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Orientation of Juvenile Wood Frogs, *Rana sylvatica*, Leaving Experimental Ponds

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ABSTRACT.—Some amphibians are able to orient toward habitat features, but it is not always clear whether (1) these animals can directly detect the habitat toward which they are moving (e.g., scenting water from a wetland); or (2) they are detecting an indirect cue that is consistently correlated with the location of suitable habitat (e.g., the location of sunrise). In 2004, we translocated 400 *Rana sylvatica* tadpoles from an isolated population on Sears Island in Maine, where emerging metamorphs travel northeast towards a forested wetland. We placed study animals in arrays consisting of a central artificial pool, with a circular drift fence at 0.2 m from the pool's edge to assess orientation of metamorphs at emergence and a similar fence at 5 m to assess orientation postemergence. Arrays were placed at 10 m and 50 m from a forested wetland, with the wetland cue to the southwest (i.e., the opposite direction of the wetland at Sears Island). *Rana sylvatica* exhibited significant orientation toward the northeast at the 0.2 m fence, indicating that emerging metamorphs retained the same directionality as at the site where they were hatched. A significant result at the 5 m fence indicated that animals continued to head toward the northeast. These results suggest that the population of *Rana sylvatica* on Sears Island may rely on indirect cues for orientation. Relying on indirect cues offers less adaptability to changes in habitat such as breeding site loss or road construction, and thus could lead frogs into ecological traps.

Juvenile and adult amphibians move up to several kilometers for a variety of reasons, including traveling between summer foraging areas and overwintering sites (Regosin et al., 2003), migrating to and from breeding sites (Stenhouse, 1985), and dispersing to new habitats (Berven and Grudzien, 1990). Numerous studies have shown that amphibians can orient nonrandomly when making such long-distance movements (Dodd and Cade, 1998; Bulger et al., 2003; Mazerolle and Desrochers, 2005). Two hypotheses predict how this orientation may occur: (1) animals directly detect the habitat features toward which they are moving (e.g., via a scent or visual cue); or (2) animals rely on indirect cues to orientate toward the habitat feature (e.g., the location of the sun). Under the second hypothesis, animals may not be able to directly detect the habitat feature.

A few studies have documented the use of direct cues. Olfactory detection of home ponds has been demonstrated for *Ambystoma maculatum* (McGregor and Teska, 1989), *Taricha rivularis* (Grant et al., 1968), and *Notophthalmus v. viridescens* (Hershey and Forester, 1980). The use of indirect cues has been more widely explored, with mechanisms including sun-compass orientation in *Acris crepitans* and *Rana catesbeiana* (Ferguson et al., 1966, 1967), detection of magnetic fields in *N. v. viridescens* (Phillips, 1986; Fischer et al. 2001; Phillips et al., 2001), and *Rana catesbeiana* tadpoles (Freak and Phillips, 2005), and the potential to use plane-polarized light in *Ambystoma tigrinum* (Taylor and Adler, 1973).

The use of indirect cues has principally been shown in the laboratory, and its prevalence under natural conditions is unclear. Relying on indirect cues limits the ability of amphibians to respond to changes in habitat location whether resulting from natural (e.g.,

beaver dam construction) or from anthropogenic causes (e.g., wetland destruction). Such changes in habitat features could occur between amphibian breeding seasons and direct detection of the actual habitat feature would allow more rapid adaptation.

Our study focused on a population of *R. sylvatica* indigenous to Sears Island, Maine, where juveniles emerging from a natal pond from 1999 to 2002 consistently orientated towards a closed canopy forested wetland to the northeast (Vasconcelos and Calhoun, 2004). Our objective was to assess whether *R. sylvatica* translocated from Sears Island orientated in the same cardinal direction as at the original site, or whether they detected and actively orientated towards suitable habitat (forested wetland) located in the opposite direction of their natal pond. We also assessed whether orientation occurred immediately upon emergence from the natal pond or after experience in the terrestrial environment and whether the distance between the natal pond and a potential cue had any influence on orientation ability.

