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To assess amphibian declines, the factors that cause natural fluctuations in population size must be considered (Pechmann et al. 1991). Interspecific competition, predation and pond drying are known to influence patterns of distribution and composition of larval amphibian assemblages (Morin 1983, Brodman 1996, Skelly 1996). While a few studies have quantified amphibian patterns across a large number of ponds, most studies on breeding pond distributions have typically focused on pond characteristics associated with pairs of coexisting species (Thompson and Gates 1982, Skelly 1996). Little has been examined about the differences among the spatial distributions of all potentially interacting amphibian populations within a region of sympatry. Detecting the degree of distribution segregation among amphibian species is the first step towards understanding multispecies interactions and their effect on the development and maintenance of community structure (Skelly 1996, Welborn et al. 1996).

Recent surveys and atlas projects are providing detailed information on the density and spatial distributions of amphibian populations in the Midwest (VanDeWalle et al. 1996, Brodman and Kilmurry 1998, Mossman et al. 1998). Questions arise as to whether the spatial distribution of a population has changed over time, or if the populations of two species have the same distribution (Syrjala 1996). Pairs of species can differ significantly in two ways: (1) their distributions are disjunct or only slightly overlapping, or (2) the distributions of the density gradients differ (Fig. 1). Syrjala (1996) has developed a nonparametric statistical procedure, based on a generalization of the Cramer-von-Mises test, to test the null hypothesis that there is no difference in the spatial distributions of two populations. This test is sensitive to differences in spatial distributions and density gradients between two populations. By applying this method to data obtained from an amphibian survey, I propose to determine the degree of breeding pond segregation among species of amphibians over an area of sympatry. This study will attempt to evaluate the usefulness of Syrjala's distributional test in determining patterns of community composition.

METHODS

A survey of amphibians was conducted in Jasper County, Indiana, in the springs and summers of 1994–96 (Brodman and Kilmurry 1998, Brodman et al. 1999). Population density data from a total of 13 species were systematically collected from wetlands throughout the county. A total of 316 wetlands had amphibian populations. Because *Siren intermedia* (western lesser siren) and *Notophthalmus viridescens* (red spotted newt) were only found at two sites each, only the 11 most common species were included in this analysis. To determine estimates of relative population abundance and breeding intensity at sites, data were gathered using nighttime anuran call surveys and catch per unit effort sampling methods and then converted to a rating on an ordinal scale of 0–5 (Karns 1986, Heyer et al. 1994).

A QuickBASIC program of the nonparametric Syrjala test (Syrjala 1996) was used to examine whether the observed differences in the distribution of each species-pair were significantly different. A spatial distribution function is constructed across the study area from measurements of population density at each location. The test statistic is the squared difference between two cumulative distribution functions summed over all sampling locations. For example, the densities of two species at each wetland are used to recalculate the test statistic for a number of randomly selected permutations. A permutation test differs from most statistical methods in that instead of comparing a computed test statistic to a known distribution of the statistic, it repeatedly and randomly recalculates the original data, each time recomputing the test statistic generating an empirical distribution of computed values (Syrjala 1996). The P-value is then determined by evaluating where that actual test statistic falls in this empirical distribution. In order to evaluate the sensitivity of the test to the number of permutations calculated, tests were run twice at both 400 and 1000 permutations. Because the hypothesis test is nonparametric, there are no assumptions required about the distributions of the two populations.

RESULTS AND DISCUSSION

All species were found to coexist with each of the other species in at least one site. The distributions of 55 species pairs were tested using the Syrjala test resulting in 38 significant differences among species at the $P < 0.05$ level (Table 1). All of the species within families or genera were significantly different from each other except among toads (*Bufo*) and leopard frogs (*Rana pipiens*) which tended not to differ from most other species.

Edgington (1980) recommends a minimum of 1000 permutations. However, there was no difference in the significant vs. non-significant differences among pairs of amphibians obtained from 400 vs. 1000 permutations. Running 400 permutations was adequate in this analysis and saved computer time.

Questions arise as to what the biological significance is when two species are shown to have statistically significant differences in spatial distributions. The next step is to characterize that difference (Syrjala 1996).

