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Orientation and migration distances of a pond-breeding salamander (*Notophthalmus perstriatus*, Salamandridae)

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Habitat loss and modification have played a significant role in the decline of amphibian populations and species. Loss of wetlands, which are used as breeding sites for many amphibians, has contributed to the decline. The protection of small, isolated wetlands and core areas of associated uplands is one way in which population declines in certain species can be slowed or prevented. Nevertheless, migration distances of individuals of most amphibian species from their breeding sites are unknown. Using drift fences and pitfall traps, I studied migration distance and orientation of striped newts (*Notophthalmus perstriatus*) at a breeding pond in northern Florida, USA. Newts entered (immigration) and exited (emigration) the pond basin in a nonrandom fashion but no obvious effects of upland habitat were apparent. Patterns of emigration and immigration differed significantly between sexes, life-history stages, and migration events. Individuals tended to exit and enter the pond basin within the same quadrant, sometimes leaving and returning at the same point. Newts moved hundreds of meters into the sandhill uplands surrounding the pond. I found an inverse relationship between the proportion of newts migrating and distance from the pond. Nonetheless, I estimated that at least 16 % of individuals breeding at the pond migrated in excess of 500 m from the pond. Thus, a core of protected upland with a radius of approximately 800 m from the pond would be needed to preserve the area used by the vast majority of individuals that breed at the pond. These data underscore the need to study upland habitat requirements for amphibians; findings for one taxon (e.g. ambystomatids) may not be applicable to others (e.g., salamandrids). Without such data, designating terrestrial core habitat to conserve aquatic-breeding amphibians will be difficult or impossible. However, without better protection of small, isolated wetlands, arguments to preserve surrounding uplands are irrelevant.

INTRODUCTION

During the past two decades, amphibian declines have received considerable attention (BARINAGA, 1990; WAKE et al., 1991; WAKE, 1991; ALFORD & RICHARDS, 1999; HOULAHAN et

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al., 2000). Although pathogens have been implicated in several die-off events (Berger et al., 1998; Lips, 1998, 1999), there is a consensus among herpetologists that the global decline is a result of multiple factors (Alford & Richards, 1999). Habitat modification and destruction have been identified as significant factors contributing to the global decline (Dodd, 1997; Alford & Richards, 1999; Duellman, 1999; Semlitsch, 2000). Although they do not attract the media attention that mass mortality or deformed amphibians receive, habitat modification and loss are insidious processes that must be addressed if amphibians are to persist. The effects of habitat changes on amphibian populations are of particular concern in areas that are characterized by a high density of small, isolated wetlands (Delis et al., 1996; Hecnar & M'Closkey, 1996; Knutson et al., 1999; Babbitt & Tanner, 2000; Semlitsch, 2000; Snodgrass et al., 2000; Russell et al., 2002). In these areas (e.g., the Southeastern Coastal Plain of North America), amphibian diversity is high (Duellman & Sweet, 1999) and many species rely solely on small, isolated wetlands as breeding sites (Dodd, 1997; Semlitsch & Bodie, 1998; Babbitt & Tanner, 2000).

Despite their size (i.e., less than a few hectares), small, isolated wetlands are of tremendous biological importance, particularly for amphibians. They play a vital role in amphibian metapopulation dynamics and therefore are essential in maintaining viable populations of amphibians at a landscape scale (Semlitsch & Bodie, 1998; Semlitsch, 2000; Snodgrass et al., 2000). In addition to amphibians, numerous other vertebrates and a suite of invertebrate species depend on small, isolated wetlands (Brown et al., 1990; Moler & Franz, 1988; Burke & Gibbons, 1995; Hart & Newman, 1995; Semlitsch & Bodie, 1998; Russell et al., 2002).

Preserving a wetland alone may not result in protection of many of the organisms that depend upon the wetland. Many amphibians have complex life cycles in which they require ponds to breed but spend the majority of their lives in surrounding upland habitats (Dodd, 1997; Dodd & Cade, 1998; Semlitsch, 1998; Semlitsch & Jensen, 2001). If sufficient upland habitat surrounding isolated breeding-ponds is not preserved, amphibians with complex life cycles are not likely to persist at a local scale. Therefore, at some point the loss of uplands may lead to extirpation of some amphibian populations because of disruption of metapopulation dynamics (Semlitsch & Bodie, 1998; Semlitsch, 2000; Marsh & Trenham, 2001), even when the ponds themselves are preserved.

One strategy to curtail the loss of amphibians associated with habitat alteration around small, isolated wetlands is to preserve "core habitat" and "buffer zones" consisting of protected uplands surrounding the wetlands (Semlitsch & Jensen, 2001). These zones provide habitat for retreats and foraging for those species with complex life cycles, many of which are now considered common. Without preservation of appropriate upland habitat, even common species will decline.

Little is known, however, about the extent of upland "core habitat" required by pond-breeding amphibians. Dodd (1996) summarized the literature on upland movements of amphibians in North America and found that this distances amphibians migrate from breeding sites are poorly known. From this summary and a review by Semlitsch (1998) on migration distances of ambystomatid salamanders, it is apparent that many amphibians move considerable distances from breeding ponds. Unfortunately, migration distances are only available for a few species and usually are based on a single or a few individuals. Clearly there is need for data on migration distances from breeding sites for most North American amphibians. These data are essential to justify establishing adequate "core habitat" of uplands around amphibian breeding ponds.

I collected data on orientation and migration distances for striped newts (*Notophthalmus perstriatus*) at a breeding pond and in the surrounding uplands in north-central Florida. Striped newts breed exclusively in small, isolated wetlands that lack fish. They have a complex life cycle and individuals spend much of their lives in uplands surrounding breeding ponds (CHRISTMAN & MEANS, 1992; DODD & LACLAIRE, 1995; JOHNSON, 2001, 2002; DODD et al., in press). Striped newts are restricted to xeric uplands (i.e., sandhill and scrub communities) and are endemic to southern Georgia and northern Florida, USA (fig. 1). The species has declined throughout its range (DODD & LACLAIRE, 1995; FRANZ & SMITH, 1999) and its biological status is under review by the US Fish and Wildlife Service (L. LaClaire, pers. comm.). The objectives of my study were (1) to determine orientation patterns of striped newts into and away from a breeding pond, and (2) to determine migration distances of individuals into the surrounding upland habitat.

