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ORIENTATION OF VERNAL POOL AMPHIBIANS IN AN
INDUSTRIAL FOREST LANDSCAPE

BY

EMMA CARCAGNO

BS Rutgers University, 2003

THESIS

Submitted to the University of New Hampshire

in Partial Fulfillment of

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in

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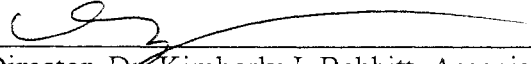
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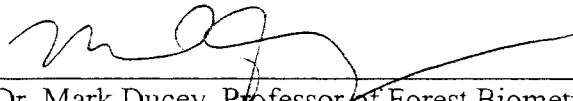
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TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	iii
LIST OF TABLES	vi
LIST OF FIGURES.....	viii
ABSTRACT.....	ix
CHAPTER	PAGE
I. INTRODUCTION	1
Vernal Pools and Amphibians.....	1
Terrestrial Habitat Requirements	3
Effects of Timber Harvesting.....	4
Buffer Zones: Current Management Strategies and Regulation	5
Orientation of Amphibian Movement.....	6
II. METHODS.....	9
Study Site	9
Study Organisms	10
Field Methods.....	11
Data Analysis	12
III. RESULTS	19
Orientation of Movements	19
Index of Non-uniformity	32

IV. DISCUSSION.....	37
Conclusions	42
REFERENCES	45
APPENDIX A. Institutional Animal Care and Use Committee Approval Letters.....	52

LIST OF TABLES

TABLE		PAGE
Table 1.	List of combinations of species, age class, and direction used in statistical analysis	13
Table 2.	List of directional bins and associated compass degrees	14
Table 3.	Summary of capture totals for <i>Ambystoma maculatum</i>	20
Table 4.	Summary of capture totals for <i>Lithobates sylvaticus</i>	21
Table 5.	Summary of chi-square results for <i>Ambystoma maculatum</i>	22
Table 6.	Summary of chi-square results for <i>Lithobates sylvaticus</i>	24
Table 7.	Summary of chi-square results for comparison among years	29
Table 8.	Results of MANOVA to compare among years for <i>Ambystoma maculatum</i>	30
Table 9.	Results of MANOVA to compare among years for <i>Lithobates sylvaticus</i>	30
Table 10.	Summary of chi-square results for comparison between species	31
Table 11.	List of Indices of Non-uniformity listed by wetland and treatment for <i>Ambystoma maculatum</i>	33
Table 12.	List of Indices of Non-uniformity listed by wetland and treatment for <i>Lithobates sylvaticus</i>	33
Table 13.	Results of ANOVA of <i>Ambystoma maculatum</i> for three buffer width treatments.	35
Table 14.	Results of ANOVA of <i>Lithobates sylvaticus</i> for three buffer width treatments	35

Table 15. Results of Tukey-Kramer posthoc test for emigrating adult <i>Lithobates sylvaticus</i>	35
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LIST OF FIGURES

FIGURE	PAGE
Figure 1. Experimental design of buffer treatments	10
Figure 2. Circular histograms depicting orientation of emigration movements for <i>Ambystoma maculatum</i> at a single wetland showing both traps and direction bins	15
Figure 3. Circular histograms depicting orientation of immigration movements for <i>Ambystoma maculatum</i> at a single wetland in three separate years	27
Figure 4. Circular histograms depicting orientation of immigration movements for <i>Lithobates sylvaticus</i> at a single wetland in three separate years	28
Figure 5. Circular histograms depicting examples of low, medium, and high indices of non-uniformity.....	34
Figure 6. Graph depicting results of paired t-test to compare movements of immigrating and emigrating adults of both species	36

ABSTRACT

ORIENTATION OF VERNAL POOL AMPHIBIANS IN AN INDUSTRIAL FOREST LANDSCAPE

By

Emma F. Carcagno

University of New Hampshire, May, 2009

Understanding the movement patterns of vernal pool amphibians is a critical aspect of effective conservation and land management. I used clearcutting to manipulate buffer widths at 11 vernal pools within an industrial forest landscape located in Maine. Forested buffers were either 30m or 100m wide, surrounded by 100m wide clearcut. Each pool was encircled with a drift fence and pitfall traps. I captured wood frogs (*Lithobates sylvaticus*) and spotted salamanders (*Ambystoma maculatum*) as they entered and exited pools and documented orientation across three years. Orientation at all pools for both species was non-uniform, differed among pools, between species, and was inconsistent among years. My results suggest that amphibian movement patterns are spatially and temporally complex, and that identifying 'corridors' of amphibian movement for protection is an ineffective approach to managing upland habitats surrounding these pools. A better understanding of how amphibians move through and use upland habitat along and a broader habitat management approach are necessary to the conservation of these species.

CHAPTER I

INTRODUCTION

Amphibians have increasingly become the focus of concern as a result of worldwide population declines (Wake 1991; Blaustein et al. 1994; Semlitsch 2000). Local habitat destruction through anthropogenic land-use is a primary factor in many declines (Semlitsch 2000; Semlitsch 2003; deMaynatier and Hunter 1998; Collins and Storfer 2003). Conservation along with careful management of anthropogenically-modified habitats at both local population and landscape levels is critical to maintaining viable populations and regional diversity (Semlitsch 2003). Our knowledge of the terrestrial ecology of amphibians and amphibian responses to anthropogenic land use is limited (Chazal and Niewiarowski 1998; deMaynadier and Hunter 1998; Semlitsch 2003). In order to develop better management and conservation strategies, it is crucial to gain a better understanding of the effects of anthropogenic land use change on amphibians.

Vernal Pools and Amphibians

Vernal pools are small, isolated wetlands common throughout the forests of northeastern North America. These pools have widely varying hydroperiods; many dry annually while others dry only every few years. Vernal pools provide breeding habitat

for large numbers of amphibians and invertebrates that are adapted to seasonal drawdown (Colburn 2004). These periods of dryness preclude the presence of established fish populations and reduce breeding populations of predatory and competing amphibians (*Rana catesbeiana*, *Rana clamitans*) (Calhoun et al. 2003; Colburn 2004). Vernal pools are particularly important as they provide breeding habitat for amphibians such as mole salamanders (Ambystomatidae) and the wood frog (*Lithobates sylvaticus*) that breed almost exclusively in small, isolated wetlands lacking fish populations. The pools also support breeding populations of other amphibians (i.e. *Bufo americanus*, *Notophthalmus viridescens*, *Pseudacris crucifer*, *Hyla versicolor*), although these amphibians also breed successfully in other types of wetlands and in permanent waters (Colburn 2004, Babbitt et al. 2003).

Vernal pools are critical in maintaining regional biodiversity by supporting an abundance and diversity of amphibian and invertebrate species (Gibbs 1993; Semlitsch and Bodie 1998). Amphibians play a crucial role in food web dynamics, consuming small invertebrates often not available to other vertebrate groups. These species also comprise a large amount of protein biomass that is an important prey source for many larger vertebrates (e.g. snakes, birds, mammals) (Semlitsch 2003). Vernal pool-breeding amphibians also serve as one of the few nutrient vectors connecting aquatic and terrestrial environments in New England forests (Russell et al. 2002, Semlitsch 2003).

Because vernal pools are relatively isolated and often occur in discrete patches within a matrix of upland habitat, vernal pool amphibian dynamics can resemble classical metapopulation models (Marsh and Trenham 2001, Zamudio and Wiczorek 2007). It is, however, important to consider that the applicability of metapopulations dynamics to

amphibian species depends greatly on the presumption that amphibians have limited ability to disperse long distances (Smith and Green 2005). Three main factors influence amphibian metapopulation dynamics; the number or density of individuals dispersing among ponds, the density and distribution of wetlands in the landscape, and the probability of successfully reaching ponds (Hanski and Gilpin 1991, Semlitsch 2003). Ecological connectance is critical to maintaining amphibian metapopulations (Semlitsch 2003). Therefore, unfragmented terrestrial habitat may be critically important to the conservation of amphibian populations (Marsh and Trenham 2001).

Terrestrial Habitat Requirements

Vernal pool-breeding amphibians exhibit a biphasic life-history, breeding and laying eggs in wetlands during a short breeding season, lasting only a few days or weeks. After breeding, these amphibians emigrate away from their breeding sites towards terrestrial habitats to forage and over-winter (Madison 1997, Semlitsch and Bodie 2003, Duellman and Trueb 1986). The quality of upland habitat affects both species richness and abundance of amphibians. Herrmann et al. (2005) found that wetlands in New Hampshire containing less than 40% forest within a 1000m radius have decreased species richness and densities. Other studies have also shown amphibian preference for closed canopy forest (Demaynadier and Hunter 1998, Rothermel and Semlitsch 2002, Walston 2008). As such, it is clear that terrestrial habitats play a key role in maintaining the overall health and biodiversity of amphibian populations in vernal pool ecosystems (Gibbons 2003, Marsh and Trenham 2001, Semlitsch and Bodie 2003).

Despite our understanding of the importance of terrestrial habitats to vernal pool-breeding amphibians, there exists a large gap in knowledge about how these habitats are utilized by amphibians (Regosin et al 2003, Semlitsch 1998). Most surveys and studies of vernal pool-breeding amphibians are concentrated around the vernal pools where they breed, rather than in terrestrial habitats where detection can be extremely difficult (Semlitsch and Bodie 2003). Similarly, current state and federal regulations and conservation strategies aim to protect only the wetland itself or arbitrarily defined portions of terrestrial habitat, if any (Semlitsch 1998, Semlitsch and Bodie 2003, Herrmann et al. 2005). Herrmann et al. (2005) suggest that, rather than conservation strategies that focus solely on the protection of upland habitats immediately surrounding vernal pools, it may be more valuable to focus on protecting a proportion of suitable upland habitat within a larger area.

