
AMPHIBIAN IMMIGRATION AND EMIGRATION AT A TEMPORARY POND IN THE FLORIDA SANDHILLS, USA: IMPLICATIONS FOR CONSERVATION

C. KENNETH DODD, JR.^{1,3} AND COREY D. ANDERSON²

¹Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611, USA

²Department of Biology, Valdosta State University, Valdosta, Georgia 31698, USA

³Corresponding author, e-mail: Terrapene600@gmail.com

Abstract.—Temporary ponds are important breeding sites for many amphibians and may serve as refugia for species crossing unfavorable habitats while dispersing. In this study, we examined the immigration and emigration patterns of six amphibian species from October 1985 through September 1990 at an isolated temporary pond in a sandhills community in north central Florida, USA. Our results indicated that the circular distribution of amphibian captures around the pond was often non-uniform, especially when capture distributions were pooled over multiple years or multiple species. Species captured more frequently tended to be found at a wider range of directions moving into and out of the pond. Many species exhibited complex multimodal distributions, with potential shifts in modal directions from year to year. Interspecies variation in the frequency of dispersion at different angles into and out of the pond basin was common and likely reflected species-specific movement capabilities. Nonrandom dispersal at our study site suggests that species may be moving to and from specific habitat types, such as nearby wetlands or terrestrial habitats used for foraging or refuge. The extensive interspecific variation in amphibian movement patterns seen at Breezeway Pond and observed in other studies, coupled with the potential for widespread and long-range dispersal, suggest that large areas of habitat should be protected to ensure the survival of amphibians breeding in temporary ponds affected by stochastic and long-term effects of climate change and isolation.

Key Words.—amphibians; immigration; emigration; movement patterns; temporary pond; sandhill community; circular statistics; landscape conservation

INTRODUCTION

The Southeastern Coastal Plain is one of the most exceptional areas of biodiversity in North America (Blaustein 2008; Jenkins et al. 2015; Noss et al. 2015). Throughout this region, depression marshes form temporary breeding sites for diverse amphibian communities that include many endemics relying solely on these wetlands for reproduction. As such, the Southeastern Coastal Plain is increasingly recognized as a biodiversity hotspot for amphibians (Semlitsch 2000; Battaglin et al. 2005; Graham et al. 2010; Barrett et al. 2014; Walls 2014). Depression marshes are typically shallow (< 1.5 m) and vegetated with varying zones of open water, aquatic vegetation, and surrounding trees or shrubs (LaClaire 1995). Canopies are usually open to direct sunlight, although some ponds with Black Gum (*Nyssa sylvatica*) and Pond Cypress (*Taxodium ascendens*) may have moderate to dense canopy cover. Ponds are often demarcated from the surrounding forest by *Panicum* grasslands of varying widths, thus forming a mosaic of open-canopied wetlands in an otherwise nearly contiguous nutrient-poor savanna-like pine forest. Historically, the upland dominant tree cover consisted of 400–500 y old Longleaf Pines (*Pinus palustris*) with a rich fire-maintained vegetative understory; in depressional areas, pine flatwoods with an understory of

Saw Palmetto (*Sabal palmetto*) were common. Most of the forest now consists of second or third growth mixed pine-hardwoods in various stages of succession. With the alteration of forest structure, most of the historic depression marshes have been lost, and those remaining are threatened unless on protected lands.

Within the Southeastern Coastal Plain, approximately 21 species of salamanders and 26 species of anurans use depression marshes for breeding, foraging, or as areas occupied while in transit between other wetlands and uplands (Dorcas and Gibbons 2008; Mitchell and Gibbons 2010). Amphibians exhibit a variety of movements, from localized wanderings within a spatially-defined home range, to long-distance dispersal as juveniles and adults (Glandt 1986; Sinsch 1997; Russell et al. 2005; Semlitsch 2008). After reproduction, many temperate zone adult amphibians disperse to the surrounding environment within 100 to 1000 m from the breeding site, thus allowing for reasonably distanced remigration during subsequent breeding seasons (Semlitsch and Bodie 2003; Crawford and Semlitsch 2007; Rittenhouse and Semlitsch 2007). Juveniles often disperse to new habitats far from the natal site or they may establish foraging areas within a nearby area that offers critical resources for growth and protection from predators and adverse environmental conditions (e.g., Vasconcelos and Calhoun 2004; Funk et al. 2005;

Gamble et al. 2007). In this way, amphibian movements transfer nutrients across a landscape, and thus become important to ecosystem structure and function (Hocking and Babbitt 2013; Capps et al. 2015).

Male amphibians typically select foraging and overwintering areas closer to ponds than females (e.g., Regosin et al. 2003; Johnson et al. 2007), presumably allowing them quick access to incoming females (for salamanders) and calling sites (for anurans) when breeding seasons commence. Nonetheless, many individuals travel great distances between breeding sites and foraging areas (Sinsch 1990; Dodd 1996; Pittman et al. 2014; Pitt et al. 2017), particularly in areas where potential breeding sites are widely scattered and ephemeral. Breeding migrations to and from ponds may take several days depending on weather and terrain, but many species move rapidly directly to or from breeding sites. As noted by Coster et al. (2014), the width of the corridor of amphibian movements varies by species, and tends to increase as the distance from a pond increases. Indeed, initial movement directions may change as an amphibian moves beyond the immediate area of the natal wetland (Pittman et al. 2014).

Amphibians may use features of the local topography, such as ravines, creek beds, or surrounding slopes to facilitate dispersal and remigration (e.g., Gibbs 1998; Anderson et al. 2015), and such features may be particularly important in juvenile dispersal. However, many breeding sites are located in regions with little topographic complexity, and the reasons animals choose a particular pathway may not be immediately evident. In north-central Florida, the landscape is generally flat or undulating, particularly in areas where Pleistocene sand dunes form the dominant topographic feature. Open temporary ponds and lakes are interspersed within sandhills with indistinct macro physical structure. In such circumstances, amphibians might be expected to enter wetlands randomly, depending upon the direction that they dispersed from a breeding site, assuming they return to their natal pond and are not responding to a particular vegetation structure that may be discontinuous around the wetland.

Understanding amphibian dispersal patterns to and from breeding ponds is critical to the management of species at both population and landscape scales. Given the extensive loss of temporary ponds on the Southeastern Coastal Plain and their vulnerability to further degradation and perturbation (Barrett et al. 2014), natural resource managers need information from a variety of habitats involving many species to incorporate adaptive management strategies (e.g., Schreiber et al. 2004; Bower et al. 2014; O'Donnell et al. 2017) into practice. In the present study, we examined the circular distribution of captures of six amphibian species around a temporary pond in the Florida sandhills over a five-

year period. Combined with previous analyses of other co-occurring species at this pond (Dodd 1993, 1994; Dodd and Cade 1998), we assess the implications of directional movements patterns in determining the extent to which lands need to be protected to ensure the viability of an entire amphibian community.

MATERIALS AND METHODS

Study site.—We collected field data from October 1985 to September 1990 at Breezeway Pond, a 0.16 ha temporary depression marsh located in a shallow 1.3 ha basin on the Ordway-Swisher Biological Station, Putnam County, Florida, USA (29°41'N, 82°00'W). The pond is located in xeric sandhill uplands near the ecotone between a Longleaf Pine (*Pinus palustris*), Turkey Oak (*Quercus laevis*), Wiregrass (*Aristida beyrichiana*) community and a xeric oak (Sand Live Oak, *Q. geminata* and Laurel Oak, *Q. hemisphaerica*) hammock community (Fig. 1). To the immediate south and west (at angles 72° to 298° from the center of the pond basin), Longleaf Pine sandhills predominated; to the north (at angles 299° to 360°, and 0° to 27°), xeric oak hammocks predominated; to the northeast, a small grassland dominated by Maidencane (*Panicum hemitomon*) was found at angles 28° to 71° from the center of the pond basin. The distance from the drift fence to the nearest forested plant association was generally 20 m but extended to about 50 m behind the *Panicum* meadow. Additional physical and vegetative details concerning the site are in Dodd (1992, 1993) and LaClaire (1992). The pond held water for two years prior to the study, but a severe drought resulted in an intermittent hydroperiod from October 1985 to December 1988, with no standing water after 23 December 1988 (see Fig. 1 in Dodd 1992).

The nearest water bodies to Breezeway Pond were Smith Lake (350 m to the north of Breezeway Pond) and three small 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). All temporary ponds within 1 km of Breezeway Pond dried completely by late 1989 and remained dry throughout the remainder of the sampling period. This was approximately 1 y after the last standing water was recorded in Breezeway Pond (Dodd 1992). Drought reduced Smith Lake from 7.55 ha surface area in 1985 to approximately 0.75 ha in 1989. The lake dried completely in May 1990.