MATERIALS AND METHODS

STUDY SITE

The study was conducted on the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam Co., Florida, USA (29°41'N, 82°00'W; fig. 1). EISENBERG & FRANZ (1995), LACLAIRE (1995) and DODD (1996) provided descriptions of the preserve and its habitats. Data were collected from 7 October 1996 to 11 September 1998 at One Shot Pond (OSP). OSP is a small, isolated pond with a variable hydroperiod (hydroperiod refers to the number of days a pond holds water between periods when it is dry) and is located in xeric sandhill uplands dominated by longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*) and wiregrass (*Aristida beyrichiana*). Small stands of planted slash pine (*Pinus elliottii*) are located north and southwest of the pond basin (fig. 2). Several water bodies are located near OSP (fig. 2). These water bodies are isolated from one another and only receive water from rainfall and ground water seepage; their hydroperiods are dictated by fluctuations in the water table. Fox Pond held water from 26 November 1997 until the end of the study, whereas OSP, Berry Pond, Lake McCloud and the Anderson Cue Lakes held water throughout the entire study period. During the study, striped newts were only present in OSP and Fox Pond. However, only 32 newts (16 adults and 16 juveniles) were captured at Fox Pond (S. A. Johnson, unpublished data). McCloud and the Anderson Cue lakes support predatory fishes, and striped newts do not breed there. No striped newts were captured during periodic sampling throughout the study period in Berry Pond. Because there were no other breeding ponds within several kilometers of OSP, I assumed that striped newts caught in upland fences around OSP originated from within OSP.

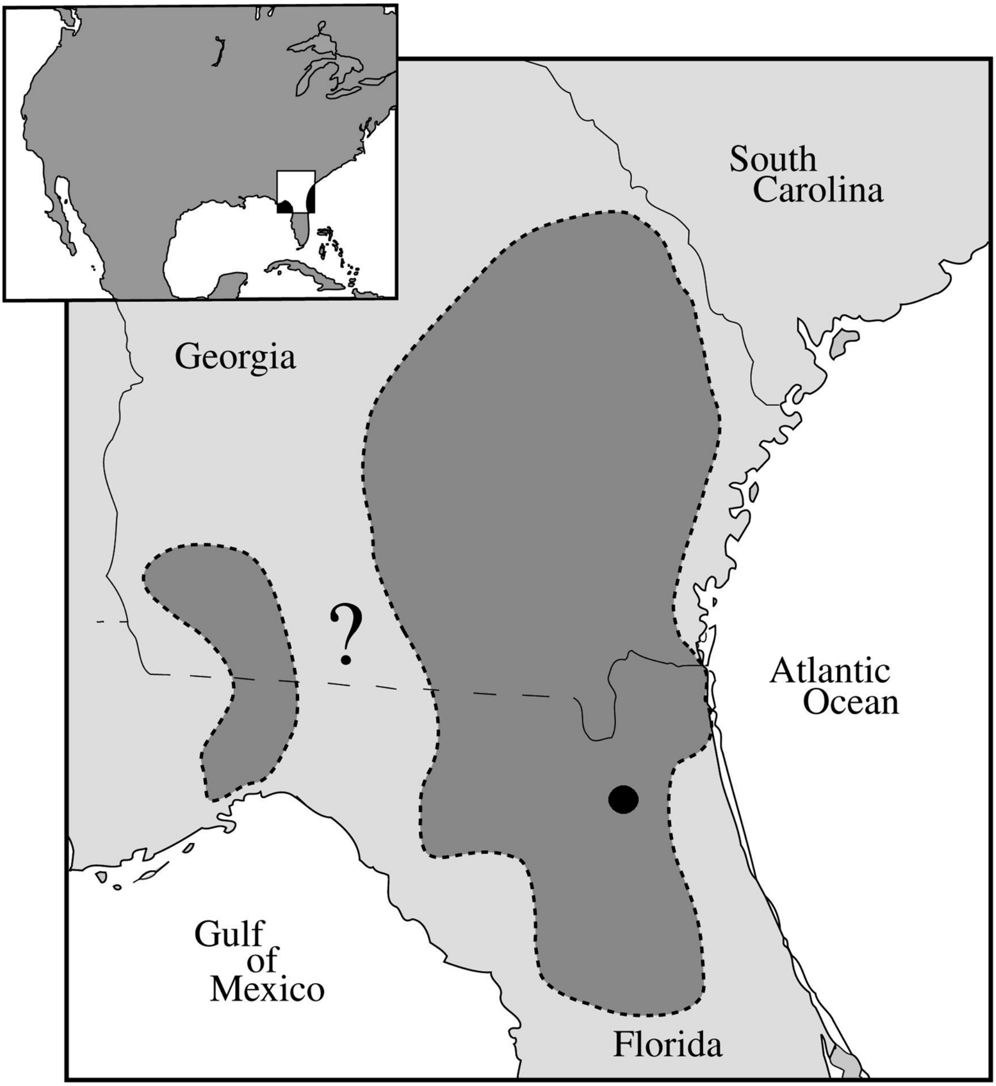


Fig. 1. – Geographic range of striped newts, which are endemic to Georgia and Florida, USA. Note the hiatus (?) between the western and eastern portions of the range. This area likely represents a true gap in the species distribution, rather than an artifact of inadequate survey effort. The black dot (•) shows the location of study area, Katharine Ordway Preserve, Putnam Co., north-central Florida, USA.

