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MOVEMENT ORIENTATION BY ADULT AND JUVENILE WOOD FROGS (*RANA SYLVATICA*) AND AMERICAN TOADS (*BUFO AMERICANUS*) OVER MULTIPLE YEARS

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Abstract.—**We conducted a four-year study of Wood Frogs (*Rana sylvatica*) and American Toads (*Bufo americanus*) occurring syntopically at a breeding site surrounded by different, but equally accessible, habitat types to investigate whether adults and juveniles had non-random movement orientations and whether those orientations differed among species, life stages, and years. Using a single drift fence encircling the breeding pond, we found that adult Wood Frogs oriented non-randomly each year and consistently avoided orientating their migration toward or away from habitat consisting of relatively younger, successional, more restricted forest, with a road edge, and with high soil moisture, and reduced canopy cover and litter depth (West). Adult American Toads oriented their migrations non-randomly to and from the pond in three or four of the years, respectively, but, orientation patterns were inconsistent across years. Wood Frog and American Toad juveniles initially oriented non-randomly each year; however, the patterns also showed no trends across years. Adult Wood Frog orientations did not seem to be affected by the differences in forest age or between residential or agricultural edges, but the road edge, the reduction in leaf litter depth, and/or tree density might have negatively impacted their orientation patterns. It remains unclear why adult American Toad patterns varied over time. Furthermore, juvenile trends showed that metamorphs did make an orientation decision, but because that predominant direction changed across years, perhaps cues other than habitat were influential. We suggest that multi-year studies may be crucial to fully understand movement patterns of a particular amphibian life stage and/or species.**

Key Words.—American Toad; amphibian; *Bufo americanus*; habitat selection; migration; orientation; *Rana sylvatica*; Wood Frog

INTRODUCTION

Pond-breeding amphibians require both aquatic breeding habitat and surrounding terrestrial habitat that they must regularly move between. Despite this dependence on multiple habitats, the majority of government regulations focus on wetlands and offers little protection to surrounding uplands (Gibbons 2003). It is becoming increasingly clear, however, that the quality and quantity of terrestrial habitat surrounding amphibian breeding ponds is a critically important determinant of amphibian species occurrence in a particular area (e.g., Gibbs 1998a,b; Homan et al. 2004; Porej et al. 2004). Understanding terrestrial habitat preferences and patterns of use for pond-breeding amphibians is essential for determining how and in what way the terrestrial habitat regulates population size, and thereby maximizes our ability to effectively protect these populations (e.g., Regosin et al. 2003).

Wood Frogs (*Rana sylvatica*) and American Toads (*Bufo americanus*) are two relatively common pond-breeding anurans in North America. These species have overlapping ranges and are often syntopic with one another, but American Toads appear to have broader habitat tolerances than Wood Frogs. Adult American Toads have been found inhabiting several habitat types including agricultural, residential, forest, and forest edge (e.g., Kolozsvary and Swihart 1999; Guerry and Hunter 2002; Forester et al. 2006). It has been further suggested that the distribution of adult American Toads is negatively associated with forest cover, emphasizing the importance of some open canopy habitat in a given area (Guerry and Hunter 2002). In contrast, adult Wood Frogs apparently prefer forested upland and forested wetland habitats (e.g., Guerry and Hunter 2002; Regosin et al. 2003; Baldwin et al. 2006). Adult Wood Frog distribution has been positively linked to the amount of forest canopy cover present (e.g., Guerry and Hunter 2002; Homan et al. 2004), and it has been suggested that there is a threshold level of forest cover below which populations are significantly less likely to persist (Homan et al. 2004).

Besides forest quality, the extent of habitat also influences adult distribution in these species. Adult Wood Frogs have been found to migrate more than 300 m from their breeding ponds (Vasconcelos and Calhoun 2004), with one study finding that 40% of a breeding population migrated more than 100 m away from the breeding pond (Regosin et al. 2005). Adult American Toads are known to be able to migrate even further, up to 1.5 km, away from their breeding ponds (Forester et al. 2006). Edge type may also influence anuran distribution and migration (e.g., deMaynadier and Hunter 1998; Gibbs 1998b). Adult Wood Frogs have been shown to be adversely impacted by road edges (Gibbs 1998b) as well as new-growth forests up to 11 years old (deMaynadier and Hunter 1998). Less is known regarding the edge habitat requirements of adult American Toads (Forester et al. 2006); however, their distribution across a broad range of habitats may indicate a greater tolerance for edge type.