Effects of Timber Harvesting

Managers of forest resources are faced with the difficult task of accommodating multiple demands of conserving biodiversity and protecting nutrient cycling and water quality, while maximizing forest productivity (Chazal and Niewiarowski 1998). Timber harvesting can have both direct and indirect negative impacts on vernal-pool-breeding amphibian populations (deMaynadier and Hunter 1998; Petranka et al. 1993; Chazal and Niewiarski 1998; Semlitsch 2003). Because amphibians are ectotherms and have a semi-permeable skin, they are more susceptible to extreme temperatures and dryness, which can lead to desiccation (Duellman and Trueb 1986). A tall, multi-layered forest canopy can help to buffer wind and temperature (Welsh and Droege 2001). Clearcutting

effectively removes this protective buffer and has a significant effect on the quality of terrestrial habitat for amphibians by eliminating shade, reducing leaf litter, increasing soil-surface temperatures, increasing temperature extremes, and reducing soil-surface moisture (Petranka et al. 1993). Altering terrestrial habitat through timber harvest may also critically affect the metapopulation dynamics of amphibian populations, by impeding amphibian dispersal among ponds and therefore increasing the probability of local population declines and extinctions (Semlitsch 2003; Hanski and Gilpin 1991).

Buffer Zones: Current Management Strategies and Regulation

Current regulation for developing around vernal pools is minimal. The upland habitats immediately surrounding vernal pools (or buffer zones) are protected through best management practices (BMPs). In most states, these BMPs are recommendations that offer no legal protection for these habitats. In New England, BMPs recommend buffer zones ranging from 0-30.5m, varying from state to state (CT 2005; MA 2005; ME 2002; NH 2008; VT 2002).

Semlitsch (1998, 2003) suggests that buffers of 15-30m are inadequate for amphibians, and found that core terrestrial habitat defined by biological criteria ranges from a mean minimum of 205m to a mean maximum of 368m for anurans, and a mean minimum of 117m to a mean maximum of 218m for urodeles. Clearly, vernal pool amphibian species are utilizing, and potentially relying, on terrestrial habitats well outside the area protected by current regulations.

Orientation of Amphibian Movements

Increasing our knowledge of amphibian movement patterns has the potential to strengthen amphibian conservation strategies, but large gaps in our knowledge of these movement patterns exist (Vasconcelos and Calhoun 2004; Semlitsch 1998). Several studies have documented non-uniform directionality by amphibians as they approach and depart from vernal pools (Shoop 1965; Guttman et al. 1991; Rothermel and Semlitsch 2001; Rothermel 2004; Vasconcelos 2004). There are several theories on how and why amphibians exhibit non-uniform directionality. Some studies have shown that the directions in which amphibians immigrate to and emigrate from breeding wetlands is associated with quality of habitat, implying that amphibians may have the ability to detect and avoid unfavorable habitat or orient towards favorable habitats (Rothermel and Semlitsch 2001). Vasconcelos and Calhoun (2004) found that both adult and juvenile *Lithobates sylvaticus* and *Ambystoma maculatum* migrated out of vernal pools preferentially towards closed-canopy forest and away from open fields, or wet meadows.

Amphibians also possess physiological mechanisms that are used in orientation. These mechanisms include the use of olfactory cues, sun-compass orientation, magnetic compass orientation, and the use of plane-polarized light for spatial orientation. Experimental evidence suggests that both anurans and urodeles exhibit sensitivity to the Earth's magnetic field and can use a light-dependent magnetic compass mediated by extraocular photoreceptors located in or near the pineal gland to direct both daily and seasonal migrations (Duetschlander et al. 2000, Phillips et al. 2001, Phillips et al. 2002, Diego-Rasilla et al. 2005, Freake and Phillips 2005). Taylor and Adler (1973)

determined that tiger salamanders (*Ambystoma tigrinum*) can perceive the plane of polarization in linearly polarized light and can learn to use that for spatial orientation.

Further documentation of amphibian terrestrial movement to and from breeding pools will provide information on the quality and extent of terrestrial habitat used by different species of pool-breeding amphibians (Vasconcelos and Calhoun 2004). This information will help develop more effective strategies for conserving upland habitat in order to maintain populations of vernal-pool breeding amphibians. For example, if amphibians have nonrandom movements in and out of vernal pools, terrestrial buffers may need both a distance and directional component in order to be effective (Dodd and Cade 1998).

I used data collected from drift fence/pitfall trap arrays encircling vernal pools with experimentally manipulated forest buffer widths to determine whether: 1) adult amphibians exhibit non-uniform orientation as they immigrate to and emigrate from vernal pools during the breeding season; 2) newly metamorphosed amphibians exhibit non-uniform orientation as they emigrate away from vernal pools post-emergence; 3) the direction of orientation varies among years, or between species; and, 4) buffer size effects orientation. In achieving these objectives, I hoped to determine whether the use of terrestrial corridors instead of or in addition to the use of buffer zones would serve as a more effective management strategy.

I hypothesized that adult wood frogs and spotted salamanders would exhibit non-uniform orientation as they immigrated to and emigrated from vernal pools. I also expected that metamorph wood frogs and spotted salamanders would exhibit non-uniform orientation post-emergence. I predicted that directionality would be consistent among

years, but not necessarily across wetlands. My 11 study sites are far enough apart to be independent from one another, such that amphibians at each wetland would be responding to different features within the local landscape. I predicted that amphibians leaving vernal pools with smaller buffers would have increased directionality, as the number of favorable terrestrial habitats proximal to the vernal pools would be decreased.

CHAPTER II

METHODS

Study Site

This study took place on land owned and managed by International Paper in Hancock and Washington Counties in eastern Maine. This region has a high abundance of vernal pools. The forests are mixed-hemlock (*Tsuga canadensis*)-hardwood (*Fagus grandifolia*, *Acer saccharum*, *Betula alleghaniensis*) in lower elevations with increasing domination by balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) at higher elevations and along riparian areas. Twelve vernal pools were selected for this study. The selection of study sites were based on several criteria. First, the selected vernal pools were initially (pre-treatment) surrounded by relatively undisturbed forest, uncut for more than 60 years within a 1,000m radius around the pool. Also, the pools were all of similar size, about 0.2 ha, which is typical of vernal pools within the region (Gibbs 1993). To ensure that the vernal pools were fishless, but held water long enough for the development of frog and salamander larvae, the hydroperiods of the selected pools were at least 5-6 months (post ice-out) during the study site selection year. After the first year one of the vernal pools was deemed unsuitable due to an undetected inlet and was removed from the study (n=11).

Between September 2003 and March 2004, International Paper created buffer zones by clear cutting forest around selected vernal pools. Each pool was randomly

assigned to one of three possible treatments (Figure 1), a buffer of >1,000m (no clearcut), which serves as a reference (n=3), a 30m buffer (n=4), or 100m buffer (n=4). The clearcuts were 100m wide surrounding the buffer. The buffer widths were chosen based on current best management practices (BMPs) and current literature. Many state BMPs recommend a 30m buffer zone for vernal pools, and both Semlitsch (1998) and Trenham (2001) recommend buffer zones close to 100m for the protection of vernal pool salamanders.

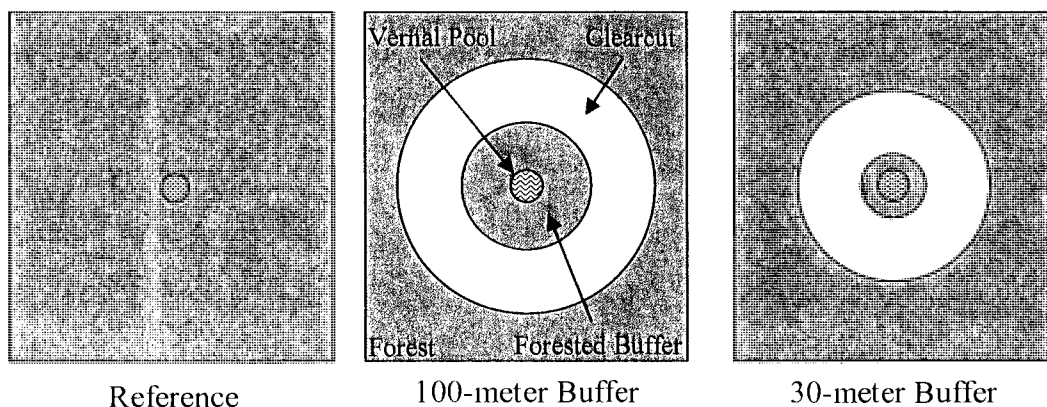


Figure 1. Experimental design; for buffer treatments either 30 or 100 meters of forest was left around the wetland, surrounded by a 100-meter-wide concentric clearcut. No cutting occurred at reference wetlands.

Study Organisms

Vernal pools provide critical breeding habitat for several amphibian species. At my study sites, these amphibian species included spotted salamanders (*Ambystoma maculatum*), blue-spotted salamanders (*Ambystoma laterale*), and wood frogs (*Lithobates sylvaticus*) (Colburn 2004). My study wetlands were also utilized by other facultative

vernal pool-breeding amphibian species including bull frogs (*Rana catesbiana*), green frogs (*Rana clamitans*), pickerel frogs (*Rana palustris*), spring peepers (*Pseudacris crucifer*), eastern red-spotted newts (*Notophthalmus viridescens*), and American toads (*Bufo americanus*). For this study, I focused on spotted salamanders and wood frogs, as these were the two most abundant vernal pool-breeding species at my study sites.

Spotted salamanders migrate to vernal pools early in the spring, and breeding lasts anywhere from a couple of weeks to a month, depending on local conditions (Colburn 2004, Hunter et al. 1999). Eggs hatch after approximately one month, though as with most amphibian species, egg development is strongly dependent on temperature (negative correlation between developmental time and temperature) (Duellman and Trueb 1986). Metamorphs emerge in mid- to late summer. After breeding, adults return to terrestrial habitat. Spotted salamanders are generally fossorial, relying heavily on rodent tunnels for habitat (Faccio 2003).

Wood frogs in Maine begin breeding in early April (Hunter et al. 1999). Breeding typically lasts 1-2 weeks. Eggs are laid in globular clusters attached to vegetation about 10cm below the water's surface. Tadpoles emerge approximately three weeks after breeding, again depending on temperature. In Maine, larvae undergo metamorphosis between late May and early August (Hunter et al. 1999). After breeding, wood frogs return to terrestrial habitat where they spend the remainder of the year.