Orientation at One Shot Pond

I encircled OSP with a 190-m drift fence made of galvanized metal flashing that was buried ca. 15 cm below the ground, with ca. 35 cm extending above the ground. Thirty-eight pitfall traps (19-l plastic buckets) were buried flush with the ground. Pitfall traps were placed

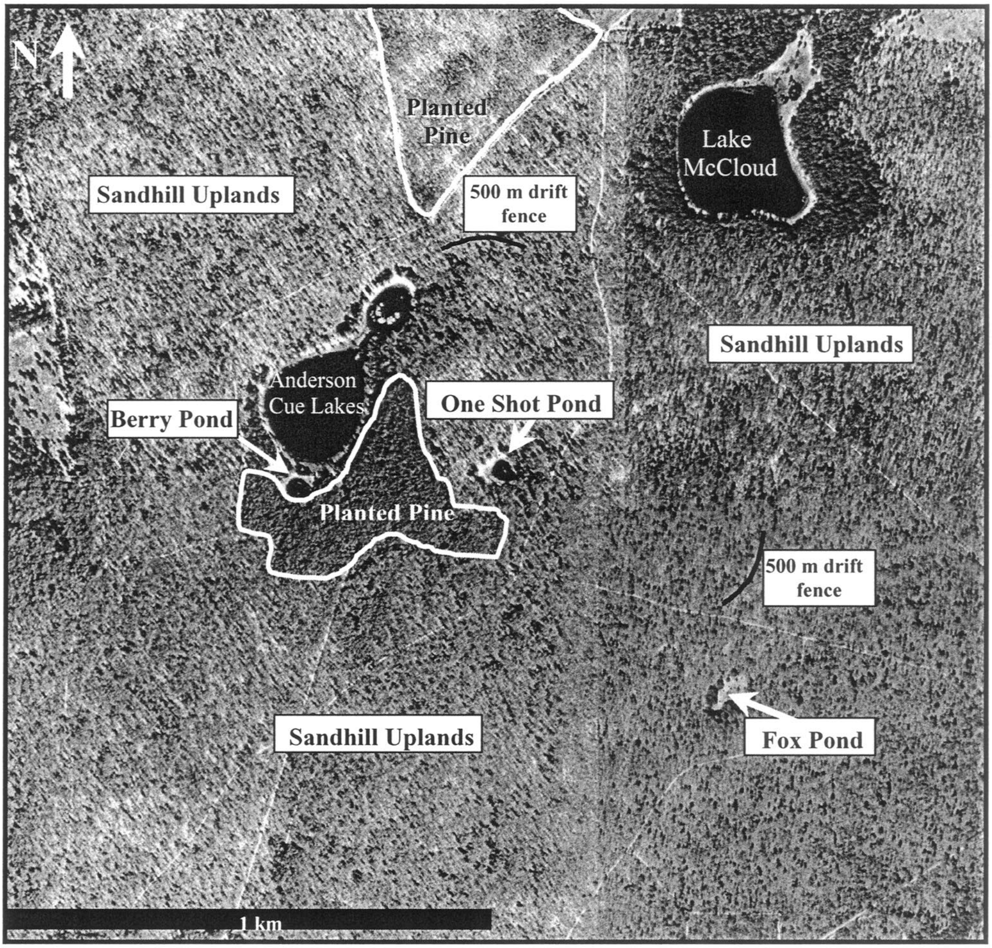


Fig. 2. – Aerial photograph of the study area in 1999. The predominant upland habitat type is xeric sandhill. The approximate locations of the 500 m drift fence sections (see fig. 3) are indicated. Dirt roads appear as thin, white lines.

in pairs, one on each side of the fence, at intervals of about 10 m. I usually checked traps three to five days per week, depending on weather and movements of animals. I weighed and measured newts caught in pitfall traps at the pond and in the surrounding uplands. Each newt was individually marked by toe clipping (DONNELLY et al., 1994) and released on the opposite side of the fence. Sex of adults was determined by the presence of a conspicuous whitish gland visible at the posterior edge of the vent in mature males. Recently transformed newts were recognized by the presence of gill vestiges visible for several days after metamorphosis. Recently transformed newts with swollen vents were presumed to be mature (JOHNSON, 2001), and aquatic sampling in the pond showed that such individuals represent paedomorphic animals that recently bred. These newts are referred to as paedomorphs. Transformed newts without swollen vents (i.e., immatures) are referred to as efts.

I obtained a compass orientation for each pair of pitfall traps surrounding OSP. To do this, I stood in the center of the pond and took a bearing on each pair of traps at the drift fence. Following the methods of Dodd & Cade (1998), I used Rao's spacing test (Rao, 1976; Batschelet, 1981) to determine if captures were distributed uniformly around the drift fence (i.e., random orientation). I analyzed orientation of newts into and away from the pond by sex and life history stage. I made comparisons between distinct migration events (Johnson, 2001) within the adult and eft life-history stages. For comparisons between sexes, life-history stages, and migration events, I ran the same multirespsonse permutation procedure (MRPP; Mielke & Berry, 2001) used by Dodd & Cade (1998). Orientation analyses were performed with the statistical software package BLOSSOM, which was developed by the US Geological Survey (Cade & Richards, 1999). BLOSSOM is available free at www.fort.usgs.gov./products/software/software.asp.

Upland migration

Migration distances of newts in the sandhill uplands around OSP were determined through captures in pitfall traps associated with drift fences. Drift fences were oriented to capture newts during movements to and from the pond (fig. 3). In year one, five fence sections were established at each of four distances from OSP (20 m, 40 m, 80 m and 160 m). Fence sections at each distance totaled 20 % of the circumference at that distance from the pond. Fence sections were distributed evenly at each distance, and they did not overlap with fence sections at the other distances (fig. 3a). Fence sections at 20 m were 10.0 m long with 4 pitfalls (2 on each side of the fence); at 40 m fence sections were 15.1 m with 6 pitfalls; at 80 m sections were 25.1 m with 8 pitfalls; at 160 m sections were 45.2 m with 10 pitfalls. Pitfall traps were installed on both sides of the upland fences (i.e., pond side and upland side; fig. 3a). This upland fence array was monitored from 7 October 1996 to 5 December 1997, and fences were constructed similarly to the fence at the pond.

