Movement Patterns and the Conservation of Amphibians Breeding in Small, Temporary Wetlands

C. KENNETH DODD, JR.* AND BRIAN S. CADE†

*Florida Caribbean Science Center, Biological Resources Division, U.S. Geological Survey, 7920 N.W. 71st Street, Gainesville, FL 32653, U.S.A., email kdodd@nervm.nerdc.ufl.edu

†Midcontinent Ecological Science Center, Biological Resources Division, U.S. Geological Survey, 4512 McMurry Avenue, Fort Collins, CO 80525, U.S.A.

Abstract: *Many amphibians breed in water but live most of their lives in terrestrial habitats. Little is known, however, about the spatial distribution of these habitats or of the distances and directions amphibians move to reach breeding sites. The amphibian community at a small, temporary pond in northcentral Florida was monitored for 5 years. Based on captures and recaptures of more than 2500 striped newts (*Notophthalmus perstriatus*) and 5700 eastern narrow-mouthed toads (*Gastrophryne carolinensis*), we tabulated the angles of orientation that these amphibians entered and exited the pond basin. Our results showed that movements of these species between the pond and terrestrial habitats were nonrandom in orientation, but that narrow corridors did not appear to be used. Differences between the species likely reflect differences in habitat preferences, whereas intraspecific differences among years and between the sexes likely reflect variation among individuals. For terrestrial buffer zones to be effective at conserving pond-breeding amphibian communities, they need both a distance and a directional component. The determination of a directional component may be obscured if studies are carried out over a short time span. Conservation efforts for wetland-breeding amphibians that concentrate solely on the wetland likely will fail without consideration of the adjacent terrestrial habitat.*

Patrones de Movimiento y Conservación de Anfibios en Humedales de Temporal Pequeños

Resumen: *Muchos anfibios se reproducen en el agua pero viven la mayor parte de sus vidas en hábitats terrestres. Sin embargo, poco se conoce sobre la distribución espacial de estos hábitats o de las distancias y direcciones en las que se mueven los anfibios para llegar a sus sitios de reproducción. La comunidad de anfibios en estanques temporales pequeños en Florida nor-central ha sido monitoreada por 5 años. En base a capturas y recapturas de mas de 2500 tritones rayados (*Notophthalmus perstriatus*) y 5700 sapos de boca chica del este (*Gastrophryne carolinensis*), tabulamos los ángulos de orientación en que estos anfibios entraron y salieron de la cuenca del estanque. Nuestros resultados muestran que los movimientos de estas especies entre el estanque y los hábitats terrestres no tuvieron una orientación azarosa, pero los corredores angostos aparentemente no son utilizados. Diferencias entre las especies parecen reflejar diferencias en las preferencias de hábitat, mientras que diferencias intraespecíficas entre años y entre sexos parece reflejar variación entre individuos. Para que las zonas terrestres de amortiguamiento sean efectivas en la conservación de comunidades de reproductores de anfibios, necesitan tener como componentes una distancla y orientación. La determinación del compopente direccional puede ser obscurecido si los estudios se llevan a cabo en un periodo de tiempo corto. Los esfuerzos conservacionistas para anfibios de reproducción en humedales tenderán a fallar si se concentran únicamente en el humedal sin tomor en consideración el hábitat terrestre adyacente.*

Paper submitted April 30, 1997; revised manuscript Accepted June 4, 1997.

Introduction

Because of their diversity and abundance, amphibians are among the most important vertebrate components of wetland ecosystems. Populations can become quite large because amphibians are ectotherms and thus use energy for growth and reproduction rather than to maintain a constant body temperature (Pough 1983). The potentially large size of both adult and larval amphibian populations has important implications for both predators and prey and for community energy dynamics (Seale 1980; Taylor et al. 1988; Holomuzki et al. 1994; Blaustein et al. 1996). The effects that amphibian declines have on ecosystem structure are thus of concern to community ecologists as well as to conservation biologists (Beebee 1996).

Many amphibians have a typical biphasic life-history pattern. Adults migrate to breeding ponds, deposit eggs, and return to terrestrial habitats (Duellman & Trueb 1986). The eggs hatch as aquatic larvae that remain in the water for various amounts of time depending on hydroperiod, thermal regime, predation, competition, and other related factors (Pechmann et al. 1989; Newman 1992; Rowe & Dunson 1995; Skelly 1996). The larvae metamorphose and emigrate from the wetland toward terrestrial habitats. A few species have been reported to move in specific directions when entering or leaving a pond or small wetland, and it has been suggested that some species follow migratory corridors as they move to and away from breeding sites (Stenhouse 1985; Verrell 1987).

The southeastern coastal plain of the United States has experienced dramatic development and landscape changes during the last 100 years. Vast areas of forests have been cleared for agriculture, plantation forestry, and human occupation (Ware et al. 1993; Means 1996). For example, approximately 2% of the 33 million ha that once comprised the longleaf pine (*Pinus palustris*) forest on the southeastern coastal plain is extant, and less than 0.01% is in old-growth forest (Means & Grow 1985; Means 1996; Noss 1989). Temporary ponds and other semipermanent small wetlands scattered throughout the coastal plain disappeared as forests were cleared. Even now, the biological importance of small wetlands is under-appreciated, and they are often ignored in wetland regulations (Hart & Newman 1995).