MATERIALS AND METHODS

Study Sites.—Sears Island (380 ha) is situated in Penobscot Bay, Searsport, Maine (44°27'N, 68°53'W), and is connected to the mainland by a 200 m long causeway. We removed *R. sylvatica* from one of three breeding ponds (namely VP3) that were constructed on the island in 1997 to replace a natural wetland (Vasconcelos and Calhoun, 2004). The constructed ponds are in a seasonally saturated wet meadow with the bay located 100 m to the southwest. A closed-canopy forested wetland is located 15 m to the northeast of VP3, with wet meadow habitat extending 60 to 100 m to the south and east before reaching further closed canopy forest. The remainder of the island is an area of undeveloped forest, dominated by red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), and yellow birch (*Betula alleghaniensis*).

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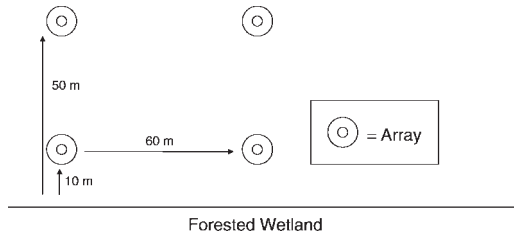


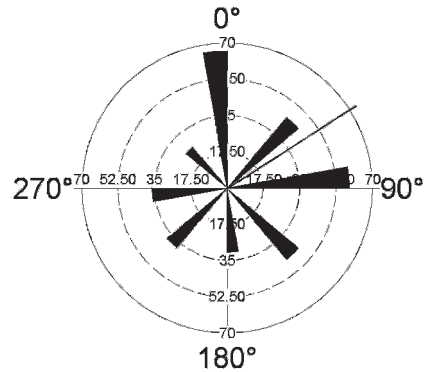
FIG. 1. Layout of artificial arrays at each site (figure approximately to scale).

Our experimental site is located in the University of Maine Dwight B. Demeritt Forest, Orono, Maine (approximately 55 km inland from Sears Island). We constructed experimental arrays in continuous forest of eastern white pine (*Pinus strobes*), balsam fir (*Abies balsamea*), and northern white cedar (*Thuja occidentalis*), with a forested wetland located to the southwest. This wetland has similar floral composition to the forested wetland on Sears Island, indicative of similar hydrology. No other wetlands are located within 100 m of any of the arrays. We established our study site at this location so that metamorphosing wood frogs orienting toward the nearby wetlands would have to shift 180° from the preferred direction at their natal pond on Sears Island (Vasconcelos and Calhoun, 2004).

Experimental Design.—Two experimental sites were chosen approximately 1 km apart. Site choice was based on maintaining a standard species, age-composition, and disturbance pattern of forest stands, and so that a clear distinction existed between the forested wetland and the surrounding upland forest. At each site, two arrays were placed at 10 m and at 50 m from the wetland edge (Fig. 1). At one site, an additional two arrays were constructed at the 10-m distance, for a total of 10 arrays (the latter two arrays were not coupled with arrays at 50 m because of the presence of a small area of damp ground (< 4 m²) approximately 80 m north of the wetland). All arrays were spaced > 60 m apart in each distance class. Also, the nearest forest edge or change in stand type was > 60 m away. All woody debris (> 1 cm in diameter) was removed from the arrays.

