribution (Rayleigh $P < 0.001$ for all tests [except for *A. maculatum* juveniles exiting VP2 $P = 0.01$]).

Terrestrial Movement.—Recapture success was low for *A. maculatum* from 2001–2002; thus, salamander recapture data were not included in the analysis. Large numbers of *R. sylvatica* adults and juveniles were recaptured at each distance, with the majority of recaptures occurring to the north for adult males, adult females, and juveniles (Table 1). Because there was unequal trapping effort, with more fences to the north at 150 m and 300 m, we compared capture data

from the matching drift fence arrays at 30 m to the north and south, each consisting of three fences. At 30 m, 90% of adults were recaptured to the north in 2002, and 79% and 92% of juveniles were recaptured to the north in 2001 and 2002, respectively. The highest number of juvenile recaptures occurred at the easternmost fence at each distance in 2002.

Mean SVL of recaptured juvenile *R. sylvatica* was significantly larger at each successive distance from VP3 in both 2001 and 2002 (Table 2). Days with high recapture rates in terrestrial traps appeared to both coincide with and follow days of high emergence rates at the pool (Fig. 3). In 2002, there was a strong correlation between captures at VP3 and terrestrial recaptures on the same day at 30 m ($r_s = 0.769$, $N = 71$, $P < 0.001$) and 150 m ($r_s = 0.501$, $N = 71$, $P < 0.001$). Omitting these same-day correlations, juvenile emergence from the pool was most positively correlated with recaptures two days later at 30 m ($r_s = 0.716$, $N = 69$, $P < 0.001$), four days later at 150 m ($r_s = 0.488$, $N = 67$, $P < 0.001$), and six days later at 300 m ($r_s = 0.365$, $N = 65$, $P < 0.004$).

Pool Fidelity.—Males and females of both species returned to breed in 2002 (Table 3). Marked male *R. sylvatica* ranged from 77.8–100% faithful to their breeding pools from 2001 to 2002, whereas marked females ranged from 37.5–97.6% faithful. VP2 had the highest percentage of males and females switching breeding pools and VP3 had the lowest. Across all pools, *R. sylvatica* marked males were 98% faithful to their breeding pools, with only 3/141 individuals breeding in a new pool in 2002. Marked females were 88% faithful, with only 7/58 individuals switching breeding pools. Male and female *A. maculatum* were 100% faithful to their breeding pools from 2001 to 2002. A higher percentage of adult *R. sylvatica* and *A. maculatum* marked in 2001 returned to VP3 in 2002 compared to the other two pools (Table 3).

Precipitation and Temperature Movement.—Correlations between amphibian movements and weather variables varied between years in many cases, often coinciding with between-year differences in the timing of migrations (Table 4). Number of male *R. sylvatica* entering the pools was not correlated with any weather variables in 2001 but was significantly correlated with minimum temperature in 2002 ($r_s = 0.619$, $P = 0.02$). Number of females entering pools was significantly correlated with maximum temperature in 2001 ($r_s = 0.787$, $P = 0.002$) and minimum temperature in 2002 ($r_s = 0.758$, $P = 0.01$). Number of males exiting pools postbreeding was significantly correlated with precipitation in 2001 ($r_s = 0.540$, $P < 0.001$) and 2002 ($r_s = 0.460$, $P = 0.005$) and with minimum