Temporary ponds serve as important breeding sites for many amphibians, and large numbers of species may be found in rather small ponds in the southeastern coastal plain. For example, 14 species of frogs were found breeding in temporary ponds in upland habitats in northcentral Florida (Moler & Franz 1987), 20 amphibians were found in a temporary pond on the coastal plain of Georgia (Cash 1994), 15 pond-breeding amphibians were captured at Breezeway Pond in northcentral northcentral Florida (Dodd 1992), and 16 species of amphibians were trapped from a series of nearby temporary ponds in managed north Florida flatwoods (O'Neill 1995). A few amphibians of critical conservation concern (*Ambystoma cingulatum, Notophthalmus perstriatus, Rana capito*; Millsap et al. 1990) breed only in temporary ponds (Dodd 1995*a*, 1997). Small wetlands also are critical to the survival of many other invertebrate and vertebrate animal species (Dickinson 1949; Moler & Franz 1987; Gibbs 1993; Hart & Newman 1995).

From 1985 to 1990 the species richness and diversity of an amphibian community inhabiting a temporary pond in northcentral Florida was monitored (Dodd 1992). The sampling design used a nearly circular drift fence around the shallow pond basin. This design allowed us to re-examine the data collected during that study in order to determine whether the most commonly captured species were moving toward and away from the pond basin in a random or nonrandom fashion and to determine if certain directions were favored over others. Coupled with information on amphibian use of upland habitats (Dodd 1996), results of the analyses of movement patterns presented here could have important applications for both amphibian conservation and for the protection of small, temporary, wetland-dependent communities.

Methods

Study Site

Field data were collected from October 1985 to September 1990 at Breezeway Pond, a 0.16-ha temporary depression marsh (Florida Natural Areas Inventory 1990) located in a shallow 1.3-ha basin on the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam County, Florida (29°41′N, 82°00′W). The pond is located in xeric sandhill uplands near the ecotone between a longleaf pine, turkey oak (*Quercus laevis*), wiregrass (*Aristida beyrichiana*) community (termed "high pine" or sandhill) and a xeric oak (*Q. geminata* and *Q. hemisphaerica*) hammock community (Fig. 1). To the immediate south and west (at angles 72° to 298° from the pond basin's center), "high pine" sandhills predominate; to the north (at angles 299° to 360°, and 0° to 27°), xeric oak hammock predominates; to the northeast, a small grassland dominated by maidencane (*Panicum hemitomon*) is found at an angle of 28° to 71° from the center of the pond basin. The distance from the drift fence to the nearest forested plant association is generally 20 m but extends to about 50 m behind the *Panicum* meadow. Additional physical and vegetative details concerning the site have been presented by Dodd (1992, 1993) and LaClaire (1992). The pond held water continuously for 2 years prior to the study (R. Franz, personal communication).

The nearest water bodies to Breezeway Pond are Smith Lake (350 m north of Breezeway Pond) and three small

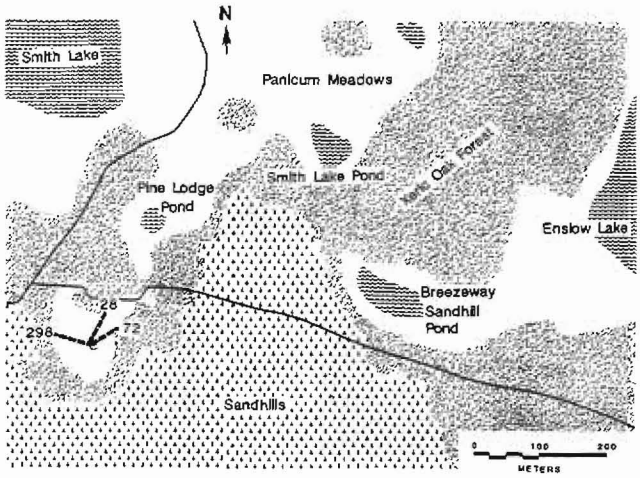


Figure 1. Breezeway Pond, Putnam County, Florida, in relation to adjacent habitat. The three dashed lines show the approximate angles between habitats immediately adjacent to Breezeway Pond. The solid lines are dirt roads.

temporary ponds, all located generally north or northeast of Breezeway Pond: Pine Lodge Pond (180 m distant), Smith Lake Pond (450 m distant), and Breezeway Sandhills Pond (400 m distant) (Fig. 1). Drought reduced Smith Lake—7.55 ha surface area in 1985—to approximately 0.75 ha in 1989; it completely disappeared on 29 May 1990. All temporary ponds dried completely in 1989 and remained dry through the remainder of the sampling period. This was approximately 1 year after the last standing water was recorded in Breezeway Pond.

Species

Of the 16 species of amphibians captured at Breezeway Pond, the striped newt (*Notophthalmus perstriatus*) and the eastern narrow-mouthed toad (*Gastrophryne carolinensis*) were the most common. The striped newt (adults to 43-mm snout-vent length) is dependent on temporary wetlands for reproduction. Found from southern Georgia through central Florida and west to the Apalachicola National Forest in the central part of the Florida panhandle, it appears to be confined to the sandy uplands associated with former beach dunes and riverine terraces (Dodd & LaClaire 1995). Breeding occurs from late autumn to early spring, with larvae completing metamorphosis as ponds dry with the coming summer (Dodd 1993). As long as water is present, however, some larvae may remain through winter; neoteny is known at several locations. When not at ponds, striped newts live in terrestrial habitats that may be quite distant from the breeding pond (Dodd 1996). Striped newts appear to have evolved a rather plastic suite of life-history traits, which allows them to exploit temporary breeding habitats that are available unpredictably both within and between years (Dodd 1993).