Sampling procedure.—The pond basin was encircled by a 230 m drift fence made of galvanized metal flashing (36 cm above ground, 10–15 cm below the surface). We sunk 23 pairs of pitfall traps (19 L black

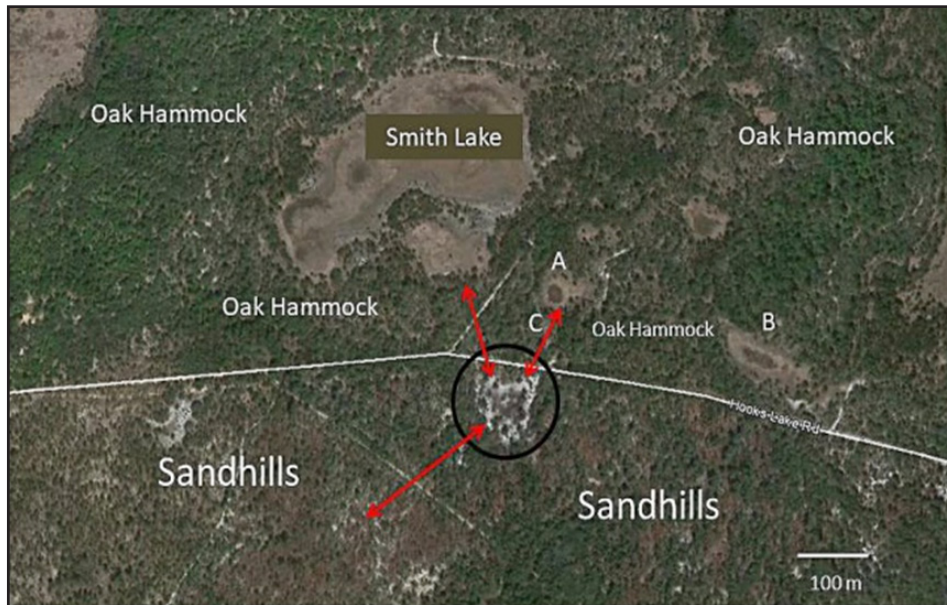


FIGURE 1. Breezeway Pond and vicinity, Ordway-Swisher Biological Station, Putnam County, Florida, USA. (A) Pine Lodge Pond; (B) Breezeway Sandills Pond; (C) *Panicum* meadow corridor toward Pine Lodge pond and other northeastern wetlands. The red arrows indicate the main directions of immigration and emigration of six amphibian species to Breezeway Pond (circle). Due north is at the top of the page.

plastic buckets, 36 cm deep) into the ground at 10 m intervals, with one trap on each side of the pitfall at each position. The pitfalls were partially shaded to minimize the effects of the direct sun. We placed coverboards flat across the openings when pitfalls were not checked to prevent desiccation; some animals were captured even though openings were covered because the seals were not complete. We checked pitfalls 5 d/week between 0700 and 0900, depending on season (corresponding to approximately 1 h after sunrise), from 1 October 1985 through 30 September 1990 (1,825 d; 83,950 bucket-nights). We obtained compass directions by standing in the center of the pond basin and measuring the angle to each pair of pitfall traps, with 0° indicating due north.

We examined captured amphibians in the field where we recorded a variety of measurements (Dodd 1992, 1993, 1994). Sixteen species of amphibians have been recorded at Breezeway Pond. Results for the four most abundant species (*Anaxyrus quercicus*, Oak Toad; *A. terrestris*, Southern Toad; *Gastrophyrne carolinensis*, Eastern Narrow-mouthed Frog; and *Notophthalmus perstriatus*, Striped Newt) are reported elsewhere (Dodd 1994; Dodd and Cade 1998). Of the remaining 12 species, sufficient sample sizes to assess immigration (coded as outside the drift fence) and emigration (coded as inside the drift fence) patterns were available for six species (Table 1): *Acris gryllus* (Southern Cricket Frog, 5 y of data); *Eurycea quadridigitata* (Southeastern Dwarf Salamander, 2 y); *Hyla femoralis* (Pine Woods Treefrog, 3 y); *Pseudacris ocularis* (Little Grass Frog, 4 y); *Lithobates sphenoccephalus* (Southern Leopard Frog,

1 y); and *Scaphiopus holbrookii* (Eastern Spadefoot, 5 y).

We collected additional data on sex and age for *S. holbrookii*. We measured spadefoots for snout-urostyle length (SUL, measured from the tip of the snout to the posterior end of the urostyle). In this population, sexual maturity is attained at 43–45 mm SUL. Males have dark keratinized patches on the fingers, a dusky or black throat, and readily produce a warning vibration and associated call; females lack these characteristics and may be distended with eggs (Pearson 1955). Sexual size dimorphism is not apparent at maturity or in the adult population.

Data analysis.—We used tests of circular uniformity suitable for count data combined into discrete groups to examine variation in the frequency of captured amphibians in the 23 pairs of pitfall traps. The response variable was the number of captures in each trap; the angle to each pitfall (or the angular boundaries for each arc around a trap) was used to classify each group. We determined the boundaries for each arc by calculating the midpoint of the angle between each trap. We analyzed capture counts in pitfalls outside of the drift fence separately from counts in pitfalls inside the drift fence.

To test whether counts in traps around the pond were non-uniform, we wrote scripts in R 3.4.0 (R Core Team 2015) to conduct the Choulakian et al. (1994) version of Watson's U^2 statistic, as described by Pewsey et al. (2013). Because the critical values for Watson's U^2

Dodd and Anderson—Amphibian immigration and emigration at a Florida pond.

TABLE 1. Summary statistics and *P*-values for three tests of circular uniformity (i.e., Watson U^2 , Kuiper, and Watson) for six amphibian species (AG = Southern Cricket Frog, *Acris gryllus*, EQ = Southeastern Dwarf Salamander, *Eurycea quadridigitata*, HF = Pine Woods Treefrog, *Hyla femoralis*, PO = Little Grass Frog, *Pseudacris ocularis*, LS = Southern Leopard Frog, *Lithobates sphenoccephalus*, and SH = Eastern Spadefoot, *Scaphiopus holbrookii*) captured over a 5-y period (1986 to 1990) at Breezeway Pond in Florida, USA. ALL: all species and/or all years combined. For *S. holbrookii* in 1988, the data were also partitioned by sex/age subclass (M: male; F: female; J: juvenile).

Species	Year(s)	SDF	Count	Circular range	$P(U^2)$	$P(\text{Kuiper})$	$P(\text{Watson})$
ALL	ALL	outside	1595	336	0.0001	0.0001	0.0001
ALL	ALL	inside	2975	336	0.0001	0.0001	0.0001
AG	86	outside	5	201	0.4863	0.4951	0.4609
AG	86	inside	60	315	0.0064	0.0040	0.0086
AG	87	outside	2	58	0.3190	0.3270	0.3270
AG	87	inside	57	301	0.0011	0.0002	0.0008
AG	88	outside	1	0	0.8978	1	1
AG	88	inside	10	242	0.3421	0.2617	0.3168
AG	89	outside	3	55	0.0747	0.0838	0.0747
AG	89	inside	30	299	0.1467	0.0624	0.1305
AG	90	outside	13	236	0.0618	0.0345	0.0567
AG	90	inside	34	296	0.3805	0.2317	0.3262
AG	ALL	outside	24	236	0.0049	0.0008	0.0041
AG	ALL	inside	191	315	0.0004	0.0002	0.0002
EQ	88	outside	5	241	0.9158	0.9255	0.9255
EQ	88	inside	25	315	0.0932	0.0935	0.0796
EQ	89	outside	13	245	0.0308	0.0144	0.0247
EQ	89	inside	67	315	0.0020	0.0023	0.0027
EQ	ALL	outside	18	296	0.1393	0.1174	0.1147
EQ	ALL	inside	92	315	0.0090	0.0051	0.0058
HF	87	outside	20	170	0.0008	0.0005	0.0013
HF	87	inside	19	204	0.0001	0.0004	0.0003
HF	88	outside	2	91	0.4969	0.5200	0.5200
HF	88	inside	5	112	0.0407	0.0787	0.0513
HF	89	outside	12	238	0.2313	0.3096	0.2152
HF	89	inside	84	320	0.0001	0.0001	0.0002
HF	ALL	outside	34	284	0.0247	0.0079	0.0362
HF	ALL	inside	108	328	0.0001	0.0001	0.0001
PO	86	outside	4	147	0.0934	0.0701	0.0897
PO	86	inside	16	258	0.0022	0.0044	0.0042
PO	87	outside	3	146	0.3495	0.3850	0.3344
PO	87	inside	45	315	0.1745	0.2493	0.1720
PO	88	outside	3	226	0.9916	0.9919	0.9919
PO	88	inside	35	288	0.0007	0.0021	0.0010
PO	89	outside	7	55	0.0001	0.0002	0.0002
PO	89	inside	36	273	0.0016	0.0024	0.0008
PO	ALL	outside	17	284	0.0127	0.0009	0.0099
PO	ALL	inside	132	336	0.0007	0.0001	0.0007
LS	89	outside	21	258	0.0009	0.0004	0.0012
LS	89	inside	41	299	0.0001	0.0001	0.0001

TABLE 1 (CONTINUED). Summary statistics and P -values for three tests of circular uniformity (i.e., Watson U^2 , Kuiper, and Watson) for six amphibian species (AG = Southern Cricket Frog, *Acris gryllus*, EQ = Southeastern Dwarf Salamander, *Eurycea quadridigitata*, HF = Pine Woods Treefrog, *Hyla femoralis*, PO = Little Grass Frog, *Pseudacris ocularis*, LS = Southern Leopard Frog, *Lithobates sphenoccephalus*, and SH = Eastern Spadefoot, *Scaphiopus holbrookii*) captured over a 5-y period (1986 to 1990) at Breezeway Pond in Florida, USA. ALL: all species and/or all years combined. For *S. holbrookii* in 1988, the data were also partitioned by sex/age subclass (M: male; F: female; J: juvenile).