The initial orientation of juvenile Wood Frogs and American Toads out of their natal pond is still relatively poorly understood, and only a few studies have successfully analyzed juvenile orientation of Wood Frogs (e.g., deMaynadier and Hunter 1999; Vasconcelos and Calhoun 2004; Patrick et al. 2006, 2007) and American Toads (e.g., Rothermel and Semlistch 2002). The studies suggest that juveniles of both species orient toward forested habitats and selectively avoid open habitats (Bellis 1965; deMaynadier and Hunter 1999; Rothermel and Semlitsch 2002; Vasconcelos and Calhoun 2004), which is consistent with the pattern of adult Wood Frog orientation but inconsistent with that of adult American Toads. The apparent preference for closed-canopy forest may exist because juveniles are especially sensitive to desiccation due to their small body size, permeable skin, and timing of migration during the warmest days of the year (Semlitsch 1981). Juvenile Wood Frogs have also exhibited preference for forested wetland habitat (Bellis 1965; Vasconcelos and Calhoun 2004), which could also be explained by their need for moisture during this sensitive period of their life. Some studies suggest that due to the tough conditions emigrating juvenile amphibians face, they may not migrate as far as adults (Semlitsch 1981, 1998; deMaynadier and Hunter 1999). However, Berven and Grudzien (1990) found that a small percentage of juvenile Wood Frogs can migrate over 2.5 km from natal ponds, suggesting juveniles may be capable of migrating relatively long distances. Overall, data regarding initial juvenile movement orientation from natal ponds is sparse and comparative data between the two species at a single pond is absent. Studying these two species together thus provides an appealing comparative analysis due to their overlapping habitat use combined with the apparent difference in habitat preferences, particularly among adults.

We used a drift fence surrounding a breeding pond that supported both Wood Frogs and American Toads to document movement orientation of adults to and from the pond in the spring and juveniles from the pond in the summer. We were particularly interested in whether and how both adults and juveniles of these species differentially orient themselves during their movements, and whether any patterns were stable across multiple years. The pond in which these particular populations bred was adjacent, in roughly equal proportions, to four different upland habitat types that varied in macrohabitat characteristics (forest age, forest extent, edge type) and microhabitat characteristics (litter depth, tree density, and soil moisture). Therefore, we also explored possible relationships between orientation patterns and the characteristics of surrounding terrestrial habitat.

MATERIALS AND METHODS

Study site.—We conducted our study at the Taylor-Ochs pond on the Denison University Biological Reserve in Granville, Ohio (40°5'N, 82°31'W) from January 2005 through August 2008. The Taylor-Ochs pond is a small (~0.1 ha) man-made pond that is bisected by a small stream. Historically this pond dries by August and refills with rain in the fall (Schultz and Mick 1998; Smith et al. 2003), and this pattern held for our four study years, with the earliest drying occurring in late May (2007) and the latest drying occurring in early August (2006, 2008). This pond was uniquely well suited for this study for two reasons. First, Wood Frogs and American Toads co-occurred there. Second, the relatively undisturbed habitat surrounding the breeding pond varied in forest age (determined using serial, decadal aerial photographs starting in 1958), linear forest extent from the pond edge, and type of forest edge. These four suitable, but variable, habitats extended to the pond edge in roughly equal proportions, and we named them East, North, South, and West quadrants after the cardinal directions with which they happened to overlap (Fig. 1). East had a more mature forest, with a linear extent > 500 m from the pond edge, North had more mature forest, with a linear extent of ~100 m and an agricultural edge, whereas South and West both have younger forests with linear extents of ~100 m, with a residential and road edge, respectively. Additionally, West contained a single private home that occupied ~5% of the total area within that quadrant (Fig. 1).

To determine whether these quadrants also differed in important microhabitat characteristics, in the summer of 2007, we randomly sampled each habitat (East, North, South, and West) 50 times up to 100 m from the center of the pond. We measured litter depth (to the nearest millimeter) and soil water content (to the nearest 2%; Kelway moisture meter) at a depth of 8 cm at each sample location. Additionally, we estimated standing tree density (minimum 10 cm diameter at breast height) within a 5-m radius of the sample location (Homan et al. 2008).