The eastern narrow-mouthed toad is a small (adults to 35-mm body length), secretive frog found throughout the southeastern United States. Unlike the habitat-specific striped newt, it breeds in a wide variety of temporary wetlands, including ponds, ditches and pools. In northern Florida, individuals may be found at any time of the year, although the majority of surface activity occurs from June through September during the breeding season (Dodd 1995*b*). Juveniles emigrate from ponds in the autumn and following spring during periods of rainfall (Dodd 1995*b*). Adults forage in the uplands, again often at considerable distance from the nearest pond (Dodd 1996), at the mouth of burrows made by vertebrates and invertebrates, and near surface debris offering refuge from heat and desiccation. Their diet consists almost entirely of ants.

Sampling Procedure

The pond basin was enclosed by a 230-m drift fence made of galvanized metal flashing (36 cm above ground, 10–15 cm below the surface). Pitfalls (19-L black plastic buckets 36 cm deep) were placed on opposite sides of the fence at 10-m intervals (Gibbons & Semlitsch 1982). To minimize the effects of direct sun, the buckets were partially shaded (Dodd 1992). Coverboards were laid flat across the buckets when pitfalls were not checked in order to prevent desiccation; animals were captured even when the boards covered the bucket openings because the seals were not complete. The pitfalls were checked 5 days per week between 0700 and 0900 hours, depending on season, from October 1985 through September 1990 (1273 days; 83,950 bucket-nights).

Striped newts and eastern narrow-mouthed toads were examined in the field (for details and results see Dodd 1993, 1995*b*). Snout-vent length (SVL: tip of snout to posterior portion of vent of newts) and snout-urostyle length (SUL: tip of snout to the posterior end of the urostyle of frogs) were measured to the nearest millimeter with a clear plastic ruler.

The sex of adult striped newts was determined by the presence in males of a clearly visible, orange-colored gland cluster on the posterior portion of the vent that is present year-round. Females lacked this gland cluster and occasionally contained eggs. The sex of striped newts captured prior to mid-January 1986 was not determined. Animals smaller than 25 mm SVL were considered juveniles (Dodd 1993). Male eastern narrow-mouthed toads have a clearly visible black chin throat that varies in level of intensity year-round (Anderson 1954). In females the throat is mottled, light, and the same color as the venter (Wright 1932). Females occasionally contained eggs visible through the body wall. Animals smaller than 21 mm SUL generally were consid-

ered juveniles (Wright 1932; Anderson 1954), although the sex of some animals was difficult to determine at 22–24 mm SUL (Dodd 1995*b*). If the sex of an individual of either species was questionable, it was classified as an "unknown adult."

Striped newts and eastern narrow-mouthed toads were marked by toe clipping following a year-specific cohort sequence; no more than one toe was clipped per foot. All captured animals were examined carefully for regenerated toes. After processing, individuals were released on the opposite side of the fence in such a manner as to minimize exposure to predators or extreme environmental conditions.

Analysis of Orientation Data

A compass orientation was obtained by standing in the center of the pond basin and taking readings on the position of the 23 paired buckets at the drift fence. Rao's spacing test (Rao 1976; Batschelet 1981) was used to determine that animal captures were distributed uniformly on the circle of buckets because it has greater power to detect departures from uniform distributions for data with multiple modes and wide angular dispersion than Rayleigh's or Watson's U^2 tests (Bergin 1991). Rao's spacing test was implemented as a special case of empirical coverage permutation tests (Mielke 1988). Analyses were run by sex (male, female) or life stage (juvenile) within each year and pooling across years for each species.

For within- and between-sex comparisons, we used a multiresponse permutation procedure (MRPP) for univariate grouped data that compares treatment groups analogous to a one-way analysis of variance. The permutation procedures, based on distance functions, allow test statistics to be based on powers of Euclidean distances. A variant of the MRPP for circular distributions, where the deviation between any two angles i and j is the minimum of $|\text{angle}_i - \text{angle}_j|$ and $360 - |\text{angle}_i - \text{angle}_j|$ (Mielke 1986), was used to compare distributions of animal captures between sexes, between immigrants and emigrants, and between years. The analyses were performed by means of a computer program (BLOSSOM) developed by the National Biological Survey (Slauson et al. 1991).

Results

Movement Patterns between Species

Striped newts and eastern narrow-mouthed toads both emigrated from and immigrated to Breezeway Pond in a nonrandom manner, regardless of sex, life stage, or year (Figs. 2 & 3). Except for juveniles, striped newts entered and exited from the pond basin in all directions. Fewer

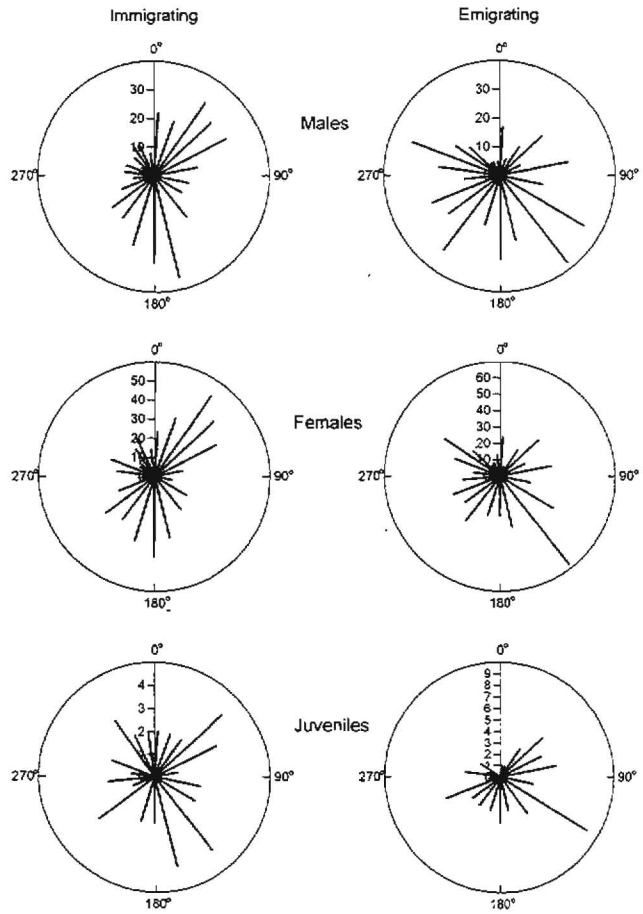


*Figure 2. Patterns of immigration and emigration for striped newts (*Notophthalmus perstriatus*) at Breezeway Pond, 1985–1990. Orientations were not uniformly distributed on the circle (Rao's spacing test, all* $p < 0.01$*). The length of the line based on the scale in each circle indicates the approximate number of animals moving to or from that direction.*