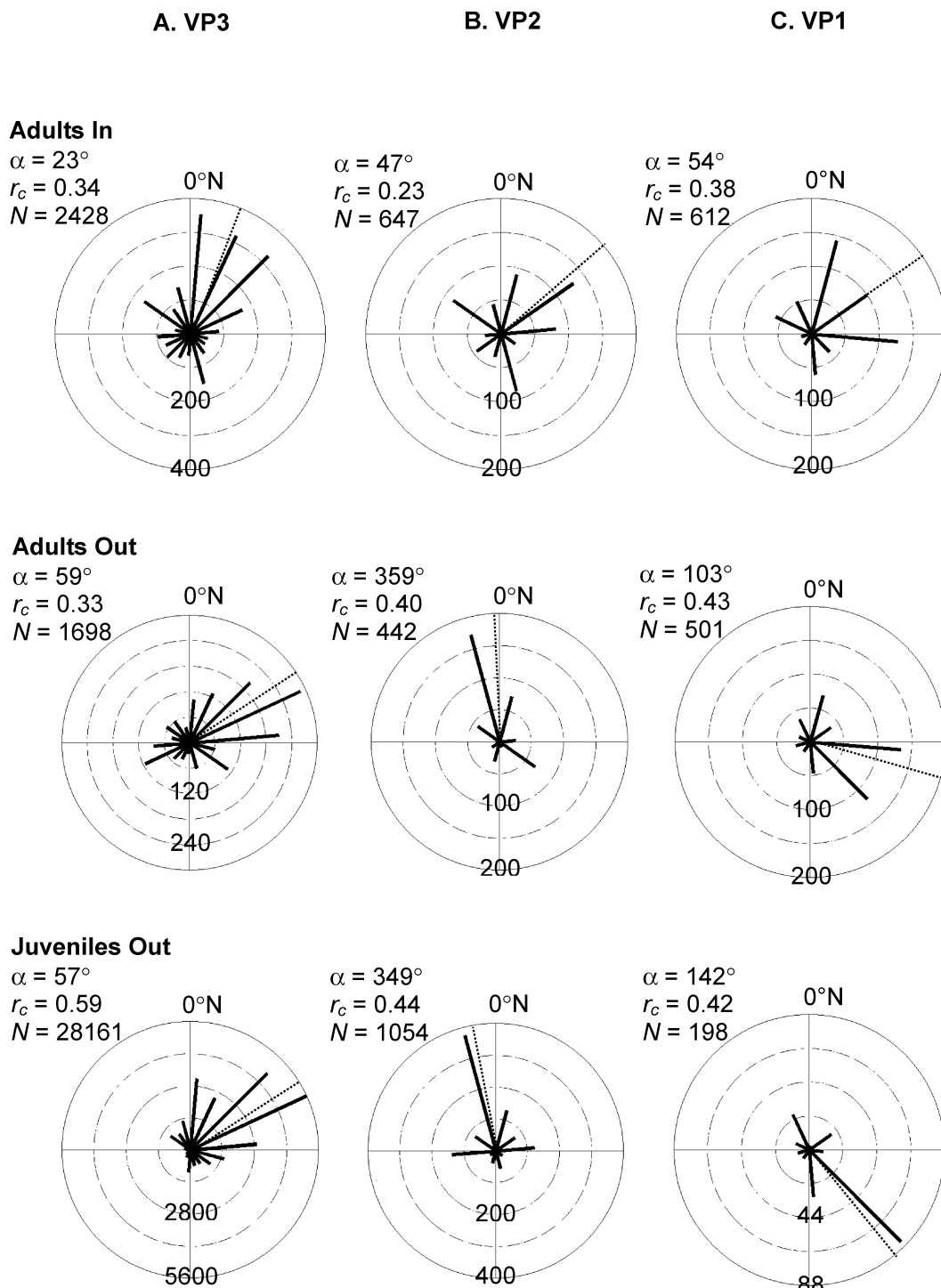


FIG. 1. Orientation of adult and juvenile *Rana sylvatica* entering and exiting VP2, VP2, and VP1. Graphs are oriented to match the landscape positions of the three pools. Bars represent the number of captures in traps at each angle over four years. Scale is given by numbered concentric rings. Dotted line represents the mean direction of movement. α = mean angle, r_c = length of mean vector, corrected for grouping, N = sample size.