Animal capture and handling.—To study anuran distribution and movement, we installed a drift fence

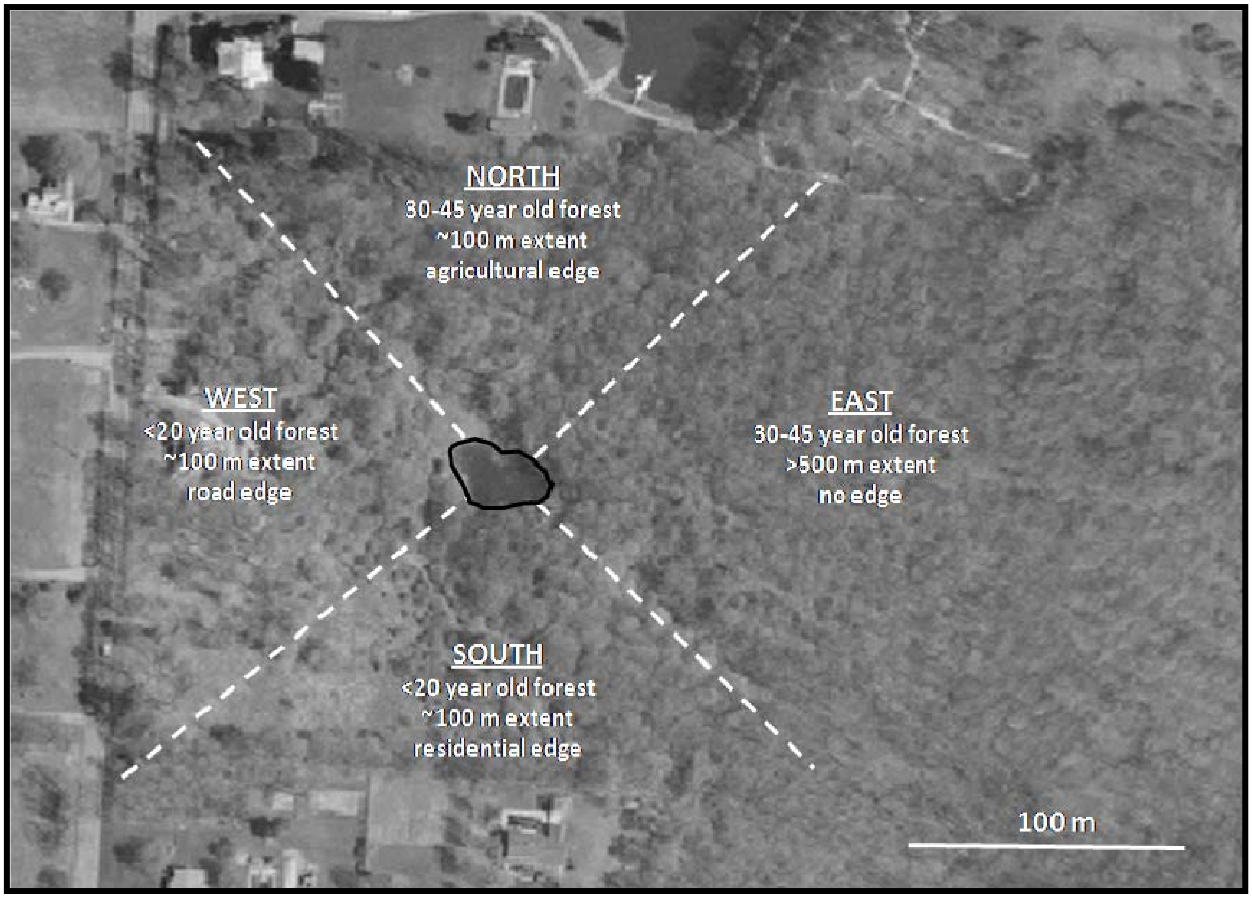

FIGURE 1. Aerial photo of Taylor-Ochs pond and surrounding habitat (1998). The black line represents the approximate location of the drift fence encircling the breeding pond, and the white dashed lines represents the nominal boundaries between four quadrants, East, North, South, and West. These areas differ in forest age, as estimated by serial photographs beginning in 1958, linear forest extent from the pond edge to the terrestrial edge, and edge type. (Aerial photograph courtesy of Licking County, Ohio).