adults were captured in buckets facing north and northwest than in buckets facing the other directions (Fig. 2), especially for immigrating and emigrating males and for emigrating females. Juveniles entered the pond primarily from the northwest through the southeast, but they appeared to avoid the northwest when emigrating (Fig. 2).

Adult eastern narrow-mouthed toads entered and exited the pond from all directions. Immigrating males entered the pond more from the northeast and southwest than they emigrated from the pond. Females had a similar pattern, although perhaps not as obvious (Fig. 3). With juveniles there were clear direction preferences. Two waves of juvenile movements were observed from 1985 to 1990. Successful reproduction occurred only once at Breezeway Pond, during the summer of 1985; a severe drought in northcentral Florida prevented successful reproduction during other years (Dodd 1995*b*).

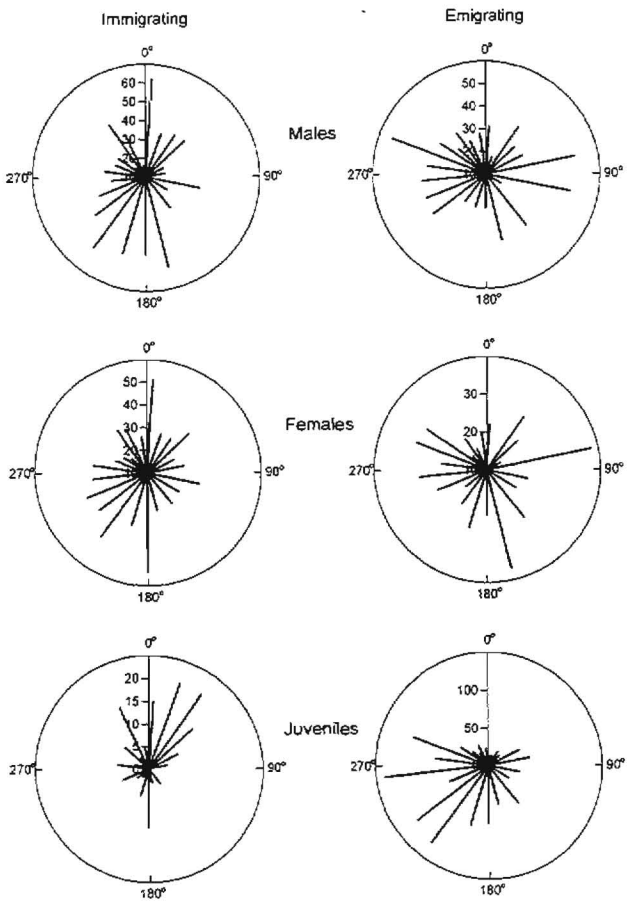


*Figure 3. Patterns of immigration and emigration for eastern narrow-mouthed toads (*Gastrophryne carolinensis*) at Breezeway Pond, 1985–1990. The figures for juveniles show patterns only during the two peaks of movement: immigration from the fall of 1988 to the spring of 1989 and emigration from the fall of 1985 to the summer of 1986. Orientations were not uniformly distributed on the circle (Rao's spacing test, all* $p < 0.01$*). The length of the line based on the scale in each circle indicates the approximate number of animals moving to or from that direction.*

During the autumn of 1985 and spring of 1986, large numbers of juvenile *G. carolinensis* left the pond basin, primarily traveling toward the west, south, and south-southeast (Fig. 3). Juveniles immigrated to Breezeway Pond in numbers only from the autumn of 1988 to the spring of 1989 because drought caused distant Smith Lake and associated wetlands to dry completely (Dodd 1995*b*). These juveniles presumably were passing through the pond basin on their way to upland habitats (Dodd 1995*b*). Most juveniles entered Breezeway Pond from the north-northeast (Fig. 3), the location of the nearest temporary wetlands.

General trends of nonrandom movement may be somewhat misleading. Significant differences in movement patterns were observed when emigration and immigration directions were examined among years (Table 1). The only exceptions were for immigrating female striped newts and for emigrating male eastern narrow-mouthed toads. Nonrandom movement to and from the ponds occurs regularly, but the directions change yearly and vary between the species.

Table 1. Among-year comparison of the directional orientation of *Notophthalmus perstriatus* and *Gastrophryne carolinensis* entering and leaving Breezeway Pond, 1986–1990.

Comparison	*Years*	n	*Standardized test statistic*	p
Notophthalmus perstriatus				
Immigrating males	86–90	396	−4.5512	<0.001
Immigrating females	86–90	562	−0.9289	0.164
Emigrating males	86–89	433	−3.8581	0.003
Emigrating females	86–90	585	−4.5391	<0.001
Gastrophryne carolinensis				
Immigrating males	86–90	826	−2.3007	0.028
Immigrating females	86–90	737	−3.4494	0.005
Emigrating males	86–90	760	0.5046	0.651
Emigrating females	86–90	526	−2.4020	0.024

Movement Patterns within Species

Male and female *N. perstriatus* did not show different emigration or immigration patterns at Breezeway Pond (Table 2). No significant differences were noted between the emigration and immigration patterns of juveniles (Table 2). Adult males, however, entered and left the pond basin in different ways, as did adult females. Both sexes emigrated more to the southeast and northwest than they immigrated to the pond from these directions.