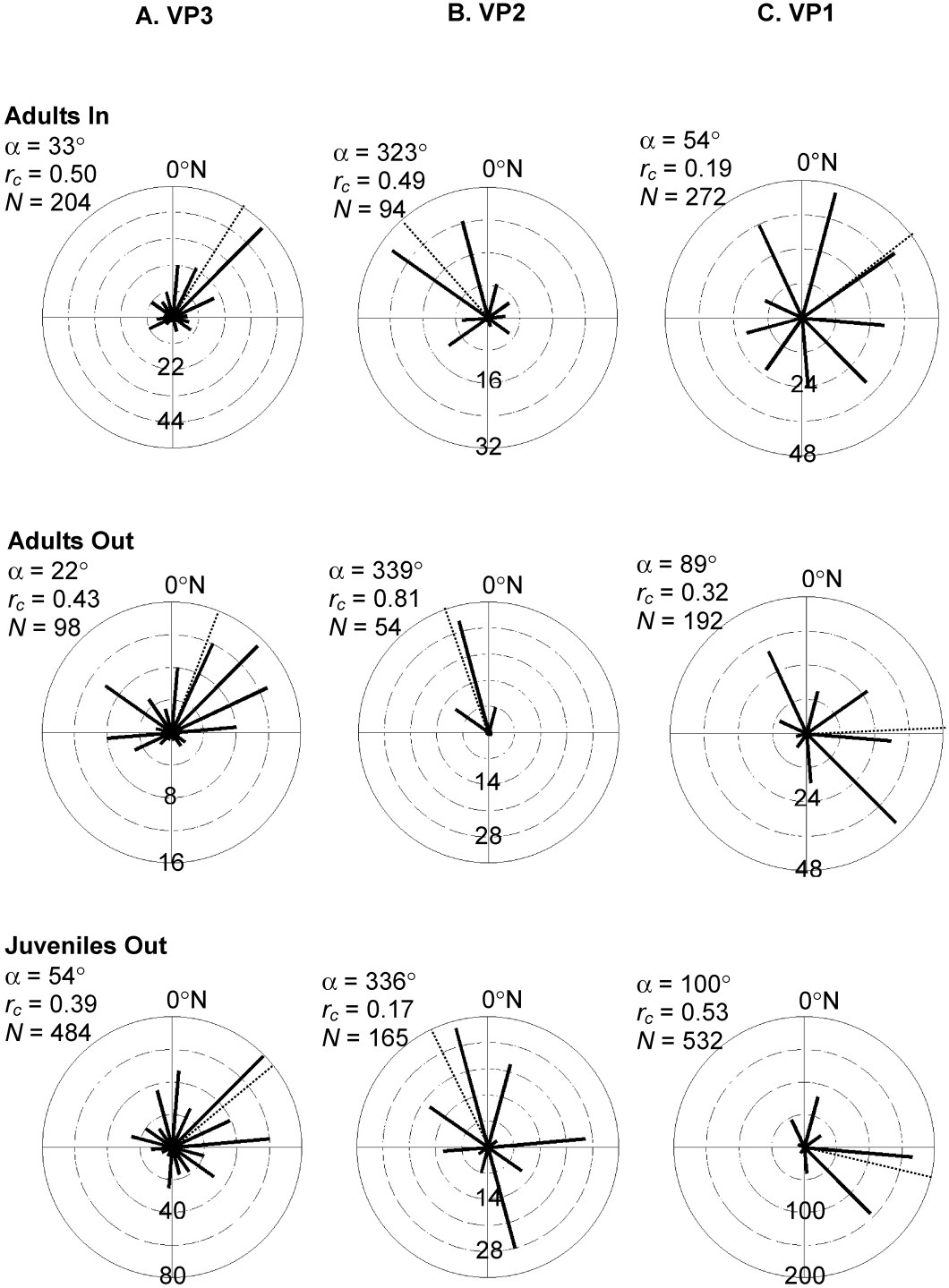


FIG. 2. Orientation of adult and juvenile *Ambystoma maculatum* entering and exiting VP3, VP2, and VP1. Graphs are oriented to match the landscape positions of the three pools. Bars represent the number of captures in traps at each angle over four years. Scale is given by numbered concentric rings. Dotted line represents the mean direction of movement. α = mean angle, r_c = length of mean vector, corrected for grouping, N = sample size.

TABLE 1. Number of adult and juvenile *Rana sylvatica* marked exiting VP3 and the number (and %) recaptured at 30 m, 150 m, and 300 m from the pool, M = male. F = female. N = north. S = south.

Class	Year	Sex	Marked	30 m		150 m		300 m
				N	S	N	S	N
Adult	2002	M	297	25 (8.4)	1 (0.3)	17 (5.7)	2 (0.7)	13 (4.4)
		F	175	10 (5.7)	3 (1.7)	12 (6.9)	4 (2.3)	8 (4.6)
Juvenile	2001	—	3306	369 (11.2)	98 (3.0)	68 (2.1)	12 (0.4)	29 (0.9)
	2002	—	9464	1385 (14.6)	127 (1.3)	588 (6.2)	18 (0.2)	237 (1.3)