system that completely encircled the pond, and animals were captured in paired pitfall traps made of plastic buckets (approximately 19 L capacity) positioned approximately every 15 m along the fence for a total of 12 pairs. Three pitfall traps fell within each of the four terrestrial quadrants, allowing equal capture area available to the amphibians if their migration orientations were uniform around the pond edge. We installed the fence in the fall of 2004 above the high water mark between 1.2 m and 6.3 m from the water's edge. However, during each spring, periods of heavy flooding pushed the high water mark beyond the drift fence in low lying areas forcing us to replace our pitfall traps with paired minnow traps until the water receded. Although the variation in trap type might have impacted our capture ability, we suspect the impact was minimal; the minnow traps were necessary only one or two times a season, for no more than a few days at a time, and we successfully caught adults in the minnow traps, with no obvious relative differences in density compared to nearby bucket traps.

We captured adult amphibians migrating to and from the pond during the breeding season, and we captured newly metamorphosed juveniles leaving the pond in the summer. Adult breeding captures were made in all four years of the study. Substantial juvenile captures, however, occurred in only 2005, 2006, and 2008, when the pond remained full through anuran metamorphosis. The drying of the pond before the end of May in 2007 resulted in near complete recruitment failure for both anuran species. Therefore, juvenile data for 2007 are not reported.

Data analysis.—To identify differences in microhabitat characteristics among quadrants, we subjected our three microhabitat variables (litter depth, tree density, and soil water content) to a principle components analysis (PCA) and compared the factor values across quadrant using ANOVA (JMP 6.0.2,SAS Institute, Cary, North Carolina, USA). To determine whether adult and juvenile movement orientations were non-random, we combined captures for the three pitfall traps in each quadrant and used a Chi-square test with α = 0.05 to look for a non-random distribution. Expected random distribution values were generated by dividing the total captured individuals of a given species in a given year by four (the number of quadrants), and we compared that value to the actual capture numbers in each quadrant. Our quadrant boundaries ran midway between traps, meaning that the interior of the three traps had 100% capture accuracy for correctly identifying an individual's migratory quadrant, while the outside traps had a capture accuracy of 75% each. Therefore, an individual had, on average, an 83% chance of falling into one of the three traps that correctly identified their movement orientation. We analyzed differences in capture location among quadrants within years first and then assigned numeric ranks (e.g., first, second, third, etc.) for associated quadrant in each year. We used these ranks to perform non-parametric Kruskal-Wallis tests to determine whether orientation patterns varied across years with α = 0.05 (JMP 6.0.2, SAS Institute, Inc., Cary, North Carolina, USA).

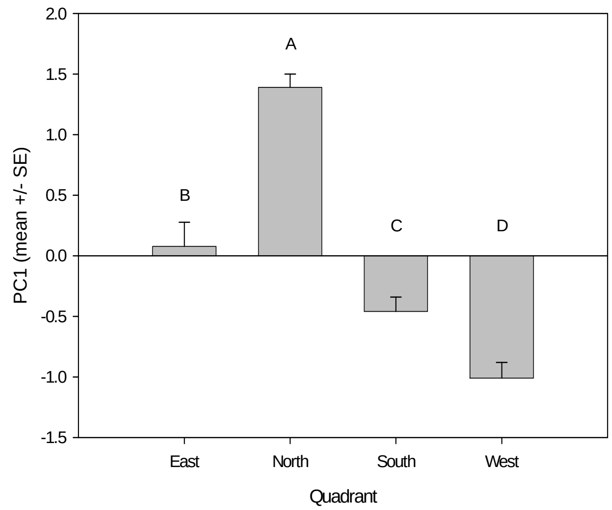

FIGURE 2. Relationships of Principle Component 1 (PC1) to the quadrants (n = 50 for each quadrant). PC1 is positively loaded by litter depth and standing tree density and negatively loaded by soil water content. Different capital letters over the bars represent statistically significant differences at α = 0.05.