An array consisted of a 60-liter plastic wading pool, 1.5 m in diameter, and 25 cm deep. Pools were placed on a leveled surface and filled to the top with water from a nearby stream that emerged from the forested wetland (approximately 100 m west-southwest of the nearest array in site 1, and > 1 km from site 2). The pools were stocked with a 5-liter bucket of packed wet leaf litter collected adjacent to the same stream a week prior to introduction of the tadpoles. The water level was maintained throughout the study, although consistent rainfall meant that little additional water was needed. Silt fencing was attached to the rim of the pool to form a continuous ramp down to the ground at an angle of approximately 45°. Two circular silt-fencing drift fences were constructed around each pool at 0.2 m and 5 m from the pools edge. The fences were 30 cm in height, with the bottom buried 10 cm into the ground. Eight pitfall traps were equally spaced at the 0.2 m fence, and 12 traps at the 5-m fence. Pitfall traps consisted of a single 10 aluminum

Inner fence



Outer fence

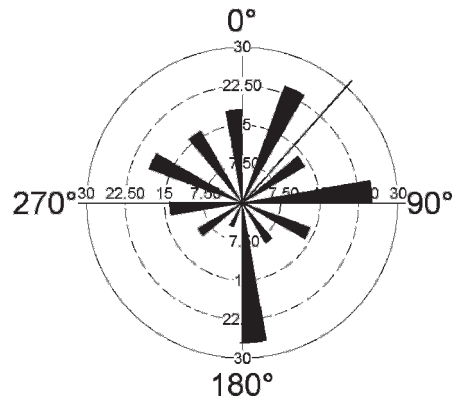


FIG. 2. Orientation of all juvenile *Rana sylvatica* captured at the inner (above) and outer (below) drift fences (pooled for all arrays). The length of the bars represents the total number of captures in each trap, with the abundance scale indicated on the concentric circles. The solid line represents the mean vector, with the 95% confidence interval indicated by the arc outside of the circle.

food can 22.5 cm deep, with a 10 cm deep funnel extending down into the trap, and were aligned at both fences such that one trap faced each of the cardinal directions, with the remaining traps equally spaced between these (i.e., one trap in between at the 0.2 m fence, and two traps at the 5-m fence). Traps remained moist throughout the study period; thus, no means of preventing dehydration (such as sponges) were needed.

On 29 June 2004, we translocated 40 randomly selected *R. sylvatica* tadpoles of Gosner stage 31–41

TABLE 1. Results of Rayleigh's test for the directionality of juvenile *Rana sylvatica* captured at the 0.2-m drift fence.

Array	Distance from wetland (m)	Sample size (N)	Mean vector (°)	Length of mean vector (r _c)	Circular variance	Significance level (Rayleigh P)
1a	10	28	300.83	0.195	0.81	0.373
1b	50	33	87.02	0.144	0.86	0.521
1c	10	32	180.85	0.267	0.74	0.123
1d	50	36	184.43	0.113	0.89	0.674
1e	10	31	58.97	0.472	0.54	0.001 *
1f	10	37	50.86	0.349	0.66	0.012 *
2a	10	40	82.72	0.287	0.72	0.043 *
2b	50	37	333.07	0.328	0.68	0.020 *
2c	10	36	12.64	0.287	0.72	0.053
2d	50	36	98.79	0.339	0.67	0.018 *
All**		144	71.647	0.328	0.67	<0.001 *

*Indicates a significant directionality as indicated by a Rayleigh $P < 0.05$. The arrays number refers to the site where it was located.

**Shows the analysis of the pooled data for those arrays that showed significant directionality in individual Rayleigh's tests.

(Duellman and Trueb, 1986) from Sears Island into each artificial pool. The number of tadpoles was based on viable ranid tadpole densities in artificial pools (Alford and Wilbur, 1985).

From 2 July through 19 July 2004, we checked pitfall traps daily except for the final week of the experiment when checks occurred every other day. Juveniles captured in pitfall traps at the enclosing 0.2-m drift fence were released on the outside of the fence directly opposite the point of capture. Juveniles recaptured at the 5 m drift fence were removed and returned to Sears Island.

Analysis.—We examined the data using both qualitative and quantitative methods (circular statistics). Graphical analysis was used as a qualitative means of looking for general patterns in orientation that may not have been evident from circular statistics. For these analyses, we pooled the circular data from all of the arrays, comparing mean directionality and the circular dispersion of individuals at the 0.2-m and 5-m fences.