temperature in 2001 ($r_s = 0.403$, $P = 0.01$) and 2002 ($r_s = 0.634$, $P < 0.001$). Counts of females exiting the pools were not correlated with any weather variables in 2001 but were significantly correlated with minimum temperature in 2002 ($r_s = 0.697$, $P = 0.03$). Number of juvenile *R. sylvatica* emerging from the pools was not correlated with any weather variables in 2001 but was significantly correlated with precipitation in 2002 ($r_s = 0.575$, $P < 0.001$). Number of juvenile *R. sylvatica* recaptured in terrestrial traps was significantly correlated with precipitation in 2001 ($r_s = 0.520$, $P < 0.001$) and 2002 ($r_s = 0.592$, $P < 0.001$).

Number of male *A. maculatum* entering pools to breed was not correlated with any weather variables in 2001, but in 2002, male counts were significantly correlated with precipitation ($r_s = 0.584$, $P = 0.01$), maximum temperature ($r_s = 0.481$, $P = 0.04$) and minimum temperature ($r_s = 0.578$, $P = 0.01$). Number of females entering pools was not correlated with any weather variables in 2001 but was correlated with minimum temperature in 2002 ($r_s = 0.744$, $P = 0.002$). Upon exiting pools, male counts were significantly correlated with precipitation in 2001 ($r_s = 0.833$, $P < 0.001$) and 2002 ($r_s = 0.536$, $P = 0.01$). Counts of females exiting pools were also correlated with precipitation in 2001 ($r_s = 0.799$, $P < 0.001$) and 2002 ($r_s = 0.535$, $P = 0.002$). Number of juvenile *A. maculatum* emerging from pools was significantly correlated with precipitation in 2001 ($r_s = 0.500$, $P < 0.001$) and 2002 ($r_s = 0.804$, $P < 0.001$) and with minimum temperature in 2001 ($r_s = 0.408$, $P = 0.004$).

DISCUSSION

Movement Patterns.—Adult *R. sylvatica* entered and exited the three breeding pools in this study in a nonrandom manner (Fig. 1). The location of VP1 makes it difficult to interpret directional orientation in terms of habitat preferences, but VP2 and VP3 have a distinct closed-canopy forest edge and forested wetland to the north and low wet meadow and clearing to the south. Adult *R. sylvatica* in these pools migrated preferentially from and toward the north in the direction of closed-canopy forested habitat, and avoided the open clearing to the south (Fig. 1A, B). Juvenile

R. sylvatica also dispersed preferentially toward closed-canopy forest in this study, in agreement with the findings of deMaynadier and Hunter (1999). Data from the terrestrial drift fences reinforce the pool orientation data for *R. sylvatica*, with the majority of recaptures occurring in the forest to the north of VP3 (Table 1).

Adult and juvenile *A. maculatum* also exhibited nonrandom movement into and out of breeding pools (Fig. 2), mirroring the findings of earlier studies (Shoop, 1965; Douglas and Monroe 1981; Kleeberger and Werner, 1983; Stenhouse, 1985; Phillips and Sexton, 1989). Like *R. sylvatica*, adult salamanders in VP2 and VP3 migrated preferentially from and toward the north in the direction of the forest (Fig. 2A, B). Juvenile *A. maculatum* followed the same pattern, with directed movement toward the forest, in agreement with the findings of Rothermel and Semlitsch (2002).

Both *R. sylvatica* and *A. maculatum* are more likely to be found in forested habitat than edge habitat during the terrestrial phase (deMaynadier and Hunter, 1998). The orientation data presented here show that the preference for travel to forested habitat (forested wetland in this case) is evident as soon as individuals leave the aquatic environment. Beyond large-scale preferences between forest and clearing, *R. sylvatica* and *A. maculatum* also demonstrated habitat preferences at a local scale, as suggested by the initial movement of individuals of both

TABLE 2. Mean SVL of juvenile *Rana sylvatica* emerging from VP3 and recaptured at 30 m, 150 m, and 300 m from the pool. SE = standard error. N = number measured. P = P value of each pairwise comparison following Bonferroni adjustment for multiple comparisons.