Field Methods

In the summer and fall of 2003 each vernal pool was completely encircled with a drift fence made of silt fencing. The fences were buried 8-10 cm below ground, and are

about 91 cm in height. They are positioned about 5 m from the high water mark to reduce the chance of flooding. Pitfall traps were constructed with #8 tin cans stacked two deep. Traps were buried flush with the ground surface on opposite sides of the fence at approximately 10 m intervals. The traps were deep enough to prevent escape by amphibians. To prevent desiccation, a sponge was placed in each trap to retain moisture. In extreme heat, or as necessary, water was added to traps. A compass bearing was taken from the center of each pool used to determine a directional bearing for each trap.

My field seasons ran from early April through mid-November. I checked traps were checked daily from April through May, and every other day from June through November. For each individual captured, date, trap ID, species, sex, snout-vent length (SVL), age (adult, juvenile, or metamorph), and mass was recorded. Adults exiting the pool during breeding season, and metamorphs leaving the pools were marked with a toe clip. Toe clip patterns were based on the wetland where the amphibian was trapped. Metamorphs trapped on the outside of the fence were not placed on the inside of the fence to ensure that I would be able to distinguish them from individuals originating at that wetland. At the end of the season, I closed traps with lids and removed sections of fence so as not to impede movement of organisms.

Data Analysis

All calculations were conducted separately on each species. In addition, I used separate calculations for adult immigrants and emigrants of both species. For metamorphs, I made calculations only on emigrating individuals, as they are emerging for

the first time. This resulted in six species-by-age class-by-direction combinations (Table 1).

Table 1. This table depicts the species-by-age class-by-direction combinations for which all calculations were done.

SPECIES	AGE CLASS	DIRECTION
<i>Ambystoma maculatum</i>	Adult	Immigrating
<i>Ambystoma maculatum</i>	Adult	Emigrating
<i>Ambystoma maculatum</i>	Metamorph	Emigrating
<i>Lithobates sylvaticus</i>	Adult	Immigrating
<i>Lithobates sylvaticus</i>	Adult	Emigrating
<i>Lithobates sylvaticus</i>	Metamorph	Emigrating

I used nonparametric statistical analyses rather than circular statistics because my data violated the assumptions of the parametric circular tests (Batschelet, 1981).

Preliminary analysis of capture totals showed that the orientation of amphibian movements was usually bi- or multi-modal, which violates the assumption of a Von Mises distribution (the normal equivalent for circular data) upon which parametric circular tests are based.

To determine whether orientation to and from wetlands was non-uniform, I used the compass bearing for each trap along with total captures for each combination described in Table 1 at each wetland in each year to calculate the expected number of individuals at each trap given uniform movement. I conducted a separate chi-square goodness of fit test for each year at each pond for all six combinations described in Table 1 to compare the observed totals to the expected totals in each trap. I used the Bonferoni adjustment for all chi-square analyses to avoid comparison-wise type I error. Rejection of the null hypothesis was interpreted as evidence of non-uniform orientation (i.e., significant orientation in one or more directions). For combinations with sample sizes

too small for chi-square test (less than 40 individuals total), I used the randomization test for goodness of fit. To determine whether movements were non-uniform over a several year period, I pooled the data by year for the six combinations described in Table 1 and performed the same set of calculations described above.

To compare movements among all wetlands, I used the compass bearings and total captures in each year for the six combinations described in Table 1 at each wetland to calculate an observed number of individuals captured per compass degree. I made this calculation using the arc lengths on either side of each trap in order to take the uneven spacing of the traps into account. I then divided the circle into eight directional bins, one each centered on N, NE, E, SE, S, SW, W and NW (Table 2). I used the individuals per degree to then calculate the number of individuals observed in each bin. This also provided a slightly more intuitive interpretation of the data, as it separated movement into eight familiar cardinal directions (Figure 2).

Table 2. Directional bins (and associated azimuths) used in evaluation of orientation of amphibians immigrating to and emigrating from vernal pools.

Directional Bin	Azimuth (Degrees)
N	337.50 - 22.49
NE	22.50 - 67.49
E	67.50 - 112.49
SE	112.50 - 157.49
S	157.50 - 202.49
SW	202.50 - 247.49
W	247.50 - 292.49
NW	292.50 - 337.49

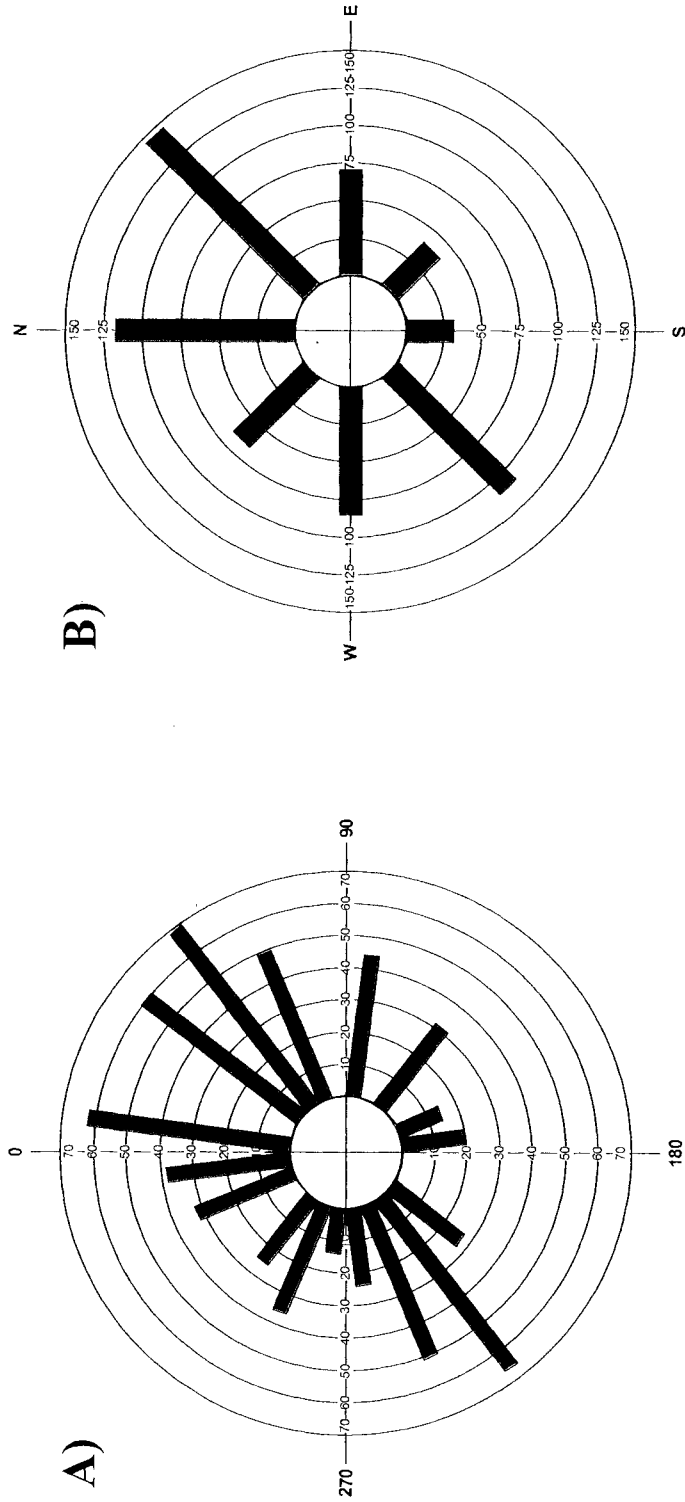


Figure 2. Circular histograms both depicting orientation of *Ambystoma maculatum* emigrating away from wetland 39. In graph A, the position of each arm represents the compass bearing of each trap and in graph B, each arm represents one of the eight directional bins. In both cases, the length of each arm represents the number of individuals captured in that trap/bin.

As with the trap data, I conducted a separate chi-square goodness of fit test for each year at each pond for all six combinations described in Table 1 to compare the observed totals to expected totals in each bin. I did this to ensure that there were no differences between calculations based on data from traps versus calculations based on directional bins. I used the Bonferoni adjustment to avoid comparison-wise type I error. A rejection of the null hypothesis was again interpreted as evidence of non-uniform orientation (i.e., significant orientation in one or more directions). A significant chi-square result only determined whether orientation was non-uniform, and did not indicate which directional bin contributed most significantly to this result (i.e., which direction the amphibians were orienting in). To determine which direction contributed most significantly to a significant chi-square result, I used the expected and observed values to calculate standardized residuals. A standardized residual \pm two in a given directional bin indicated that that trap was a major contributor to the rejection of the null hypothesis.

To compare movements among wetlands, I used the Pythagorean theorem, to calculate unit vectors to describe the mean X (East-West) and Y (North-South) movement at each wetland and year for each of the six combinations described in Table 1. I conducted a multivariate analysis of variance (MANOVA) using the mean X and Y values to determine if there was a net directional movement among all wetlands. I used the Bonferoni adjustment to avoid comparison-wise type I error. A significant result would indicate an overall pattern in movement across all wetlands. I performed these calculations for each year, as well as on data pooled across the three years, to further explore the differences across wetlands.

To compare patterns of orientation between the two study species, I used a chi-square test of heterogeneity for each wetland for both immigrating and emigrating adults. I used a 2 x 8 contingency table (where 2 = the number of species and 8 = the number of directional bins). I only performed this test for those combinations for which I had more than 40 individuals total for each species and wetland, and did not perform the test for the metamorph age class due to the variability of data from year to year and wetland to wetland. I used the Bonferoni adjustment to avoid comparison-wise type I error.

I compared orientation among years, by performing a chi-square test of heterogeneity for each pond-by-species-by-direction combination using a 3 x 8 contingency table (where 3 = the number of years and 8 = the number of directional bins). I only performed this calculation for those combinations for which I had more than 40 individuals in each year. I did not perform this test for the metamorph age class due to the variability of the data from year to year. I used the Bonferoni adjustment to avoid comparison-wise type I error.

