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Amphibians and Reptiles Captured in Drift Fences in Northwest Wisconsin Pine Barrens

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Amphibian Use of Constructed Ponds on Maryland's Eastern Shore

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Amphibian assemblages were sampled at nine constructed ponds (three in each age category: new ponds—age <1 yr, young ponds—age 4–5 yr, old ponds—age >30 yr) on Maryland's eastern shore (May–October 1994, March–August 1995) using a total of 27 drift fence and funnel trap arrays. The importance of habitat and landscape variables including pond age was considered in explaining amphibian use and distribution across ponds. Specifically, amphibian (1) abundance; (2) composition; (3) diversity; (4) richness; and (5) reproductive success were studied. During both years, we captured 1904 individuals comprising ten species. The most frequently collected species (species found in all treatments) were *Bufo fowleri*, *Rana sphenoccephala utricularius*, and *Rana catesbeiana*. *Bufo fowleri* comprised the majority of the collections in 1994 and 1995, 60.6% and 49.4% respectively. Some species were only collected at new ponds (*Hyla chrysoscelis*, *H. cinerea*), some only at young and old ponds (*Acris crepitans*, *Rana clamitans*), and some only at old ponds (*Scaphiopus holbrookii*, *Ambystoma opacum*). Despite these differences in composition, no statistically significant differences in reproductive success or numbers collected were found across treatments. Brillouin diversity indices indicated amphibian diversity was greatest at young ponds in both years. Results suggest that, in the ponds studied, pond age affects amphibian composition, richness, and diversity but is not particularly useful in predicting reproductive success or the sizes of amphibian collections. However, because canonical correspondence analysis showed age to be a relatively important variable, it should not be discounted. Species-specific habitat requirements, regional abundance, and pond placement in the landscape (e.g., next to agriculture) appear to be more important in explaining amphibian use of constructed ponds.

INDEX DESCRIPTORS: Amphibian assemblages, constructed ponds, wetland use, pond age.

Wetland habitats are biologically diverse and productive areas that support numerous species of both aquatic and terrestrial organisms. Because most amphibian species in North America have biphasic (aquatic larvae to terrestrial adult) and complex life cycles where adults move to aquatic habitats to reproduce (Wilbur 1980, Heyer et al. 1994), wetlands are essential. The long-term survival of many amphibian populations is therefore closely tied to the presence of aquatic habitats (e.g., wetlands, ponds, etc.) as places for reproduction.

At present, amphibians appear to be particularly vulnerable to population losses (Fellers and Drost 1993, Blaustein 1994, Blaustein et al. 1994, Heyer et al. 1994, Pechman and Wilbur 1994) although the causes of many documented population declines remain elusive. Destruction of essential aquatic breeding habitats negatively impacts amphibian persistence and may act synergistically with other factors causing amphibian declines. One easily implemented conservation measure is the construction of ponds and other wetland habitats.

Unfortunately, amphibians have been largely neglected from studies addressing species' colonization and use of constructed wetlands. It is not clear how constructing wetlands may affect amphibian populations. However, Laan and Verboom (1990) showed that spatial relationships among amphibian sub-populations are important for predicting the occurrence of species at newly created sites. They also suggested the importance of landscape connectivity and proximity to source populations when planning new wetlands for amphibians. Lacki et al. (1992) studied herpetofaunal use of mine-drainage treatment wetlands and showed that these sites could provide adequate habitat. Moreover, their study suggested that species composition was dependent upon construction design, water pH and heavy metal concentration, and the proximity to source populations. Briggler

(1998) found that the abundance and distribution of amphibian species at constructed ponds was influenced by pond age. In his study, *Rana sphenoccephala utricularius* was found predominantly in newly created ponds of three years or less. Other recent studies addressing amphibian use of constructed wetlands have been undertaken (N. Gerber and T. Touré pers. comm.).

In this project, we focused on some characteristics of amphibian assemblages present at constructed ponds of various ages at a 6,000 ha privately-owned wildlife management area located in Dorchester County, Maryland. We also examined attributes of the surrounding landscape, including physical characteristics of the constructed ponds, that could potentially affect the resident amphibian assemblages. Specifically, we considered how these habitat variables, including pond age, might affect (1) abundance; (2) composition; (3) diversity; (4) richness; and (5) reproductive success of amphibian assemblages present at the constructed ponds. Findings from this and other similar studies are necessary to predict impacts of creating wetlands on local amphibian populations. Moreover, it is unlikely that future efforts to conserve amphibians will be complete without studies addressing amphibian colonization and use of constructed wetlands.

METHODS

Nine constructed ponds were chosen as study sites at Tudor Farms, a 6000-ha privately-owned wildlife management area, located in Dorchester County, Maryland (Fig. 1). Ponds were constructed to encourage wildlife such as waterfowl, gallinaceous birds, and deer and to provide agricultural irrigation. Ponds were grouped into three different age categories (new, young, and old) and three ponds were assigned to each group. At the outset of the study in 1994, the age

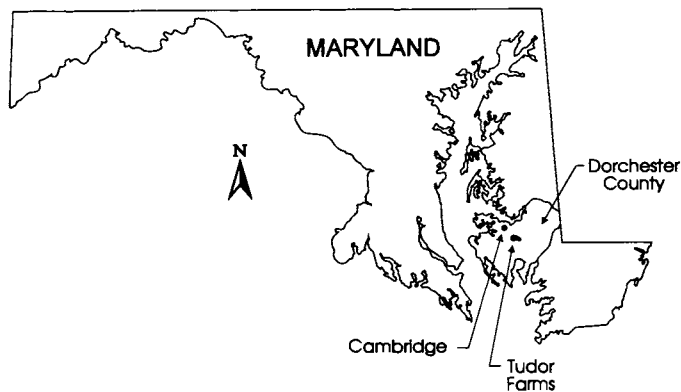


Fig. 1. Map of Maryland showing the study location in Dorchester County, Maryland.

groups corresponded to <1 year of age, between 4–5 years of age, and >30 years of age.

New ponds included: Raleigh Pond (RA), Merrill Pond (ME), and Pound Pond (PO). Surface areas for each new pond were 0.32 ha, 0.33 ha, and 0.80 ha, respectively. Pond perimeters were 192.0 m, 511.67 m, and 608.25 m, respectively. Young ponds included: Triangle Pond (TR), Circle Pond (CI), and Foundation Pond (FO). Surface areas for each young pond were 0.48 ha, 0.12 ha, and 0.02 ha, respectively. Pond perimeters were 311.25 m, 186.75 m, and 133.5 m, respectively. Old ponds included: Old Pond One (OP1), Old Pond Two (OP2), and Lilypad Pond (LI). Surface areas for each old pond were 0.09 ha, 0.16 ha, and 0.16 ha, respectively. Pond perimeters were 135.75 m, 134.25 m, and 276.0 m, respectively.