Results from year one demonstrated that striped newts regularly moved more than 160 m. Therefore, a new upland fence array was installed in year two, with upland drift fences erected much farther away from OSP. On 5 December 1997, the upland drift fences described above were replaced with a different array of fence sections (fig. 3b) and the new fences were in place by 7 December 1997. These fences were constructed of heavy-gauge silt-fence material buried ca. 15 cm into the ground – ca. 40 cm extended above ground. Two fence sections were installed at each of five distances (100 m, 200 m, 300 m, 400 m and 500 m) from the pond. Fence sections at each distance totaled 13.4 % of the circumference at that distance from the pond, and fence sections overlapped (fig. 3b). The two fence sections at 100 m were each 42 m long with 6 pitfalls (3 on each side of the fence), installed evenly throughout each section; at 200 m sections were 84 m long with 10 pitfalls; at 300 m sections were 126 m long with 14 pitfalls; at 400 m sections were 168 m long with 18 pitfalls; at 500 m sections were 210 m long with 22 pitfalls. Pitfall traps were oriented in the same manner as year one; pond-side traps were on the side of the fences toward OSP and upland-side traps were away

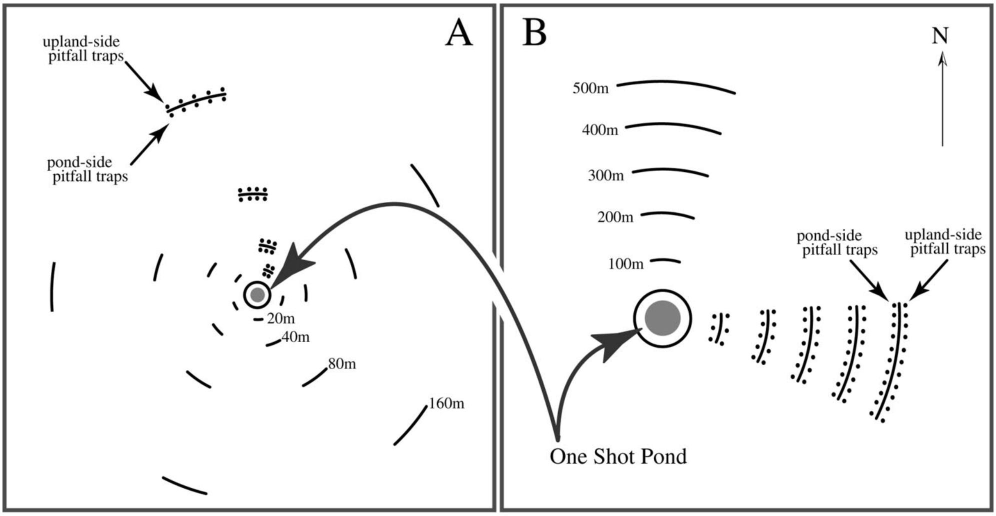


Fig. 3. – Upland drift fence arrays around One Shot Pond, Putnam Co., Florida, USA. The upland array design in year one of the study is depicted in A and the year two design is depicted in B. One Shot Pond is shown as a solid circle, and the circle around it represents the drift fence at the pond.

from OSP (fig. 3b). The upland fence array in year two was monitored until the study ended on 11 September 1998.

In total, 280 pitfall traps were installed at upland fence sections and were monitored during the 2-year study, for a total of 98,140 trap-nights (one trap-night means one pitfall trap open for 24 hours). Upland traps were checked on the same schedule as those at the pond and newts were processed as described above.

Based on captures at upland fence sections and at the outside of the drift fence encircling OSP, I estimated the proportion of the newt population that migrated different distances from the pond. Data used in the estimates were confined to 7 December 1997 through 31 March 1998. During this period, there was a mass migration of newts toward the pond and very little movement away from the pond (JOHNSON, 2001). Ninety-one percent of upland fence captures during year two occurred during this period. These captures, however, only represented newts that migrated through a subset of the surrounding uplands. Because upland drift fences sampled only 13.4 % of the uplands at each distance, I multiplied the number of captures in the outside pitfalls by 7.5. The product of this calculation is an estimate of the number of captures expected at each distance had the upland fence sections sampled 100 % of the uplands at each distance. For each upland fence section, I divided the estimate by the number of total newt captures on the outside of the fence at OSP to approximate the proportion of individuals that had migrated various distances (i.e., 100 m to 500 m, at 100 m intervals). I assumed there was no strong nonrandom orientation of newts moving through the uplands. Nonetheless, movement of newts into and away from the pond was nonrandom (see below), but there was no overwhelmingly strong directionality that would violate this assumption.

However, estimates of the proportion of newts that migrated various distances from the pond are probably conservative.

I use the term "migration" to indicate seasonal, two-way movements of newts away from and toward a breeding pond. "Immigration" indicates a general pattern of migration toward the breeding pond, whereas "emigration" indicates migration away from the pond (Semlitsch & Ryan, 1999). "Dispersal" refers to "once-in-a-lifetime" movement away from a pond and infers that the dispersing individual will not return to its natal pond.

RESULTS

ORIENTATION AT ONE SHOT POND

All patterns of adult immigration and emigration were significantly nonrandom (fig. 4; Rao's spacing tests, all $P < 0.001$). Adult striped newts entered and exited the pond in all directions. They tended to enter the pond basin primarily from the east and west (fig. 4). Adults emigrated in all directions but there was a single, distinct angle of emigration, as indicated by the relatively high number of captures in a pitfall trap located at a south-southeast direction (fig. 4). Emigration of paedomorphs and efts also was nonrandom (fig. 5; Rao's spacing tests, both $P < 0.001$). There was no obvious pattern to paedomorph emigration, but emigrating efts exited the pond basin most often in the southwest quadrant (fig. 5).

Overall patterns of immigration differed significantly from emigration for females and males (tab. 1). Although the directionality of immigrating adults appeared similar between the sexes (fig. 4), patterns were significantly different (MRPP test, $P = 0.002$). There were three distinct immigration events of adults, but orientation patterns were significantly different between the sexes only during the third, and largest of these events (tab. 2). Differences in emigration between males and females (fig. 4) were not significant overall or when distinct emigration events were compared (tab. 1-2).