We used Oriana 1.0 (Kovach Computing Services, Anglesey, Wales, U.K.) to quantitatively analyze circular data. We used the Rayleigh test to test for nonrandom directionality in animals leaving the ponds at the 0.2-m and 5.0-m fences, and to compare between arrays at 10 m and 50 m. Although a V -test is more powerful than a Rayleigh test when there is an expected direction of movement, the design of the experiment presented two alternative hypotheses: (1) that the emerging juveniles would orient toward the northeast; or (2) that they orient toward the southwest. The V -test would only have indicated whether the frogs had orientated in the same direction, and the multiple comparisons needed to evaluate several alternative hypotheses would have reduced the power of the test (Batschelet, 1981). Because of the small circumference of the 0.2-m drift fence, we felt that to be able to evaluate these hypotheses, we would need evidence of specific directionality toward the northeast or the southwest, rather than simply nonrandom movement. A significance level of 0.05 was used for all tests, corrected for the grouping of data resulting from the low number of traps at both fences (Batschelet, 1981). Watson-Williams tests were used

to test for differences in the mean angles of those arrays that demonstrated significant results with the Rayleigh test. If no significant differences were shown in these mean angles, the data were pooled, and a further Rayleigh's test was conducted.

RESULTS

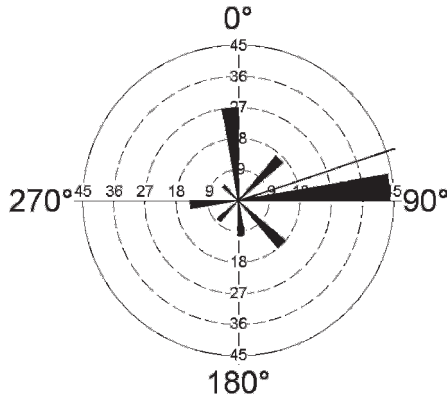
Of the 400 tadpoles released, 346 were captured as metamorphs at the 0.2-m drift fences, and 195 were recaptured at the 5-m fence. Those individuals that were not captured at the 0.2-m fence presumably died before leaving the artificial ponds; individuals not captured at the 5-m fence presumably either settled or died between the two drift fences.

Graphical analysis of all the data (pooled for all arrays regardless of individual significance levels) showed mean directions of 57.35° at the 0.2-m fence and 41.84° at the 5-m fence (Fig. 2). This analysis also revealed that at the 5-m fence, 14% of captures were in traps to the south of the artificial ponds, that is, the direction of the wetland at the experimental site.

The results of statistical analyses showed similar patterns to the graphical analyses. Juvenile frogs were significantly orientated in a specific direction at five of the 10 arrays at the 0.2-m drift fences (Table 1). Watson-Williams tests of these five significant arrays showed a significant difference between sample means, indicating that one or more of the arrays differed in directionality (Watson-Williams $F_{4,176} = 8.271$; $P < 0.001$). Analysis showed that the 95% confidence intervals for the mean directions overlapped for four of the arrays, with one array differing in directionality. When this one array was removed from the analysis, the remaining arrays did not significantly differ in mean directionality (Watson-Williams $F_{3,141} = 2.024$; $P = 0.093$). The removal of this array from the pooled data is justified as it had little effect on the mean directionality (a change from 57.076–71.647° after removal) and no effect on the significance level of the Rayleigh's test ($P < 0.001$). Mean directionality was 71.647° for these pooled data (95% CI from 52.044–91.250°; Fig. 3).