Amphibians were sampled at the ponds from May–October 1994 and March–August 1995 using 27 drift fence and funnel trap arrays. Sites were visited weekly through the end of May and then daily for the remainder of the sampling season.

Description of Study Location

Dorchester County lies on Maryland's eastern shore and extends as a peninsula into the Chesapeake Bay. Like other areas on the Atlantic Coastal Plain, Dorchester County is characterized by flat topography and low elevation. Southern Dorchester County is mostly marshland with altitudes of 0.61 m (2 feet) or less (Rasmussen and Slaughter 1957), giving it more wetlands than any other county in Maryland (Metzger 1973).

The study location in Dorchester County is bordered by secondary tidal rivers, the Transquaking and its chief tributary, the Chicamacomico. Surrounding these rivers are tidal marsh soils subject to flooding by salt water (Owens and Denny 1986). Other soils at the study site are mostly textured to medium textured and are poorly drained (Matthews 1963).

Extensive woodlands composed of many tree species including loblolly pine (*Pinus taeda*), red maple (*Acer rubrum*), white oak (*Quercus alba*), willow oak (*Quercus pbellos*), swamp oak (*Quercus prinus*), sweetgum (*Liquidambar styraciflua*), and black gum (*Nyssa sylvatica*) characterize the landscape. Common understory species near the pond sites include greenbrier (*Smilax rotundifolia*), sweet pepperbush (*Clethra alnifolia*), poison ivy (*Toxicodendron radicans*), bay berry (*Myrica cerifera*), and many species of grasses. Agricultural crops such as soybean, corn, winter wheat, and sunflower are also in close proximity to several ponds.

Adult and Juvenile Sampling

We placed three drift fence and funnel trap arrays parallel to the shoreline (between 0.75 m and 9.75 m away from the edge) of each pond and examined traps for captured amphibians. Four funnel traps were required for each of the three drift fences per study site for a total of 108 traps. Two traps were placed at both ends of each drift fence to capture animals arriving or leaving the pond. Amphibians were marked by a site-specific toe clip (Martof 1953). Calling amphibians were also documented while in the field in order to report the occurrence of species not revealed by trapping.

Larval Sampling

We sampled larvae May–July (1995) by dip netting along the shore of each pond and by trapping. Dip netting used a sampling scheme stratified by distance from the shore and shoreline location (modeled after Shaffer et al. 1994). Three sampling transects were established along the perimeter of each pond. Each transect was fixed by the location of the three drift fences along the perimeter. The end of the drift fence located at the southern-most edge of each pond served as the starting point for the first sampling transect. The second and third sampling transects were marked by the first end of the next two drift fences encountered moving in a clockwise direction. Two separate sets of dip netting occurred at each transect location (twenty sweeps at 1 m from the shore and another twenty sweeps at 2 m from the shore). Sixty sweeps in each set (1 m and 2 m from the shore) were conducted for a total of 120 net sweeps at each sampling time. The shallow sweeps were conducted first and in a clockwise direction from the transect origin. These were followed by deeper water sweeps in the same direction. Shallow water samples and deep water samples were separated by approximately 5 m to assure independence. Individual sweeps were separated from each other by 1-m intervals. Each dip net sweep was perpendicular to the shore and approximately 1 m in length.

We also placed four larval traps at the cardinal compass points at each pond at a depth of approximately 6 cm. These traps (PVC pipe with a screen funnel at one end) were checked once a week for tadpoles. During periods when there were fluctuations in water levels, the traps were moved closer to the ponds' interiors so they were always partially submerged.

Transformed amphibians captured while dip netting or in the larval traps were identified and released but not included in subsequent analyses. Larvae were counted and identified in the lab (Gosner 1960, Altig 1970, Gibbons and Semlitsch 1991) and released at the site of capture within one week.

Landscape Characteristics

Habitat and landscape variables (Table 1) were studied during the second season (March–July 1995). Pond-to-pond and pond-to-marsh distances were measured from the nearest shore of each site on aerial photographs (scale: 1 cm = 0.168 km, dated December 1993). Aerial photographs were also used to measure the percent area composed of woodland, marsh, and agricultural fields using circular areas containing grids. The measurements were made within a circular area of 1 km² centered on the ponds (radii = 0.564 km) and each overlaid circle contained a grid with 540 1 mm² squares.

Aquatic Vegetation Sampling

Vegetation was sampled in all ponds except two (OP1, OP2) that dried early in the season. A 1 m² sampling grid, divided into 16 equal squares, was used to sample vegetation at random locations within the ponds (interior zone) and along the pond perimeters (shore zone). Pond perimeters were first divided into 30 m segments

Table 1. Codes and descriptions of habitat and landscape variables.

Code	Description
DWATER	Distance to the nearest freshwater wetland (km)
DMARSH	Distance to the nearest brackish marsh (km)
WOODS	Percent woodland within 1 km ² of each pond
MARSH	Percent brackish marsh within 1 km ² of each pond
FIELDS	Percent agricultural fields within 1 km ² of each pond
EAV	Percent emergent aquatic vegetation
SAV	Percent submerged aquatic vegetation
DEAV	Percent dead emergent vegetation
ALGAE	Percent algae
PERIMETER	Pond perimeter (m)
%AGRI	Percent perimeter directly abutted by agricultural fields
%WOOD	Percent perimeter directly abutted by woods
SAREA	Pond surface area (ha)
DEPTH	Pond average depth (m)
AGE	Pond age
PH	Pond pH

to sample shore-zone vegetation. Within each 30 m segment, the sampling grid was placed with one edge resting on the land-water interface at a single location chosen randomly. Parallel transects across the ponds were constructed to sample vegetation within the interior zones. A square on the grid was counted for each vegetation category (Table 1) if coverage was at least 50%. Measurements from the shore and interior zones for all vegetative categories were summed to calculate the percent cover of each vegetation type for the ponds.

Pond Profile and Water Quality

Surface areas were estimated (in ha) from aerial photographs and pond perimeters were determined from pacing the shorelines. Pond depth was measured every two meters along two perpendicular transects across the pond (north-to-south and west-to-east transects). Water samples were taken during larval sampling dates to determine pH. One water sample was collected from each pond at the initial point of the first set of larval samples. The water samples were analyzed in the lab with a HACH wide-range (4–10) pH test kit (Model 17-N).

Data Analyses

The data were checked for normality using Shapiro-Wilk's *W* statistics. The hypotheses of differing amphibian numbers across pond treatments were tested with Kruskal-Wallis tests since the data were not normally distributed. Total captures at all sites were examined with Kruskal-Wallis tests for differences among treatments. A non-parametric multiple contrast analysis of the sums of ranks was used for both significant and marginally non-significant tests to determine where differences existed (Zar 1984). Kruskal-Wallis tests were also used to examine differences in habitat and landscape variables. In

cases where only two treatments could be compared, Mann Whitney *U* tests were performed. Spearman's rank correlation coefficients (r_s) were also conducted to assess correlations among the habitat and landscape variables.