RESULTS

In addition to the macrohabitat differences among quadrants (Fig. 1), there were also differences in microhabitat characteristics. Our PCA generated three factors, and we conducted further analyses on the one factor that had an eigenvalue > 1.0 (PC1, eigenvalue = 1.82). PC1 represented 60.6% of the variation. Litter depth and tree density loaded positively on PC1 and soil water content loaded negatively. We found that PC1 scores differed significantly across all quadrants ($F_{3,196}$ = 50.8, P < 0.0001; Tukey's HSD, all P < 0.05), with North having the highest mean value, followed by East, South, and West (Fig. 2).

The capture distributions of adult Wood Frogs migrating to the pond (inbound) and away from the pond (outbound) were non-random in all four years (Inbound- 2005: χ^2_3 = 143.0, P < 0.001; 2006: χ^2_3 = 275.9, P < 0.001; 2007: χ^2_3 = 343.4, P < 0.001; 2008: χ^2_3 = 425.3, P < 0.001, Fig. 3a.; Outbound- 2005: χ^2_3 = 28.4, P < 0.001; 2006: χ^2_3 = 145.4, P < 0.001; 2007: χ^2_3 = 355.4, P < 0.001; 2008: χ^2_3 = 489.3, P < 0.001, Fig. 3b).

Additionally, there were significant differences among annual ranks of movement orientations for the inbound and outbound frogs (Inbound: χ^2_3 = 10.0, P = 0.0186; Outbound: χ^2_3 = 10.9, P = 0.0120). For inbound adult Wood Frogs, West had a significantly lower median rank (i.e., relatively few animals captured migrating from West) than the other three quadrants across those four years (P ≤ 0.05). Although there was a trend of East having a higher median capture location rank relative to the other three quadrants over those years, it was not significant.

The outbound adult Wood Frog pattern was similar to the inbound pattern, with West's median rank being significantly lower than South's, which was significantly lower than East's (both P ≤ 0.05). North's rank was lower than that of East (P ≤ 0.05) but not different from the ranks of South or West (both P > 0.05).

The capture distributions of inbound and outbound adult American Toads were non-random in all years, with the exception of inbound toads in 2005 (Inbound- 2005: χ^2_3 = 5.6, P > 0.10; 2006: χ^2_3 = 14.7, P < 0.005; 2007: χ^2_3 = 287.0, P < 0.001; 2008: χ^2_3 = 27.5, P < 0.001, Fig. 3d.; Outbound- 2005: χ^2_3 = 34.1, P < 0.001; 2006: χ^2_3 = 24.8, P < 0.001; 2007: χ^2_3 = 107.9, P < 0.001; 2008: χ^2_3 = 23.1, P < 0.001, Fig. 3e). There was no significant pattern among ranks of migration orientations across years for either inbound or outbound American Toads (Inbound: χ^2_3 = 1.3, P = 0.70; Outbound: χ^2_3 = 4.9, P = 0.17). For inbound toads, each quadrant's capture locations supported the greatest number of toads in at least one year. For outbound toads, East was typically among the quadrants supporting the greatest number of individuals, though not significantly. Notably, traps in South never had the fewest number of toads either inbound or outbound, suggesting that along with East it may have been among the best quadrants for toads.

The juvenile anurans were first captured leaving the pond between late May and early June for both species in 2005, 2006, and 2008. There were only three juvenile American Toads and 28 juvenile Wood Frogs captured in 2007 because the pond dried in mid-May. Due to these low recruitment rates, 2007 was excluded from our