As with striped newts, male and female *G. carolinensis* also did not show different immigration or emigration patterns between the sexes (Table 2). In contrast to *N. perstriatus*, male and female frogs entered and exited the pond basin to and from similar directions (Table 2). Juvenile eastern narrow-mouthed toads had significantly different patterns of immigration than of emigration (Table 2). They moved primarily toward the "high pine" habitats rather than toward the xeric oak hammock and *Panicum* meadow. Immigrating juvenile *G. carolinensis* entered the pond through the xeric oak hammock from the direction of the nearest water bodies.

To examine the directional orientation of these two species, we conducted within-year comparisons of directional orientation. Of the 42 possible comparisons (two species, two directions, two or three sex/life stages, 5 years; data were insufficient for many juvenile comparisons), only 4 comparisons were significantly different in any one year (Table 3).

In 1987 male and female striped newts emigrated and immigrated differently from each another: females generally entered the pond basin from the sandhills to the

Table 2. Overall comparison of the directional orientation of *Notophthalmus perstriatus* and *Gastrophryne carolinensis* entering and leaving Breezeway Pond, 1985–1990.

Comparison	n	*Standardized test statistic*	p
Notophthalmus perstriatus			
Immigrating vs. emigrating males	396, 435	−9.3190	<0.01
Immigrating vs. emigrating females	564, 585	−6.0922	<0.01
Immigrating vs. emigrating juveniles	46, 63	−0.5900	0.21
Immigrating males vs. females	396, 564	−0.4525	0.23
Emigrating males vs. females	435, 585	−0.3533	0.26
Gastrophryne carolinensis			
Immigrating vs. emigrating males	826, 760	−1.6796	0.07
Immigrating vs. emigrating females	737, 526	0.1727	0.44
Immigrating vs. emigrating juveniles*	159, 1267	68.6737	<0.01
Immigrating males vs. females	826, 737	0.2950	0.49
Emigrating males vs. females	760, 526	0.4371	0.57

**Immigration only from fall 1988 to spring 1989; emigration only from fall 1985 to summer 1986.*

southwest and west-northwest (angles 233° to 304°) in greater proportion than males, whereas males immigrated at a greater proportion than females at eight scattered locations around the perimeter of the pond (angles of 4°, 63°, 79°, 102°, 142°, 197°, 313°, and 352°). When emigrating, males left the pond at 13 angles in greater proportion than females, whereas females exited the pond basin at only three angles in greater proportion than males; neither sex showed any directionality. In 1989 male and female striped newts also immigrated differently, but the sample size was small ($n = 64$) and spread out over 23 directions, making the determination of patterns impossible. However, only four females and one male entered the pond from the sandhills to the south-southwest and west (angles of 197° and 304°).

In 1988 male and female eastern narrow-mouthed toads emigrated differently. Males emigrated toward the west (angles 278° and 291°) in greater proportion than females, whereas females emigrated at seven angles proportionally more than males. Directionality was apparent (four of the seven angles grouped together) because females moved toward the high pine sandhills southeast and south-southwest of Breezeway Pond (at angles 121° to 197°).

Discussion

Our data show that striped newts and eastern narrow-mouthed toads inhabiting the uplands of the Katharine Ordway Preserve do not move toward and away from breeding ponds randomly. Furthermore, neither species appears to use movement corridors, although the spacing of the pitfall buckets may cause some blurring of recorded directional tendencies. Emigrating animals may adjust their movement direction after they move away from the pond, whereas immigrating animals might be funneled in different directions as they contact the fence. The placement of the drift fence likely did not influence migration because the patterns of emigration and immigration are rather broad, even accounting for displacement as animals traveled along the fence.

Movement patterns also changed somewhat from one year to the next. If corridors or scent trails were used in migration, the migratory pathways should be as precise as they are in certain other amphibians (Shoop 1965, 1968; Stenhouse 1985). For example, Shoop (1968) detected a travel corridor approximately 30 m wide for the salamander *Ambystoma maculatum* at a Massachusetts breeding pond. Although corridor use was not apparent by the species in our study, individual animals may follow the same pathways from one year to the next as they travel to the breeding pond. Stenhouse (1985) found that individual *A. maculatum* tended to enter and exit a pond at the same location from one year to the next, although for all animals taken together there was no specific directional tendency. Variation in movement patterns among individuals could account for the observed differences in orientation patterns among years in our study.

Table 3. Within-year comparison of the directional orientation of *Notophthalmus perstriatus* and *Gastrophryne carolinensis* entering and leaving Breezeway Pond, 1986–1990.[a]

Species[b]	*Comparison*	*Year*	n	*Standardized test statistic*	p
NP	Male vs. female Emigrating	1987	452	−2.3851	0.033
NP	Male vs. female Immigrating	1987	468	−4.2037	0.005
NP	Male vs. female Immigrating	1989	64	−2.4078	0.034
GC	Male vs. female Emigrating	1988	436	−3.2624	0.014

[a] *Only significant differences are presented; all other comparisons within years were not significant at the* $p > 0.05$ *level.*
[b] *NP,* Notophthalmus perstriatus; *GC,* Gastrophryne carolinensis.