Species diversity was examined by calculating Brillouin indices (Krebs 1989), all of which are significantly different by definition (Magurran 1988). Species richness was estimated by rarefaction (Krebs 1989) and 95% confidence intervals for each curve were determined. Correlations between habitat/landscape variables and amphibian abundances were assessed using Spearman's rank correlation coefficients (r_s). Species associations with pond age were tested with χ^2 goodness-of-fit analyses, assuming equal distributions across treatments as the expected values and adjusting numbers for differences in pond perimeter. Amphibian numbers were adjusted by a multiplication factor (unique to each pond) relative to the smallest pond perimeter. Yates' correction for continuity (χ_c^2) was used when the analysis involved pooling frequencies with only one degree of freedom (Zar 1984).

Reproductive success was examined with Kruskal-Wallis tests by comparing both total larval captures and ratios of juveniles to adults (of each amphibian species) across treatments. For the ratio tests, if a denominator contained a zero, indicating that no adults were captured, a value of two was assigned since at least two adults had to be present at ponds where metamorphosed juveniles were captured. A value of zero in the numerator, indicating that no juveniles were captured, remained unchanged.

A multivariate analysis (Canonical Correspondence Analysis; CCA) was applied to the data gathered in 1994 and 1995 to infer species-environment relationships from the amphibian assemblage and habitat data (ter Braak 1986). CCA can select those aspects of the environment that best explain variation in species composition (Palmer 1993). CCA was conducted with CANOCO Version 2.1 (ter Braak 1988). Data input consisted of a site-by-species matrix and a site-by-environment matrix. Pond age was also included in the CCA to determine its relative importance in explaining the variation in amphibian distributions. Adult amphibian captures were used to generate ordination diagrams so that the analyses would not be affected by large numbers of juveniles. Pond surface area (SAREA) was omitted in both analyses because it was highly correlated with pond perimeter.

Alpha levels were adjusted when multiple tests were conducted (e.g. Kruskal-Wallis tests) to hold the experimentwise error rate at $\alpha = 0.05$, in which case the Dunn-Sidak method was used (Sokal and Rohlf 1995), and for multiple correlations, the sequential Bonferroni technique was used (Rice 1989).

RESULTS

Abundance and Composition

A total of 1465 transformed amphibians comprising nine species was collected in 1994 (Table 2, Fig. 2). Of this total, 253 were adults and 1212 were juveniles (Figs. 3, 4). Fewer individuals were captured in 1995 (134 adults and 305 juveniles) but an additional species, the spring peeper (*Pseudacris crucifer*), was collected (Table 2, Fig. 2). Most adults were captured at old ponds and fewest at young ponds during both years (Fig. 3). Most juveniles were captured at new ponds and fewest at old ponds in each season (Fig. 4). Captures were greatest at new ponds and lowest at old ponds in 1994 (Table 2). In 1995, captures were still greatest at new ponds but lowest in young ponds (Table 2).

In both years, the most frequently collected species were the same: Fowler's toad (*Bufo fowleri*), southern leopard frog (*Rana sphenoccephala utricularius*), and bullfrog (*R. catesbeiana*). Fowler's toads constituted the majority of the collections. Overall, the three most abundant

Table 2. Number of transformed amphibians collected by species and treatment in 1994 and 1995. Percentages are given for each species in parentheses out of the total captures for that year.

Species	Total (%)		New (%)		Young (%)		Old (%)	
	1994	1995	1994	1995	1994	1995	1994	1995
Anura								
<i>Bufo fowleri</i>	888 (60.61)	217 (49.43)	463 (73.96)	90 (44.22)	172 (33.01)	41 (37.27)	253 (79.56)	86 (67.19)
<i>Acris crepitans</i>	10 (0.68)	2 (0.46)	0 (0)	0 (0)	8 (1.54)	1 (0.91)	2 (0.63)	1 (0.78)
<i>Hyla chrysoscelis</i>	1 (0.068)	0 (0)	1 (0.16)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>H. cinerea</i>	4 (0.27)	1 (0.23)	4 (0.64)	1 (0.50)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Pseudacris crucifer</i>	0 (0)	1 (0.23)	0 (0)	0 (0)	0 (0)	0 (0)	3 (0.91)	1 (0)
<i>Scaphiopus holbrookii</i>	3 (0.20)	1 (0.23)	0 (0)	0 (0)	0 (0)	0 (0)	3 (0.94)	1 (0.78)
<i>Rana catesbeiana</i>	245 (16.72)	21 (4.78)	7 (1.12)	7 (3.48)	216 (41.46)	13 (11.2)	22 (6.92)	1 (0.78)
<i>R. clamitans</i>	16 (1.10)	2 (0.46)	0 (0)	0 (0)	12 (2.30)	2 (1.82)	4 (1.26)	0 (0)
<i>R. s. utricularius</i>	290 (19.80)	194 (44.19)	151 (24.12)	103 (51.24)	113 (21.69)	52 (47.27)	26 (8.18)	39 (30.47)
Caudata								
<i>Ambystoma opacum</i>	8 (0.55)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	8 (2.52)	0 (0)
Grand Total	1465 (100)	439 (100)	626 (100)	201 (100)	521 (100)	110 (100)	318 (100)	128 (100)

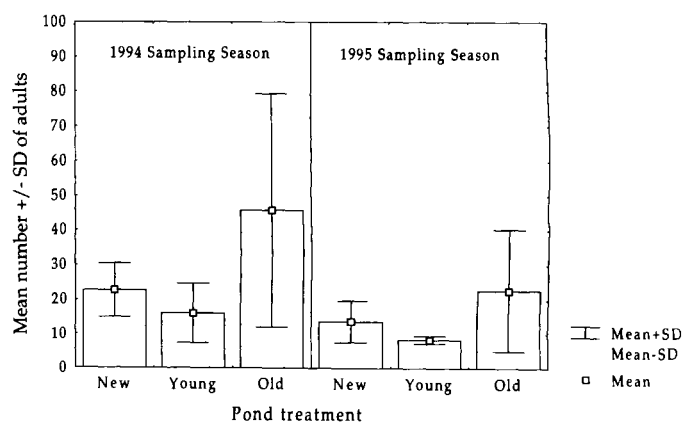
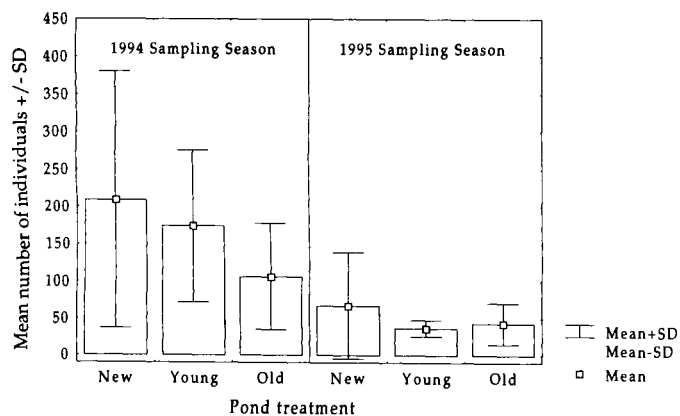


Fig. 2. Mean number \pm standard deviation (SD) of transformed amphibians collected within each treatment in 1994 and 1995.