Year	Location	Mean SVL (mm)	SE	N	P
2001	VP3	13.57	0.02	3290	
	30 m	14.06	0.06	448	0.000
	150 m	14.92	0.14	72	0.000
	300 m	16.90	0.22	29	0.000
2002	VP3	13.60	0.01	9464	
	30 m	14.09	0.03	1404	0.000
	150 m	14.91	0.04	587	0.000
	300 m	16.93	0.07	222	0.000

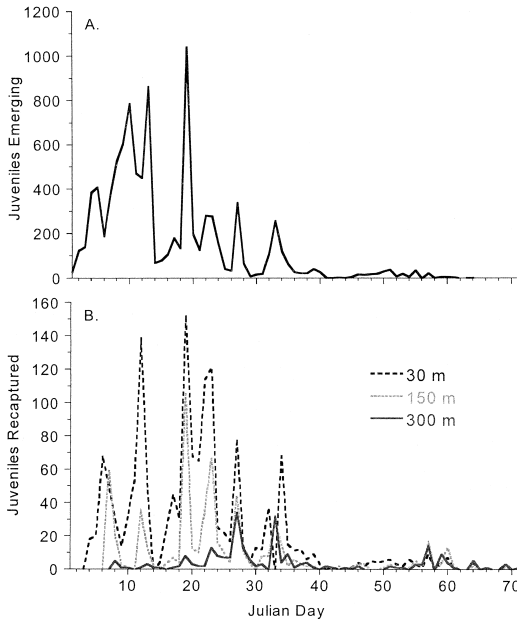


FIG. 3. Number of juvenile *Rana sylvatica* emerging from VP3 and number recaptured at 30 m, 150 m, and 300 m from VP3 from day 1 (first juvenile emergence) through 71 (final terrestrial recapture).

species from VP2 and VP3 toward the wooded wetland on the forest edge.

Adult and juvenile *R. sylvatica* readily traveled in excess of 300 m from their pools of origin in this study (Table 1). Bellis (1965) determined that adult and juvenile *R. sylvatica* in a peat bog had traveled at least 410 m from the nearest breeding pool, and Berven and Grudzien (1990) determined that dispersing *R. sylvatica* juveniles traveled an average of 1208 m from their natal pools. Our data suggest that the long distance movements reported in these earlier studies may

not be the exception, particularly for juvenile *R. sylvatica*. Despite trapping over proportionally less circumference at progressively greater distances from the pool, number of adult *R. sylvatica* recaptures did not decrease proportionally at greater distances. At 300 m, 4% of the total circumference was covered with drift fences, and yet we recaptured 4.4% of males and 4.6% of females, whereas at 30 m, with 64% of the total circumference covered, we recaptured less than 10% of males and females (Table 1). This suggests that adults may have established summer activity areas near the fences located 300 m from the breeding pool, leading to greater than expected recapture success. Juvenile recapture success decreased more dramatically at greater distances, suggesting that the majority of juveniles were still dispersing, as opposed to establishing summer home ranges, at 300 m.

Previous studies indicate that adult *A. maculatum* travel an average of 153 m (range = 6–249 m) from breeding pools into the surrounding terrestrial habitat (Douglas and Monroe, 1981; Kleeberger and Werner, 1983; Madison, 1997), and juvenile *A. maculatum* can disperse at least 40 m from their pool of origin (Rothermel and Semlitsch, 2002). We were unable to add to these previous studies because of a low recapture rate for *A. maculatum*. The low recapture rate for *A. maculatum* in this study was likely a result of the relatively low breeding and recruitment at VP3 (nine adults and 44 juveniles total) coupled with the difficulty of capturing semifossorial salamanders in pitfall traps.

Recaptures of juvenile *R. sylvatica* were concentrated in the easternmost fences at each distance to the north. This pattern mirrors the concentrated dispersal pattern observed for juveniles exiting VP3 in the northeastern corner of the pool, suggesting fairly straight, directed movements may continue after juveniles leave

TABLE 3. Number of adult *Rana sylvatica* and *Ambystoma maculatum* marked in 2001 (marked), number (and % of total) returning in 2002, and number (and %) of those returning adults that bred in the same pool or a different pool. M = male. F = female.