Although striped newts and eastern narrow-mouthed toads did not use narrow migratory corridors in our study, they did not move randomly between terrestrial habitats and breeding ponds. Certain directions were favored over others. Unlike in other studies that relate corridors to physical features of the local environment (Stein 1938; Hurlbert 1969; Healy 1975; Hershey & Forester 1980), there are no obvious topographic cues surrounding Breezeway Pond to funnel migrating amphibians toward or away from the pond basin. Hence, it seems likely that the newts and frogs moved directly toward the pond from their nonbreeding habitats.

The declination at which individuals entered and left the pond basin is likely a reflection of the direction of favorable terrestrial habitats. In this regard, most striped newts favored high pine sandhill habitats, whereas eastern narrow-mouthed toads were likely to use a wider range of habitats. These results are consistent with previous observations of the ecology and biogeography of these species (Carr 1940; Dodd 1993, 1995*b*).

There are still many questions concerning the movements of these animals to ponds. For example, some amphibians, including the eastern narrow-mouthed toad (personal observation), do not breed every year. Hence, the number of animals at a pond represents only a fraction of the total population (Crump 1982). Perhaps the annual variation that we observed in orientation patterns, as well as the differences between the sexes, resulted solely from individual variation in propensity to move to a breeding site. The direction of immigration and emigration observed in any one year then would reflect that part of the population that bred in that particular year. General tendencies reflecting specific habitat preferences still would be apparent.

Conservation Implications

Many amphibians use terrestrial sites at substantial distances from the nearest breeding ponds (Glandt 1986; Sinsch 1988; Denton & Beebee 1993; reviewed by Dodd 1996; Means et al. 1996). On the Katharine Ordway Preserve, striped newts have been found at distances up to 709 m, and eastern narrow-mouthed toads to 914 m, from the nearest possible breeding pond (Dodd 1996). Unfortunately, we do not know what percentage of the total breeding population is found at various distances from the pond. Still, long-distance movements by amphibians to and from terrestrial habitats, sometimes occurring in specific directions from breeding sites, have important consequences for conserving wetlands and their dependent amphibian communities.

Most regulations affecting wetlands address the wetland itself or areas immediately adjacent to the wetland. Indeed, wetlands smaller than 0.2 ha (0.5 acre), such as Breezeway Pond, receive no protection in Florida (Hart & Newman 1995). One partial solution to wetlands conservation is the requirement for terrestrial buffer zones around wetlands to reduce direct impacts. The width of buffer zones varies with the management objective involved. Even when terrestrial buffer zones are considered as part of regulations, as they are in some states (e.g., Massachusetts), they may be inadequate to protect wetland-breeding amphibian communities.

To our knowledge, very few studies have addressed the need for terrestrial buffer zones to protect wetland-dependent herpetofaunal communities. Burke and Gibbons (1995) pointed out the need for terrestrial buffer zones to protect aquatic turtle communities; they recommended a zone extending 275 m around an elliptical Carolina Bay to conserve 100% of nesting and hibernation sites. Smaller zones would protect proportionally smaller portions of required habitat, but even the most stringent state statute would protect only 44% of the critical terrestrial habitat. Brown et al. (1990) suggested only a 15-m buffer zone for "semi-aquatic reptile" nesting; for sandhill ponds, they recommended a buffer width of 223 m to ensure "high quality" habitat for wildlife around sandhill wetlands. Based on our results and data on distances amphibians move to breeding ponds (Dodd 1996), these recommendations are inadequate to protect sandhill amphibian communities.

No studies have empirically addressed the need for or size of buffer zones specifically for amphibian communities. Dubois (1991) suggested that a buffer zone 100–500 m alongside watercourses would protect a large portion of the amphibians using the site. Although Dodd (1996) trapped 83% of the amphibians captured incidentally to another study within 600 m of the nearest potential breeding source, sampling problems precluded a recommendation for exact buffer zone width.

Our results suggest that a directional component that takes amphibian habitat use into consideration should be evaluated when buffer zones surrounding wetlands are planned, especially isolated temporary wetlands. Drawing a regulatory circle around a pond (as in Brown et al. 1990) will not be sufficient to ensure amphibian community survival if certain species are preferentially using habitats at specific directions from the pond.

For terrestrial buffer zones to be effective at conserving pond-breeding amphibian communities, they need both a distance and a directional component. Managers will need to consider the many types of amphibian migratory patterns (Glandt 1986) and not just movements directly between a terrestrial home range and a breeding pond. Because of annual variation in individual movement patterns, the determination of the directional component may be obscured if studies are carried out over short time spans. It is imperative, therefore, that data be gathered on terrestrial habitat requirements during the nonbreeding times of the year.

Conservation efforts for amphibians that concentrate

solely on wetlands likely will fail without consideration of the adjacent terrestrial habitat. Although much media attention has focused on the unexplained loss of amphibian species and communities in many parts of the world (Wyman 1990; Blaustein & Wake 1995; Stebbins & Cohen 1995), the potential decline of even so-called common species due to landscape alteration of terrestrial habitats needs much further investigation.

Acknowledgments

We thank B. Charest, K. Enge, J. Stuart, M. Blouin, K. Studenroth, and R. Burke, who ran the buckets at various times during the study. B. Charest prepared Fig. 1. R. Franz, D. Jackson, and D. B. Means read drafts of the manuscript and offered helpful suggestions. We especially thank R. Franz for encouragement, and the Katharine Ordway Preserve-Swisher Memorial Sanctuary for allowing this research to be carried out.

Literature Cited

Anderson, P. K. 1954. Studies in the ecology of the narrow-mouthed toad, *Microbyla carolinensis carolinensis*. Tulane Studies in Zoology 2:15–46.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, London.