Fig. 3. Mean number \pm standard deviation (SD) of adult amphibians collected across treatments in 1994 and 1995.

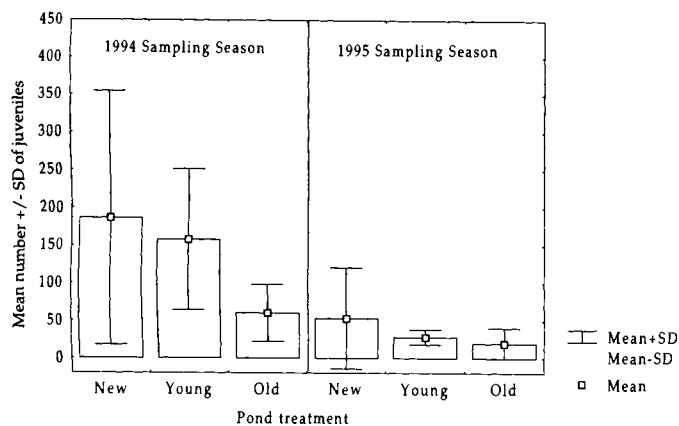


Fig. 4. Mean number \pm standard deviation (SD) of juvenile amphibians collected across treatments in 1994 and 1995.

species accounted for 97.1% and 98.4% of the total sample in 1994 and 1995, respectively, and were the only species found at ponds of all ages. Cope's gray treefrog (*Hyla chrysoscelis*) and green treefrog (*Hyla cinerea*) were collected only at new ponds. An individual spring peeper (*Pseudacris crucifer*) was collected at one young pond in 1995. *Acris crepitans* and *R. clamitans* were collected only at young and old ponds. Species collected only at old ponds were eastern spadefoot toads (*Scaphiopus holbrookii*) and marbled salamanders (*Ambystoma opacum*). Marbled salamanders were found only at OP2 in 1994.

Amphibian Associations with Pond Age

Using a conservative alpha level ($\alpha = 0.01$) because multiple Kruskal-Wallis tests were conducted, no significant differences were found for amphibian captures across treatments; however, differences in the numbers of *Rana s. utricularius* and of juvenile ranid frogs collected in 1994 were marginally non-significant across treatments ($H = 6.49$, $P = 0.039$ for both tests). In the case of *R. s. utricularius* captures, an examination of the sum of ranks (nonparametric Tukey-type multiple comparison, Zar 1984) indicated that captures were greater at new ponds (sum of ranks = 23) compared to old ponds (sum of ranks = 6, $q = 3.59$, $P < 0.05$). Juvenile ranid numbers were greater at young ponds (sum of ranks = 23) than at old ponds (sum of ranks = 6, $q = 3.59$, $P < 0.05$). No significant differences in mean amphibian captures were found for animals collected in 1995; however, for many species the sample sizes were too small to permit a powerful test.

Adult *B. fowleri*, and *R. s. utricularius* were captured in sufficient numbers to perform χ^2 goodness-of-fit analyses in both years. *Rana catesbeiana* yielded adequate sample sizes in 1994 only. Numbers of these species were adjusted for pond perimeter to consider differences in relative abundance across treatments. *Bufo fowleri* adults from both years were collected least often at young ponds ($\chi_c^2 = 61.02$, $P < 0.0001$ and $\chi_c^2 = 32.61$, $P < 0.0001$, respectively). Distributions of *R. s. utricularius* were also heterogeneous across treatments and were collected most often at new ponds in 1994 ($\chi_c^2 = 44.05$, $P < 0.0001$). No other specific associations between the relative abundance of amphibians and pond age were observed.

Amphibian Richness and Diversity

Nine amphibian species (eight frogs, one salamander) were collected in 1994 and eight species (all frogs) were collected in 1995 (Table 2). A total of ten amphibian species was collected during the study. Additionally, New Jersey chorus frogs (*Pseudacris triseriata kal-*

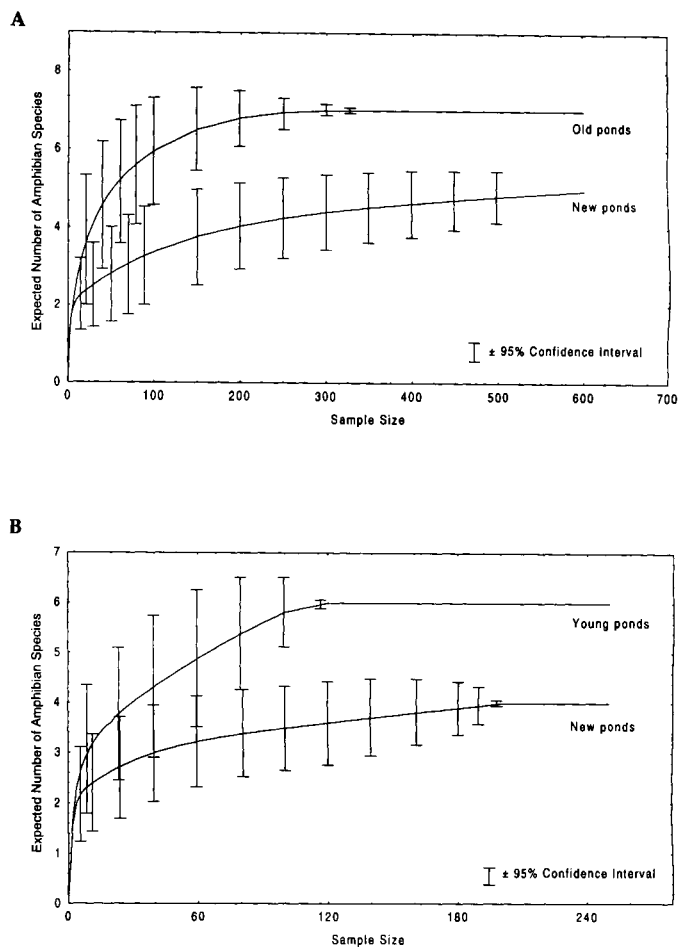


Fig. 5. Rarefaction estimates of amphibian richness by treatment in (A) 1994 and (B) 1995.

mi) were heard in early spring of both years but were never captured. Species composition between years was similar with the exceptions of *Hyla chrysoscelis* and *Ambystoma opacum* which were collected only in 1994 and *Pseudacris crucifer* collected only in 1995. In 1994, the number of amphibian species at each new pond was between three and five species, at each young pond was between four and five species, and at each old pond was five species. In 1995, variability in the number of species collected at each old pond was between 2–4 species and was equal among new (three species) and young ponds (four species). We found no statistically significant differences in the mean number of amphibian species collected across pond treatments either in 1994 or 1995 ($P = 0.24$ and $P = 0.10$, respectively).