Species	Pool	Sex	Marked	Returned	Same Pool	Different Pool
<i>R. sylvatica</i>	VP1	M	138	18 (13.0)	17 (94.4)	1 (5.6)
		F	88	9 (10.2)	8 (88.9)	1 (11.1)
	VP2	M	124	9 (7.3)	7 (77.8)	2 (22.2)
		F	114	8 (7.0)	3 (37.5)	5 (62.5)
	VP3	M	304	114 (37.5)	114 (100.0)	0 (0.0)
		F	237	41 (17.3)	40 (97.6)	1 (2.4)
<i>A. maculatum</i>	VP1	M	21	10 (47.6)	10 (100.0)	0 (0.0)
		F	24	9 (37.5)	9 (100.0)	0 (0.0)
	VP2	M	7	0 (0.0)	0 (0.0)	0 (0.0)
		F	5	5 (100.0)	5 (100.0)	0 (0.0)
	VP3	M	14	14 (100.0)	14 (100.0)	0 (0.0)
		F	5	5 (100.0)	5 (100.0)	0 (0.0)

TABLE 4. Spearman rank correlation coefficients between captures of males (M), females (F), and juveniles (J) entering and exiting pools or captured in terrestrial traps on dates of first through 95% of captures and precipitation (PPT), maximum temperature (Max), and minimum temperature (Min). *N* = number of days. (* = significance at *P* = 0.05).

Species	Year	Movement	Sex/class	Dates	PPT	Max	Min	<i>N</i>	Critical value
<i>R. sylvatica</i>	2001	Entering	M	4/13–4/25	–0.376*	0.435*	0.359*	13	0.56
			F	4/13–4/25	–0.504*	0.787	0.514*	13	0.56
		Exiting	M	4/23–5/29	0.540	0.135*	0.403	37	0.325
			F	4/22–5/16	0.147*	0.199*	0.190*	25	0.398
	Terrestrial	J	6/24–8/7	0.027*	–0.088*	0.142*	45	0.294	
		J	7/6–8/14	0.520	–0.153*	0.030*	40	0.313	
	2002	Entering	M	3/31–4/13	0.458*	0.160*	0.619	14	0.538
			F	4/3–4/13	0.491*	0.488*	0.758	11	0.618
		Exiting	M	4/10–5/15	0.460	0.020*	0.634	36	0.330
			F	4/9–4/18	0.473*	0.116*	0.697	10	0.648
Terrestrial		J	6/28–7/31	0.575	0.280*	0.312*	34	0.340	
		J	7/1–8/21	0.592	–0.230*	0.045*	52	0.274	
<i>A. maculatum</i>	2001	Entering	M	4/13–5/16	0.191*	0.042	0.251*	34	0.340
			F	4/13–5/17	0.292*	0.079*	0.236*	35	0.335
		Exiting	M	5/5–5/28	0.833	–0.047*	0.309*	24	0.406
			F	5/5–5/28	0.799	–0.225*	0.154*	24	0.406
	Terrestrial	J	8/7–9/26	0.500	0.259*	0.408	51	0.276	
		2002	Entering	M	3/31–4/18	0.584	0.481	0.578	19
	F			4/3–4/18	0.467*	0.419*	0.744	16	0.503
	Exiting	M	4/19–5/10	0.536	0.128*	0.335*	22	0.425	
		F	4/13–5/14	0.535	–0.107*	0.101	32	0.350	
		Terrestrial	J	7/24–9/28	0.804	–0.077*	–0.098*	67	0.241
J									

their natal pools. Juvenile *R. sylvatica* were larger at greater distances from their pool of origin (Table 2). More work is needed to determine whether this is caused by the growth of individual juveniles as they travel to greater distances or an inherently greater ability of larger juveniles to rapidly travel greater distances and be recaptured. Individual movements would have to be tracked to determine juvenile time-budgets and microhabitat characteristics that may influence juvenile movement patterns. Studies in Maine are currently examining this question.

The strong correlation between juvenile captures at the pool and recaptures at 30 m and 150 m on the same day is likely a result of the correlation between juvenile movement and precipitation, since precipitation was correlated both with juvenile dispersal from the pools and terrestrial activity (Table 4). Ignoring these same-day correlations, the next most significant correlation between pool captures and recaptures at 30 m occurred after two days. This suggests that, on average, juvenile *R. sylvatica* exiting the pool reached the fences at 30 m in two days. Similarly, the next highest correlation between pool captures and recaptures at 150 m, after the same-day correlation, occurred after four days, and the highest correlation between pool captures and recaptures at 300 m occurred after six

days. This suggests that, on average, juveniles were reaching 150 m in four days and 300 m in six days.