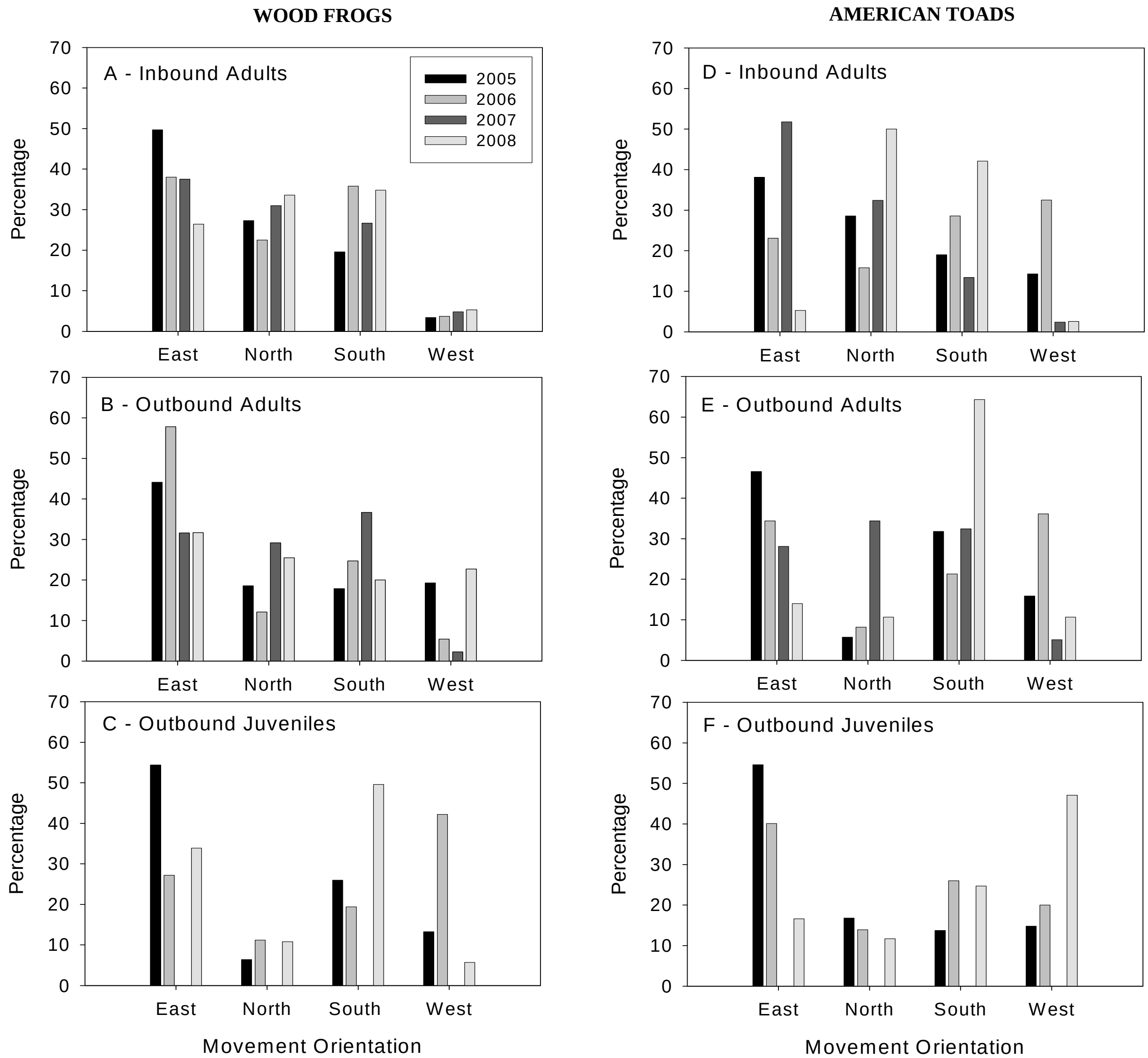

FIGURE 3. Percentage of the population of (A-C) Wood Frogs and (D-F) American Toads immigrating to (A, D) or emigrating from (B, C, E, F) the breeding pond oriented from or toward one of four quadrants. The four quadrants and there habitats were: East (older, more extensive forest, with no edge within ~500 m from the pond), North (older forest with an agricultural edge ~100 m from the pond), South (younger forest, with a residential edge ~100 m from the pond), and West (younger forest, with a road edge ~100 m from the pond) in 2005 through 2008. Total population sizes for Wood Frogs in 2005, 2006, 2007, and 2008, respectively were: Inbound Adults: 322, 924, 1,428, and 1,897; Outbound Adults: 145, 223, 1,237, and 1,557; Outbound Juveniles: 894, 12,705, 28 (not shown), and 76,809. Total population sizes for American Toads in 2005, 2006, 2007, and 2008, respectively were: Inbound Adults: 42, 234, 506, and 38; Outbound Adults: 88, 122, 491, and 28; Outbound Juveniles: 3,224, 1,268, 3 (not shown), and 429.