To further explore the patterns of orientation, I used the method described by Timm et al. (2007) to calculate a relative “index of non-uniformity” as the mean across bins of the absolute difference between observed and expected percentage of captures. This index provides an intuitive interpretation of the magnitude of non-uniformity in capture distribution. The index was calculated for each wetland and year for each combination described in Table 1, as well as on data pooled across years.

I used the index of non-uniformity to compare orientation across experimental buffer treatments. I used an analysis of variance (ANOVA) to test whether there was a difference in magnitude of non-uniformity of orientation among the three treatments (30-

meter buffers, 100-meter buffers, and reference), and then performed a Tukey-Kramer posthoc test to determine which treatments were significantly different from the others. Lastly, I used the index to compare orientation of immigrating and emigrating amphibians for each species and each wetland using a paired t-test.

CHAPTER III

RESULTS

I captured a total of 35,972 individuals over the three field seasons from 2004-2006. This combined total consisted of 7,372 spotted salamanders comprised of 5,385 adults and 1,987 metamorphs; and 25,134 wood frogs comprised of 8,467 adults and 20,133 metamorphs. Refer to Table 3 for a summary of spotted salamander captures and Table 4 for a summary of wood frog captures.

Orientation of Movements

Immigration and emigration movements for both species in all years were consistently non-uniform. There were a total of 179 unique species-by-pond-by-year-by-direction combinations, of which 151 had non-uniform distributions. Specifically, I found that 19/33 combinations were non-uniform for immigrating adult spotted salamanders, 21/33 (significant at $p < 0.0015$) for emigrating adult spotted salamanders, 16/19 (significant at $p < 0.0026$) for emigrating metamorph spotted salamanders, 28/33 for immigrating adult wood frogs, 30/33 (significant at $p < 0.0015$) for emigrating adult wood frogs, and 19/28 (significant at $p < 0.0018$) for emigrating metamorph wood frogs. This pattern was even stronger when capture data were pooled across all three years: 54/63 species-by-pond-by-direction combinations had non-uniform distributions. For a summary of results from the chi-square analysis, refer to Tables 5 and 6.

Table 3. Summary of capture totals for *Ambystoma maculatum* at 11 vernal pools in Maine.

Wetland	<u>Immigrating Adults</u>			<u>Emigrating Adults</u>			<u>Emigrating Metamorphs</u>					
	2004	2005	2006	TOTAL	2004	2005	2006	TOTAL	2004	2005	2006	TOTAL
7	100	34	42	176	77	39	70	186	0	0	29	29
19	70	33	64	167	40	56	38	134	107	8	48	163
20	155	112	147	414	122	91	158	371	44	51	195	290
25	306	193	110	609	278	154	103	535	65	39	29	133
30	97	63	62	222	66	58	51	175	0	0	0	0
39	329	296	232	857	242	216	203	661	105	295	466	866
55	33	25	9	67	18	19	4	41	0	0	30	30
59	47	58	14	119	35	22	8	65	0	0	107	107
124	46	17	25	88	27	17	18	62	0	57	0	57
129	12	6	3	21	7	8	3	18	0	0	0	0
141	80	73	58	211	72	65	49	186	91	90	131	312
TOTAL	1,275	910	766	2,951	984	745	712	2,434	412	540	1,035	1,987

Table 4. Summary of capture totals for *Lithobates sylvaticus* at 11 vernal pools in Maine.

Wetland	<u>Immigrating Adults</u>			<u>Emigrating Adults</u>			<u>Emigrating Metamorphs</u>					
	2004	2005	2006	TOTAL	2004	2005	2006	TOTAL	2004	2005	2006	TOTAL
7	213	64	95	372	86	48	116	250	9	51	7677	7,737
19	90	47	308	445	69	77	168	314	557	248	1137	1,942
20	234	325	385	944	147	167	218	532	619	3	898	1,520
25	155	96	163	414	92	76	114	282	140	7	104	251
30	129	148	154	431	72	121	178	371	0	0	0	0
39	409	210	233	852	211	177	182	570	62	1	16	79
55	96	45	53	194	96	33	57	186	239	12	1716	1,967
59	60	156	46	262	32	110	50	192	21	5	212	238
124	440	88	261	789	204	61	204	469	0	5905	17	5,922
129	7	23	32	62	7	9	28	44	0	350	12	362
141	107	78	43	228	99	93	72	264	1	109	5	115
TOTAL	1,940	1,280	1,773	4,993	1,115	972	1,387	3,474	1,648	6,691	11,794	20,133

Table 5. Summary of chi-square analysis results for orientation of *Ambystoma maculatum* at 11 vernal pools in Maine.
DF= degrees of freedom.

Wetland	Immigrating Adults			Emigrating Adults			Emigrating Metamorphs		
	2004	2005	2006	2004	2005	2006	2004	2005	2006
7									
Chi-square value	72.463	25.848	66.424	53.560	41.042	174.554			66.426
DF	14	14	14	14	14	14			14
p-value	<0.0001	0.0271	<0.0001	<0.0001	0.0002	<0.0001			<0.0001
Randomization test	<0.0001	0.0283	<0.0001	0.00002	0.00051	<0.0001			<0.0001
19									
Chi-square value	75.277	11.205	26.476	45.260	50.639	55.216	59.513	3.768	150.794
DF	6	6	6	6	6	6	6	6	6
p-value	<0.0001	0.0822	0.0002	<0.0001	<0.0001	<0.0001	<0.0001	0.7080	<0.0001
Randomization test	<0.0001	0.0788	0.00028	<0.0001	<0.0001	<0.0001	<0.0001	0.7390	<0.0001
20									
Chi-square value	67.897	44.893	244.243	48.495	79.308	162.390	51.917	38.919	219.139
DF	7	7	7	7	7	7	7	7	7
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Randomization test	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
25									
Chi-square value	317.212	163.152	224.003	244.328	156.215	152.735	31.662	147.461	19.334
DF	15	15	15	15	15	15	15	15	15
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0072	<0.0001	0.1990
Randomization test	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0074	<0.0001	0.1875
30									
Chi-square value	11.718	29.679	56.336	31.399	20.616	59.466			
DF	11	11	11	11	11	11			
p-value	0.3852	0.0018	<0.0001	0.0010	0.0376	<0.0001			
Randomization test	0.3818	0.0022	<0.0001	0.0014	0.0375	<0.0001			
39									
Chi-square value	73.505	130.289	161.102	124.353	65.656	113.930	44.362	178.933	295.834
DF	16	16	16	16	16	16	16	16	16
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0002	<0.0001	<0.0001
Randomization test	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.00028	<0.0001	<0.0001
55									
Chi-square value	19.877	41.286	16.879	24.4044	24.5880	23.0165			31.2918
DF	11	11	11	11	11	11			11
p-value	0.0471	<0.0001	0.1115	0.0111	0.0105	0.0176			0.0010
Randomization test	0.0456	<0.0001	0.0930	0.0116	0.0120	0.0177			0.0012
59									
Chi-square value	15.583	33.101	15.959	16.6158	16.5660	14.1987			384.3097
DF	13	13	13	13	13	13			13
p-value	0.2724	0.0016	0.2514	0.2175	0.2199	0.3600			<0.0001
Randomization test	0.2665	0.0020	0.2325	0.2075	0.2088	0.3249			<0.0001

Table 5. Continued from page 22

Wetland	Immigrating Adults			Emigrating Adults			Emigrating Metamorphs		
	2004	2005	2006	2004	2005	2006	2004	2005	2006
124	16.001	9.4331	25.936	26.5290	30.9047	48.1050		63.7190	
Chi-square value	16	16	16	16	16	16		16	
DF	0.4529	0.8945	0.0549	0.0470	0.0138	<0.0001		<0.0001	
p-value	0.4514	0.9130	0.0537	0.0473	0.0162	0.0004		<0.0001	
Randomization test									
129	13.358	8.6213	7.6396	11.6346	10.6565	13.4977			
Chi-square value	10	10	10	10	10	10			
DF	0.2043	0.5684	0.6640	0.3103	0.3849	0.1972			
p-value	0.1850	0.5758	0.7584	0.2693	0.3544	0.1833			
Randomization test									
141	66.240	8.749	20.089	25.8473	22.3365	17.5454	78.6295	29.7626	52.6806
Chi-square value	4	4	4	4	4	4	4	4	4
DF	<0.0001	0.0677	0.0005	<0.0001	0.0002	0.0015	<0.0001	<0.0001	<0.0001
p-value	<0.0001	0.0664	0.00066	<0.0001	0.00022	0.0015	<0.0001	<0.0001	<0.0001
Randomization test				5				1	

Table 6. Summary of chi-square analysis results for orientation of *Lithobates sylvaticus* at 11 vernal pools in Maine. DF = degrees of freedom.