Species	Year(s)	SDF	Count	Circular range	$P(U^2)$	$P(\text{Kuiper})$	$P(\text{Watson})$
SH	86	outside	37	262	0.0005	0.0014	0.0019
SH	86	inside	41	262	0.0001	0.0001	0.0001
SH	87	outside	98	330	0.2794	0.2789	0.2291
SH	87	inside	159	336	0.0001	0.0001	0.0001
SH	88	outside	1202	336	0.0001	0.0001	0.0001
SH	88	inside	2152	336	0.0001	0.0001	0.0002
SH	89	outside	127	336	0.0271	0.0400	0.0571
SH	89	inside	32	246	0.0012	0.0004	0.0017
SH	90	outside	17	284	0.5670	0.5498	0.5646
SH	90	inside	27	309	0.8396	0.6266	0.8645
SH	ALL	outside	1481	336	0.0001	0.0001	0.0001
SH	ALL	inside	2411	336	0.0001	0.0001	0.0001
SH	M88	outside	346	336	0.0017	0.0050	0.0080
SH	M88	inside	666	336	0.0048	0.0038	0.0059
SH	F88	outside	223	336	0.0426	0.0604	0.1159
SH	F88	inside	367	336	0.0003	0.0001	0.0002
SH	J88	outside	21	289	0.0522	0.0613	0.0673
SH	J88	inside	21	265	0.0020	0.0037	0.0035

statistic were developed under the assumption that the circular data being analyzed are continuously distributed (rather than grouped), to determine the significance of Watson's U^2 statistic, we used a Monte Carlo testing procedure (with 9,999 iterations). For each iteration, the 23 traps were randomly sampled n times, with n equal to the total number of captures (over all 23 traps) in the observed data set. To simulate the U^2 statistic under the null hypothesis of a discrete circular uniform distribution, we based the probability of sampling from a particular trap on the length of the arc surrounding each bucket. We calculated the P -value for each test as the proportion of times the simulated test statistic was greater than or equal to the observed test statistic.

Recent methodological assessments (e.g., Humphreys and Ruxton 2017) have found that grouping has little effect on Type I error rates and power of commonly applied tests of circular uniformity. Although some commonly encountered grouping schemes, such as months and seasons, do not have perfectly equal intervals, the effect of grouping with unequal intervals on tests of circular uniformity has not been formally evaluated to date. For this reason, to examine the agreement of our testing procedure with other potential statistics, we compared results for Watson's U^2 statistic to results for two other tests of circular uniformity (Watson, Kuiper)

from the package circular (Agostinelli, C., and U. Lund. 2017. circular: Circular Statistics. Available from <https://cran.r-project.org> [Accessed 14 February 2017]) in R. Because the critical values for the Watson test and Kuiper tests were also developed under the assumption of a continuous circular distribution, we used Monte Carlo tests (analogous to those described above for Watson's U^2 statistic) to generate null distributions and calculate P -values. We evaluated the effect of sample size on the nominal Type I error rate (of 5%) computationally for all three tests of circular uniformity (i.e., Watson U^2 , Watson, and Kuiper) by sampling ($n = 5, 10, 20, 100, 500, \text{ and } 1,000$) from a uniform distribution, conducting a Monte Carlo test at a significance level of 5% (= 19 permutations for a one-tailed test), and then estimating the proportion of times (out of 10,000 tests) that a false positive occurred.

Because tests of circular uniformity (described above) are sensitive to variation in the counts of captured amphibians in the pitfall traps around the pond, it was possible that the null hypothesis of circular uniformity could be rejected even in cases where amphibians were captured in all 23 traps (as long as the capture frequencies in the traps were sufficiently uneven). Hence, to provide additional information about the angular extent of dispersion, we also used

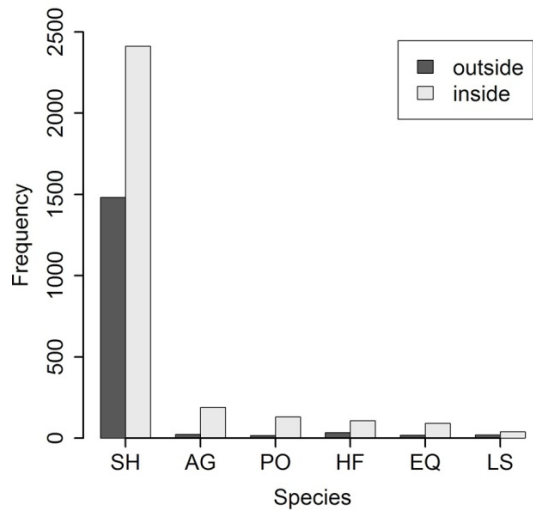


FIGURE 2. Barplots representing cumulative capture frequencies (from 1986 to 1990) on the outside (dark gray) and inside (light gray) of the drift fence surrounding Breezeway Pond, Putnam County, Florida, USA. Species are AG (Southern Cricket Frog, *Acris gryllus*), EQ (Southeastern Dwarf Salamander, *Eurycea quadridigitata*), HF (Pine Woods Treefrog, *Hyla femoralis*), PO (Little Grass Frog, *Pseudacris ocularis*), LS (Southern Leopard Frog, *Lithobates sphenoccephalus*), and SH (Eastern Spadefoot, *Scaphiopus holbrookii*).

the circular package in R to calculate the circular range (i.e., the shortest arc on the circle containing all pitfall traps where captures occurred). For the Breezeway Pond study, the maximum potential circular range was 336° (representing the shortest possible arc on the circle when there were captures in all 23 buckets). For heuristic purposes, we also evaluated the relationship between circular range and sample count by calculating Spearman’s rank correlation coefficient (r_s). We did not calculate the significance of the correlation coefficient due to potential non-independence of samples from the same species over successive years. We calculated the circular range and tested whether counts were non-uniform around the unit circle for the pooled sample (over all species and all years), for each species (pooled across all years), and for species/year subsets.

RESULTS

We captured 4,570 individuals of six species between 1986 and 1990, with all species exhibiting higher capture counts in pitfalls on the inside of the drift fence (Table 1; Fig. 2). The most frequently captured species was *S. holbrookii*, with 3,354 of 3,892 captures occurring in 1988; the least abundant species was *L. sphenoccephalus* with all 62 captures in 1989. For the total sample (over all species and all years), the circular range was the maximum value of 336°, indicating that amphibians were captured in all pitfalls around the pond, on both sides of the drift fence. For species/year subsets, the circular range varied from 0° (*A. gryllus*: 1988 inside,

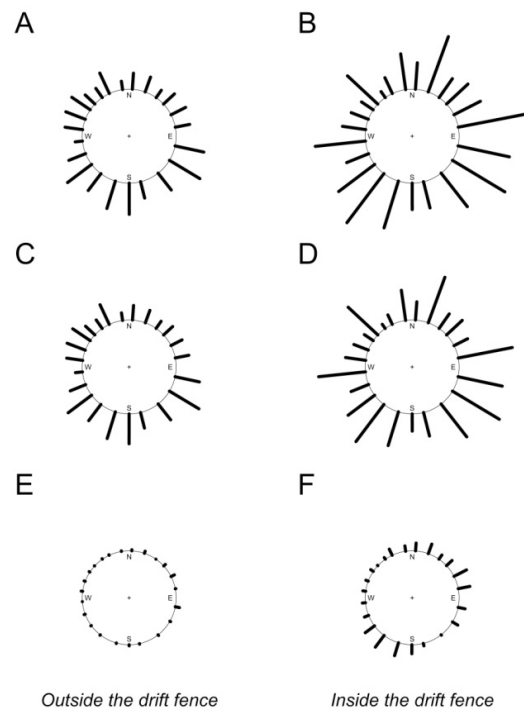


FIGURE 3. Circular barplots (A-F) representing the relative frequency of individuals captured in the 23 pairs of pitfall traps (one outside and one inside the drift fence) around Breezeway Pond, Putnam County, Florida, USA. (A, B) All six species combined over all sample years. (C, D) Eastern Spadefoot (*Scaphiopus holbrookii*) over all sample years. (E, F) All species combined over all sample years, excluding *S. holbrookii*. Note that the circular distribution for all six species combined over all sample years (A, B) mirrored the circular distribution of the most frequently captured species: *S. holbrookii* (C, D).