There were two distinct emigration events of recently transformed striped newts comprising the 1996-97 cohort. The first emigration event took place from October through November 1996, and the second event from April through June 1997 (Johnson, 2002). Immature newts (i.e., efts) comprised the first event, whereas emigration later consisted mostly of recently transformed paedomorphs (Johnson, 2002). Patterns of emigration were significantly different between the eft and paedomorph life-history stages of the same cohort (tab. 1). In addition to the eft emigration of 1996, a second emigration event of efts took place from June through early September 1998 (Johnson, 2002). Patterns of eft captures at OSP differed significantly between these two emigration events and, considering all efts and all adults, efts exited the pond basin in a different pattern from adults (tab. 1-2).

Data for 44 individually marked efts initially caught leaving the pond in the winter of 1996 and recaptured when they returned to breed in the winter of 1997 indicated that individuals tended to enter and exit the pond within the same quadrant. Sixty-four percent of these newts left and returned to OSP in the same quadrant, and four individuals (9 %) were caught leaving and returning to the pond at the same pair of pitfall traps. The vast majority of

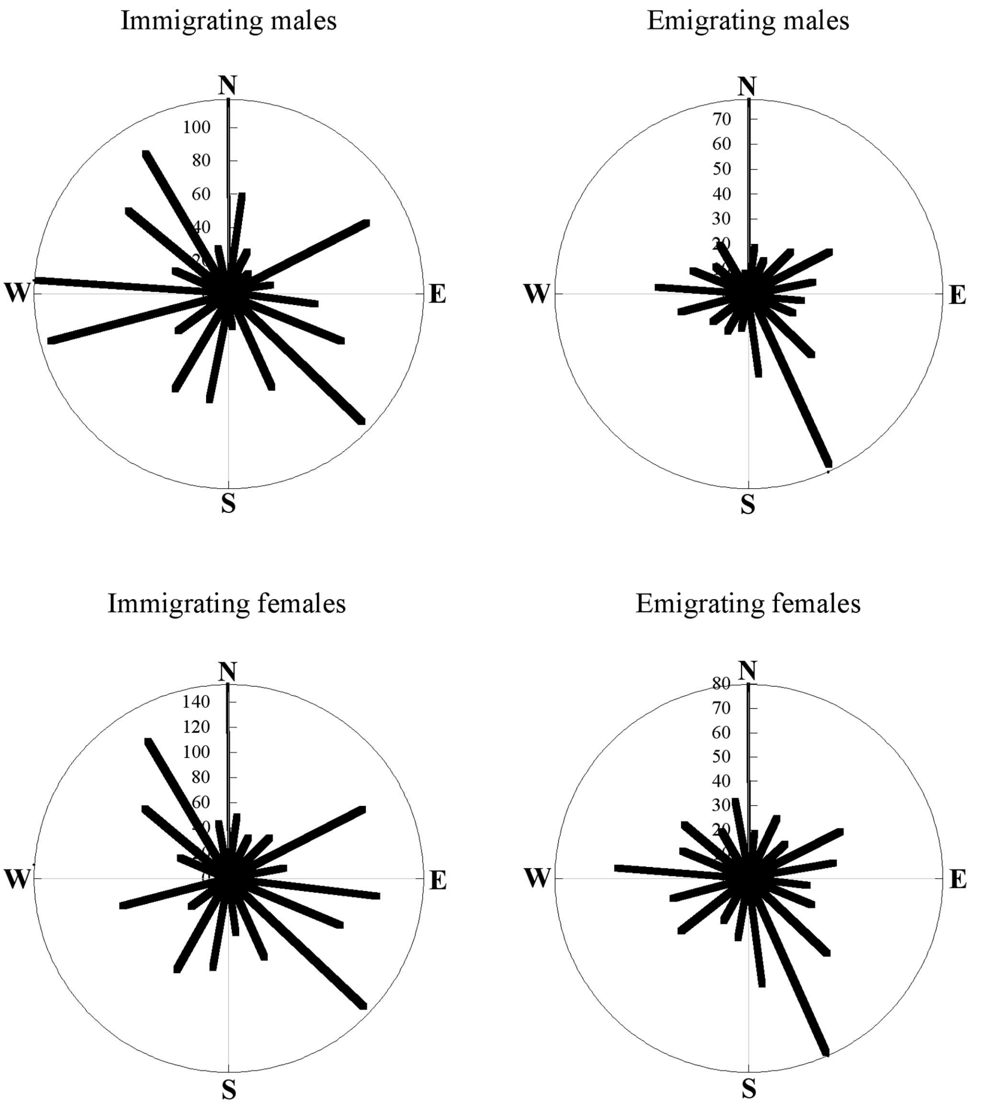
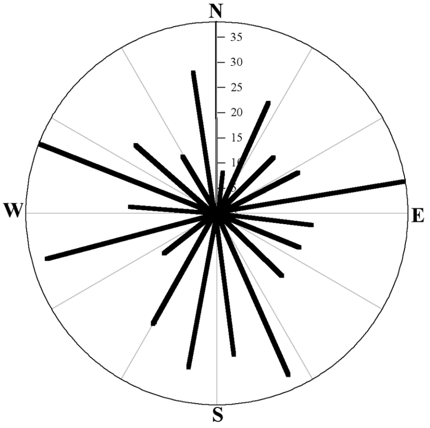


Fig. 4. – Orientation patterns of immigrating and emigrating striped newt adults captured in pitfall traps at a drift fence encircling One Shot Pond, Putnam, Co., Florida, USA. Orientation was significantly different from random for all four patterns. The length of the lines indicates the number of newts entering and exiting the pond basin at each pitfall trap.