Wetland	Immigrating Adults			Emigrating Adults			Emigrating Metamorphs		
	2004	2005	2006	2004	2006	2005	2004	2005	2006
7									
Chi-square value	103.598	24.908	95.051	47.499	49.040	218.566	22.561	154.260	24952.4
DF	14	14	14	14	14	14	14	14	14
p-value	<0.0001	0.0355	<0.0001	<0.0001	0.0005	<0.0001	0.0678	<0.0001	<0.0001
Randomization test	<0.0001	0.0355	<0.0001	<0.0001	0.00077	<0.0001	0.0601	<0.0001	<0.0001
19									
Chi-square value	77.310	17.359	98.195	58.648	142.256	262.001	273.158	102.191	1083.65
DF	6	6	6	6	6	6	6	6	6
p-value	<0.0001	0.0080	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Randomization test	<0.0001	0.0079	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
20									
Chi-square value	32.179	200.460	595.801	259.487	216.174	544.847	177.532	11.163	1075.55
DF	7	7	7	7	7	7	7	7	7
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.1316	<0.0001
Randomization test	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.1328	<0.0001
25									
Chi-square value	66.708	45.506	138.950	215.487	140.522	109.157	88.654	14.904	82.521
DF	15	15	15	15	15	15	15	15	15
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.4583	<0.0001
Randomization test	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.4432	<0.0001
30									
Chi-square value	33.315	64.764	154.776	35.769	42.281	100.950			
DF	11	11	11	11	11	11			
p-value	0.0005	<0.0001	<0.0001	0.0002	<0.0001	<0.0001			
Randomization test	0.00059	<0.0001	<0.0001	0.00022	<0.0001	<0.0001			
39									
Chi-square value	217.965	95.882	171.831	153.881	65.1340	100.845	60.789	12.089	44.889
DF	16	16	16	16	16	16	16	16	16
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.7378	0.0001
Randomization test	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.7471	0.00096
55									
Chi-square value	64.575	38.102	99.252	75.581	51.283	64.097	265.029	31.116	2128.63
DF	11	11	11	11	11	11	11	11	11
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0011	<0.0001
Randomization test	<0.0001	0.0002	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0019	<0.0001
59									
Chi-square value	51.709	141.984	34.947	37.851	146.531	67.345	31.042	10.025	205.233
DF	13	13	13	13	13	13	13	13	13
p-value	<0.0001	<0.0001	0.0009	0.0003	<0.0001	<0.0001	0.0033	0.6918	<0.0001
Randomization test	<0.0001	<0.0001	0.0011	0.00047	<0.0001	<0.0001	0.0045	0.5909	<0.0001

Table 6. Continued from page 24

	Immigrating Adults			Emigrating Adults			Emigrating Metamorphs		
	2004	2005	2006	2004	2005	2006	2004	2005	2006
124 <i>Lithobates sylvaticus</i>									
Chi-square value	91.228	96.865	250.604	144.900	45.905	202.769	7248.16	26.205	
DF	16	16	16	16	16	16	16	16	16
p-value	<0.0001	<0.0001	<0.0001	<0.0001	0.0001	<0.0001	<0.0001	0.0512	
Randomization test	<0.0001	<0.0001	<0.0001	<0.0001	0.00022	<0.0001	<0.0001	0.0498	
129									
Chi-square value	12.447	26.365	21.257	11.229	20.978	17.323	339.149	22.186	
DF	10	10	10	10	10	10	10	10	10
p-value	0.2563	0.0033	0.0194	0.3399	0.0212	0.0675	<0.0001	0.0142	
Randomization test	0.2159	0.0043	0.0190	0.3020	0.0217	0.0632	<0.0001	0.0143	
141									
Chi-square value	64.272	37.262	45.347	49.200	36.370	39.944	5.545	84.331	23.345
DF	4	4	4	4	4	4	4	4	4
p-value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.2358	<0.0001	0.0001
Randomization test	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.1536	<0.0001	0.00022

The orientation of movements differed among years. There were 29 unique combinations of species, wetlands, and direction for which there were sufficient sample sizes, of which 25 had significant differences among years. This total included 4/5 (significant at $p < 0.01$) for immigrating adult spotted salamanders, 3/6 (significant at $p < 0.0083$) for emigrating adult spotted salamanders, 10/10 (significant at $p < 0.005$) for immigrating adult wood frogs and 4/8 (significant at $p < 0.0063$) for emigrating adult wood frogs. Figures 3 and 4 illustrate the differences in direction of orientation among years at one wetland for both spotted salamanders and wood frogs, respectively (Table 7). I also found that though there was strong directionality for both species at individual wetlands, there was no congruence in the direction of orientation among all wetlands for either species. (Tables 8 and 9).

Orientation of adults differed between species for most wetlands. There were a total of 22 unique pool-by-direction combinations, 20 of which had large enough sample sizes to perform the chi-square analysis. Of those 20 combinations, 12 showed significant differences between species (significant at $p < 0.005$) (Table 10).

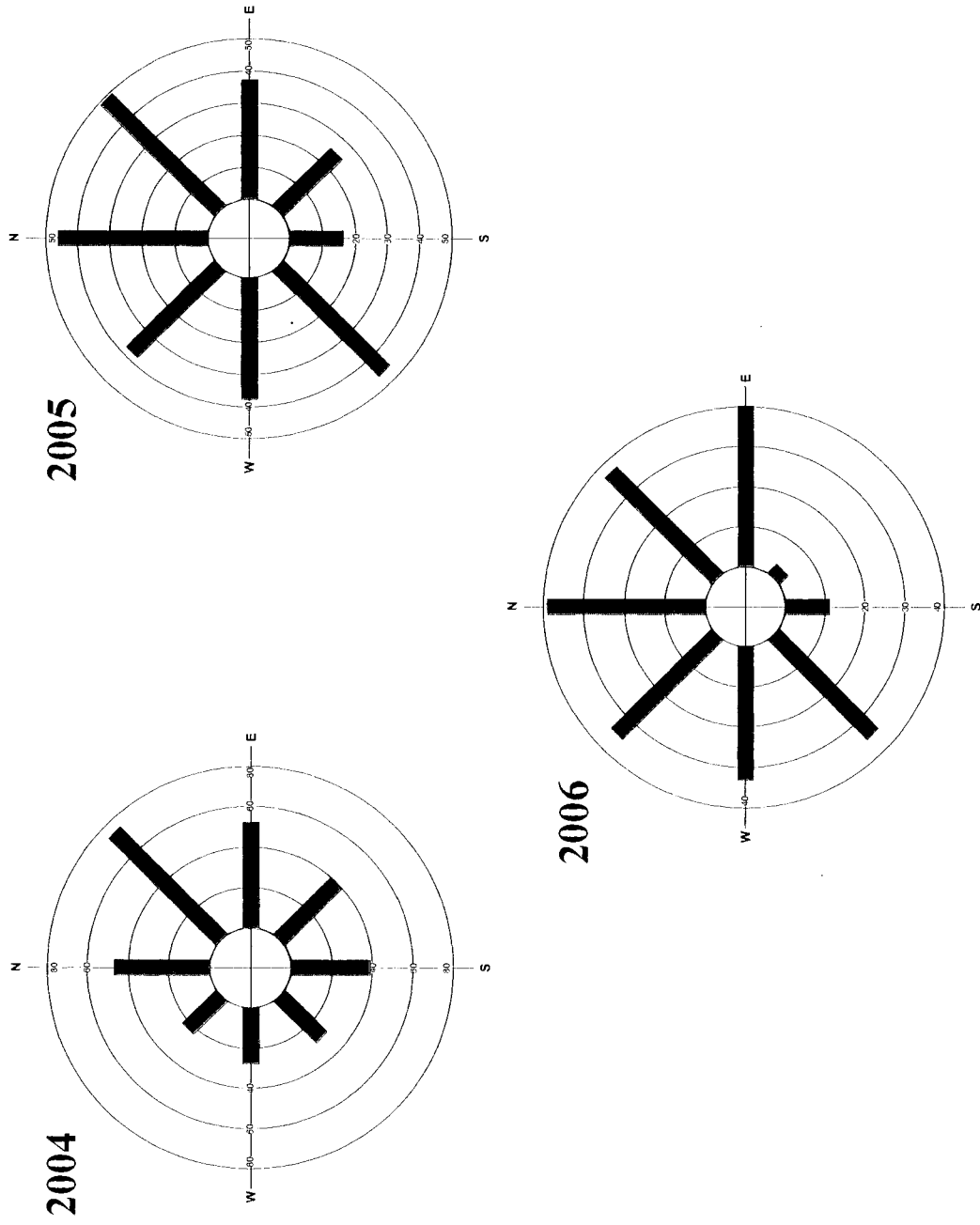


Figure 3. Circular histograms depicting orientation movements for *Ambystoma maculatum* immigrating to wetland 39 over three separate breeding seasons. Each arm represents one of the eight directional bins, and the length of each arm represents the number of individuals captured in each bin.

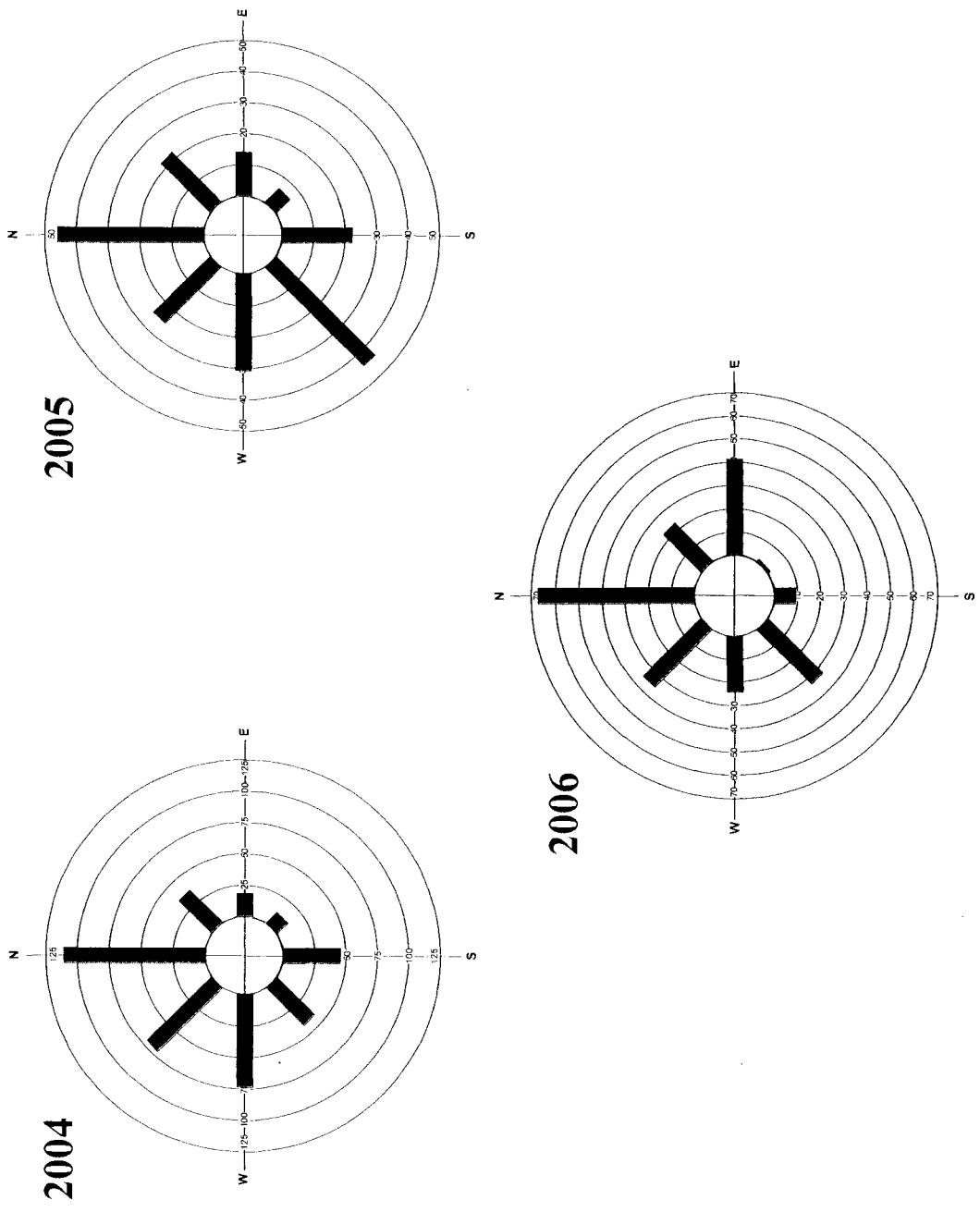


Figure 4. Circular histograms depicting orientation movements for *Lithobates sylvaticus* immigrating to wetland 39 over three separate breeding seasons. Each arm represents one of the eight directional bins, and the length of each arm represents the number of individuals captured in each bin.