$n = 1$) to the maximum of 336° (*S. holbrookii*: 1987 inside, $n = 159$; 1988 outside, $n = 2,152$; 1988 inside, $n = 1,202$; and 1989 outside, $n = 127$). Species that were captured more frequently tended to be found over a wider range of angles around the pond basin ($r_s = 0.92$). When we pooled data for each species across all years, there also was a positive correspondence between counts and circular range ($r_s = 0.85$), with the circular range varying from 236° (*A. gryllus*: ALL outside, $n = 24$) to the maximum of 336° (*P. ocularis*: ALL inside, $n = 132$; *S. holbrookii*: ALL outside, $n = 1,481$; ALL inside, $n = 2,411$).

The null hypothesis of uniformity of counts in pitfalls around the pond was rejected in 107 of 174 tests (= 62%; Table 1). There were only four instances (*A. gryllus* 1990 outside, *H. femoralis* 1988 inside, *S. holbrookii* 1989 outside, and *S. holbrookii* 1988 outside females) where the test outcome was not the same for all three statistics (at $\alpha = 0.05$). For the total sample (over all species and years), there was strong evidence against the null hypothesis of circular uniformity for captures on the outside ($n = 1,595$; Fig. 3A) and inside ($n = 2,975$; Fig. 3B) of the drift fence (Table 1), with the overall

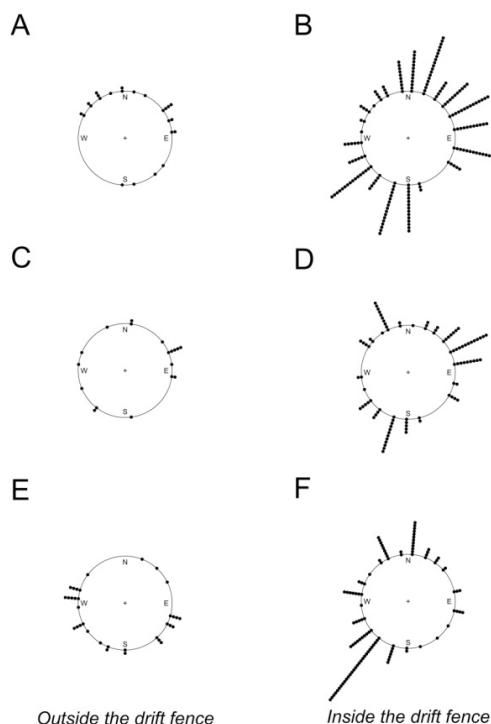


FIGURE 4. Circular barplots (A-F) representing the relative frequency of individuals captured in the 23 pairs of pitfall traps (one outside and one inside the drift fence) around Breezeway Pond, Putnam County, Florida, USA. (A, B) Southern Cricket frog (*Acris gryllus*). (C, D) Southeastern Dwarf Salamander (*Eurycea quadridigitata*). (E, F) Pine Woods Treefrog (*Hyla femoralis*).

pattern of dispersion being heavily biased by the most frequently encountered species, *S. holbrookii* (Figs. 3, 6). When we pooled data across years for each species (Figs. 3C-D,4,5), circular uniformity was rejected for all six species inside of the drift fence, and for five of six species outside of the drift fence (Table 1). For tests based on species/year subsets (Table 1), circular uniformity was rejected in 7 of 20 tests for captures on the outside of the drift fence (Fig. 7A) and in 14 of 20 tests for captures on the inside of the drift fence (Fig. 7B). Assessment of Type I error rates indicated that test results were not sensitive to small sample size (Table 2).

Species accounts.—Although *A. gryllus* was captured during each year of the study, very few individuals entered the pond over the 5-y period ($n = 24$; Fig. 4A), except in 1990 when there was a small surge of immigration from the general direction of the northern wetlands. For *A. gryllus* entering the pond, the null hypothesis of circular uniformity could not be rejected in any one of the 5 y they were encountered, but when we pooled *A. gryllus* captures across all years, the null hypothesis of circular uniformity was rejected (Table 1).

Large numbers of *A. gryllus* left the pond basin in all years ($n = 191$; Fig. 4B), with a peak in 1990 during the

TABLE 2. The effect of sample size (top row) on the nominal Type I error rate (of 5%) for a Monte Carlo version of the Watson U^2 , Watson, and Kuiper tests of circular uniformity. The Type I error rate for different sample sizes ($n = 5, 10, 20, 100, 500,$ and 1000) was evaluated by sampling from a uniform distribution, conducting a test at a significance level of 5% (= 19 permutations for a one-tailed test), and then estimating the proportion of times (out of 10,000 tests) that a false positive occurred. Results suggest that the high number of significant tests observed in our study cannot be explained by Type I error alone.

Tests	5	10	20	100	500	1000
Watson U^2	0.048	0.049	0.049	0.051	0.049	0.048
Kuiper	0.050	0.050	0.050	0.051	0.051	0.053
Watson	0.050	0.051	0.048	0.052	0.049	0.051

worst of the drought. Emigration was generally to the northeast through the *Panicum*-grass area, and especially toward the sandhills to the east and southwest. Circular uniformity was rejected for *A. gryllus* captures on the inside of the drift fence in 1986 and 1987, but not in subsequent years (Table 1). When we pooled *A. gryllus* captures inside the drift fence across all years, the null hypothesis of circular uniformity was rejected (Table 1).

Movement data were available for *E. quadridigitata* from 1988 to 1989. Relatively few *E. quadridigitata* were captured outside the drift fence ($n = 18$; Fig. 4C). In 1988, there were five captures outside the drift fence, each in a different bucket on the southwest and northeast sides of the pond. In 1989, eight of the 13 captures outside the drift fence were clustered into three buckets on the east side of the pond. Circular uniformity was rejected for the 1989 sample, but not for the multiyear sample (Table 1), even though the modal direction was to the east/northeast.

In contrast, substantial numbers of adult *E. quadridigitata* left the basin ($n = 92$; Fig. 4D) as the drought intensified during the summer of 1988 and throughout 1989. By 1990, it appears that *E. quadridigitata* had vacated the dry basin. In both 1988 and 1989, there was substantial emigration toward the southwest sandhills. In 1988, counts were notably high in one bucket on the north side of the pond (towards the wetlands), with the mode shifting towards the northeast in 1989, resulting in a multiyear pattern with three peaks (Fig. 4D). The null hypothesis of circular uniformity was rejected for *E. quadridigitata* leaving the pond in 1989 and for the multiyear sample, but not for the 1988 sample (Table 1).

Hyla femoralis successfully bred in Breezeway Pond only once during the 5-y study (late summer 1988). Standing water did not occur during the breeding season of this species except in 1987 (no juveniles produced) and the latter half of 1988. Movement data were available for 1987 to 1989 (Table 1). Relatively few *H. femoralis* were captured entering the pond basin ($n =$

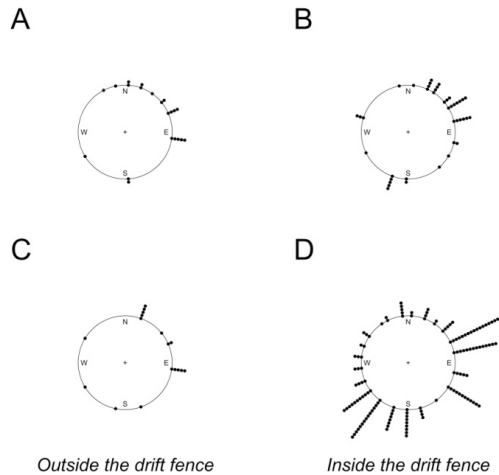


FIGURE 5. Circular barplots (A-D) representing the relative frequency of individuals captured in the 23 pairs of pitfall traps (one outside and one inside the drift fence) around Breezeway Pond, Putnam County, Florida, USA. (A, B) Southern Leopard Frog (*Lithobates sphenocephalus*). (C, D) Little Grass Frog (*Pseudacris ocularis*).