Significant orientation was also seen in three of the 10 arrays at the 5-m fence (Table 2), with Watson-Williams tests revealing no significant differences

Inner fence



Outer fence

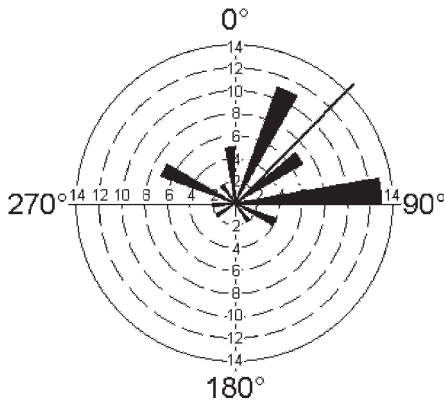


FIG. 3. Orientation of juvenile *Rana sylvatica* captured at the 0.2 m (above) and 5 m (below) drift fences. The figures represent pooled data from those individual arrays that showed significant directionality as evaluated by Rayleigh's test. The length of the bars represents the total number of captures in each trap, with the abundance scale indicated on the concentric circles. The solid line represents the mean vector, with the 95% confidence interval indicated by the arc outside of the circle.

between these mean directions. The pooled data had a mean direction of 44.541° (95% CI: $23.247\text{--}65.836^\circ$; Fig. 3).

Both of these mean angles at the 0.2-m and 5-m fences approximate a northeasterly direction (45°). The lack of significant differences in the Watson-Williams tests also indicates that there were no significant differences in the directionality of juvenile frogs when comparing between arrays at 10 m and 50 m from the wetland.

DISCUSSION

Finding that emerging juvenile *R. sylvatica* showed evidence of orientation toward the northeast, that is, the same directionality found at Sears Island from 1999–2002 (Vasconcelos and Calhoun, 2004), and the opposite direction to the forested wetland at the experimental arrays, was unexpected given that previous research indicates that emerging wood frog juveniles move toward wetlands (Heatwole, 1961; Bellis, 1965; Mazerolle, 2001). It is important to notice that this directionality was only seen at five of the 10 inner fences and three of the 10 outer fences. However, there were no arrays where frogs were significantly orientated in a direction corresponding to our alternative hypothesis of southwest. At the one statistically significant array where frogs at the 0.2-m fence did not orientate northeast, the frogs exhibited a mean orientation of 333° (i.e., north-northwest). This represents < 1 m change in direction as represented by position on the circumference of the 0.2-m fence. At Sears Island the frogs emerging from the pools showed highly significant directionality (Rayleigh $P < 0.001$ for all tests) moving toward a forested wetland and away from open habitat (Vasconcelos and Calhoun, 2004). Although our sites were uniformly forested, we also documented a similar significant directionality. The mean direction at Sears Island was 57° (Vasconcelos and Calhoun, 2004), compared with 71.6° at our 0.2-m fence and 44.5° at our 5-m fence.

Our results were unlikely to be a function of suitable habitat being too distant for direct-cue detection, because there were no significant differences when comparing orientation at 10 m and 50 m from the wetland edge at the experimental sites. The wetlands at the experimental sites were suitable habitat for juvenile *R. sylvatica* (Heatwole, 1961; Bellis, 1965) and presumably would have generated direct cues similar to those of the Sears Island wetland. Although 50 m could be too distant for animals to detect direct cues, it is unlikely 10 m is too distant, especially if the cue is of value in orientation. The use of a drift fence to capture animals may have presented a barrier to olfactory cues, although this is unlikely because a porous fencing material was used and previous studies have indicated that drift fences do not block such cues (Hershey and Forester, 1980). Visual cues could have been limited, but Maine forests are usually too dense to allow visual detection of forest wetlands at 50 m even without a fence.