Beebee, T. J. C. 1996. Ecology and conservation of amphibians. Chapman & Hall, London.

Bergin, T. M. 1991. A comparison of goodness-of-fit tests for analysis of nest orientation in Western Kingbirds (*Tyrannus Verticalis*). Condor **93**:164–171.

Blaustein, A. R., and D. B. Wake. 1995. The puzzle of declining amphibian populations. Scientific American **272(4)**:56–61.

Blaustein, L., J. Friedman, and T. Fahima. 1996. Larval Salamandra drive temporary pool community dynamics: evidence from an artificial pool experiment. Oikos **76**:392–402.

Brown, M. T., J. M. Schaefer, and K. H. Brandt. 1990. Buffer zones for water, wetlands, and wildlife in east central Florida. Publication 89-07. Center for Wetlands, University of Florida, Gainesville.

Burke, V. J., and J. W. Gibbons. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina Bay. Conservation Biology **9**:1365–1369.

Carr, A. F., Jr. 1940. A contribution to the herpetology of Florida. Publication 3, Biological Science Series. University of Florida, Gainesville.

Cash, W. B. 1994. Herpetofaunal diversity of a temporary wetland in the southeast Atlantic Coastal Plain. M.S. thesis. Georgia Southern University, Statesboro.

Crump, M. L. 1982. Amphibian reproductive ecology on the community level. Pages 21–36 in N. J. Scott, editor. Herpetological communities. Wildlife research report **13**. U.S. Fish and Wildlife Service, Washington, D.C.

Denton, J. S., and T. J. C. Beebee. 1993. Summer and winter refugia of natterjacks (*Bufo calamita*) and common toads (*Bufo bufo*) in Britain. Herpetological Journal **3**:90–94.

Dickinson, J. C., Jr. 1949. An ecological reconnaissance of the biota of some ponds and ditches in northern Florida. Quarterly Journal of the Florida Academy of Science **11**:1–28.

Dodd, C. K., Jr. 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodiversity and Conservation **1**:125–142.

Dodd, C. K., Jr. 1993. The cost of living in an unpredictable environment: the ecology of striped newts *Notophthalmus perstriatus* during a prolonged drought. Copeia **1993**:605–614.

Dodd, C. K., Jr. 1995*a*. Reptiles and amphibians in the endangered longleaf pine ecosystem. Pages 129-131 in E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources. National Biological Service, Washington, D.C.

Dodd, C. K., Jr. 1995*b*. The ecology of a sandhills population of the eastern narrow-mouthed toad, *Gastrophryne carolinensis*, during a drought. Bulletin of the Florida Museum of Natural History **38**: 11–41.

Dodd, C. K., Jr. 1996. Use of terrestrial habitats by amphibians in the sandhill uplands of north-central Florida. Alytes **14**:42–52.

Dodd, C. K., Jr. 1997. Imperiled amphibians: a historical perspective. Pages 159–196 in G.W. Benz and D.E. Collins, editors. Aquatic fauna in peril: the southeastern perspective. Special publication no. 1. Southeast Aquatic Research Institute, Lenz Design and Communications, Decatur, Georgia.

Dodd, C. K., Jr., and L. V. LaClaire. 1995. Biogeography and status of the striped newt (*Notophthalmus perstriatus*) in Georgia, USA. Herpetological Natural History **3**:37–46.

Dubois, A. 1991. Les amphibiens des régions tropicales: facteurs de déclin et d'extinction. Cahiers d'Outre-Mer **42**:393–398.

Duellman, W. E., and L. Trueb. 1986. Biology of amphibians. McGraw Hill, New York.

Florida Natural Areas Inventory. 1990. A guide to the natural communities of Florida. Florida Natural Areas Inventory and Florida Department of Natural Resources, Tallahassee.

Gibbons, J. W., and R. D. Semlitsch. 1982. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimelyana **7**:1–16.

Gibbs, J. P. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands **13**:25–31.

Glandt, D. 1986. Die saisonalen Wanderungen der mitteleuropäischen Amphibien. Bonner Zoologische Beiträge **37**:211–228.

Hart, R., and J. R. Newman. 1995. The importance of isolated wetlands to fish and wildlife in Florida. Nongame wildlife program project report. Florida Game and Fresh Water Fish Commission, Tallahassee.

Healy, W. R. 1975. Breeding and postlarval migrations of the red-spotted newt, *Notophthalmus viridescens*, in Massachusetts. Ecology **56**:673–680.

Hershey, J. L., and D. C. Forester. 1980. Sensory orientation in *Notophthalmus v. viridescens* (Amphibia: Salamandridae). Canadian Journal of Zoology **58**:266–276.

Holomuzki, J. R., J. P. Collins and P. E. Brunkow. 1994. Trophic control of fishless ponds by tiger salamander larvae. Oikos **71**:55–64.

Hurlbert, S. H. 1969. The breeding migrations and interhabitat wandering of the vermillion-spotted newt *Notophthalmus viridescens* (Rafinesque). Ecological Monographs **39**:465–488.

LaClaire, L. V. 1992. Ecology of temporary ponds in north-central Florida. M.S. thesis. University of Florida, Gainesville.

Means, D. B. 1996. Longleaf pine forest, going, going... Pages 210–229 in M. B. Davies, editor. Eastern old-growth forests. Island Press, Washington. D.C.

Means, D. B., and G. Grow. 1985. The endangered longleaf pine community. ENFO (Florida Conservation Foundation) **September**:1–12.

Means, D. B., J. G. Palis, and M. Baggett. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. Conservation Biology **10**:426–437.