34; Fig. 4E), with most captures outside the drift fence located on the south and west sides of the pond basin in 1987 ($n = 20$) and 1988 ($n = 2$), with a shift towards the north and east in 1989 ($n = 12$). We rejected the null hypothesis of circular uniformity for immigrating *H. femoralis* in 1987 and for the multi-year sample, but not for the 1988 and 1989 samples separately.

We found relatively few *H. femoralis* on the inside of the drift fence (Fig. 4F) in 1987 ($n = 19$) and 1988 ($n = 5$), with captures oriented towards the south and west. Substantially greater emigration occurred in October 1988 ($n = 84$) and only involved juveniles (17–20 mm SUL), with most captures occurring on the north and southwest sides of the pond, presumably in the direction of the surrounding oak hammock forest. Adults could easily climb over the drift fence and may be underrepresented in the dataset, although all other captures outside 1988 were adults. There was strong evidence against the null hypothesis of circular uniformity for *H. femoralis* leaving the pond in the multi-year sample, as well as in the years 1987 and 1989 (Table 1). For the 1988 sample, only Watson's U^2 statistic was significant.

The only year data were available for *L. sphenocephalus* was in 1989, when mostly juvenile *L. sphenocephalus* moved back and forth within the pond basin as it dried in December; we observed only a few adults. Movements into the basin ($n = 21$; Fig. 5A) were mostly from the north and east. Because most movements into the basin occurred when juveniles were otherwise dispersing and all captures occurred during a narrow time-frame, these captures likely do not represent true immigration, but rather back and forth

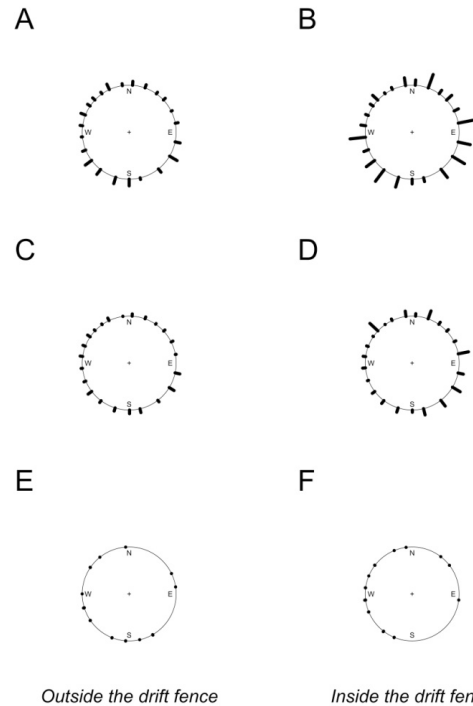


FIGURE 6. Circular barplots (A-F) representing the relative frequency of Eastern Spadefoot (*Scaphiopus holbrookii*) captured in 1988 in the 23 pairs of pitfall traps (one outside and one inside the drift fence) around Breezeway Pond, Putnam County, Florida, USA. (A, B) Males. (C, D) Females. (E, F) Juveniles.

movements within the basin. Movements away from the pond ($n = 41$; Fig. 5B) were in the general direction of the *Panicum*-grass area with a few individuals dispersing toward the adjacent southwest sandhills. The null hypothesis of circular uniformity was rejected for *L. sphenocephalus* entering and leaving the pond basin (Table 1).

Relatively few *P. ocularis* entered the pond basin over the 5-y period ($n = 17$; Fig. 5C), and none at all after the winter of 1988–1989. Immigration occurred primarily from the northeast, with the most conspicuous non-uniformity in 1989, when five of seven captures occurred in one bucket on the east side of the pond. We rejected the null hypothesis of circular uniformity for the 1989 sample and the multiyear sample, but not for 1986, 1987, or 1988 (Table 1).

Most emigration of *P. ocularis* ($n = 132$; Fig. 5D) occurred towards the sandhills adjacent to Breezeway Pond to the southwest and east. Circular uniformity was rejected for the multiyear sample and for all years except 1987 (Table 1). Because most dispersal occurred from November to February, these frogs presumably were moving toward retreats as the pond basin dried in December 1988.

Mass reproduction of *S. holbrookii* occurred at Breezeway Pond only once during the 5-y study, in September 1988, although some spadefoots entered

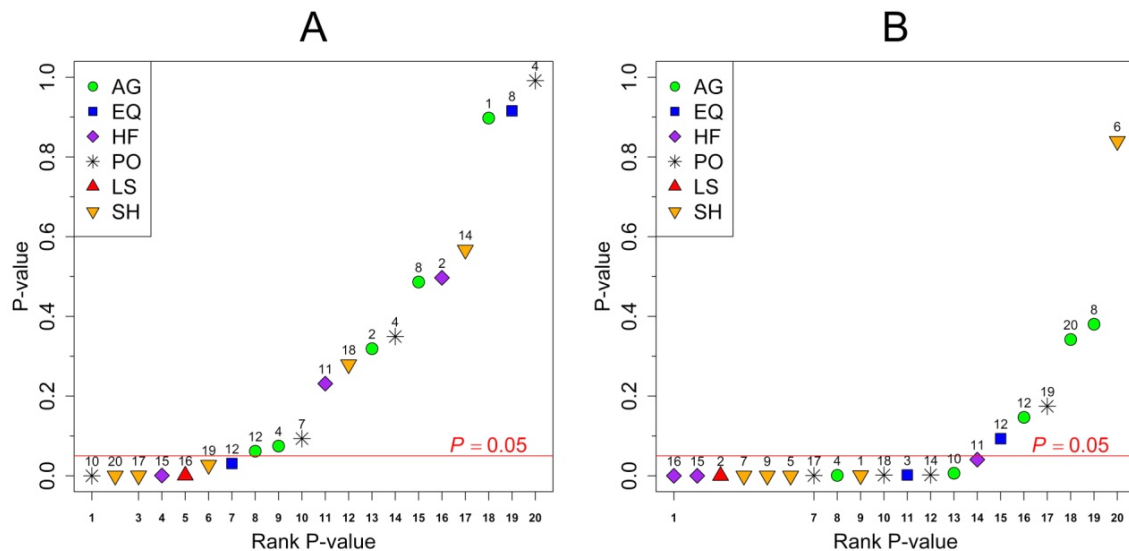


FIGURE 7. P -values in ascending rank order for Watson's U^2 test of circular uniformity. Results are presented for each species (AG = Southern Cricket Frog, *Acris gryllus*; EQ = Southeastern Dwarf Salamander, *Eurycea quadridigitata*; HF = Pine Woods Treefrog, *Hyla femoralis*; PO = Little Grass Frog, *Pseudacris ocularis*; LS = Southern Leopard Frog, *Lithobates sphenoccephalus*; and SH = Eastern Spadefoot, *Scaphiopus holbrookii*). (A) Outside the drift fence for each sample year and (B) inside the drift fence for each sample year. The red line in each panel represents a significance level (α) of 0.05. Missing labels on the abscissa represent tied ranks; for example, there were six species-year subsets with a P -value equal to 0.001 in panel B (see Table 1 for the exact P -values for all subsets).

and exited the pond basin during all years of the study. Despite the large numbers of breeding adults in 1988, reproduction was not very successful, with only a few metamorphs produced. *Scaphiopus holbrookii* entered the pond in large numbers from all directions over the course of the study ($n = 1,481$; Fig. 3C), especially from adjacent sandhills to the south, but with considerable inter-annual variation in the shape of the circular frequency distribution. *Scaphiopus holbrookii* left the pond in even larger numbers in all directions ($n = 2,411$; Fig. 3D). Although *S. holbrookii* were captured in all pitfall traps around the pond, counts in each trap were sufficiently uneven that there was strong evidence against the null hypothesis of circular uniformity for most years both outside and inside the drift fence (Table 1). The exception was *S. holbrookii* captured outside the drift fence in 1987 and for *S. holbrookii* outside and inside the drift fence in 1990.

Because we captured a relatively large number of *S. holbrookii* in 1988, we further partitioned the data to examine dispersion patterns for sex/age subclasses (Fig. 6A-F). Patterns for males and females entering and leaving the pond in 1988 (Fig. 6A-D) mirrored patterns observed for all spadefoots captured over the five-year study (Fig. 3C, D). Males ($n = 346$) and females ($n = 223$) were captured in all 23 traps on the outside of the drift fence, but with the highest counts on the south side of the pond, towards the sandhills. Males ($n = 666$) and females ($n = 367$) captured on the inside of the drift fence (Fig. 6B, D) exhibited a similar pattern, but with

some buckets on the north side of the pond also having relatively high counts. Capture counts for juveniles entering ($n = 21$; Fig. 6E) and leaving ($n = 21$; Fig. 6F) the pond basin were high also on the south and west sides, but with relatively low counts (relative to adults) on the southeast side of the pond basin.