Table 7. Results of chi-square analysis to compare orientation patterns among all years. This analysis was only performed for those species-by-age class-by-direction combinations for which there were more than 40 individuals in each year (see Table 3). DF = degrees of freedom.

		<i>Ambystoma maculatum</i>		<i>Lithobates sylvaticus</i>	
		Immigrating Adults	Emigrating Adults	Immigrating Adults	Emigrating Adults
W7	total individuals			369	251
	Chi-square value			23.996	26.476
	DF			14	14
	p-value			0.046	0.023
W19	total individuals		134	447	313
	Chi-square value		9.488	25.398	27.650
	DF		14	14	14
	p-value		0.799	0.031	0.016
W20	total individuals	414	369	942	531
	Chi-square value	49.507	30.180	306.450	72.001
	DF	14	14	14	14
	p-value	<0.0001	0.007	<0.0001	<0.0001
W25	total individuals	609	535	414	282
	Chi-square value	65.439	51.111	72.408	35.678
	DF	14	14	14	14
	p-value	<0.0001	<0.0001	<0.0001	0.001
W30	total individuals	224	175	430	370
	Chi-square value	21.712	25.6114	32.244	25.464
	DF	14	14	14	14
	p-value	0.085	0.029	0.004	0.030
W39	total individuals	858	663	851	572
	Chi-square value	57.880	36.053	67.546	37.872
	DF	14	14	14	14
	p-value	<0.0001	0.001	<0.0001	0.001
W55	total individuals			194	
	Chi-square value			53.481	
	DF			14	
	p-value			<0.0001	
W59	total individuals			263	
	Chi-square value			24.863	
	DF			14	
	p-value			0.036	
W124	total individuals			788	470
	Chi-square value			142.771	32.455
	DF			14	14
	p-value			<0.0001	0.003
W129	total individuals				
	Chi-square value				
	DF				
	p-value				
W141	total individuals	212	185	225	264
	Chi-square value	50.876	16.316	50.641	21.817
	DF	14	14	14	14
	p-value	<0.0001	0.294	<0.0001	0.082

Table 8. Results of the MANOVA comparing directional orientation among all wetlands for *Ambystoma maculatum*.

		Wilk's λ	F	p-value
Immigrating Adults	2004	0.857	0.611	0.900
	2005	0.912	0.356	0.995
	2006	0.873	0.532	0.949
Emigrating Adults	2004	0.866	0.568	0.929
	2005	0.891	0.453	0.979
	2006	0.861	0.592	0.914
Emigrating Metamorphs	2004	0.885	0.479	0.971
	2005	0.830	0.742	0.777
	2006	0.874	0.530	0.950

Table 9. Results of the MANOVA comparing directional orientation among all wetlands for *Litobates sylvaticus*.

		Wilk's λ	F	p-value
Immigrating Adults	2004	0.917	0.336	0.997
	2005	0.884	0.485	0.969
	2006	0.781	0.999	0.467
Emigrating Adults	2004	0.847	0.659	0.861
	2005	0.838	0.701	0.820
	2006	0.899	0.416	0.987
Emigrating Metamorphs	2004	0.868	0.560	0.934
	2005	0.813	0.830	0.674
	2006	0.953	0.184	0.497

Table 10. Results of chi-square analysis to compare patterns of orientation between *Lithobates sylvaticus* and *Ambystoma maculatum*. This analysis was only performed for species-by-age class-by-direction combinations for which there were more than 40 individuals total for each species and wetland. DF = degrees of freedom

		Immigrating Adults	Emigrating Adults
W7	total individuals	546	435
	Chi-square value	23.747	21.045
	DF	7	7
	p-value	0.001	0.004
W19	total individuals	613	448
	Chi-square value	18.133	14.567
	DF	7	7
	p-value	0.011	0.042
W20	total individuals	1358	900
	Chi-square value	41.383	33.107
	DF	7	7
	p-value	<0.0001	<0.0001
W25	total individuals	1023	818
	Chi-square value	136.874	163.553
	DF	7	7
	p-value	<0.0001	<0.0001
W30	total individuals	654	544
	Chi-square value	12.029	37.272
	DF	7	7
	p-value	0.100	<0.0001
W39	total individuals	1711	1229
	Chi-square value	103.518	37.225
	DF	7	7
	p-value	<0.0001	<0.0001
W55	total individuals	261	230
	Chi-square value	14.191	7.798
	DF	7	7
	p-value	0.048	0.351
W59	total individuals	381	256
	Chi-square value	30.233	14.646
	DF	7	7
	p-value	<0.0001	0.041
W124	total individuals	877	532
	Chi-square value	6.722	10.401
	DF	7	7
	p-value	0.458	0.167
W129	total individuals		
	Chi-square value		
	DF		
	p-value		
W141	total individuals	439	451
	Chi-square value	25.958	28.729
	DF	7	7
	p-value	0.001	<0.0001

Index of Non-uniformity

The index of non-uniformity was calculated for each species, both immigrating and emigrating adults, and for emigrating metamorphs, at each wetland. The index values ranged from 2.23 to 10.27 (Table 11 and 12), with lower values indicating more uniform movement and higher values indicating a greater magnitude of non-uniformity (Figure 5). In almost all cases, treatment had no effect on the magnitude of non-uniformity (Table 13 and 14). The only exception was emigrating adult wood frogs ($p=0.0238$). The Tukey-Kramer test revealed that the 30-meter and 100-meter treatments were significantly different from one another (Table 15).

Directionality was less uniform for both species during emigration than immigration. The index of non-uniformity was significantly different between immigrating and emigrating adults for both spotted salamanders (d.f.=10, $t = -2.99$, $p=0.0137$) and wood frogs (d.f.=10, $t = -4.70$, $p=0.0008$) (Figure 6).

Table 11. Summary of index of non-uniformity by treatment for *Ambystoma maculatum*. The lower the value of the index, the more uniform the movements.

Treatment	Wetland	Immigrating Adults	Emigrating Adults	Metamorphs
30-meter Buffer	7	6.01	7.26	--
	19	7.02	8.9	7.41
	20	4.29	6.95	7.76
	59	3.61	3.6	10.27
mean		5.23	6.68	8.48
100-meter Buffer	25	6.83	6.47	4.71
	39	2.98	4.78	5.33
	55	4.96	4.6	--
	129	6.28	5.82	--
mean		5.26	5.42	5.02
Reference	30	4.19	5.11	--
	124	3.67	5.7	6.22
	141	2.77	5.24	3.8
mean		3.54	5.35	5.01

Table 12. Summary of index of non-uniformity by treatment for *Lithobates sylvaticus*. The lower the value of the index, the more uniform the movements.

Treatment	Wetland	Immigrating Adults	Emigrating Adults	Metamorphs
30-meter Buffer	7	5.03	7.26	8.42
	19	5.52	8.9	6.79
	20	3.83	8.47	7.08
	59	4.92	7.34	6.25
mean		4.82	7.99	7.13
100-meter Buffer	25	2.84	6.12	5.29
	39	5.19	3.94	7.78
	55	5.34	7.13	8.7
	129	2.23	4.18	7.18
mean		3.9	5.34	7.24
Reference	30	5.7	6.3	--
	124	2.48	6.13	8.06
	141	4.44	6.58	7.68
mean		4.21	6.34	7.87