We documented that some of the frogs moved northeast even though the habitat located in this direction was less suitable than in other directions. This suggests that the movement of some of the translocated *R. sylvatica* is based on the use of indirect cues that remain consistent between Sears Island and our experimental site (e.g., the direction of the sun or the earth's magnetic field). Those animals that showed significant directionality at the 0.2-m fence provide evidence that orientation in response to indirect cues may manifest itself prior to, or during emergence from, the natal pond. Orientation prior to emergence has been demonstrated for other amphibian species such as *Triturus vulgaris* (Malmgren, 2002) and *Rana catesbeiana* (Justis and Taylor, 1976), but we believe that this is the first time the use of indirect cues has

TABLE 2. Results of Rayleigh's test for the directionality of juvenile *Rana sylvatica* captured at the 5-m drift fence.

Array	Distance from wetland (m)	Sample size (N)	Mean vector (α)	Length of mean vector (r_c)	Circular variance	Significance level (Rayleigh P)
1a	10	20	245.10	0.020	0.98	0.992
1b	50	23	178.71	0.263	0.74	0.215
1c	10	19	355.14	0.607	0.40	0.001 *
1d	50	24	320.49	0.293	0.71	0.141
1e	10	18	80.68	0.779	0.23	<0.001 *
1f	10	21	254.14	0.223	0.78	0.363
2a	10	18	48.43	0.425	0.58	0.042 *
2b	50	25	75.60	0.263	0.74	0.179
2c	10	16	90.57	0.222	0.78	0.452
2d	50	11	270.00	0.273	0.73	0.451
All**		55	44.54	0.473	0.527	<0.001 *

* Indicates a significant directionality as indicated by a Rayleigh $P < 0.05$. The arrays number refers to the site where it was located.

** Shows the analysis of the pooled data for those arrays that showed significant directionality in individual Rayleigh's tests.

been shown as a potential mechanism for orientation of larval *R. sylvatica*.

Although we found evidence that dispersing wood frog metamorphs use indirect environmental cues, we were not able to determine specifically which cue(s) the metamorphs were using to orientate. Nevertheless, our results raise the question as to how widespread the use of indirect cues is in amphibian orientation. At Sears Island, we expected strong selection for directionality of emerging metamorphs because of the ocean's proximity to the southwest of the breeding pond. The size of the Wood Frog population is not known, but as an island population, immigration is most likely reduced; thus, selection pressure increased (Ridley, 1993). The fact that amphibians in large populations (e.g., those found at the Savannah River Site, Aiken, SC), continue to show philopatry following destruction of their breeding sites (Pechmann et al., 2001), suggests that indirect cues may be prevalent in many populations.

Using indirect cues could lead metamorphs into an ecological trap where the proximate cues used to orientate in the terrestrial environment no longer maximize survival and fitness (Schlaepfer et al., 2002). Evidence for this has been shown for several species of amphibian including *Ambystoma talpoideum* and *Notophthalmus viridescens*, with adults continuing to return to breeding pools that have been destroyed (Pechmann et al., 2001). If the use of indirect cues is widespread in amphibian populations, the potential for disrupted breeding success resulting from habitat loss will be increased. Wetland mitigation often involves wetlands being created to replace those that are lost (Roberts, 1993). If wetland removal not only leads to the loss of a breeding site, but also to high rates of breeding failure resulting from adults returning to the destroyed location, effects on amphibian populations may be more significant than first thought.

In addition to potentially creating an ecological trap, the use of indirect cues may have a strong link to the degree of philopatry in a population. If all the juvenile amphibians emerging from a natal pond head in the same direction, then the chance of their locating

a different breeding site will be reduced. High levels of philopatry for *R. sylvatica* have been demonstrated; for example approximately 80% of adults breeding at study ponds in Appalachia emerged as juveniles from the same pond (Berven and Grudzien, 1990). Interestingly, the 14% of juveniles we documented changing direction toward the wetland at the 5-m drift fence is similar to the 18% of juveniles dispersing to different breeding sites found by Berven and Grudzien (1990).

Our results highlight the need for more research into how amphibian populations respond to changes in the location of potential breeding sites and links between directionality and levels of philopatry. The extension of experimental studies such as ours to different locations and species would help in determining how widespread the use of indirect cues is.

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