The null hypothesis of circular uniformity was rejected for males entering and leaving the pond basin, as well as for females leaving the pond basin (Table 1). For females entering the pond basin, the null hypothesis of circular uniformity was only rejected by Watson's U^2 statistic and not by the Watson or Kuiper tests (Table 1). The null hypothesis of circular uniformity was rejected for juveniles leaving the pond and was only near significant for juveniles entering the pond (Table 1).

DISCUSSION

Our results indicate that the circular distribution of amphibian captures around the pond is often non-uniform, especially when capture distributions are pooled over multiple years and/or multiple species. Species that were captured more frequently tend to be found at a wider range of angles around the pond, and many species exhibit complex multimodal distributions, with potential shifts in modal directions from year to year. Visual inspection of circular bar plots reveals substantial interspecies variation in the frequency of dispersion at different angles into and out of the pond basin. Such intraspecific and interspecific variation in

direction of dispersion likely reflects species-specific movement capability, whether the pond basin is used as a potential breeding site or as a temporary refuge, the life histories of the species, and the effects and timing of an increasingly severe drought.

The low failure rate of the tests, even at small sample sizes, implies that Type I error does not adequately explain the large number of significant tests. However, we could not rule out the possibility that such tests may have had low power to detect non-uniform counts when sample sizes were small (i.e., Type II error). For example, we captured fewer amphibians on the outside of the drift fence than on the inside of the drift fence, and (for species/year subsets) the lower frequency of positive tests for amphibians captured outside the drift fence potentially could be explained by low power to detect deviations from circular uniformity for small sample sizes. On the other hand, we rejected uniformity for species such as *P. ocularis* (1989 outside) despite small sample sizes ($n = 7$), suggesting that the power of these tests may be high when angular modes develop early.

Our results highlight great variation in the timing and direction of amphibian movements around the drying pond basin, suggesting complex patterns of spatial and temporal dispersion to nearby terrestrial and aquatic habitats. On the Ordway-Swisher Biological Station, many amphibians, including species captured at Breezeway Pond, have been found as far away as 900 m from the nearest water body (Dodd 1996; Johnson 2003), easily within the distance of the nearest ponds and wetlands to Breezeway Pond.

Amphibian immigration and emigration patterns, particularly of metamorphs first exiting a pond, often suggest a random orientation, at least initially (Pittman et al. 2014). As juveniles move away from a pond edge, habitat quality becomes more important in determining a movement direction. Nonrandom movements also may be assumed by adults that use topographical features, such as ravines, steep slopes, or connecting streams or rivulets, to move between breeding sites, temporary refuges, or non-breeding terrestrial habitats. Although topographical features that might aid in orientation are not evident at Breezeway Pond, both random and broadly non-random movements appear common.

These results are consistent with previous studies of other species captured at the pond. For example, most adult Oak Toads (*Anaxyrus quercicus*) tend to move to and from a sandhill community at Breezeway Pond; whereas, Southern Toads (*A. terrestris*) move back and forth between the temporary pond and the xeric hammock (Dodd 1994). In contrast, adult Striped Newts (*Notophthalmus perstriatus*) and Eastern Narrow-mouthed Frogs (*Gastrophryne carolinensis*) exhibit non-random movement patterns that vary by year and

sex (Dodd and Cade 1998). In all four species, there is a considerable amount of annual variation in immigration and emigration patterns directly at the pond. This probably also reflects a mixture of intra-population movements, juvenile dispersal, and landscape-level variation of individual movements in response to drought.

Whereas some researchers have observed amphibians entering and exiting ponds using corridors at their study sites (e.g., Semlitsch 1981), we find no evidence of corridor use at Breezeway Pond, except in a very broad sense. Animals entering and exiting the basin from the northeast may use the *Panicum*-grass open area toward Pine Lodge Pond to facilitate movement, but even this habitat corridor through the surrounding oak hammock is narrow, approximately 30 m in width. Amphibians may alter their pathways upon leaving the pond, either constricting their movements toward a particular site (e.g., a wetland) or dispersing more widely as distance from the pond increases. Individuals entering the pond might be coming in a more or less straight direction from another wetland, or they may be coming from a widely dispersed terrestrial area and narrowing their angle of entry as they approach the pond basin. Because we did not track amphibians entering and dispersing from the basin beyond the drift fence, our data cannot be used to make a definitive inference about corridor usage. At this stage, we can only assert that species oriented both randomly and non-randomly in broadly defined directions that appeared to be toward or away from distant wetlands or adjacent terrestrial habitats. It seems likely that whether amphibians use vegetative or topographic corridors to facilitate movements depends entirely on the topography surrounding a pond basin or wetland.

Temporary ponds interspersed among rolling sandhill topography likely serve two important functions for an amphibian community. During wet years when rainfall and groundwater allow for a sustained hydroperiod, the ponds serve as breeding sites for amphibians that require or prefer fishless habitats for reproduction (e.g., *Anaxyrus quercicus*, *Gastrophryne carolinensis*, *Hyla femoralis*, *Lithobates sphenoccephalus*, *Notophthalmus perstriatus*, and *Pseudacris ocularis* at Breezeway Pond). Even a small temporary pond can produce thousands of metamorph amphibians (Gibbons et al. 2006), which then populate adjacent terrestrial habitats. Even if temporary ponds do not have sufficient hydroperiod every year for successful reproduction, some species may benefit as long as ponds fill every few years. This is particularly true of opportunistic explosive breeders such as *Scaphiopus holbrookii*.

In consecutive wet years, temporary ponds normally hold water for long periods of time or have very short periods without standing water interspersed between

periods with extended hydroperiods. This appears to have been the case at Breezeway Pond prior to our study, when the extended hydroperiod over several years allowed for a resident amphibian community that included even small salamanders (e.g., *Eurycea quadridigitata*) in an otherwise hostile dry and hot region, as well as some frogs (e.g., Gopher Frog, *Lithobates capito*) that normally breed in larger more stable wetlands. *Eurycea quadridigitata* moved toward the southwest sandhills where individuals presumably sought subterranean refuge. Southeastern Dwarf Salamanders (*Eurycea quadridigitata*) move to breeding sites during rainfall, especially in the fall and winter, although movements can occur throughout the year (Semlitsch and McMillan 1980). They can travel at least 180 m from a breeding site (Palis and Aresco 2007), although the nearest wetlands from Breezeway Pond are well beyond this distance. Non-random movement toward adjacent forest from breeding ponds by this species also was noted by Palis and Aresco (2007). The capture histories for *A. gryllus* also suggest that a population may have resided in the pond basin during the previous wet years and subsequently dispersed as drought conditions intensified. However, *A. gryllus* also may have used the Breezeway Pond basin as a stop-over as they moved between wetlands. It is thus not only the duration and timing of hydroperiod that is important for a temporary pond-breeding amphibian community inhabiting a patchy landscape, but also the reliability of the hydroperiod through the years.

Sandhill temporary ponds may also serve a secondary function as short-term amphibian refuges in an otherwise hostile habitat. Temporary ponds may be used both during immigration to and emigration from distant breeding sites, with the length of stay possibly determined by hydroperiod and environmental conditions, presumably rainfall, humidity, and cloud cover. In extreme cases, extended drought may result in the drying of normally reliable water bodies, causing dispersal of their resident species. At Breezeway Pond, the timing and direction of movements suggest that *A. gryllus* used the pond basin primarily as a way station as they dispersed away from distant drying wetlands (e.g., Breezeway Sandhills Pond) on their way to other potential wetlands (large Smith Lake or deep Pine Lodge Pond) or to terrestrial retreats (the sandhill southwest of Breezeway Pond). Breezeway Pond and its distant isolated wetlands thus appear illustrative of a classic source-sink landscape in terms of amphibian occupancy. Breezeway Pond is not so reliable over a long period of time as to form a permanent amphibian community, but it may be important in terms of periodic reproduction; it also serves as a refuge for amphibians moving across a landscape among patchily-distributed wetlands. If Breezeway Pond or other temporary

wetlands dry, amphibians have no choice but to move much further distances across inhospitable habitats or to seek terrestrial refugia and wait out the drought.

The cues amphibians use to locate breeding sites and, presumably, foraging areas, range from chemoreceptive, magnetic, and celestial to acoustic (Sinsch 1992; Wells 2007; Buxton et al. 2015), with adults often returning to sites used in previous years. Some amphibians also use landscape markers, such as the position of a tree line or familiar logs or debris to help with orientation (Heusser 1969). Many, if not most, pond-breeding anurans are sensitive to light in the blue spectrum suggesting that they can use areas of increasing illumination in orientation, such as would be present in the open horizon above lakes and ponds (Hailman and Jaeger 1974). The open sky and lack of tree canopy surrounding a wetland *Panicum* habitat within a landscape of darker pine trees should provide landscape and illumination cues by which amphibians could locate breeding sites or temporary refugia. The directional movements of amphibians would seem likely facilitated by the open horizons above the ponds and lakes in the vicinity of Breezeway Pond.