Rarefaction (Krebs 1989) was used to estimate the number of amphibian species expected across pond treatments for given sample sizes. By this method, amphibian richness in 1994 would be expected to be greater at old ponds than at new ponds (Fig. 5A), although at small sample sizes 95% confidence intervals overlap. Young ponds were not significantly different from either new or old ponds. The expected number of amphibian species across treatments in 1995 was expected to be greater at young ponds than at new ponds (Fig. 5B). Again, at small sample sizes there was overlap of the 95% confidence intervals. Old ponds in this year were not significantly different than either new or young ponds.

Amphibian diversity was estimated with the Brillouin index (H). Total amphibian diversity in 1994 was greatest at young ponds (H

Table 3. Number of amphibian larvae (all species combined) collected across treatments in 1995.

Month and distance from shore	Total	New	Young	Old
May 1 m	382	198	171	13
May 2 m	198	121	65	12
June 1 m	228	130	82	16
June 2 m	74	41	33	0
July 1 m	199	58	64	77
July 2 m	76	38	15	23

= 1.72) followed by old ponds ($H = 1.09$) and then new ponds ($H = 0.93$). Young ponds again had the most diverse amphibian assemblages in 1995 ($H = 1.53$) but in contrast to 1994, old ponds were the least diverse ($H = 1.01$).

Correlations of Habitat and Landscape Variables with Abundance

Differences in habitat/landscape variables across treatments were tested with Kruskal-Wallis tests (DWATER, DMARSH, WOODS, MARSH, FIELDS, PERIMETER, SAREA). Some data for old ponds could not be obtained (EAV, SAV, DEAV, ALGAE, DEPTH, and PH); thus these variables were compared between new and young ponds using Mann-Whitney U tests. Distance to nearest freshwater (DWATER) was significantly different among all treatments ($H = 6.49$, $P = 0.039$). New ponds (sum of ranks = 24) were located at greater distances from other freshwater sources than were young ponds (sum of ranks = 7, $P < 0.05$). Average depth of new ponds was significantly greater than that of young ponds ($U = 0.0$, $P = 0.05$). The percentage of submerged aquatic vegetation (SAV) was significantly higher in young ponds compared to new ponds ($U = 0.0$, $P = 0.05$).

Results of Spearman's rank correlations (r_s) between landscape variables showed that perimeter and surface area were positively correlated ($r_s = 0.88$, $P = 0.001$). The percentages of pond perimeters directly abutted by fields (%AGRI) and woods (%WOOD) were negatively correlated ($r_s = -1.00$). When P-values were adjusted for multiple tests, no other significant correlations among habitat and landscape variables were observed.

For 1994, significant negative correlations were found between pond surface area (SAREA) and juvenile *Rana clamitans* abundances ($r_s = -0.86$, $P = 0.002$). Percent fields (FIELDS) was negatively correlated with three amphibian abundances: total *Acris crepitans* ($r_s = -0.83$, $P = 0.005$), total *Rana clamitans* ($r_s = -0.86$, $P = 0.002$), and juvenile *R. clamitans* ($r_s = -0.82$, $P = 0.006$). The numbers of *R. s. utricularius* adults were positively correlated with the percent of pond perimeter directly abutted by fields (%AGRI) ($r_s = 0.68$, $P = 0.04$). No significant correlations were found between habitat/landscape variables and 1995 abundance data.

Reproductive Success

The abundance of amphibian larvae (all species combined) sampled 1 m from the shore in 1995 were not significantly different across treatments (Kruskal-Wallis test, $H = 1.87$, $P = 0.39$, Table 3); nor did samples taken at 2 m from the shore differ ($H = 2.17$, $P = 0.34$). Larvae captured in traps were combined with the 1 m samples

Table 4. Species scores generated by CCA on numbers of adult amphibians collected in 1994.

Species	Species Scores	
	Axis 1	Axis 2
<i>Acris crepitans</i>	1.3732	0.2981
<i>Ambystoma opacum</i>	-1.0066	0.8114
<i>Bufo fowleri</i>	-0.3999	0.1494
<i>Hyla chrysoscelis</i>	0.3467	-1.9230
<i>Hyla cinerea</i>	0.3580	-1.4180
<i>Rana catesbeiana</i>	1.5481	0.5611
<i>Rana clamitans</i>	1.8589	0.9136
<i>Rana s. utricularius</i>	0.3351	-0.6173
<i>Scaphiopus holbrookii</i>	-0.7963	0.5817

taken in 1995 only and the differences among treatments were non-significant ($H = 1.87$, $P = 0.39$).

In both years, only Fowler's toads, bullfrogs, and southern leopard frogs were captured with sufficient frequency for comparing ratios of juveniles: adults across treatments (Table 3). Juvenile: adult ratios were not significantly different across treatments for each of these species.

Canonical Correspondence Analysis

The overall ordination generated by CCA from 1994 data was significant (Monte Carlo test, $P = 0.03$) although the first axis was not (Monte Carlo test, $P = 0.18$). The first axis and overall test for 1995 data were not significant (Monte Carlo tests, $P = 0.52$ and $P = 0.13$ respectively) but the biplots were similar to those produced with the 1994 data. Accordingly, we restrict the discussion to the 1994 CCA.

The importance of the association between species and environment is expressed by the eigenvalues produced by CCA. In other words, eigenvalues measure how much variation in the species data is explained by the environmental variables. Eigenvalues generated for the most important canonical axes were: axis 1 (0.4279) and axis 2 (0.1987).

The percentage of variability in species scores explained by each axis was 50.13 and 23.27 (axes 1 and 2 respectively). Amphibians with the highest scores on axis 1 were *R. clamitans*, *R. catesbeiana*, and *A. crepitans* and those with the lowest scores on axis 1 were *A. opacum* and *S. holbrookii* (Table 4).

Species-environment correlations (Pearson's correlation coefficients) for axes 1 and 2 were 0.974 and 0.993 respectively. Correlations of environmental variables with axis 1 were greatest for percent woods surrounding ponds (WOODS) and perimeter (PERIMETER) (Table 5). The variables age (AGE) and percent marsh surrounding ponds (MARSH) had the highest correlations with axis 2 (Table 5).