Data on habitat use and interactions with other species need to be collected. For example, the two most common species in my study area, spring peeper (*Pseudacris crucifer*) and western chorus frog (*P. triseriata*) tadpoles occur together in 40.4% of the breeding ponds utilized by these species. They were found to have significantly different spatial distributions (Table 1). Skelly (1996) found that these species co-occurred in most of the ponds studied in southeastern Michigan, but there was a large amount of variation in relative abun-

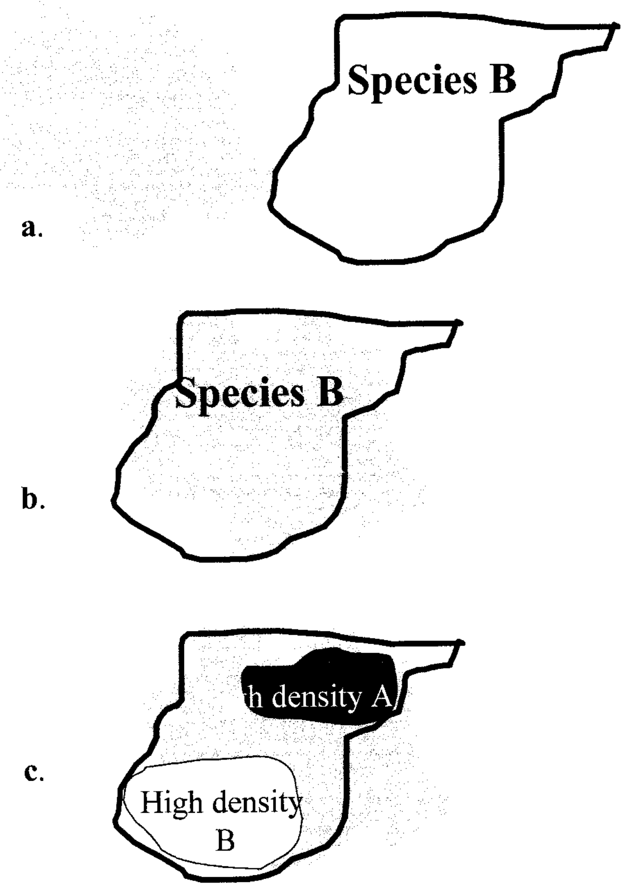

Fig. 1. Three theoretical spatial distributions of species 1 and species 2 are (a) clearly different and non-overlapping, (b) broadly overlapping with no differences in density gradients, and (c) broadly overlapping but with differences in density gradients. The Syrjala test can determine that scenario a and c indicate significant differences in the way that species 1 and 2 are distributed.

dance. Chorus frogs grew faster to metamorphosis and were more common in the most temporary ponds while spring peepers were most abundant in the more permanent ponds and avoided predation more effectively. Similar analyses should be done on other commonly co-occurring species that have significantly different spatial distributions.

The Syrjala test on population density data can be useful in studying amphibian communities in several ways. First, it can indicate the heuristic value of which pairs of co-occurring species are likely to demonstrate microhabitat partitioning, differential predator avoidance abilities or interspecific competition that affect community structure. I predict that closely related species that do not differ significantly in spatial distribution, such as American toads (*Bufo americanus*) and Fowler's toads (*B. fowleri*), are less likely to be experiencing intense interspecific competition or microhabitat partitioning than the hylid treefrogs (*Hyla* and *Pseudacris*), which have significantly different spatial distributions. Another use of this procedure is to detect changes in the distribution of a species over time. This may be important in long-term amphibian population monitoring programs because of some findings that high rates of species turnover can occur at sites within a metapopulation (Hecnar and M'Closkey 1996, Skelly et al. 1998). Preliminary findings here indicate that the northern leopard frog (*Rana pipiens*) is one such species that has significantly different spatial distributions from year to year (1994–96, P = 0.002) because of high turnover rates at specific sites within a metapopulation context. Some declines in amphibians may be confounded by changes in spatial distribution resulting from declines in some areas and increases in others. More studies should be done on differences among the spatial distribution of sympatric amphibians in other areas where population density data have been collected.

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Table 1. Results of the Syrjala test on the spatial distribution of amphibians. Data are given as P-values, significant differences ($\alpha \leq 0.05$) are underlined. Species are: Hylidae—*Pseudacris crucifer* (pc), *P. triseriata* (pt), *Hyla versicolor* (hv), *H. chrysoscelis* (hc); Bufonidae—*Bufo americanus* (ba), *B. fowleri* (bf); Ranidae—*Rana pipiens* (rp), *R. clamitans* (rcl), *R. catesbeiana* (rct); Ambystomatidae—*Ambystoma laterale* (al), *A. tigrinum* (at).

	pc	pt	hv	hc	ba	bf	rp	rcl	rct	al	at
pc	—	0.014	0.003	0.008	0.161	0.088	0.171	0.004	0.002	0.167	0.002
pt		—	0.002	0.018	0.131	0.094	0.071	0.006	0.004	0.146	0.001
hv			—	0.002	0.011	0.112	0.304	0.045	0.002	0.321	0.001
hc				—	0.178	0.008	0.092	0.004	0.006	0.802	0.001
ba					—	0.157	0.132	0.019	0.004	0.179	0.001
bf						—	0.364	0.121	0.002	0.633	0.001
rp							—	0.694	0.126	0.421	0.001
rcl								—	0.012	0.227	0.002
rct									—	0.423	0.001
al										—	0.002
at											—

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