Many researchers have expressed concern about the effect of climate change on amphibians, particularly the predicted effects of increasing droughts in various parts of North America (Corn 2005; Daszak et al. 2005; Lawler et al. 2009; Duarte et al. 2012; Walls et al. 2013). Drought is not uncommon in Florida and the Southeastern U.S. (Seager et al. 2009), and indeed droughts are frequently out of phase, with wet springs followed by dry summers and vice versa (Stahle and Cleaveland 1992). Although precipitation amounts in Florida are projected to increase during the autumn through spring seasons under some projections of climate change impacts, summer precipitation is actually projected to decrease throughout the peninsula (Ingram et al. 2013). The timing of precipitation and the amounts of rainfall are also projected to become more stochastic, leading to periods of excessive rainfall punctuated by severe droughts. These alternating effects of climate change increase the likelihood of boom or bust years for amphibians breeding in isolated temporary ponds, particularly summer breeders. Species that are not long-lived, such as *A. gryllus*, would be especially vulnerable in such scenarios when faced with a xeric sandhill landscape such as surrounds Breezeway Pond.

Prior to extensive human encroachment, amphibian populations in small depression marshes, such as Breezeway Pond, undoubtedly waxed and waned with drought cycles; populations temporarily extirpated by drought were recolonized as environmental conditions improved (e.g., Dodd and Johnson 2007). Today, temporary wetlands are frequently isolated by human activity, except on very large tracts of protected lands,

thus thwarting recolonization. Although much has been written about the need for protecting both wetlands and adjacent areas surrounding them (Semlitsch 2000; Semlitsch and Jensen 2001; Semlitsch and Bodie 2003), we concur with Hossack et al. (2013) that large areas of habitat need to be protected, perhaps in conjunction with the creation of additional breeding ponds and wetlands, to ensure the survival of temporary pond-breeding amphibians from the stochastic and long-term effects of climate change and isolation.

Our results and conclusions are not unique to the amphibians of the imperiled Longleaf Pine ecosystem; numerous other studies in widely different regions have noted the necessity for extensive tracts of land as non-breeding habitats and dispersal corridors for amphibians. What is sufficient for one species may not be sufficient for an amphibian community through time. Simply put, amphibians require extensive tracts of habitat to maintain community function, a consideration necessary when making management and restoration decisions. Unless large contiguous areas are protected, it may be impossible to maintain Southeastern U.S. temporary pond-breeding amphibian communities in their diverse composition, especially considering the additive effects of threats (Hof et al. 2011) and the extensive random and non-random movements of amphibians over large terrestrial areas.

Acknowledgments.—We thank the technicians, particularly Bert Charest, who collected and recorded the data daily on herpetofaunal captures throughout this long study, and the Ordway-Swisher Biological Station (formerly the Katharine Ordway Preserve-Swisher Memorial Sanctuary) for permission to conduct this research. This study was supported by the Division of Research (then Region 8) of the U.S. Fish and Wildlife Service. Research was carried out according to ASIH-HL-SSAR guidelines for the use of amphibians in research (1987); there were no specific animal care and use guidelines established by the U.S. Fish and Wildlife Service when the fieldwork was carried out.

LITERATURE CITED

- Anderson, N.L., C.A. Paszkowski, and G.A. Hood. 2015. Linking aquatic and terrestrial environments: can beaver canals serve as movement corridors for pond-breeding amphibians? *Animal Conservation* 18:287–294.
- Barrett, K., N.P. Nibbelink, and J.C. Maerz. 2014. Identifying priority species and conservation opportunities under future climate scenarios: amphibians in a biodiversity hotspot. *Journal of Fish and Wildlife Management* 5:282–297.
- Battaglin, W., L. Hay, G. McCabe, P. Nanjappa, and A. Gallant. 2005. Climate patterns as predictors of amphibian species richness and indicators of potential stress. *Alytes* 22:146–167.
- Blaustein, R.J. 2008. Biodiversity hotspot: the Florida Panhandle. *Bioscience* 58:784–790.
- Bower, D.S., E.J. Pickett, M. P. Stockwell, C.J. Pollard, J.I. Garnham, M.R. Sanders, J. Clulow, and M.J. Mahony. 2014. Evaluating monitoring methods to guide adaptive management of a threatened amphibian (*Litoria aurea*). *Ecology and Evolution* 4:1361–1368.
- Buxton, V.L., M.P. Ward, and J.H. Sperry. 2015. Use of chorus sounds for location of breeding habitat in 2 species of anuran amphibians. *Behavioral Ecology* 26:1111–1118.
- Capps, K.A., K.A. Berven, and S.D. Tiegs. 2015. Modeling nutrient transport and transformation by pool-breeding amphibians in forested landscapes using a 21-year dataset. *Freshwater Biology* 60:500–511.
- Choulakian, V., R.A. Lockhart, and M.A. Stephens. 1994. Cramér-von Mises statistics for discrete distributions. *Canadian Journal of Statistics* 22:125–137.
- Corn, P.S. 2005. Climate change and amphibians. *Animal Biodiversity and Conservation* 28:59–67.
- Coster, S.S., J.S. Veysey Powell, and K.J. Babbitt. 2014. Characterizing the width of amphibian movements during post breeding migration. *Conservation Biology* 28:756–762.
- Crawford, J.A., and R.D. Semlitsch. 2007. Estimation of core terrestrial habitat for stream-breeding salamanders and delineation of riparian buffers for protection of biodiversity. *Conservation Biology* 21:152–158.
- Daszak, P., D.E. Scott, A.M. Kilpatrick, C. Faggioni, J.W. Gibbons, and D. Porter. 2005. Amphibian population declines at Savannah River Site are linked to climate, not chytridiomycosis. *Ecology* 86:3232–3237.
- 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. 1994. The effects of drought on population structure, activity, and orientation of toads (*Bufo quercicus* and *B. terrestris*) at a temporary pond. *Ethology Ecology & Evolution* 6:331–349.
- 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., and B.S. Cade. 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. *Conservation Biology* 12:331–339.
- Dodd, C. K., Jr., and S.A. Johnson. 2007. Breeding ponds colonized by Striped Newts after 10 or more years. *Herpetological Review* 38:150–152.
- Dorcas, M., and W. Gibbons. 2008. *Frogs & Toads of the Southeast*. University of Georgia Press, Athens, Georgia, USA.
- Duarte, H., M. Tejedo, M. Katzenberger, F. Marangoni, D. Baldo, J.F. Beltrán, D. A. Martí, A. Richter-Boix, and A. Gonzalez-Voyer. 2012. Can amphibians take the heat? Vulnerability to climate warming in subtropical and temperate larval amphibian communities. *Global Change Biology* 18:412–421.
- Funk, W.C., A.E. Greene, P.S. Corn, and F.W. Allendorf. 2005. High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. *Biology Letters* 1:13–16.
- Gamble, L.R., K. McGarigal, and B.W. Compton. 2007. Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: implications for spatio-temporal population dynamics and conservation. *Biological Conservation* 139:247–257.
- Gibbons, J.W., C.T. Winne, D.E. Scott, J.D. Willson, X. Glaudas, K.M. Andrews, B.D. Todd, L.A. Fedewa, L. Wilkinson, R.N. Tsaliagos, et al. 2006. Remarkable amphibian biomass and abundance in an isolated wetland: implications for wetland conservation. *Conservation Biology* 20:1457–1465.
- Gibbs, J.P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *Journal of Wildlife Management* 62:584–589.
- Glandt, D. 1986. Die saisonalen Wanderungen der mitteleuropäischen Amphibien. *Bonner Zoologische Beiträge* 37:211–228.
- Graham, S.P., D.A. Steen, K.T. Nelson, A.M. Durso, and J.C. Maerz. 2010. An overlooked hotspot? Rapid biodiversity assessment reveals a region of exceptional herpetofaunal richness in the southeastern United States. *Southeastern Naturalist* 9:19–34.
- Hailman, J.P., and R.G. Jaeger. 1974. Phototactic responses to spectrally dominant stimuli and use of colour vision by adult anuran amphibians: a comparative survey. *Animal Behaviour* 22:757–795.
- Heusser, H. 1969. Die Lebensweise der Erdkröte, *Bufo bufo* (L.); Das Orientierungsproblem. *Revue Suisse de Zoologie* 76:443–518.
- Hocking, D.J., and K.J. Babbitt. 2014. Amphibian contributions to ecosystem services. *Herpetological Conservation and Biology* 9:1–17.
- Hof, C., M.B. Araújo, W. Jetz, and C. Rahbek. 2011. Additive threats from pathogens, climate and land-use for global amphibian diversity. *Nature* 480:516–519.
- Hossack, B.R., M.J. Adams, C.A. Pearl, K.W. Wilson, E.L. Bull, K. Lohr, D. Patla, D.S. Pilliod, J.M. Jones, K.K. Wheeler, et al. 2013. Roles of patch characteristics, drought frequency, and restoration in long-term trends of a widespread amphibian. *Conservation Biology* 27:1410–1420.
- Humphreys, R.K., and G.D. Ruston. 2017. Consequences of grouped data for testing departure from circular uniformity. *Behavioral Ecology and Sociobiology* 71:167.
- Ingram, K., K. Dow, L. Carter, and J. Anderson (Eds.). 2013. *Climate of the Southeastern United States: Variability, Change, Impacts, and Vulnerability*. Island Press, Washington, D.C., USA.
- Jenkins, C.N., K.S. Van Houtan, S.L. Pimm, and J.O. Sexton. 2015. US protected lands mismatch biodiversity priorities. *Proceedings of the National Academy of Science USA* 112:5081–5086.
- Johnson, J.R., J.H. Knouft, and R.D. Semlitsch. 2007. Sex and seasonal differences in the spatial terrestrial distribution of Gray Treefrog (*Hyla versicolor*) populations. *Biological Conservation* 140:250–258.
- Johnson, S.A. 2003. Orientation and migration distances of a pond-breeding salamander (*Notophthalmus perstriatus*, Salamandridae). *Alytes* 21:3–22.
- LaClaire, L.V. 1992. Ecology of temporary ponds in north-central Florida. M.S. thesis, University of Florida, Gainesville, Florida, USA. 174 p.
- LaClaire, L.V. 1995. Vegetation of selected upland temporary ponds in north and north-central Florida. *Bulletin of the Florida Museum of Natural History* 38:69–96.
- Lawler, J.J., S.L. Shafer, and A.R. Blaustein. 2009. Projected climate impacts for the amphibians of the Western Hemisphere. *Conservation Biology* 24:38–50.
- Mitchell, J., and W. Gibbons. 2010. *Salamanders of the Southeast*. University of Georgia Press, Athens, Georgia, USA.
- Noss, R.F., W.J. Platt, B.A. Sorrie, A.S. Weakley, D.B. Means, J. Costanza, and R.K. Peet. 2015. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. *Diversity and Distributions* 21:236–244.
- O'Donnell, K.M., A.F. Messerman, W.J. Barichivich, R.D. Semlitsch, T.A. Gorman, H.G. Mitchell, N. Allan, D. Fenolio, A. Green, F.A. Johnson, et al. 2017. Structured decision making as a conservation tool for recovery planning of two endangered salamanders. *Journal for Nature Conservation* 37:66–72.