DISCUSSION

Understanding the influence of constructed wetlands on amphibians is an important issue in amphibian conservation. Only a few studies have specifically addressed amphibian colonization and use of constructed wetlands (e.g., Laan and Verboom 1990, Lacki et al. 1992, Edenhamn and Salonen 1996) and more are needed.

Several differences in the characteristics of amphibian assemblages using the ponds in this study were revealed. However, variation in amphibian captures within treatments was large, especially within new ponds in 1994. Not surprisingly, no significant differences in

Table 5. Inter set correlations of environmental variables with axes. The number of variables used in the analysis (7) was equal to the number of pond sites (9) minus 2.

Variable	Axis 1	Axis 2
PERIMETER	0.2003	-0.4692
DWATER	-0.1256	-0.5936
DMARSH	-0.1530	-0.4172
WOODS	0.6573	-0.4036
MARSH	-0.4167	0.6238
FIELDS	-0.2747	-0.4594
AGE	-0.4376	0.8174

the mean number of amphibians collected across pond treatments were detected in either year.

Differences in overall amphibian collections were present between 1994 and 1995 despite equal sampling effort (six months of study in both seasons). However, in the first year of the study, 1026 more individuals (mostly juveniles) were collected than in the second year which could be attributed to a summer drought. Rainfall in the summer months of 1994 (June, July, and August) was 35.28 cm while for the same months the following year was 15.49 cm (L. Lane, Weather Station, Horn Point Laboratory, pers. comm.) Although numbers collected in 1995 were much smaller, similar proportions of species were collected in both years.

Species composition was different among pond age categories as predicted. Pond treatments had only three species in common: *B. fowleri*, *R. catesbeiana*, and *R. sphenoccephala utricularius*. These species comprised the vast majority of the collections in both years. Numbers of each of these three species were also greater than all other species collected. Thus, *B. fowleri*, *R. catesbeiana*, and *R. s. utricularius* appear to be the most successful colonizers of newly-created ponds. However, the ability to colonize new ponds is probably facilitated by the large numbers of individuals of these species at the study location. Also, these three species colonized ponds within the first year of construction. Presumably, the ability to rapidly colonize ponds also contributes to large abundances in the area. In other studies, the European tree frog, *Hyla arborea*, colonized 60% of constructed ponds by the second season after construction (Edenhamn and Salonen 1996) and the tiger salamander, *Ambystoma tigrinum*, was found one year after wetland restoration (Sewell 1989).

Other, less frequently collected species were found only in certain treatments. For example, *A. crepitans* and *R. clamitans* were found only at young and old ponds. Similarly, *Ambystoma opacum* and *S. holbrookii* were found exclusively at old ponds. *Ambystoma opacum* was found only at OP2 in 1994. Restricted distributions observed in these species were also revealed by CCA.

In addition, the soil type of both old pond sites where *A. opacum* and *S. holbrookii* were collected (OP1, OP2) was sandy instead of the silty-clay loam types found at the other locations. Because *A. opacum* and *S. holbrookii* are both fossorial species, the substrate differences may explain their distributions although this was not analyzed.

Moreover, the temporary nature of OP1 and OP2 also excludes species with longer larval periods and eliminates fish predation. Fish predation would also be low at new ponds because fishes have not had sufficient time to become established, although a few small sunfish (*Enneacanthus gloriosus*) were dip-netted at Merrill pond. Fishes were also collected while dip-netting for larvae at all young ponds and at Lilypad pond. Blue-spotted sunfish (*Enneacanthus gloriosus*), eastern mosquitofish (*Gambusia holbrookii*), brown bullhead (*Ameiurus nebulosus*), red fin pickerel (*Esox americanus*), and eastern mudminnow (*Umbra limi*) were typically encountered. For the infrequently en-

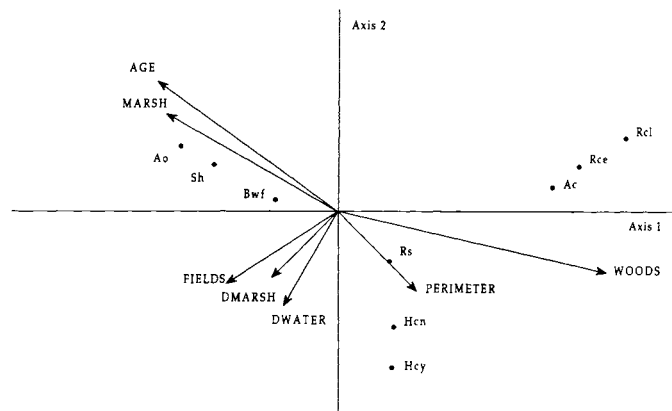


Fig. 6. CCA ordination diagram from 1994 data with amphibian species (●) and pond age and environmental variables (vectors). Codes for species are from Table 2 and codes for environmental variables are from Table 1.

countered amphibian species (*A. opacum* and *S. holbrookii*), apparently habitat type (soil and wetland duration) is especially important. Also, CCA showed that these species tended to avoid ponds extensively surrounded by woods. This could be due to the fact that no ephemeral ponds were sampled in heavily forested locations.

Hylid frogs were collected at two new ponds, Raleigh and Merrill, although their numbers were small. These frogs may have been collected only at new ponds because all new ponds were located on the eastern side of the study area. A single spring peeper (*Pseudacris crucifer*) was collected at Triangle Pond in 1995.

These distributional differences in composition and in the numbers collected are not easily explained by pond age. In fact, pond age does not appear to be the sole factor determining how many and which amphibians will use a given pond. Vectors representing environmental variables from the CCA ordination diagram (Fig. 6) can extend theoretically through the origin as axes. Longer environmental vectors are more strongly correlated with the ordination axes than shorter vectors and are thus more closely related to the pattern of variation in species composition depicted in the ordination diagram. Vectors depicting pond age (AGE), percent woods surrounding ponds (WOODS), and percent marsh surrounding ponds (MARSH) were relatively long (Fig. 6). Thus, these were the three most important environmental variables explaining species' distributions. These results also show that older ponds tended to be found in more marshy areas than younger ponds, which tended to be found in more wooded areas. Thus, because CCA showed age to be an important variable relative to the others, it should not be discounted entirely. Pond age, according to CCA, was most important for explaining the distributions of *A. opacum*, *B. fowleri*, and *S. holbrookii*. Overall, additional factors influenced the characteristics of the amphibian assemblages as evidenced by the large within-treatment variation.

Additionally, adult *R. sphenoccephala utricularius* from 1994 samples were found at new ponds more often than expected by chance. CCA supported this result by showing that this frog was associated with younger ponds with large perimeters. Also, *B. fowleri* adults were found less often at young ponds. It is not apparent from these data why toads were infrequently collected at young ponds.