Emigrating paedomorphs



Emigrating efts

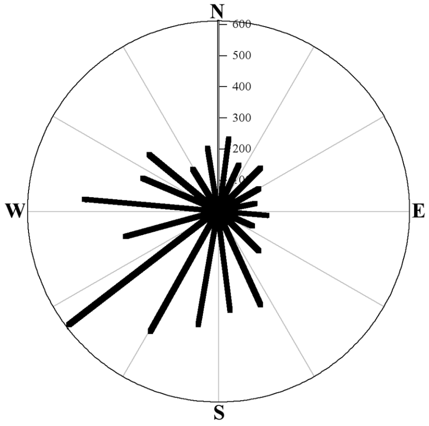


Fig. 5. – Orientation patterns of emigrating striped newt paedomorphs and efts captured in pitfall traps at a drift fence encircling One Shot Pond, Putnam, Co., Florida, USA. Orientation was significantly different from random for both patterns. The length of the lines indicates the number of newts exiting the pond basin at each pitfall trap.

Table 1. – Overall comparisons of directional orientation patterns for striped newts entering (immigrating) and leaving (emigrating) One Shot Pond, Putnam Co., Florida, USA.

Comparison	*n*	Standardized test statistic	*P*
Immigrating vs. emigrating males	1159, 486	– 13.317	< 0.001
Immigrating vs. emigrating females	1489, 645	– 3.798	0.008
Immigrating males vs. females	1159, 1489	– 5.524	0.002
Emigrating males vs. females	486, 645	– 0.437	0.2
Emigrating efts vs. emigrating adults	5008, 1131	– 67.639	< 0.001
Emigrating efts vs. emigrating paedomorphs of the same cohort	745, 407	– 9.506	< 0.001

Table 2. – Comparisons of directional orientation patterns for striped newts entering (immigrating) and leaving (emigrating) One Shot Pond, Putnam Co., Florida, USA.

Comparison	n	Standardized test statistic	P
Immigrating males vs. immigrating females	°	°	°
– Immigration Event 1	23, 13	0.697	0.7
– Immigration Event 2	22, 66	– 0.130	0.3
– Immigration Event 3	1049, 1290	– 4.008	0.006
Emigrating males vs. emigrating females	°	°	°
– Emigration Event 2	15, 68	0.686	0.7
– Emigration Event 3	430, 484	– 0.005	0.3
Emigrating efts during metamorphic Event 1 vs. emigrating efts during metamorphic Event 3	745, 4237	– 3.599	0.01

individuals (84 %) entered the pond basin within the same half they had exited from the previous year.

MIGRATION INTO UPLANDS

I captured 831 newts in the upland drift fences during year one (fig. 3a, tab. 3). Pond-side captures accounted for 73 % of total captures, and migration in year one consisted primarily of recently transformed efts that were moving into the uplands. I captured newts at all of the upland fence sections (fig. 3a; tab. 3) and in most (91.4 %) of the pond-side pitfall traps.

Table 3. – Numbers of striped newts captured in pitfall traps at drift fence arrays in the sandhill uplands surrounding One Shot Pond, Putnam, Co., Florida, USA. Drift fences were located at various distances from the pond. See fig. 3 for a depiction of the arrays.

	Year 1				Year 2				
	20 m	40 m	80 m	160 m	100 m	200 m	300 m	400 m	500 m
Pond-side	140	126	169	172	11	6	10	12	7
Upland-side	79	39	64	42	121	108	86	86	48
Total	219	165	233	214	132	114	96	98	55

During each period of migration most newts were captured on the same sides of upland drift fences. However, for some movement events, a few newts were captured in pitfalls on the opposite side of fences from the majority of captures. I believe this is because there was a small degree of wandering by some newts in the uplands as they moved to or from OSP. Pond-side captures at upland fences in year one represented three distinct periods of newt migration, two emigration events and one immigration event (tab. 4). Most newts captured on the pond-side of upland fences in year one (76 % of pond-side captures) were caught during the first emigration event (i.e., E1), which occurred from October 1996 through February 1997 (tab. 4). Emigration during this period consisted almost exclusively of immature efts that had recently transformed. I captured far fewer newts (15 % of pond-side captures) during emigration event two (E2), which occurred from April through July of 1997 (tab. 4). This emigration event was comprised of recently transformed paedomorphic newts (54 % of the migrating newts), as well as recently transformed efts and several adults that likely had finished breeding and were moving back into the uplands. The third period of migration, indicated by pond-side fence captures in year one, was the result of an immigration event (i.e., I3) that began in October 1997 (tab. 4). There was a major breeding migration of adults to the pond that began in October 1997 and pond-side captures at this time probably resulted from adults that were moving toward the pond but happened to be captured on the pond-side of the upland drift fences (tab. 4).

Upland-side captures of striped newts accounted for 27 % of captures in year one. I captured newts at each of the five fence sections (fig. 3a), at each distance from OSP (tab. 3) and in most (81.4 %) of the pitfall traps on the upland-side of the fences in year one. Upland-side captures occurred during three distinct periods of migration, all of which were immigration events. These migration events (I1, I2 and I3; tab. 4) occurred during the same time periods as described above for pond-side captures (tab. 4). Immigration event I3 accounted for the largest proportion (54 %) of upland-side captures in year one, followed by event I1 (29 %) and I2 (17 %). All of these migration events consisted of adult newts moving toward OSP to breed (tab. 4).

I captured 495 newts in the upland drift fences during year two (fig. 3b, tab. 3). In contrast to year one, migration consisted primarily of immigrating adults. Pond-side captures accounted for only 9 % of total captures. I captured newts at each of the two fence sections (fig. 3b) and at each distance from OSP (tab. 3), but captures were recorded in less than half of the pitfall traps (42.8 %) on the pond-side of the upland fences in year two. Pond-side captures at

Table 4. – Captures of striped newts in upland fences around One Shot Pond, Putnam Co., Florida, USA, during distinct periods of movement. *: fence arrays modified in early December 97.