- Palis, J.G., and M.J. Aresco. 2007. Immigration orientation and migration distance of four pond-breeding amphibians in northwestern Florida. *Florida Scientist* 70:251–263.
- Pearson, P.G. 1955. Population ecology of the spadefoot toad, *Scaphiopus h. holbrookii* (Harlan). *Ecological Monographs* 25:233–267.
- Pewsey, A., M. Neuhäuser, and G.D. Ruxton. 2013. Circular statistics in R. Oxford University Press, Oxford, UK.
- Pitt, A.L., J.J. Tavano, R.F. Baldwin, and B.S. Stegenga. 2017. Movement ecology and habitat use of three sympatric anuran species. *Herpetological Conservation and Biology* 12:212–224.
- Pittman, S.E., M.S. Osbourn, and R.D. Semlitsch. 2014. Movement ecology of amphibians: a missing component for understanding population declines. *Biological Conservation* 169:44–53.
- R Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria. <https://cran.r-project.org>
- Regosin, J.V., B.S. Windmiller, and J.M. Reed. 2003. Terrestrial habitat use and winter densities of the Wood Frog (*Rana sylvatica*). *Journal of Herpetology* 37:390–394.
- Rittenhouse, T.A.G., and R.D. Semlitsch. 2007. Distribution of amphibians in terrestrial habitat surrounding wetlands. *Wetlands* 27:153–161.
- Russell, A.P., A.M. Bauer, and M.K. Johnson. 2005. Migration in amphibians and reptiles: an overview of patterns and orientation mechanisms in relation to life history strategies. Pp.151–203 *In* *Climatology, Geography, Ecology: Causes of Migration in Organisms*. Elewa, A.M. (Ed.). Springer-Verlag, Heidelberg, Germany.
- Schreiber, E.S., A.R. Bearlin, S.J. Nicol, and C.R. Todd. 2004. Adaptive management: a synthesis of current understanding and effective application. *Ecological Management & Restoration* 5:177–182.
- Seager, R., A. Tzanova, and J. Nakamura. 2009. Drought in the southeastern United States: causes, variability over the last millennium, and the potential for future hydroclimate change. *Journal of Climate* 22:5021–5045.
- Semlitsch, R.D. 1981. Terrestrial activity and summer home range of the Mole Salamander (*Ambystoma talpoideum*). *Canadian Journal of Zoology* 59:315–322.
- Semlitsch, R.D. 2000. Size does matter: the value of small isolated wetlands. *National Wetlands Newsletter* 22:5–6, 13.
- Semlitsch, R.D. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. *Journal of Wildlife Management* 72:260–267.
- Semlitsch, R.D., and J.R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats. *Conservation Biology* 17:1219–1228.
- Semlitsch, R.D., and J.B. Jensen. 2001. Core areas, not buffer zone. *National Wetlands Newsletter* 23:5–6, 11.
- Semlitsch, R.D., and M.A. McMillan. 1980. Breeding migrations, population size structure, and reproduction of the Dwarf Salamander, *Eurycea quadridigitata*, in South Carolina. *Brimleyana* 3:97–105.
- Sinsch, U. 1990. Migration and orientation in anuran amphibians. *Ethology Ecology & Evolution* 2:65–79.
- Sinsch, U. 1992. Sex-biased site fidelity and orientation behaviour in reproductive Natterjack Toads (*Bufo calamita*). *Ethology, Ecology & Evolution* 4:15–32.
- Sinsch, U. 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. *Oecologia* 112:42–47.
- Stahle, D.W., and M. K. Cleaveland. 1992. Reconstruction and analysis of spring rainfall over the southeastern US for the past 1000 years. *Bulletin of the American Meteorological Society* 73:1947–1961.
- Vasconcelos, D., and A.J.K. Calhoun. 2004. Movement patterns of adult and juvenile *Rana sylvatica* (LeConte) and *Ambystoma maculatum* (Shaw) in three restored seasonal ponds in Maine. *Journal of Herpetology* 38:551–561.
- Walls, S.C. 2014. Identifying monitoring gaps for amphibian populations in a North American biodiversity hotspot, the southeastern United States. *Biodiversity and Conservation* 23:3341–3357.
- Walls, S.C., W.J. Barichivich, and M. E. Brown. 2013. Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. *Biology* 2:399–418.
- Wells, K.D. 2007. *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago, Illinois, USA.



C. KENNETH DODD, JR. (Ken) received his Ph.D. in Zoology at Clemson University, Clemson, South Carolina, USA, in 1974. Most of his career was with the U.S. Department of Interior: Office of Endangered Species 1976-1984; Research division of the U.S. Fish and Wildlife Service, later transferred to the U.S. Geological Survey (USGS; 1984–2007). Ken retired from the USGS in early 2007 as Project Leader of the USGS Amphibian Research and Monitoring Initiative in the southeastern United States, and is currently Courtesy Associate Professor in the Department of Wildlife Ecology and Conservation at the University of Florida. Ken has published more than 220 papers, reviews, and books, mostly on turtle and amphibian ecology and conservation. His book *Frogs of the United States and Canada* was published by Johns Hopkins University Press in 2013, and an edited volume *Reptile Ecology and Conservation: A Handbook of Techniques* was published by Oxford University Press in 2016. Ken lives in Gainesville, Florida, USA, with his wife Marian Griffey and their six cats and numerous turtles. (Photographed by Marian Griffey).



COREY D. ANDERSON received his Bachelor's degree in Integrative Biology from the University of California at Berkeley, USA, in 1997 and his Ph.D. (in Evolution, Ecology and Population Biology) from Washington University in St. Louis, Missouri, USA (Alan Templeton's lab) in 2006. After completing his Ph.D., Corey did postdoctoral work at The Biodesign Institute at Arizona State University, Tempe, Arizona, USA, where he assisted Michael Rosenberg in developing the popular PASSaGE 2 spatial statistics software. Corey is currently an Associate Professor at Valdosta State University, Valdosta, Georgia, USA. His research examines the ecological and micro-geographic processes that drive dispersion of organisms at the local landscape scale, with much of this work focused on the ecology and conservation of organisms that use underground refuges. The photograph was taken with Corey's youngest son, Miles Berkeley Anderson. (Photographed by Corey D. Anderson).