Mielke, P. W., Jr. 1986. Non-metric statistical analyses: some metric alternatives. Journal of Statistical Planning and Inference **13**:377–387.

Mielke, P. W., Jr. 1988. Goodness-of-fit and g-sample omnibus tests based on coverages. Pages 9–19 in J.N. Srivastava, editor. Probability and statistics: essays in honor of Franklin A. Graybill. Elsevier Science Publishers B.V., North Holland, New York.

Millsap, B. A., J. A. Gore, D. E. Runde, and S. I. Cerulean. 1990. Setting

priorities for the conservation of fish and wildlife species in Florida. Wildlife Monographs **111**.

Moler, P. E., and R. Franz. 1987. Wildlife values of small isolated wetlands in the southeastern coastal plain. Pages 234-241 in R. R. Odom, K. A. Riddleberger, and J. C. Ozier, editors. Proceedings of the third southeastern nongame and endangered wildlife symposium. Georgia Department of Natural Resources, Atlanta.

Newman, R. A. 1992. Adaptive plasticity in amphibian metamorphosis. Bioscience **42**:671-678.

Noss, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. Natural Areas Journal **9**:211-213.

O'Neill, E. D. 1995. Amphibian and reptile communities of temporary ponds in a managed pine flatwoods. M.S. thesis. University of Florida, Gainesville.

Pechmann, J. H. K., D. E. Scott, J. W. Gibbons, and R. D.Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management **1**:3-11.

Pough, F. H. 1983. Amphibians and reptiles as low-energy systems. Pages 141-188 in W. P. Aspey and S. I. Lustick, editors. Behavioral energetics: the cost of survival in vertebrates. Ohio State University Press, Columbus.

Rao, J. S. 1976. Some tests based on arc-lengths for the circle. Sankhya, Series B **38**:329-338.

Rowe, C. L., and W. A. Dunson. 1995. Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. Oecologia **102**:397-403.

Seale, D. B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology **61**:1531-1550.

Shoop, C. R. 1965. Orientation of *Ambystoma maculatum*: movements to and from breeding ponds. Science **149**:558-559.

Shoop, C. R. 1968. Migratory orientation of *Ambystoma maculatum*: movements near breeding ponds and displacements of migrating individuals. Biological Bulletin **135**:230-238.

Sinsch, U. 1988. Seasonal changes in the migratory behaviour of the toad *Bufo bufo*: direction and magnitude of movements. Oecologia **76**:390-398.

Skelly, D. K. 1996. Pond drying, predators, and the distribution of *Pseudacris* tadpoles. Copeia **1996**:599-605.

Slauson, W. L., B. S. Cade, and J. D. Richards. 1991. User manual for BLOSSOM statistical software. Midcontinent Ecological Science Center, Biological Resources Division, U.S. Geological Survey, Fort Collins, Colorado.

Stebbins, R. C., and N. W. Cohen. 1995. A natural history of amphibians. Princeton University Press, Princeton, New Jersey.

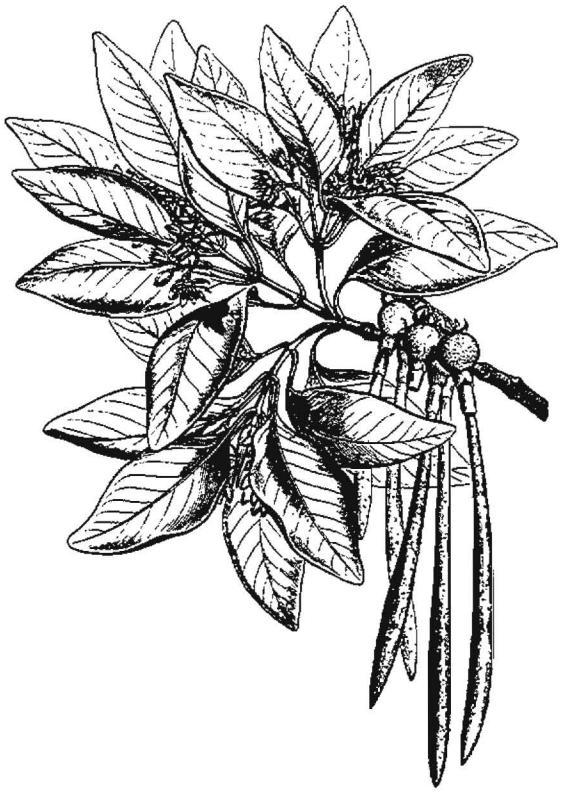
Stein, K. F. 1938. Migration of *Triturus viridescens*. Copeia **1938**:86-88.

Stenhouse, S. L. 1985. Migration, orientation and homing in *Ambystoma maculatum*. Copeia **1985**:631-637.

Taylor, B. E., R. A. Estes, J. H. K. Pechmann, and R. D. Semlitsch. 1988. Trophic relations in a temporary pond: larval salamanders and their microinvertebrate prey. Canadian Journal of Zoology **66**:2191-2198.

Verrell, P. A. 1987. The directionality of migrations of amphibians to and from a pond in southern England, with particular reference to the smooth newt, *Triturus vulgaris*. Amphibia-Reptilia **8**:93-100.

Ware, S., C. Frost, and P. D. Doerr. 1993. Southern mixed hardwood forest: the former longleaf pine forest. Pages 447-493 in W. H. Martin, S. G. Boyce, and A. C. Echternacht, editors. Biodiversity of the southeastern United States. Lowland terrestrial communities. John Wiley & Sons, New York.

Wright, A. H. 1932. Life-histories of the frogs of the Okefinokee Swamp, Georgia. Macmillan, New York.

Wyman, R. L. 1990. What's happening to the amphibians? Conservation Biology **4**:350-352.