Fence side of captures	Migration event	Predominant direction of newt movement	Time period of event	Number of newts captured	Description
Year 1					
Pond-side	E1	Away from pond	October 96 through February 97	461	Emigrating efts
Pond-side	E2	Away from pond	April 97 through July 97	91	Primarily emigrating paedomorphs and efts
Pond-side	I3	Toward pond	October 97 through December 97*	55	Immigrating adults
Upland-side	I1	Toward pond	October 96 through January 97	65	Immigrating adults, some emigrating efts
Upland-side	I2	Toward pond	April 97 through July 97	36	Immigrating adults
Upland-side	I3	Toward pond	November 97 through December 97*	123	Immigrating adults
Year 2					
Pond-side	I3	Toward pond	December 97* through March 98	16	Immigrating adults
Pond-side	E3	Away from pond	June 98 through September 98	25	Emigrating efts
Upland-side	I3	Toward pond	December 97* through March 98	449	Immigrating adults

upland fences in year two represented two distinct periods of newt migration, one immigration event (i.e., I3) and one emigration event (i.e., E3). I captured few newts during both of these events; 16 during I3 and 25 newts during E3 (tab. 4). Captures during migration event I3 were adults that were moving to the pond to breed but were captured in pond-side traps as they wandered toward the pond. Captures during E3 were recently transformed newts that were leaving OSP.

In year two, I captured far more newts (91 % of total upland captures) on the upland-side of drift fences than on the pond-side (tab. 3). I captured newts at all sections of drift fence and in almost all of the upland-side pitfalls (88.6 %). Captures occurred during a single immigration event (I3; tab. 4) and were exclusively of adults that were immigrating to OSP to breed. The number of captures declined as the distance from the pond increased (tab. 3). Based on estimated values, at least 360 newts (16 % of the breeding migration) migrated more than 500 m from OSP (fig. 6). I estimated that 645 newts (29 % of the breeding migration) migrated at least 400 m. The estimate was the same for 300 m (645 newts). I estimated that 810 (36 % of the breeding migration) and 908 (41 % of the breeding migration) of newts migrated from the pond at least 200 and 100 m, respectively (fig. 6). Based on these estimates, it appears that roughly 60 % of the striped newts emigrated less than 100 m. However, as indicated by captures at the 500 m fences, a substantial percentage of individuals comprising the 1997-98 breeding migration immigrated to OSP from farther than 500 m. In fact one newt that was marked leaving OSP as an eft on 18 November 1996 was recaptured on 4 February 1998 as it colonized Fox Pond, a dispersal distance of approximately 685 m.

DISCUSSION

ORIENTATION

The distribution of habitats surrounding a breeding pond should influence patterns of immigration revealed by captures of salamanders at the pond. Habitat preferences among species and/or differential survivorship in various habitat types might be apparent as individuals arrive at the breeding pond. For example, imagine an amphibian breeding-pond in which one half of the uplands surrounding the pond were pine plantation (i.e., marginal habitat) whereas the other half remained native uplands (i.e., preferred habitat). The pattern of captures at the pond would be expected to reflect the distribution of upland habitats. One might predict significantly fewer captures along the half of the pond adjacent to the pine plantation as compared to the native upland half. This is because pond-breeding salamanders have the ability to select appropriate upland habitats and accurately navigate through uplands during migration, often using specific habitat types (SHOOP, 1968; HURLBERT, 1969; SEMLITSCH, 1981; STENHOUSE, 1985; MADISON, 1997; MADISON & FARRAND, 1998; DEMAYNADIER & HUNTER, 1999; MALMGREN, 2002; ROTHERMEL & SEMLITSCH, 2002).

In this study, although newts entered and exited the pond basin from all directions, migration was nonrandom. Some directions were preferred over others, but there were no obvious upland habitat features that could explain the newts' orientation behavior. However, I did not measure habitat variables in the uplands and individuals could have used micro-

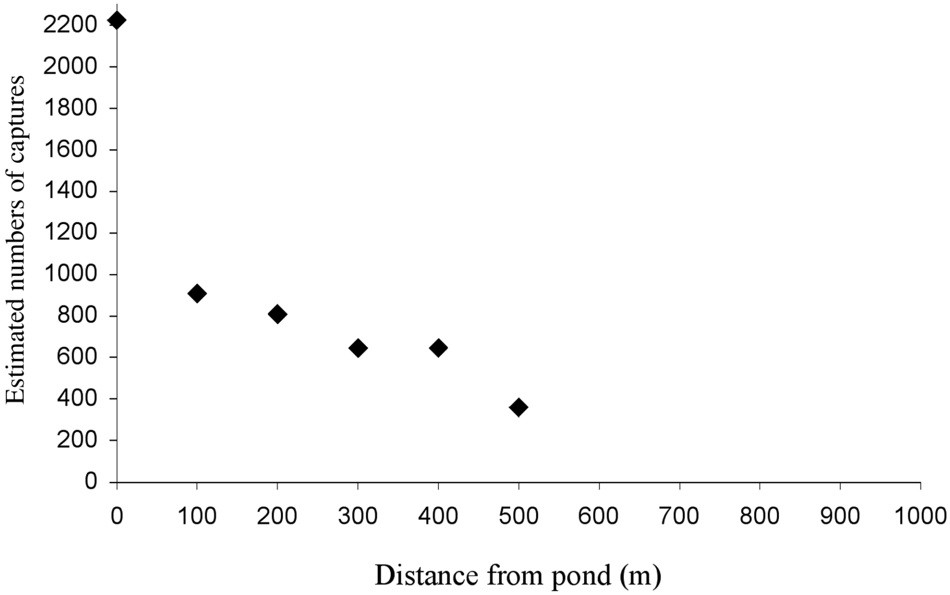


Fig. 6. – Estimated numbers of striped newt captures in pitfall traps at drift fences in the sandhill uplands around One Shot Pond, Putnam Co., Florida, USA. Drift fences were located at 100 m intervals up to 500 m from the pond. The zero point represents captures at a drift fence encircling the pond. See *Materials and methods* for an explanation of how the estimated numbers were calculated.

topographic features as cues to navigate toward the pond. In a similar study, DODD & CADE (1998) concluded that movements of striped newts and narrowmouth toads were a reflection of the distribution of favorable upland habitats around the pond. Although the uplands at OSP were primarily sandhill habitat, a small plantation of slash pine (with intact groundcover) was well within the dispersal capabilities of migrating newts (fig. 2). In year one I often caught newts at a section of drift fence in the pine plantation. Newts could have resided within the plantation or have traveled through it en route to native sandhill. Nevertheless, this plantation represented only a small portion of the uplands and had no detectable effect on striped newt movements.