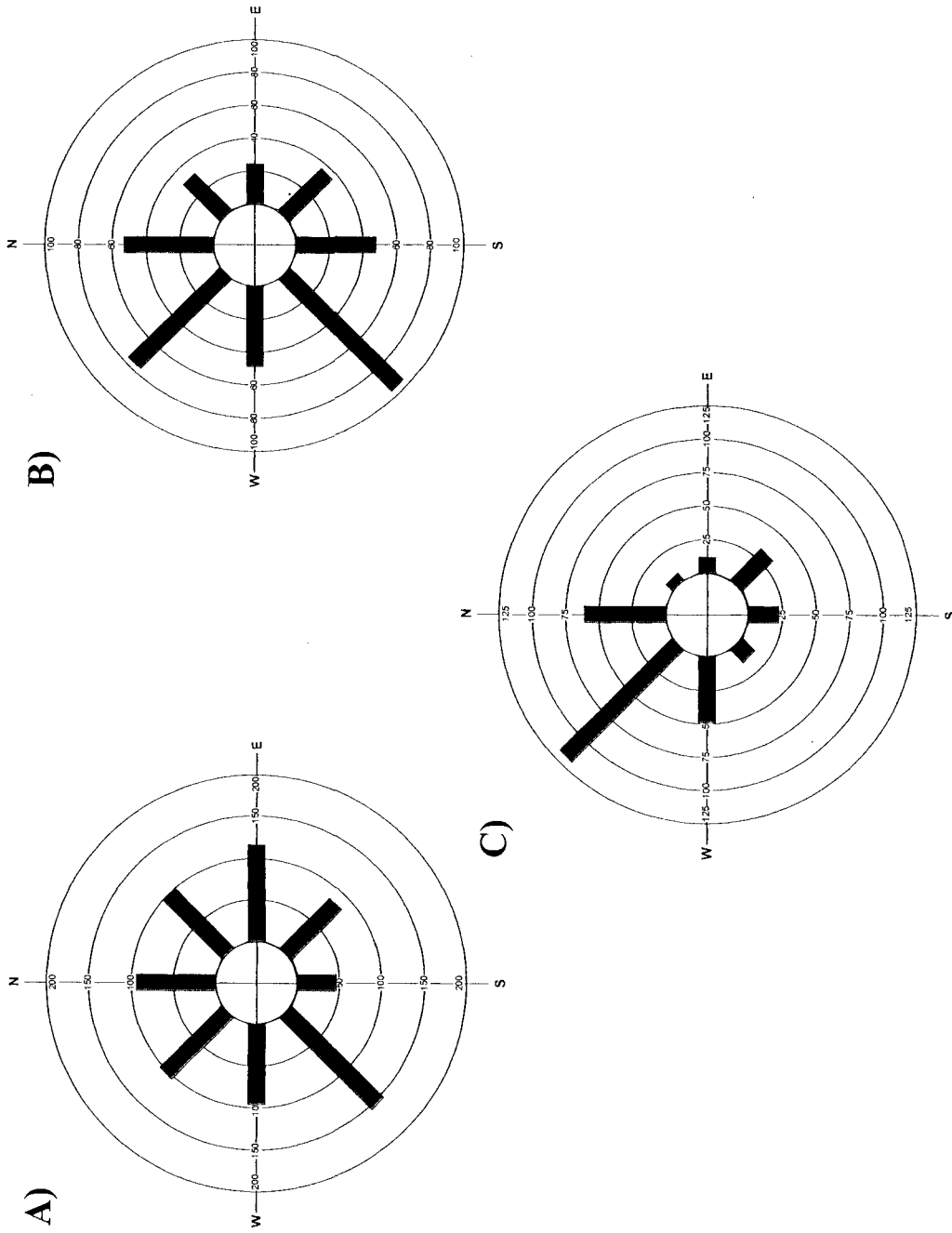


Figure 5. Circular histograms depicting examples of A) low (2.48, *Lithobates sylvaticus*, wetland 124), B) medium (4.29, *Ambystoma maculatum*, wetland 20), and C) high (8.9, *Lithobates sylvaticus*, wetland 19) indices of non-uniformity. Each arm represents one of the eight directional bins, and the length of each arm represents the number of individuals captured in each bin.

Table 13. Results of one-way ANOVA to compare the index of non-uniformity across all three buffer treatments for *Ambystoma maculatum* during 2004, 2005, and 2006 at 11 vernal pools in Maine. DF = degrees of freedom.

	<u>Immigrating Adults</u>			<u>Emigrating Adults</u>			<u>Emigrating Metamorphs</u>					
	DF	MS	F	P	DF	MS	F	P	DF	MS	F	P
among groups	2	3.1691	1.48	0.2842	2	2.11833	0.98	0.4175	2	10.2911	5.15	0.0782
within groups	8	2.1433			8	2.17009			4	1.9969		
Total	10				10				6			

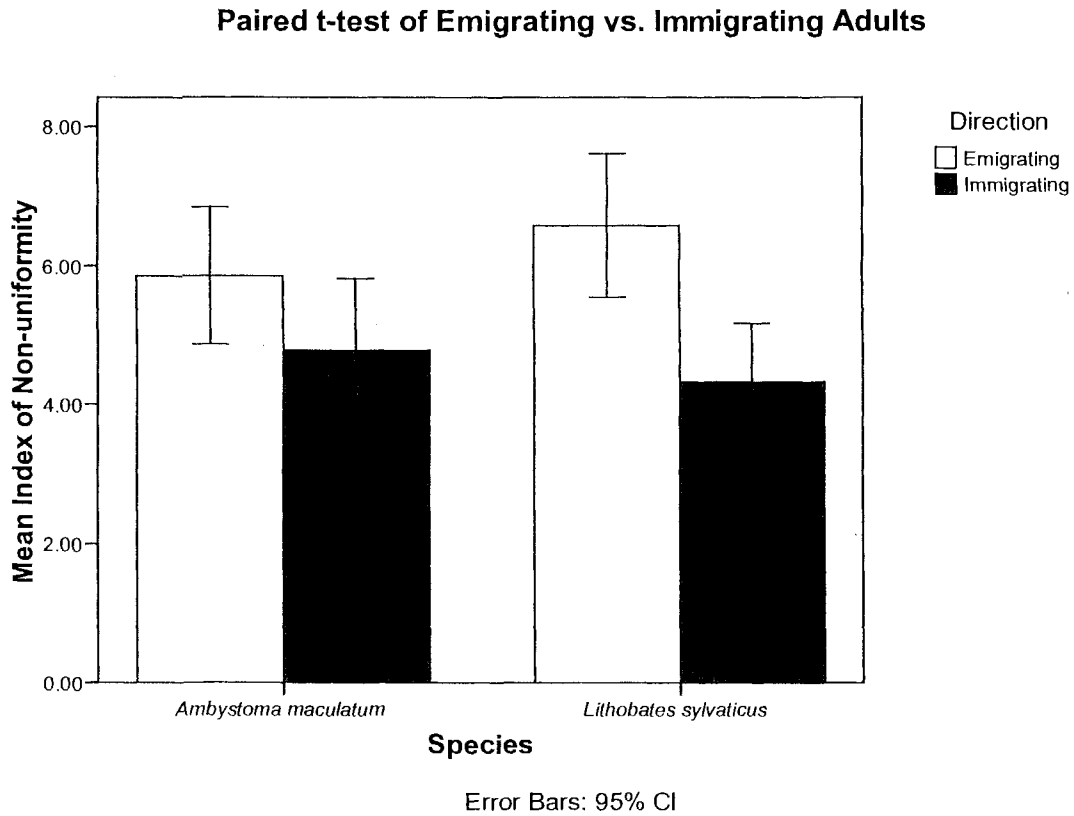
Table 14. Results of one-way ANOVA to compare the index of non-uniformity across all three buffer treatments for *Liithobates sylvaticus* during 2004, 2005, and 2006 at 11 vernal pools in Maine. DF = degrees of freedom.

	<u>Immigrating Adults</u>			<u>Emigrating Adults</u>			<u>Emigrating Metamorphs</u>					
	DF	MS	F	P	DF	MS	F	P	DF	MS	F	P
among groups	2	0.88212	0.49	0.6306	2	7.14190	6.19	0.0238	2	0.38452	0.30	0.7472
within groups	8	1.80502			8	1.15440			7	1.26542		
Total	10				10				9			

Table 15. Results of Tukey-Kramer posthoc test for emigrating adult *Liithobates sylvaticus*.

Treatment	Treatment	Mean Difference	Std. Error	p-value
0	30	-1.66	0.821	0.170
	100	0.994	0.821	0.480
30	0	1.66	0.821	0.170
	100	2.65*	0.760	0.020
100	0	-0.994	0.821	0.480
	30	-2.65*	0.760	0.020

Figure 6. Bar graph showing results of paired t-test between emigrating and immigrating adults for both *Ambystoma maculatum* and *Lithobates sylvaticus*. The bars represent the mean index of non-uniformity. Error bars show 95% confidence interval of the mean. For spotted salamanders the degrees of freedom (DF) =10, $t = -2.99$, $p = 0.0137$, and for wood frogs DF=10, $t = -4.70$, $p = 0.0008$.



CHAPTER IV

DISCUSSION

The complexity and variability of vernal pool ecosystems prove a challenge to land managers and conservationists alike. The amphibian species that utilize vernal pools rely not only on the wetlands themselves, but on the upland habitats that surround them. It was my goal in this study to determine whether the amphibian species that rely on vernal pools exhibit non-uniform orientation in an industrial forest landscape. Being able to predict the direction of movement towards and away from vernal pools has significant management implications. Current BMPs only recommend the protection of a small, forested buffer immediately surrounding the vernal pool, but if amphibians orient in specific and predictable directions, the use of corridors may be a more effective management strategy for the protection of upland habitats and the overall conservation of these amphibian species.

I found amphibian that orientation was non-uniform for both adult and metamorph wood frogs and spotted salamanders immigrating to and emigrating from vernal pools, but these movements varied among years, among wetlands, and between species. That is, these movements, though concentrated in one or more specific directions, were not predictable and cannot be used to dictate management decisions within this industrial forest landscape without further understanding of amphibian

movements and upland habitat use. However, these results do suggest patterns in amphibian orientation that warrant further exploration.

Orientation was significantly non-uniform a majority of the time for both species at all wetlands in all years. This result suggests at least two explanations for amphibian orientation within this landscape. First, in a given year at a given wetland, individual amphibians of each species are independently orienting using similar cues, whether physiological or environmental or a combination. The second explanation is that these species are using some trailing behavior, for example using a pheromone trail to “follow” one another as they immigrate to and emigrate from the wetlands.

Many studies have documented non-uniform orientation of amphibians (Shoop 1965, Dodd and Cade 1997, Patrick et al. 2007, deMaynadier et al. 1998, Vasconcelos and Calhoun 2004, Walston 2008). Some of these studies have considered only one year of data (Shoop 1965, Patrick et al. 2007). Others, while considering several years of data, have been conducted in landscapes in which favorable habitat is limited with amphibians showing significant orientation in the direction of favorable habitat (Demaynadier et al. 1998, Vasconcelos and Calhoun 2004, Walston 2008). A few studies have been conducted over multiple years at sites with relatively undisturbed landscapes (Timm et al. 2007, Jenkins et al 2006). Many studies also only explored the movements of only one species (Shoop 1965, Patrick et al. 2007, Jenkins et al. 2006). My study is unique in that I investigated the orientation of two vernal pool amphibian species over a several-year period, in a heavily managed, industrial forest landscape where habitat alteration, though substantial, is not permanent.