Movement patterns of *R. sylvatica* and *A. maculatum* to and from breeding pools documented in this study suggest that current recommendations for conservation of terrestrial habitat adjacent to vernal pools are realistic, if not conservative. Both adult and juvenile *R. sylvatica* exceeded our 300 m fences. We lack data on *A. maculatum* and on what percent of the *R. sylvatica* population traveled 300 m, but our sample numbers were sufficiently high to suggest that the 230 m zone recommended by Calhoun et al. (in press) for conserving pool-breeding amphibians in developing landscapes is reasonable. The nonrandom movement of both species, adults and juveniles, suggests that quality of nonbreeding habitat is important at both metamorph and adult stages. Adult frogs were commonly found in the adjacent forested wetland and associated small stream, suggesting this habitat was an attractive summer refugia.

Our study of movement patterns suggests that in developing landscapes with limited open space options it may be possible to conserve key areas around breeding pools (perhaps forested or forested wetland habitat) without having to conserve the entire area around a pool. Data on the relationship between size and quality

of nonbreeding habitat required to maintain local breeding populations have to be quantified for each pool-breeding species. Continued research to confirm preferred nonbreeding habitat should target conservation of nonbreeding habitat in a way that may allow strategies to be both more flexible and effective.

Pool Fidelity.—Adult *R. sylvatica* and *A. maculatum* exhibited high levels of breeding-pool fidelity despite the fact that the three pools were close together and only recently created (Table 3). Berven and Grudzien (1990) reported that adult *R. sylvatica* were 100% faithful to the breeding pool in which they first bred, and Whitford and Vinegar (1966) speculated that adult *A. maculatum* were similarly faithful to their breeding pools. Our adult pool-fidelity values support the findings of these earlier studies. The close proximity of the three pools may explain the 2% of male and 12% of female *R. sylvatica* that changed breeding pools. Indeed, the majority of *R. sylvatica* that bred in different pools came from VP2, most likely because of the location of VP2 between the other two pools. Higher return rate of marked amphibians to VP3 may be a reflection of the preferred temporary water regime which prevented the establishment of breeding *Rana clamitans* Latrielle (Green Frog) populations associated with the permanent and semi-permanent regimes of VP1 and VP2 (Vasconcelos, 2003). Certainly for *R. sylvatica*, recruitment would not be expected in VP1 and in VP2 in some years owing to little or no metamorph production.

Literature on pool fidelity suggests that location of detention basins or other created pools next to natural pools may attract breeding amphibians to less suitable sites. These findings also suggest that mitigating for vernal pool losses outside of the impact area may do little to mitigate losses to local amphibian populations.

Temperature and Precipitation Cues.—Activity of *R. sylvatica* during the nonbreeding season has been shown to increase with increasing temperature (Heatwole, 1961) and precipitation (Bellis, 1962, 1965). This pattern was consistent in our study for animals (male and female) entering breeding pools. Movement of male *R. sylvatica* from breeding pools was not correlated with precipitation in both years and was correlated with juvenile exiting only in 2001. Spring 2001 was characterized by a cold, late spring with little rainfall. The inconsistencies in movement patterns may be related to broader weather conditions including winter conditions (i.e., snow pack or condition of the animals) and rate of warming in the spring.

Previous studies have concluded that the stimulus to the breeding migration of adult *A. maculatum* is associated with increasing precipi-

tation (Blanchard 1930), humidity and temperature (Baldauf 1952). Sexton et al. (1990) found that, although all immigration of *A. maculatum* to breeding pools was associated with some rainfall, mean temperature was the best predictor of the number of immigrating adults. Our findings were less consistent between sexes and years (Table 4). Precipitation was the most important weather variable for entering males and females in 2001 (likely because of drought conditions). However, our data from 2001 and 2002 indicate a strong positive correlation between precipitation and the postbreeding emigration of *A. maculatum* adults from breeding pools and the dispersal of juveniles from their natal pools (Table 4).

In summary, our findings suggest that peak migrations of *A. maculatum* and *R. sylvatica* adults and juveniles are linked to both temperature and precipitation events. Monitoring events, studies looking at terrestrial habitat use, and conservation of migratory routes (such as timing of road closings in amphibian breeding areas) may benefit from taking into account these cues associated with peak movement.

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