Although upland-habitat preferences and microenvironmental features I did not measure could have influenced the nonrandom pattern of immigration observed at OSP, if measured over several seasons, orientation may in fact be random. It is possible that striped newts are roughly evenly distributed in the uplands around OSP but that only a portion of the population migrates to the pond during any particular breeding event. If the portion of individuals moving was not indicative of the whole population, then what truly should be random orientation would appear as nonrandom because data were collected for a relatively short time.

Patterns of newt emigration were also nonrandom, and newts exited the pond basin in all directions. Efts emigrated predominantly in the southwest quadrant of the pond. The slope of the pond basin was shallowest in this quadrant, and water depth during metamorphic events could have influenced the behavior of recently transformed efts as they left the pond. On the other hand, adults emigrated most often in the south-southeast portion of the basin. Differences in aquatic habitat preference (e.g., depth) between adult and immature newts might explain the varying emigration patterns, although habitat preferences of both life history stages are unknown.

UPLAND MIGRATION

Using upland drift fence arrays in year two, I was able to estimate the percentage of the striped newt breeding population that migrated different distances (in increments of 100 m) from the pond. Captures at drift fences in the sandhill uplands surrounding OSP indicated that many striped newts (16 %) migrated more than 500 m from the pond. This is a conservative estimate because newts captured in traps closer to the pond may have migrated further than indicated by the traps. Captures at the drift fence surrounding the pond and at upland drift fences at the end of year one showed that a breeding migration of newts into OSP had begun before the installation of fences for year two (JOHNSON, 2001, 2002). Although the proportion of individuals caught at the pond before the new upland fence arrays were established was small (7 % of the total), some newts already had moved toward the pond before the upland arrays were in place. Moreover, immigrating adults did not arrive at the pond in a random fashion during this breeding migration. The upland fence arrays in year two were located north and southeast of OSP and newts were caught at the pond with lowest frequency toward the north. Therefore, the proportion of the breeding population caught at each distance from the pond in year two is likely an underestimate of the actual proportion that migrated to that particular distance.

Many pond-breeding amphibians have complex life-cycles and spend much of their adult lives in terrestrial habitats away from breeding sites. Distances that individuals disperse or migrate from breeding ponds have been reported for some species (DODD, 1996; SEMLITSCH, 1998 and references therein). It is clear that individuals disperse and migrate hundreds of meters from breeding sites into upland habitats, some even thousands of meters. With few exceptions, however, distance values usually have been presented for less than 10 individuals per species. The results from my study appear to be the first estimates of migration distances for a breeding population of North American amphibians based on a substantial sample size.

CONSERVATION IMPLICATIONS

Central to a successful amphibian conservation strategy is the protection of sufficient breeding and nonbreeding habitat (i.e., the pond and appropriate "core habitat": SEMLITSCH & JENSEN, 2001). Studies of amphibian migration and dispersal can provide the scientific basis for determining directional and distance components that can be used to establish protected areas around breeding ponds. BROWN et al. (1990) used spatial requirements (i.e., distance moved from a wetland), among other data, to recommend width of "buffer zones" for wildlife protection at wetlands in Florida. Nevertheless, lack of data for amphibians forced them to use rough estimates for most of the species considered. Further utility of movement distance data can be found in regulations to protect the flatwoods salamander (*Ambystoma cingula-*

tum) which, as a result of severe population decline (MEANS et al., 1996), was federally listed as threatened in the USA (ANONYMOUS, 1999). The US Fish and Wildlife Service restricts specific silvicultural practices within 450 m of flatwoods salamander ponds. Additionally, only selective timber harvest at specific times is allowed within a primary radius of 164 m around breeding ponds (ANONYMOUS, 1999). The width of the primary zone (164 m) was derived from a review of migration distances for pond-breeding salamanders of the genus *Ambystoma* (SEMLITSCH, 1998), despite the fact that no data for *A. cingulatum* were presented. This example underscores the need to determine migration and dispersal distances for all pond-breeding amphibians. SEMLITSCH (1998) acknowledged that the extent of protected upland recommended for *Ambystoma* species may apply to some species of pond-breeding amphibians, but certainly not all. My data show that recommendations for protecting terrestrial habitat for ambystomatid salamanders are inadequate for *Notophthalmus perstriatus*. Therefore, it is not defensible to extrapolate data across taxa. Clearly, a 164 m protected zone would not protect all of the striped newts breeding at OSP. Based on extrapolation of migration distances revealed by upland drift fences, a protected area of "core habitat" extending ca. 1000 m from OSP would likely be needed to encompass almost all of the newts that breed there.

Although they have great value as wildlife habitat, small, isolated wetlands in the United States are afforded little protection from development. Overall, more than 50 % of wetlands have been destroyed by development in the United States (DAHL, 1990), and much of this loss has been small wetlands. In Florida, a state with an extremely large number and diversity of wetlands, isolated wetlands less than 0.2 ha receive no protection from development. This size threshold was adopted by the state's water management districts "based on a consensus of scientific and regulatory opinion rather than on biological and hydrological evidence" (HART & NEWMAN, 1995). Small wetlands are just as vulnerable at the national level as they are in Florida.

There is strong evidence that protection of core areas of terrestrial habitat surrounding breeding sites is crucial for persistence of amphibian populations and species. Data from OSP demonstrate that small, isolated wetlands can support breeding populations of salamanders that migrate hundreds of meters into the surrounding uplands. Similar studies at other ponds and in different upland types are necessary because data on upland habitat requirements (quality and quantity) of most amphibian species are lacking. Without this information, designating terrestrial "core habitat" to conserve aquatic-breeding amphibians will largely remain guesswork, with generalizations made from data on relatively few individuals of a few species. However, unless more protection is afforded to small, isolated wetlands, arguments to preserve uplands surrounding the wetlands are irrelevant.

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