In my study, directional orientation differed among years at the majority of wetlands for both species. Those few instances where there was no statistically significant difference in orientation among years tended to occur in those wetlands where sample sizes were low in all years, and therefore had low power to detect directionality. This result strengthens the value of using several years of data when investigating the orientation of amphibian movements, specifically when the results of the study may mediate management strategies. Had I sampled for only one year, I would have found significant non-uniform orientation, but would not have known that the direction of orientation would change from year to year. The variation in direction of orientation among years in this study suggests that suitable habitat is not limited in this landscape. Timm et al. (2007) also found year-to-year variation when comparing amphibian orientation among several years in a relatively unaltered landscape. This result also points to the complexity of amphibian orientation, suggesting that wood frogs and spotted salamanders are likely using a complex combination of physiological and environmental cues to orient to and from breeding sites.

Directional orientation also differed when compared among all 11 study sites. My study sites were located relatively far from one another, with distance between wetlands ranging from approximately 0.5-18 miles, and are likely functioning independently from one another, with amphibians cueing into different local features of the upland habitats. While the use of physiological cues for amphibian orientation has been well documented (Phillips 1986, McGregor and Teska 1989, Grant et al. 1968, Hershey and Forester 1980, Ferguson et al 1967, Fischer et al. 2001, Phillips et al. 2002, Taylor and Adler 1973), the variability of my data across wetlands suggests that

amphibians are not relying solely on these cues for orientation to and from breeding sites. For example, if wood frogs were only using magnetic compass orientation, I would expect to find that wood frogs were orienting in similar directions at all 11 study sites. Again, this further exemplifies the complexity of cues likely used for orientation by amphibians.

Although both wood frogs and spotted salamanders demonstrated strong directionality, these directions differed between the two species. Again, this result has important management implications. Data from one species cannot inform the management of others. It also strengthens the case that corridors would not be an effective management strategy in this landscape. Timm et al. (2007), found similar results when comparing the direction of orientation between wood frogs, spotted salamanders, marbled salamanders (*Ambystoma opacum*), and eastern red-spotted newt (*Notophthalmus viridescens*) at 14 vernal pools in Western Massachusetts with orientation varying among all species. Wood frogs and spotted salamanders are known to utilize different post-breeding habitats. Wood frogs have been shown to be associated with small wetlands, wet seeps and drainages during summer months (Heatwole 1961, Bellis 1965, Rittenhouse 2007), whereas spotted salamanders, which are semi-fossorial, rely heavily on rodent tunnels (Faccio 2003). It is worth noting that overwintering habitat requirements also differ between the two species as spotted salamanders cannot tolerate below-freezing temperatures, and must spend the winter far enough below ground in order to survive. Wood frogs, conversely, are freeze-tolerant and overwinter under leaf litter or in shallow burrows (Schmid 1982, DeGraaf and Yamasaki 2001).

This may lead the two species to utilize different parts of the forest for overwintering habitat.

To further examine the patterns of amphibian orientation, I calculated an “index of non-uniformity” to describe the magnitude of non-uniformity found at each wetland. This also allowed me to compare among the three buffer treatments, and between immigrating and emigrating adults. I expected to find increased directionality (less uniform movements) at the 30-meter buffer treatment wetlands, as the amount of suitable habitat would be diminished in close proximity to the wetland. I found no treatment effect for either species, except for emigrating adult wood frogs. There was a significant difference between the 30-meter and 100-meter buffer treatments for adult wood frogs, with a higher mean index of non-uniformity at the 30-meter buffer treatment. This suggests that wood frogs exiting 30-meter treatment wetlands may encounter fewer suitable post-breeding habitats and therefore show decreased uniformity as they orient towards the few remaining suitable habitats.

For both species, the magnitude of non-uniformity differed significantly between immigrating and emigrating adults. That is, movements of adults immigrating towards the wetlands were consistently more uniform than movements of adults emigrating away from wetlands. To the best of my knowledge, no other study has compared the movements of immigrating and emigrating amphibians in this way. This result speaks to the differences between over-wintering and post-breeding habitats for both species, as described previously. It may also indicate that amphibians use different cues to mediate their orientation movements before and after breeding.

This result also suggests that over-wintering habitats are not a limiting factor in this landscape. Previous studies have shown that both wood frogs and spotted salamanders will orient towards favorable habitat when the availability of such habitats is low (Demaynadier et al. 1998, Vasconcelos 2004, Walston 2008). Conversely, when the favorable habitat is abundant, others have found that though movements are non-uniform, they are directionally variable and difficult to predict (Shoop 1965, Timm et al. 2007). I would then expect that if favorable habitat were limited, the index of non-uniformity would be higher, as the amphibians would have movements directed towards remaining favorable habitats. Therefore, the difference in indices of non-uniformity between immigrating and emigrating adults may indicate that suitable overwintering habitats are more abundant in this landscape than post-breeding habitats.

Conclusions

Previous studies have demonstrated a conflicting number of different cues that may mediate amphibian orientation. The use of direct cues, such as olfactory detection of breeding wetlands, has been demonstrated for *Ambystoma maculatum* (McGregor and Teska 1989) and other species (Grant et al. 1968, Hershey and Forester 1980). The use of indirect cues such as sun-compass orientation (Ferguson et al 1966, 1967), detection of magnetic fields (Phillips 1986, Fischer et al. 2001, Phillips et al. 2002), and the potential to use plane polarized light (Taylor and Adler 1973) have also been demonstrated in a wide variety of amphibian species. Patrick et al. (2007) showed that wood frog tadpoles taken from a pool where emerging metamorphs are known to travel northeast, towards favorable habitat, still orient towards the northeast when emerging from artificial pools.

This result suggests that wood frog metamorphs are relying on indirect cues for orientation; however, it is important to note that these tadpoles were taken from a wetland where suitable habitat surrounding the wetland was limited.

The landscape surrounding my study sites, though impacted by anthropogenic land use, still retains an overall abundance of suitable habitat. My study sites were located within a nearly 300,000-acre block of forest managed almost exclusively for timber with little other development. While the effects of timber management have been shown to be detrimental to amphibians in certain cases (deMaynadier and Hunter 1998; Petranka et al. 1993; Chazal and Niewiarski 1998; Semlitsch 2003), it is important to note that these effects are temporary. Morris and Marnet (2005) found no difference in the distribution of salamanders between mature forest and 11-12 year old clearcuts. It is likely that the cues amphibians rely on for orientation to and from breeding wetlands changes with the abundance of suitable habitat surrounding the wetland.

Vernal pools ecosystems are extraordinarily complex and dynamic, as they can show significant variation in hydroperiod, species richness, breeding adult abundance, and reproductive success (Berven 1990, Semlitsch et al. 1996, Babbitt 2005). These variations occur not only from wetland to wetland but can occur from year to year at one wetland. The results of my study further illustrate the highly variable nature of vernal pool ecosystems. I found no predictable patterns of orientation at either the landscape or the local scale. I determined that orientation varied across wetlands, years, treatments, and between species. There were also differences in orientation between immigrating and emigrating adults. Further research is needed to determine what local environmental

and microhabitat cues amphibians are using for orientation in systems where there is an abundance of suitable habitat.

It was my aim to use the results of this study to determine whether the use of corridors in addition to or as an alternative to buffers would be a valid management strategy for the upland habitats surrounding these pools. My results suggest that in a landscape where anthropogenic land use does not permanently alter habitat (such as clearcuts), and suitable habitat is abundant surrounding the altered forest, the direction of orientation, though non-uniform, is highly variable and therefore not predictable. As such, corridors do not offer a practical strategy for managing in these ecosystems. It is worth noting that in systems where other, more permanent types of anthropogenic land use such as agriculture and development, are prominent, corridors may provide safer travel to the remaining suitable habitats. Buffers, which help to protect the forest immediately surrounding the pool and maintain the overall integrity of the wetland itself, may be the best approach until we have a more complete understanding of the use of upland habitats by these amphibian species.

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APPENDIX A

Institutional Animal Care and Use Committee Approval Letters



UNIVERSITY of NEW HAMPSHIRE

June 1, 2004

Babbitt, Kimberly J
Natural Resources
James Hall
Durham, NH 03824

IACUC #: 020601
Approval Date: 06/26/2002
Review Level: C

Project: Experimental testing of buffer requirements for amphibians inhabiting vernal pools in a forested landscape

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category C on Page 4 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *the research potentially involves minor short-term pain, discomfort or distress which will be treated with appropriate anesthetics/analgesics or other assessments.*

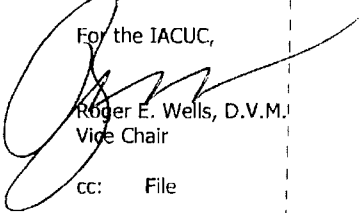
Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this study. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:

1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladi Porsche, UNH Health Services.

If you have any questions, please contact either Van Gould at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,


Roger E. Wells, D.V.M.
Vice Chair

cc: File

**Research Conduct and Compliance Services, Office of Sponsored Research, Service Building,
51 College Road, Durham, NH 03824-3585 * Fax: 603-862-3564**



UNIVERSITY of NEW HAMPSHIRE

June 30, 2005

Babbitt, Kimberly J
Natural Resources, Nesmith 206
Durham, NH 03824

IACUC #: 050604
Approval Date: 06/29/2005
Review Level: C
Project: Experimental Testing of Buffer Requirements for Amphibians Inhabiting Vernal Pools in a Forested Landscape

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category C on Page 4 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *the research potentially involves minor short-term pain, discomfort or distress which will be treated with appropriate anesthetics/analgesics or other assessments.* The IACUC made the following comments on this protocol:

1. *The Committee suggested that the investigator might consider using surgical glue/tissue cement instead of sutures.*
2. *In the future, the investigator should include references for any citations included in the protocol.*

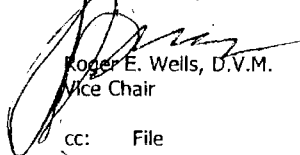
Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

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For the IACUC,



Roger E. Wells, D.V.M.
Vice Chair

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