Pond age can be used to predict some aspects of species composition. In both years some species were never found at new ponds (*A. crepitans*, *A. opacum*, *R. clamitans*, and *S. holbrookii*). CCA showed that in the case of *A. crepitans* and *R. clamitans*, the amount of woodland surrounding the ponds was more important than pond age. However, finding significant associations with pond age may be lim-

ited by sample size as no other associations were found for species less frequently captured and because dispersal capacities differ between species.

In CCA, species points can be projected perpendicularly upon the environmental axes showing the central position of a species' distribution along the environmental variable (ter Braak 1987). When a species point is projected toward the head of the environmental variable vector, it is more strongly and positively associated with that vector than a species that is projected near the origin or tail end of the vector. Species points projected near the origin of the environmental variable vector are associated with the average value of that variable. Thus, the order of the species points corresponds approximately to the ranking of the weighted averages of the species with respect to the magnitude of a particular environmental variable (ter Braak 1987).

Species points for *R. clamitans*, *R. catesbeiana* and *A. crepitans* show that these species preferred ponds surrounded by large areas of woods and tended to avoid the oldest ponds surrounded by large brackish marshes (Fig. 6). In contrast, species points for *B. fowleri*, *S. holbrookii*, and *A. opacum* show that these species preferred the oldest ponds surrounded by large marshy areas and avoided the ponds surrounded by large areas of woods (Fig. 6).

Estimates of amphibian diversity by Brillouin's index showed greatest overall diversity in young ponds, followed by old ponds and then new ponds in 1994. Higher diversity indices in young ponds can be attributed to the larger evenness found in this treatment. Measures of overall diversity in 1995 were still greatest in young ponds, but in contrast to the previous year, new ponds were the next most diverse followed by old ponds. Because 1995 was a drier year, captures were larger in new ponds where water remained than in two of the old ponds where desiccation occurred more rapidly than in the previous year.

In addition, amphibian richness was also different among the ponds and among the treatments overall. Rarefaction estimated greater amphibian richness in old ponds (given the same sample size) than in new ponds in 1994 and greater richness in young ponds than in new ones in 1995. Hemesath and Dinsmore (1993) showed that the age of restored wetlands (1, 2, and 3 years post-restoration) did not affect bird species richness. Wetland age in my study did affect amphibian richness presumably because the range of pond ages considered was larger and because amphibians may colonize sites more slowly.

Reproductive success was also examined by comparing abundances of larvae and ratios of juveniles: adults across treatments. Larval abundances were highly variable among the ponds and no differences in mean larval abundances were detected. Pond age does not appear to influence these reproductive measures. Aquatic conditions (pH, vegetative cover, average depth, predation by fishes, pond duration etc.) are likely to affect reproductive success more than pond age alone. However, no correlations were detected between those habitat variables measured and the abundances of larvae and juveniles in this study.

Although pond age does not account for many differences in abundance or for reproductive success of amphibians found at the constructed ponds, correlations between habitat/landscape variables and abundances yield some insights. For example, numbers of *A. crepitans* and *R. clamitans* were negatively correlated with percent agricultural fields. Although the percentage of agricultural fields surrounding new ponds was not significantly different from young and old ponds, all three new ponds directly abutted a field on one side (Merrill Pond), two sides (Pound Pond), and all sides (Raleigh Pond). Young and old ponds had agricultural fields nearby but the perimeters of all six ponds were completely surrounded by woods. This suggests that agricultural fields may be barriers for these species. Moreover,

cricket frogs (*A. crepitans*) are largely restricted to some immediate source of moisture (Pyburn 1958) which could make movements across fields difficult. CCA supported this finding by showing that these species were found at ponds with more surrounding woods and avoided ponds surrounded by large areas of agriculture. The detrimental impact of agricultural fields on amphibian migration and survival was documented by Wenderkinch (1988). Nitrogenous fertilizers associated with agriculture could also negatively affect amphibians (Tyler 1997). In contrast, *R. s. utricularius* adults seemed to prefer ponds which directly abutted fields and this could explain why they were associated with new ponds.

Other species found only at a particular pond age treatment were *A. opacum* and *S. holbrookii*. Both species were found at OP1 and OP2, which were temporary ponds that completely dried in early summer. Marbled salamanders migrate to dry pond basins in late summer and early fall to breed and deposit eggs (Shoop and Doty 1972). At the outset of the study it was not known that these two sites were ephemeral. *Scaphiopus holbrookii* is also known to prefer temporary breeding sites (Gibbons and Bennett 1974).

In conclusion, the construction of aquatic habitats for amphibian conservation is likely to become increasingly important as natural ponds and other wetlands are destroyed or altered. What appears to be most important for explaining differences in amphibian assemblages using constructed wetlands is the placement of these sites in the landscape (e.g., next to agricultural fields).

Wetland age in this study could not solely predict which species would be present at all pond ages or the extent of amphibian use (e.g., numbers collected) but it was closely related to the pattern of species composition revealed by CCA. However, differences in richness, diversity, and to some degree composition and abundance could be predicted by pond age. Some species were never found at new ponds. In fact, a large proportion of the species captured in both years were never sampled at new ponds (4/9 species in 1994 and 5/10 species in 1995). These ponds should be sampled in the future to determine if they ever become accessible or suitable for these species. As new ponds mature they may be colonized. Initially, new ponds will likely increase the abundance of rapidly colonizing species (e.g., *B. fowleri*, *R. catesbeiana*, and *R. s. utricularius*) and if given enough time and succession they could become suitable habitat for some of the species found at the older sites. We predict that *A. crepitans* is likely to use new ponds in the future because a few individuals were observed in 1995 near Merrill Pond. Additional sampling methods (in addition to drift-fences) should be used in future studies (Jones 1986) because some species (e.g., hylids) can circumvent the drift-fences.

Also, the effect of wetland age could have been obscured by site fidelity intrinsic to some amphibians. Site fidelity is common in many species of amphibians and could affect the distribution of amphibian assemblages sampled in this study. If amphibians return to their natal site to breed as adults, they would be unlikely to colonize newly-created ponds. If migration to the natal site results in higher fitness than random search, selection should act in favor of homing behavior (Sinsch 1992). However, homing behavior and site fidelity may have reduced importance for some species in locations where there are extensive wetlands. In fact, Fowler's toads (*B. fowleri*) have been shown to exhibit somewhat less site fidelity to the natal pond as the number of suitable sites in the area increases (Sinsch 1992). *Bufo fowleri* were always found using new sites in this study.