juvenile analysis. As with the adults, juveniles of both species oriented themselves in a non-random pattern (Wood Frogs - 2005: $\chi^2_3 = 481.53$, $P < 0.001$; 2006: χ^2_3 2666.99, $P < 0.001$; 2008: $\chi^2_3 = 38840.16$, $P < 0.001$; Fig. 3c; American Toads - 2005: $\chi^2_3 = 5451.95$, $P <=$ 0.001; 2006: $\chi^2_3 = 19.05$, $P < 0.001$; 2008: $\chi^2_3 = 126.53$, $P < 0.001$; Fig. 3f). By contrast, the ranks of migration orientations showed no obvious trends across the four years for either species (Wood Frogs: $\chi^2_3 = 5.133$, $P =$ 0.1623; American Toads: $\chi^2_3 = 3.64$, $P = 0.3031$). Juvenile Wood Frogs were captured with the greatest numbers in East in 2005, West in 2006, and South in 2008. Juvenile American Toads were captured with the greatest numbers in East in 2005 and 2006, and West in 2008. It is worth noting that North was never the favored orientation of juveniles and, in fact, supported the least number of juveniles in two of the three years.

DISCUSSION

Our goal was to determine whether adults and newly metamorphosed juvenile Wood Frogs and American Toads demonstrated non-random capture distributions at the pond edge, and whether the orientations were uniform across years. We found that Wood Frog adults demonstrated non-random capture distributions in all four years, with discernable trends across years, while American Toad adults were distributed non-randomly in three of the four years but demonstrated no significant trends across years. Juveniles migrated non-randomly in each year, but neither species showed discernable trends across years.

While we do not know what paths individual anurans took before and/or after the fence capture, we assume that capture location is indicative of terrestrial habitat use. We acknowledge that radio telemetry, more extensive drift fencing, or otherwise tracking individuals would provide a more precise analysis of habitat use; however, we base our assumption on a number of supportive studies. For example, straight line migrations to and from the breeding locations have been found for many adult anurans, especially in suitable forested habitats like ours, including American Toads (e.g., Forester et al. 2006), California Red-legged Frogs (*Rana aurora draytonii*; e.g., Bulger et al. 2003), Mountain Yellow-legged Frogs (*Rana muscosa*; Matthews and Pope 1999), Japanese Toads (*Bufo japonicus formosus*; Kusano et al. 1995), Natterjack Toads (*Bufo calamita*; Sinsch 1992), and the Common European Toad (*Bufo bufo*; van Gelder et al. 1986). Additionally, previous studies have assumed that capture location along a drift fence was indicative of habitat distribution (e.g., Sjögren-Gulve 1998). Although there are fewer data for juveniles, studies that have monitored metamorphic Wood Frog movements from the natal pond found similar non-random capture distributions at fences at the pond edge and then subsequently at distances ranging from 5 to 300 m from the pond edge (Vasconcelos and Calhoun 2004; Patrick et al. 2006, 2007), suggesting that juvenile Wood Frogs remain in the habitat toward which they originally oriented for some time. However, one recent study (Roznik and Johnson 2009) on movements of juvenile Gopher Frogs (*Lithobates capito*), found a pattern of random orientation at the pond edge and non-random distribution further away from the pond.

Thus, assuming capture location indicates terrestrial habitat use, it appears that Wood Frog adults selectively avoided West, a habitat with low litter depth and tree density, and high soil water content. Our findings contrast with other studies where emigrating adult Wood Frogs have preferred forested wetlands, much like West, in the summer (Heatwole 1961; Baldwin et al. 2006). It is possible that the relatively low litter depth and tree density in West made the habitat less appealing, despite its relatively high soil moisture. Or perhaps West's soil is not wet enough to result in Wood Frogs choosing it for its moisture. In either case, the other three habitats may have been more appealing because of their greater leaf litter and tree density. It is also possible that West was avoided because of its road edge. This explanation of the migration pattern matches a previous study indicating that Wood Frogs are negatively influenced by roads (Gibbs 1998b). However, other studies indicate that Wood Frogs may not be particularly inhibited by roads (deMaynadier and Hunter 2000), and are more likely to be caught at road edges than at field edges (Regosin et al. 2005), suggesting that edge may impact populations differently. Finally, the trend toward a preference for East among adults may have resulted because of East's greater linear extent from the pond edge (>500 m vs. 100 m), given that a study done in Massachusetts found that 40% of Wood Frogs over-wintered >100 m from the pond edge (Regosin et al. 2005).

Adult migration orientations of American Toads were somewhat different than we expected. American Toads are commonly considered habitat generalists (e.g., Guerry and Hunter 2002), so we expected to see a more muted orientation pattern for American Toads than we saw for Wood Frogs. Interestingly, there were clear migration orientation patterns in three of the four years, but they differed considerably across those years. It is possible that their habitat tolerance allows them to survive successfully in all four habitats. Furthermore, they appear to be unaffected by edge, suggesting that they may be less sensitive to different edges than Wood Frogs. Their use of multiple different habitats across years may also signify that they have less terrestrial fidelity. To test the question of reduced habitat fidelity, future research could attempt to complete a mark-recapture study to assess whether individuals at this site frequently switch between our four habitats between breeding seasons.

Among juveniles, the migration patterns were non-random, but inconsistent across years. Juvenile Wood Frogs have previously been shown to move toward either forested wetlands (Bellis 1965; Vasconcelos and Calhoun 2004) or forested uplands (deMaynadier and Hunter 1999) and may follow a movement pattern similar to the adult population (Vasconcelos and Calhoun 2004). There is also evidence to suggest that Wood Frog juveniles use indirect cues to orient during migrations (Patrick et al. 2007). In our population, the initial orientation pattern was non-random and was not uniform between years. Given the choice between more mature terrestrial uplands (East and North), less mature forested uplands (South), and less mature forested lowlands (West), juveniles preferentially oriented toward

East in 2005, West in 2006, and South in 2008. Multiple year studies are rare for juvenile anurans emerging from their natal ponds, although Vasconcelos and Calhoun (2004) did not find significant differences in juvenile Wood Frog orientations across three years. However, like our study, a multi-year study of emerging Great Crested Newts (*Triturus cristatus*) and Smooth Newts (*Triturus vulgaris*) found juveniles oriented non-randomly each year with differences between years (Malmgren 2002). Malmgren (2002) suggested the possibility of juveniles following the chemical cues of other juveniles emerging from the pond before them, which is a possibility in our study, as well. Despite the orientation inconsistencies in our study, it is interesting that Wood Frog juveniles never preferentially headed North. North is the only habitat with a visibly steep incline adjacent to the pond edge, which may act as a deterrent. More research is needed to discern what cues, both direct and indirect, are used by emerging juvenile Wood Frogs.

American Toad juveniles also initially oriented non-randomly, heading East in 2005 and 2006 and West in 2008. Previous research has shown that juvenile American Toads are more selective in habitat than are adults and prefer closed-canopy forests over open fields (e.g., Rothermel and Semlitsch 2002). In the first two years of this study, juveniles preferentially oriented toward the more mature forested upland habitat (East). Interestingly, in our study, East and North should seem similarly mature and forested to a newly metamorphosed juvenile using direct cues, given the juvenile's naiveté to the extent of forest patches, yet American Toads moved toward the more extensive East in significantly greater numbers than they moved to the less extensive North. The avoidance of North mimics the trend of Wood Frog juveniles and may again be attributed to the slope present in North, but absent in East. In 2008, the preference changed from East to West, a habitat characterized by higher soil moisture, but lower tree density and leaf litter than East. We find it interesting that for both juvenile anuran species, initial orientation is non-random, but that is inconsistent across years. Cues other than habitat may be influencing their orientation; however, this is a largely unexplored research topic, and to the best of our knowledge, no one has studied whether American Toad metamorphs use direct or indirect cues for orientation.

Our results suggest that there are clear non-random patterns in migration orientation for both Wood Frogs and American Toads. Assuming that these orientations reflect habitat use, the more mature, extensive secondary forest habitat appears to be commonly preferred for adults of both species, suggesting that forest extent is important for maintaining populations of these species. Juveniles, despite their non-random distribution within years, initially oriented towards both the relatively mature and immature forests covering a wide range of habitat variables. Some species or life stages may rely on different cues, or cues other than habitat characteristics, for orientation, which may have important implications for conservation. Furthermore, as juveniles are naïve to long-distance edge effects, they may fall victim to ecological traps as they move toward road, residential, or agricultural areas. The habitat use and requirements of juveniles should continue to be monitored so as to aid in conservation efforts of terrestrial habitats surrounding wetlands. Furthermore, the variability of habitat use across years emphasizes the importance of long-term studies and suggests that single-year studies to determine migration orientation patterns may be insufficient for some species.

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