Finally, the effect of wetland age on the characteristics of amphibian assemblages in this study could have been hindered by tidal disturbances that essentially returned older ponds to an earlier stage of succession. Severe disturbances were observed in August of 1995 when high tides and the effect of hurricane Felix inundated many of the study ponds with brackish water. Salinity became as high as 14

% in one pond. Flooding with brackish water was extensive and larval traps were found under 30 cm of water at some ponds. Large mortality was observed for fishes, amphibians and other aquatic species including vegetation. Therefore, in other locations where disturbance is less likely to impact wetland communities, the effect of pond age on amphibian assemblages may be easier to observe.

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LITERATURE CITED

- ALTIG, R. 1970. A key to the tadpoles of the continental United States and Canada. *Herpetologica* 26:180-207.
- BLAUSTEIN, A. R. 1994. Chicken little or Nero's fiddle? A perspective on declining amphibian populations. *Herpetologica* 50:85-97.
- BLAUSTEIN, A. R., D.B. WAKE, and W.P. SOUSA. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology* 8:60-71.
- BRIGGLER, J. T. 1998. Amphibian use of constructed woodland ponds in the Ouachita National Forest. Unpubl. M.S. Thesis, University of Arkansas, Fayetteville, Arkansas.
- EDENHAMN, P. and A. C. SALONEN. 1996. The colonization ability of the European tree frog (*Hyla arborea* L.) in a landscape mosaic. Pages 65-87. *In* Spatial dynamics of the European tree frog (*Hyla arborea* L.) in a heterogeneous landscape. P. Edenhamn, PhD Thesis, Swedish University of Agricultural Sciences, Uppsala.
- FELLERS, G. M. and C. A. DROST. 1993. Disappearance of the cascades frog *Rana cascadae* at the southern end of its range, California, USA. *Biological Conservation* 65:177-181.
- GIBBONS, J. W. and D. H. BENNETT. 1974. Determination of anuran terrestrial activity patterns by a drift fence method. *Copeia* 1974:236-243.
- GIBBONS, J. W. and R. D. SEMLITSCH. 1991. Guide to the reptiles and amphibians of the Savannah River site. University of Georgia Press, London.
- GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183-190.
- HEMESATH, L. M. and J. J. DINSMORE. 1993. Factors affecting bird colonization of restored wetlands. *Prairie Naturalist* 25:1-11.
- HEYER, W. R., M. A. DONNELLY, R. W. MCDIARMID, L.-A. C. HAYEK, and M. S. FOSTER, eds. 1994. Measuring and monitoring biological diversity: Standard methods for amphibians. Smithsonian Institution Press, Washington, D.C.
- JONES, K. B. 1986. Amphibians and reptiles. Pages 267-290. *In* Inventory and monitoring of wildlife habitat. A.Y. Cooperrider, R.J. Boyd, and H.R. Stuart, eds. U.S. Department of Interior, Bureau of Land Management, Denver, Colorado.
- KREBS, C. J. 1989. Ecological methodology. Harper Collins, New York.
- LAAN, R. and B. VERBOOM. 1990. Effects of pool size and isolation on amphibian communities. *Biological Conservation* 54:251-262.
- LACKI, M. J., J. W. HUMMER, and H. J. WEBSTER. 1992. Mine-drainage treatment wetland as habitat for herpetofaunal wildlife. *Environmental Management* 16:513-520.
- MAGURRAN, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.
- MARTOF, B. S. 1953. Territoriality in the green frog *Rana clamitans*. *Ecology* 34:165-174.
- MATTHEWS, E. D. 1963. Soil survey of Dorchester County, Maryland. U.S. Department of Agriculture, Soil Conservation Service 26. Washington, D.C.
- METZGER, R. G. 1973. Wetlands in Maryland. Maryland Department of State Planning Publication No. 157, Baltimore, Maryland.
- OWENS, J.P. and C.S. DENNY. 1986. Geologic map of Dorchester County. State of Maryland Department of Natural Resources, Maryland Geological Survey, Baltimore, Maryland.
- PALMER, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74:2215-2230.
- PETCHMANN, J. H. K. and H. M. WILBUR. 1994. Putting declining amphibian populations in perspective: natural fluctuations and human impacts. *Herpetologica* 50:65-84.
- POLSON, S. H. 1997. Amphibian assault. *National Parks* 71:2215-2230.
- PYBURN, W. F. 1958. Size and movements of a local population of cricket frogs (*Acris crepitans*). *Texas Journal of Science* 10:325-342.
- RASMUSSEN, W. C. and T. H. SLAUGHTER. 1957. The ground-water resources. Pages 1-13. *In* The water resources of Caroline, Dorchester, and Talbot Counties. W. C. Rasmussen, T. H. Slaughter, A. E. Hulme, and J. J. Murphy, eds. Maryland Department of Geology, Mines and Water Resources. Waverly Press, Inc., Baltimore, Maryland.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223-225.
- RITTER, M. W. 1993. Rapid colonization of a human-made wetland by Mariana common moorhenon Guam. *Wilson Bullerin* 105:685-687.
- SEWELL, R. W. 1989. Flora and faunal colonization of restored wetlands in west-central Minnesota and Northeastern South Dakota. Unpubl. M.S. Thesis. South Dakota State University, Brookings, South Dakota.
- SHAFFER, H. B., R. A. ALFORD, B. D. WOODWARD, S. J. RICHARDS, R. G. ALTIG, and C. GASCON. 1994. Quantitative sampling of amphibian larvae. Pages 130-141. *In* Measuring and monitoring biological diversity: Standard methods for amphibians. W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster, eds. Smithsonian Institution Press, Washington.
- SHOOP, R. C. and T. L. DOTY. 1972. Migratory orientation by marbled salamanders (*Ambystoma opacum*) near a breeding area. *Behavioral Biology* 7:131-136.
- SINSCH, U. 1992. Amphibians. Pages 213-233. *In* Animal Homing. F. Papi, ed. Chapman and Hall, New York.
- SOKAL, R. R. and F. J. ROHLF. 1995. Biometry: The principles and practice of statistics in biological research. Freeman and Company, New York.
- TER BRAAK, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167-1179.
- TER BRAAK, C. J. F. 1987. Ordination. Pages 91-173. *In* R.H.G. Jongman, C. J. F. ter Braak, and O. F. R. van Tongeren, eds. Data analysis in community and landscape ecology. Pudoc, Wageningen, The Netherlands.
- TER BRAAK, C. J. F. 1988. CANOCO: a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis (Version 2.1). Report LWA-88-02. Agricultural Mathematics Group, Wageningen, The Netherlands.
- TYLER, M. J. 1997. Herbicides kill frogs. *Froglog* 21:2.
- WENDERKINCH, E. 1988. Population size, migration barriers, and other features of *Rana dalmatina* populations near Krge, Zealand, Denmark. *Memoranda Societatis pro Fauna et Flora Fennica* 64:101-103.
- WILBUR, H. M. 1980. Complex life cycles. *Annual Review of Ecology and Systematics* 12:167-93.
- ZAR, J. H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey.