

IDENTIFYING THE MINIMAL DEMOGRAPHIC UNIT FOR MONITORING POND-BREEDING AMPHIBIANS

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Abstract. Amphibians are declining globally, and efforts are underway to establish long-term programs to monitor population trends. Because researchers are constrained to sampling a small subset of populations that occur across a landscape, monitoring units should be selected that maximize the statistical independence of population responses to environmental stressors. Breeding sites of pond-breeding amphibians are often clustered locally, and habitat switching between neighboring ponds could significantly compromise both demographic and statistical independence. This raises a fundamental issue of whether the basic monitoring unit for trend analysis should be an individual pond or a cluster of local ponds. To help resolve the degree of demographic independence within a cluster of local ponds, we conducted a spatial-scale analysis of breeding-population synchrony of the wood frog (*Rana sylvatica*) and spotted salamander (*Ambystoma maculatum*) in four national parks in Kentucky, North Carolina, and Tennessee, USA. We used the number of egg masses deposited annually from 1993 through 2002 as an index of relative breeding-population size and used correlation coefficients of annual percentage change in population size as an index of synchrony.

Within parks, synchrony for both species was independent of the distance between ponds and was lower between paired ponds within a local cluster compared with paired comparisons of geographically isolated groups. These patterns indicate a lack of demographic independence within clusters and are consistent with field observations of wholesale shifting of local pond populations to adjoining ponds. Habitat shifting occurred primarily in response to beaver activity that created new ponds or allowed fish to invade fish-free habitats. *Ambystoma maculatum* shifted habitats less frequently and exhibited higher levels of within-cluster population synchrony than *R. sylvatica*. Turnovers occurred for local pond populations for both species and at higher rates for *R. sylvatica*. However, no local pond cluster experienced a turnover event during the study. Our data suggest that pond populations that are only a few hundred meters apart are not demographically independent and are best treated as subpopulations of the same monitoring unit. We discuss the implications of these findings for amphibian-monitoring programs that are designed to assess population trends.

Key words: *Ambystoma maculatum*; amphibian monitoring; amphibians, declining; amphibians, pond breeding; disturbance and site philopatry; monitoring unit, minimal size to assess trends; population synchrony; population turnover; *Rana sylvatica*; spatial-scale analysis.

INTRODUCTION

Amphibians are undergoing a global decline (e.g., Stebbins and Cohen 1995, Beebee 1996, Drost and Fellers 1996, Sarkar 1996, Green 1997, Houlihan et al. 2000, Davidson et al. 2002). However, long-term studies of North American species have rarely been conducted, and population trends for most species are undocumented. Monitoring efforts to date have gravitated towards two general approaches: documenting changes in the total number of populations found across the landscape, and monitoring trends of local populations using repeated annual censuses. Long-term stud-

ies of population trends have rarely been conducted and have involved one or a few local populations (e.g., Hairston and Wiley 1993, Semlitsch et al. 1996, Cortwright 1998, Meyer et al. 1998). As a result, the extent to which local population trends reflect landscape or regional patterns is largely unknown.

Pond-breeding amphibians are important faunal elements of small freshwater wetlands and are the primary ecological group used in most monitoring programs in north-temperate regions. A critical but unresolved issue with respect to monitoring pond breeders concerns the minimal demographic unit that should be used to assess trends. Breeding ponds are spatially discrete and often exhibit varying degrees of clustering across the landscape. Researchers typically are constrained to monitoring a small subset of all populations within a region. Ideally, the smallest unit used for mon-

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PLATE 1. Gum Swamp (PC in Fig. 4) is a seasonal pond in the Great Smoky Mountains National Park that provides breeding habitat for several amphibians. The inset shows an egg mass of the wood frog, *Rana sylvatica*. Photo credit: J. W. Petranka.

itoring should have a high degree of demographic and statistical independence. That is, the basic monitoring unit should provide a relatively independent measure of the effects of environmental stressors on focal species.

Pond populations that are in very close proximity may lack demographic independence if adults treat a cluster of ponds (i.e., a set of local ponds with adjoining ponds separated by a distance that is less than the average dispersal distance of a species) as a single breeding habitat and switch freely among sites. Ecological experiments demonstrate that gravid females will avoid ovipositing in experimental ponds or natural pools where future offspring may experience intense competition or high predation risk (Resetarits and Wilbur 1989, Kats and Sih 1992, Hopey and Petranka 1994, Petranka et al. 1994, Spieler and Linsenmair 1997). Although the ecological scale of behavioral avoidance is poorly resolved, wholesale shifts in breeding congregations between local ponds in response to predators, competitors, altered seasonal hydrology, or the creation of new habitats would severely compromise demographic independence. As a result, selection of a single pond within a cluster as a monitoring unit might provide a false representation of true demographic trends. For example, a local pond population might decline following fish invasion due to behavioral switching to adjoining sites, even though the population utilizing the entire pond cluster remains stable. Alternatively, if site fidelity to natal ponds is high as suggested by some studies (Gill 1978, Richter 1997, Pechmann et al. 2001), then local pond populations within a cluster may have sufficient demographic independence to qualify as basic monitoring units.

Pond breeders have traditionally been viewed as showing strong site fidelity and as being organized as metapopulations; however, this characterization may or may not hold depending on spatial scale (Marsh and

Trenham 2001). An issue particularly relevant to developing efficient monitoring programs and conservation management plans is whether local populations that utilize clusters of ponds function as a single, essentially panmictic, population or as a metapopulation consisting of several discrete populations. The former would occur if movement between local ponds is so high that subgroups behave as a single breeding unit (Harrison 1991). The latter would occur if movement between ponds is greatly restricted due to site philopatry, barriers to dispersal, or distances between ponds exceeding the average dispersal distances of metamorphs.

Studies of population synchrony at different spatial scales can provide insights into the extent to which local clusters of populations are demographically independent. Studies of a variety of organisms indicate that population synchrony usually declines with the distance between adjoining populations (e.g., Moran 1953, Ranta et al. 1998, Ripa 2000). Several factors may contribute to relatively high levels of synchrony between local populations, including exposure to common stochastic events such as annual weather patterns (the Moran effect), dispersal of large numbers of juveniles from a large population to surrounding smaller populations, or the effects of wide-ranging predators that feed on patches of prey. These factors would all operate to produce higher positive synchrony between local populations of pond-breeding amphibians compared with more geographically isolated populations.

In contrast, behavioral switching between local habitats would counter factors that generate positive synchrony. In the simplest case where a local cluster contains only two ponds, strong switching could produce negative (inverse) synchrony. Where more than two ponds occur within a local cluster, strong behavioral switching might reduce local synchrony to levels that

are lower than those of more geographically isolated and demographically independent populations.

Our present work provides an analysis of spatial patterning of population synchrony for two seasonal pond specialists in the southeastern United States. It is the first that we are aware of to examine long-term population dynamics in a broad array of local and regional populations, and overcomes limitations of past demographic studies that have been confined to one or a few populations. It also spans a sufficient length of time to provide insights into the dynamics of breeding habitats with respect to physical and biotic perturbations. The primary objectives of the study when initiated in 1993 were: (1) to analyze patterns of spatial synchrony to gain insights into the smallest demographic unit that is suitable for monitoring these species, (2) to examine how estimates of non-trend variation and statistical power for detecting trends are influenced by duration of study, population grouping, population size, level of local disturbance, and other relevant factors, and (3) to examine long-term population trends of the focal species at different spatial scales and population groupings. This work focuses on (1); the remaining aspects of the study will be addressed in future publications.

METHODS

Overview of monitoring program and site dynamics

We began a long-term monitoring program for the wood frog (*Rana sylvatica* Le Conte) and spotted salamander (*Ambystoma maculatum* [Shaw]) in 1993–1994 using 31 ponds that comprised four regional clusters (Fig. 1; specific locations are in Petranka and Smith [1995] and are available through the U.S. National Park Service). These included nine ponds in southeastern Kentucky (USA) within Cumberland Gap National Historical Park (CUGA), six ponds in west-central Kentucky within Mammoth Cave National Park (MACA), nine ponds in northwestern North Carolina (USA) within the Blue Ridge Parkway (BLRI), and seven ponds in eastern Tennessee (USA) within the Great Smoky Mountains National Park (GRSM; see Plate 1). We selected ponds that would facilitate an analysis of breeding-population synchrony at different spatial scales. These include population trends for individual ponds, for local clusters of ponds, for geographically isolated ponds or pond clusters within parks, and for entire park populations across the study region. Where clusters occurred, we monitored all ponds within a cluster.

We phased in the monitoring program over two years (first year of sampling = 1993 for GRSM and CUGA, 1994 for BLRI and MACA) and estimated relative breeding-population size annually through 2002 using egg-mass counts. At most sites we obtained data on breeding-population size for 9 (BLRI) or 10 (CUGA; GRSM) breeding seasons. We terminated the program at MACA after 1998 (5 breeding seasons) due to funding and logistical constraints.

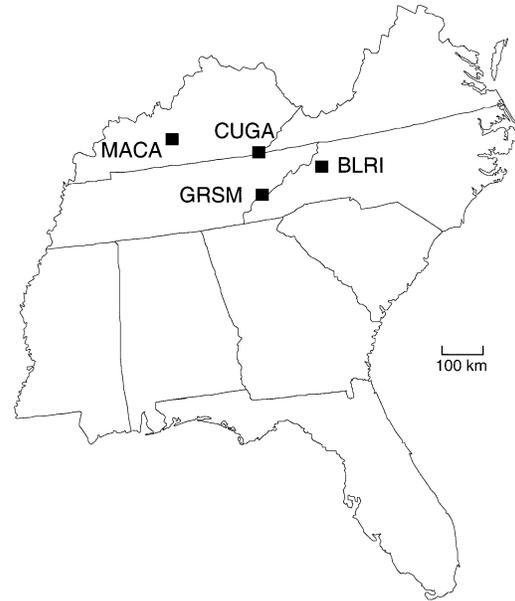


FIG. 1. Location of the four national parks in the United States where monitoring programs were conducted. Exact locations of ponds within parks are in Petranka and Smith (1995). BLRI = Blue Ridge Parkway (9 ponds), CUGA = Cumberland Gap National Historical Park (9 ponds), GRSM = Great Smoky Mountains National Park (7 ponds), and MACA = Mammoth Cave National Park (6 ponds).

Several ponds were isolated from nearest known ponds by a distance that exceeded the average reported dispersal distance of *R. sylvatica* (~1200 m for juveniles; Berven and Grudzien 1990; $N = 8$ ponds) or *A. maculatum* (<200 m for adults; Petranka 1998, Semlitsch 1998; $N = 8$ ponds). We treated each of these as a local pond population and designated each as a “geographic isolate.” One exception is that we treated two pond populations that were an estimated 360 m apart in BLRI as being separate geographic isolates because they were isolated by a major barrier, the Linville River. All other ponds were members of local clusters.

Ponds within a cluster occurred within 400 m of adjoining ponds and 83% were within 100 m of nearest neighbors. Breeding-population structure within these clusters could range along a gradient from sets of ponds that support a single panmictic population due to high rates of inter-pond movement, to metapopulation organization (McCullough 1996). We designated each cluster of local ponds as a geographic isolate (mean distance between isolates = 9.7 km) and treated three pairs of clusters in relatively close proximity (0.8–0.9 km apart) as being separate because of major barriers to dispersal. As used here, the term “geographic isolate” refers to either an isolated pond or an isolated cluster of ponds, i.e., groups in which immigration from adjoining isolates is assumed to be a rare event. When comparing similarities among geographic isolates, we used either the number of egg masses in an

isolated pond or the total number of masses for a local cluster of ponds.

At the initiation of the study all ponds were fish free, <1 ha in extent, and surrounded by hardwood or mixed conifer-hardwood forests that provided habitat for juveniles and adults. Perturbations during the study altered some of these original conditions. In BLRI and CUGA new ponds were created within 200 m of existing ponds due to beaver activity. In a few instances ponds that adjoined streams were connected to streams for one year or more, allowing fish invasion. These typically reverted to fish-free status within one to three years after dams washed out or were eliminated by park personnel. Fish invaded a few ponds that adjoined streams following bank overflow. One pond in CUGA dramatically increased in size (<0.5 ha to >1–2 ha) in certain years due to impoundment by beavers. In addition, a cluster of three seasonal ponds was created at CUGA in autumn of 1998 as part of a wetlands-mitigation project. These were within 250 m of three ponds selected in 1993 for monitoring, and to a degree mimicked the creation of fish-free ponds by beavers. All ponds created during the study were monitored and the initial year of filling was treated as year 1. At sites where new ponds were created within 400 m of existing ponds, we included egg-mass counts in new ponds as part of the total for a local geographic isolate.

Sampling protocol for egg masses

Rana sylvatica and *A. maculatum* are seasonal-pond specialists. They rarely use permanent ponds with predatory fish but may use permanent ponds that lack fish. Most breeding sites that were selected were vernal ponds or abandoned beaver ponds. Seasonal habitats fill in late fall or early winter, and *R. sylvatica* and *A. maculatum* begin breeding with the late-winter warm-up.

Wood frogs are synchronized breeders. Each female lays a single egg mass and >90% of females in a local population often breed within a 1-wk period. Adults congregate locally in ponds to breed and the egg masses are laid in large rafts (dense aggregates of egg masses). Adults at our sites typically breed from February through mid-March following one or more days of warm weather. Rainfall is not required to stimulate adults to migrate to ponds or to breed. In contrast, *A. maculatum* migrates and breeds during rainy weather. Local populations usually have two or three major breeding bouts from February through early April with successive rainfall events. Females deposit 1–4 conspicuous egg masses, usually attached to tree limbs or other support structures (Petranka 1998).

Breeding activity of both species varies within and between parks. In particular, sites in BLRI are at relatively high elevations and breeding normally occurred two to three weeks after breeding in other parks. Within CUGA, BLRI, and GRSM breeding at one or two sites occurred consistently later than at the remaining sites

within each park. These sites received less solar insolation due to shading or local topography and often were exposed to different rainfall regimes compared with other park populations. Within a cluster of local ponds, seasonal breeding activity was similar for all pond populations.

We selected *R. sylvatica* and *A. maculatum* as focal species because the egg masses can be accurately censused to provide a quantitative measure of the relative size of female breeding populations (e.g., Crouch and Paton 2000). Our goal was to estimate relative changes in breeding-population size using the cumulative number of egg masses laid each year. We conducted an initial census shortly after the first breeding bout, then made 2–5 additional seasonal censuses until no new masses were observed following conditions that were suitable for breeding. Because the large egg masses of the two focal species can be counted with little error, our seasonal counts provide a reliable estimate of relative reproductive effort and a quantitative basis for detecting long-term population trends.

At each site we systematically waded through all areas of the pond and counted egg masses. One or more individuals often assisted and we used polarizing sunglasses when needed to reduce surface glare. We attempted to initially sample *R. sylvatica* within 5–10 d after the initial major breeding bout because the masses in egg rafts fuse with time and are difficult to distinguish. In a few instances, egg masses in rafts fused prior to the initial site visit and could not be counted directly. In such cases we estimated the number of masses using a regression equation derived from previous data on raft surface area vs. the number of egg masses (number of masses = $30.7 \times [\text{raft area in square meters}] + 11.6$; $P < 0.0001$; $r^2 = 0.88$). For *R. sylvatica* we estimated the relative size of the breeding population based on the cumulative number of masses laid each season.

Ambystoma maculatum has a prolonged embryonic period. Inspection of data and field observations indicated that egg masses are often lost to predators such as wood frog tadpoles (Petranka et al. 1998) near the end of the incubation period. Because penultimate counts often slightly exceeded final seasonal counts, we used the highest egg-mass count for the season as an estimate of relative breeding effort.

Population turnover and site perturbations

For comparative purposes, we adopted Hecnar and M'Closkey's (1996) criterion of considering a pond population to have gone locally "extinct" if no egg masses, larvae, or breeding adults were observed during the breeding season at a site where breeding occurred the previous year. We calculated annual turnover rates as the number of ponds where a species was absent divided by the total number of ponds occupied during the previous year. The absence of breeding adults or egg masses at a site for one year may not reflect a true

demographic extinction (Marsh and Trenham 2001), particularly for spotted salamanders that are long lived and are known to occasionally skip a breeding season. As such, we view our estimates of turnover rates as a relative index that is useful for comparing between groups and with other published studies.

The systems that we monitored were dynamic with respect to site perturbations, and we recorded events that might trigger habitat switching among local ponds. Beaver activity was the most conspicuous source of perturbations and often resulted in the creation of new ponds or the invasion of fish-free ponds by fish. Other significant changes included the creation of three constructed ponds in CUGA, the elimination of the deepest area of one breeding pond in CUGA by storm damage that resulted in a large tree falling in a pond, the progressing filling of one small pond by growth of *Sphagnum* moss, and the failure of some small ponds ($N = 2$ ponds in GRSM) to fill during a regional drought that occurred from 1998 through 2002. Years when ponds did not fill were excluded when calculating turnover rates.

Statistical analyses

Because the absolute number of egg masses in ponds differed markedly, we expressed changes in breeding effort as the percentage difference from year 1. Ponds that contained <9 masses during the first year of sampling ($N = 1$ and 7 ponds for *A. maculatum* and *R. sylvatica*, respectively) were excluded from analyses of individual ponds because of small sample size and the unreliability associated with expressing change as a percentage of year 1 when values are small (e.g., a change from 1 to 15 masses would constitute a 1500% increase in population size). However, egg-mass counts for these ponds were included as part of egg-mass tallies for geographic isolates.

To examine whether population synchrony is influenced by geographic distance between ponds or population membership (e.g., within vs. between geographic isolates), we generated Pearson product-moment correlation coefficients for all pairwise comparisons of different groupings using the change in numbers of egg masses for yearly increments (e.g., 1994–1995; 1995–1996; etc.), expressed as a percentage of year-1 values. We estimated distances between paired ponds from topographic maps or direct field measurements and classified pairs as being members either of the same geographic isolate or of different isolates.

Correlation coefficients can be used as an index to indicate both positive and negative synchrony. The former would generate positive coefficients and the latter negative coefficients. Paired populations that fluctuate randomly with respect to each other should have correlation coefficients that approximate zero. However, data points derived from all pairwise comparisons of ponds are not fully independent because data for individual ponds are used in multiple calculations of cor-

relation coefficients. To minimize the problem we relied on randomization methods (Edgington 1995, Driskell et al. 2001).

To examine synchrony in annual changes in population size we compared the observed mean for correlation coefficients to a set of 1000 correlation coefficients that were derived through randomization procedures. Annual changes in population size for all ponds or geographic isolates were pooled, then randomized with respect to year and site. We ran correlations between two sets of randomly selected data points ($N = 1000$ iterations), with sample sizes corresponding to the number of actual pairs for each groupings. The 1000 values were ranked and the proportion that were higher than the mean correlation coefficient provided an exact P value. We compared correlation coefficients for three groups: (1) ponds within the same geographic isolate, (2) ponds in different isolates within the same park, and (3) different isolates within the same park. Estimated mean distances, d , between paired groups were: ponds within the same isolate, $d = 87$ m (range, 1–400 m); ponds in different isolates, $d = 8.34$ km (range = 0.7–26.9 km); and different isolates, $d = 9.7$ km (range = 0.8–26.9 km). Randomization tests were also used for pairwise comparisons of means using the observed difference between means compared with differences generated by randomly assigning values to treatments ($N = 1000$ iterations). We used the Mantel test with 1000 iterations to examine relationships between the distance between paired ponds or geographic isolates and synchrony. Relationships were examined for all ponds within a park, all geographic isolates within a park, and all geographic isolates, irrespective of park affinity (regional trends).

RESULTS

Evidence of habitat switching and lack of site philopatry

Although *Rana sylvatica* and *Ambystoma maculatum* have been characterized as being moderately to strongly philopatric to breeding ponds (Shoop 1968, Berven and Grudzien 1990), we observed several instances in which site disturbances greatly decreased philopatry. At both BLRI (Blue Ridge Parkway) and CUGA (Cumberland Gap National Historic Park), beavers invaded areas with study ponds and either created new ponds or allowed predatory fish to invade fish-free habitats. A common response that was most evident for *R. sylvatica* was for a significant portion (often the majority) of the population to breed in adjoining ponds following site disturbance. We discuss three examples in detail below.

At BLRI beavers created a pond-marsh complex (PA4) during fall 1996 within 50 m of an isolated cluster of three shallow ponds (PA1–PA3). During the spring of 1997 an estimated 63% of all *A. maculatum* and 61% of *R. sylvatica* females in this geographic

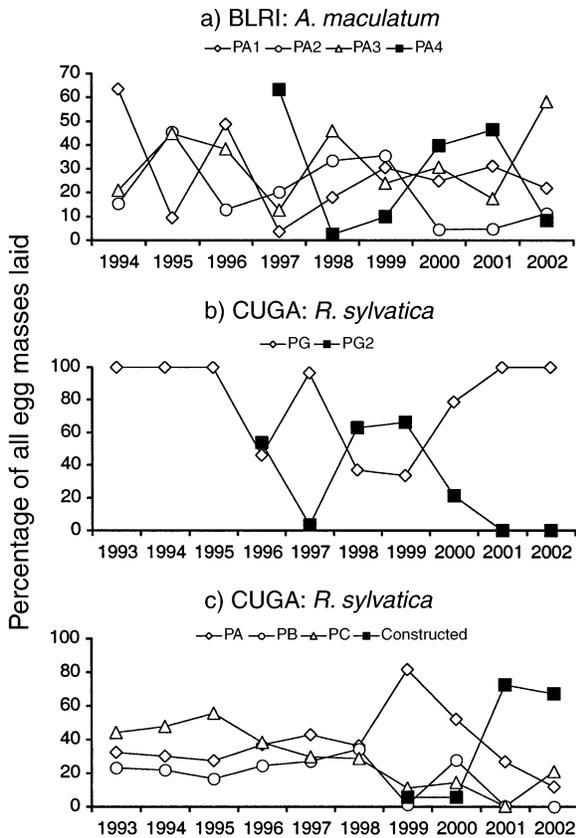


FIG. 2. Changes in relative reproductive effort among pond populations of *Ambystoma maculatum* and *Rana sylvatica* within the same geographic isolate. Data are the number of egg masses laid annually and are expressed as a percentage of the total number of masses for each geographic isolate (cluster of local ponds). New breeding sites that were created during the study are indicated with solid squares. Codes are for individual ponds except for PA4 (a pond-marsh complex), PG2 (two connected beaver ponds), and "Constructed" (three constructed ponds in close proximity [see *Methods: Overview of monitoring* . . .]).

isolate used PA4, while the remainder bred in PA1–PA3. The dam of PA4 washed out in 1997 and the site was reduced to a series of small pools that provided marginal breeding habitat. The following year only 3% of *A. maculatum* and no *R. sylvatica* used the remnants of PA4, while the remainder of the isolate used PA1–PA3. PA4 reformed in 1999 following dam reconstruction by beavers, washed out again in 2000, and was rebuilt and remained intact from 2001 through 2002. During 2001 and 2002 fish invaded PA4 and *R. sylvatica* did not use the site in either year (egg masses = 0). Use by *A. maculatum* also declined markedly relative to the initial year when fish were absent (Fig. 2a).

Example 2 concerns a site in CUGA that supported an isolated vernal pond (PG) from 1993 through 1995. During autumn of 1995 beavers invaded the area and connected the site to an adjoining stream that allowed

fish invasion. Two new connected beaver ponds were created within 200 m of PG, changing the site from an isolated pond to a cluster of local ponds. In 1996, 54% of *R. sylvatica* females bred in the two newly constructed beaver ponds that contained very few fish (PG2; Fig. 2b). In 1997 fish were conspicuously more abundant in the PG2 complex and almost all adults bred in PG. Park personnel eliminated all beaver dams and associated fish populations in 1998 and 1999, and *R. sylvatica* extensively utilized both PG and a small pool that remained where PG2 drained. In 2000 beavers reformed the PG2 ponds and *R. sylvatica* responded by primarily breeding in the fish-free habitat (PG). In 2001 and 2002 beavers reinvaded all sites and both PG and PG2 held fish. Adults responded by breeding only in PG and laying eggs in a very shallow extension of the pond that lacked fish. Despite much evidence of habitat shifting, the population trend for 1993–2002 did not deviate significantly from zero (regression analysis of total egg-mass count on year: $P = 0.74$, $r^2 = 0.12$, slope = 8.14).

Surprisingly, *A. maculatum* females at PG did not respond by shifting to the newly created beaver ponds as seen in BLRI (<6 masses laid in PG2 annually from 1996 through 2002). Instead, annual breeding effort at PG declined by 99% from 178 egg masses in 1994 to only 2 egg masses in 1997. Numbers of egg masses have remained relatively low since 1997 (mean = 23 masses per year from 1997 through 2002). This suggests that fish predation and lack of juvenile recruitment may have acted demographically to reduce breeding-population size of *A. maculatum* from 1994 through 2002.

Fig. 2c shows the dynamics of *R. sylvatica* populations within a second geographic isolate at CUGA. Documented site perturbations from 1993 through 2002 included the invasion of fish into PC during certain years (1996, 1997), heavy siltation of PC in 1998 from overbank flow, the construction of three vernal ponds within 250 m of existing ponds as part of a wetlands mitigation site (1999–2002), and the reduction in effective breeding habitat at PB due to a large tree that fell into the deepest section of the pond in 1996. The most conspicuous pattern at the site was a marked shift of the breeding population from forested vernal ponds (PA–PC) to the sunnier and warmer mitigation ponds. An estimated 73% of females in this local geographic isolate bred in the created ponds two years after their initial filling. At PC the population responded to fish and siltation by decreasing relative use from 1996 through 1998. Relative use of PC increased markedly in 1999, but then declined in subsequent years as adults bred primarily in the newly constructed ponds. Use of PB declined markedly from 1999 through 2002, apparently in response to treefall and shifting of adults to newly created ponds. As at the PG complex, *A. maculatum* did not respond by utilizing newly created ponds (<5 masses per year from 1999 through 2002).

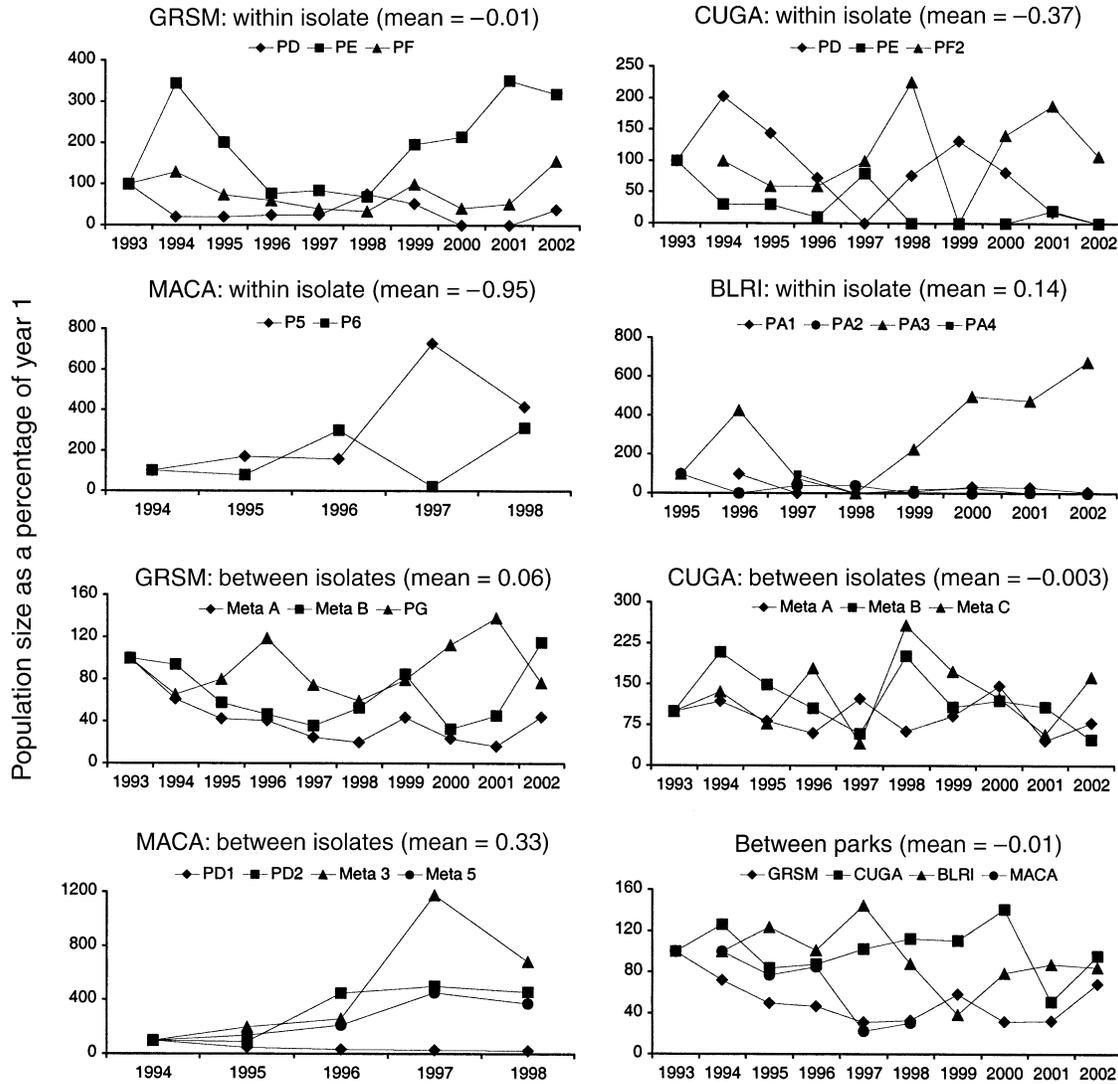


FIG. 3. Relative changes in the size of breeding populations of female wood frogs based on annual egg-mass counts. For comparative purposes, egg-mass counts are expressed as a percentage of the number laid in year 1 (first census). Labels above each panel indicate the park and group. Values for “mean” are the mean correlation coefficients for all pairings within the group and reflect the degree of synchrony in annual population change.

The response of *A. maculatum* to fish invasions and siltation at PC was similar to PG, with the population undergoing a general decline from a peak of 171 masses in 1994 to 0 masses in 2002.

Synchrony in annual population change

Examples of breeding population dynamics, variation in population synchrony, and calculated synchrony indices for different population groupings and spatial scales are in Figs. 3 and 4. Examples of both strong positive and negative synchrony occurred for both species. At the broadest geographic scale synchrony between entire park populations was relatively weak for both species (lower right panels of Figs. 3 and 4). Within parks, *Ambystoma maculatum* exhibited higher synchrony in annual population change than did *R. syl-*

vatica (Table 1). Synchrony in annual population change was statistically significant or nearly so for all three within-park pairings for *A. maculatum*, but no pairing was significant for *R. sylvatica* (Table 1). For both species, average population synchrony was similar for pairs within the same geographic isolate vs. pairs in different isolates (means for correlation coefficients for *A. maculatum*: = 0.32 vs. 0.26, $P = 0.67$; means for *R. sylvatica*: = 0.06 vs. 0.09, $P = 0.74$; Table 1). Average synchrony was also greater between geographic isolates than for paired populations from the same isolate, but differences were not significant ($P = 0.36$ and 0.79 for *A. maculatum* and *R. sylvatica*, respectively; means = 0.54 vs. 0.32 and 0.19 vs. 0.06, respectively; Table 1). This pattern is consistent with widespread evidence of habitat shifting among pond

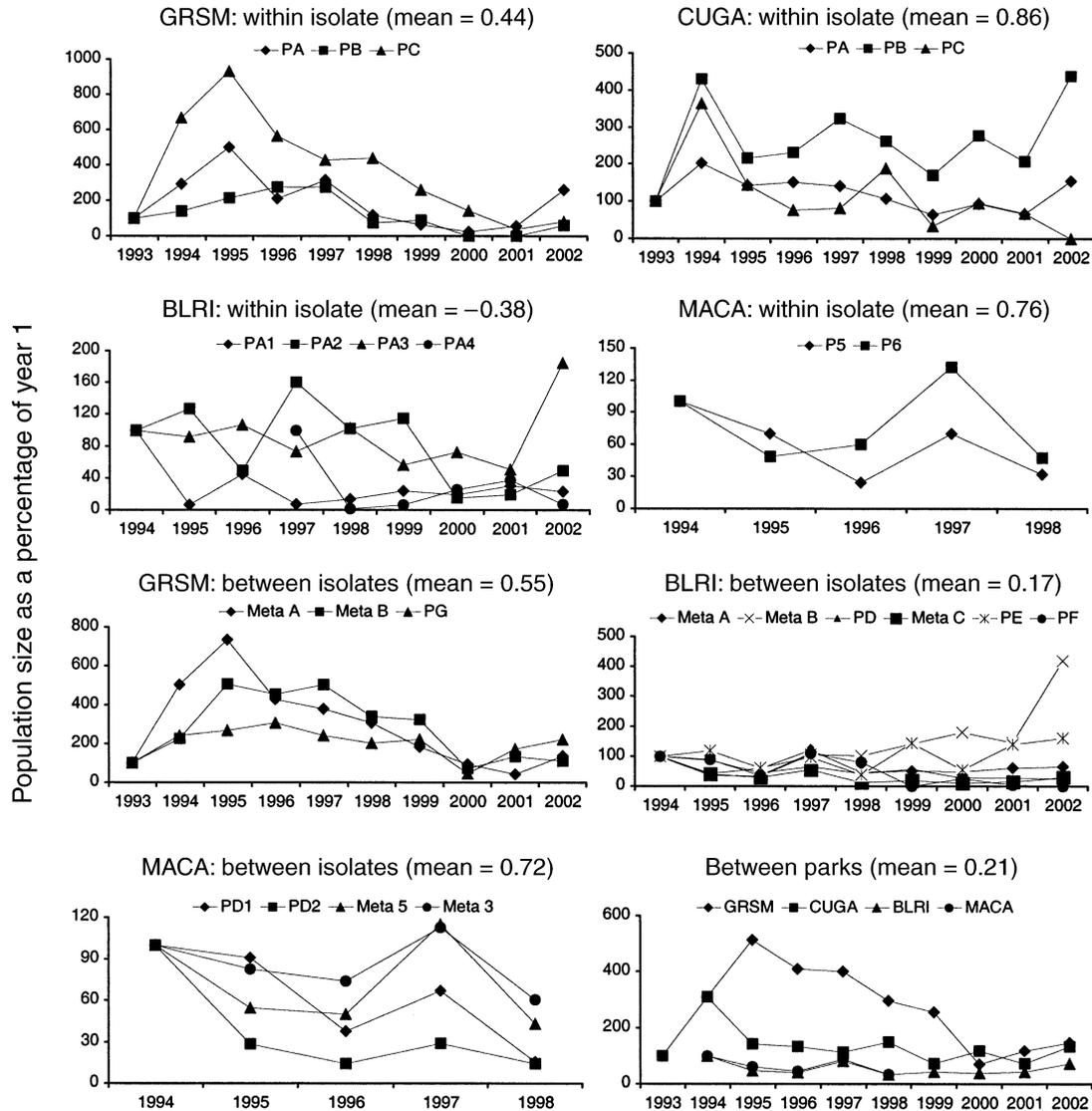


FIG. 4. Relative changes in the size of breeding populations of female spotted salamanders based on annual egg-mass counts. For comparative purposes, egg-mass counts are expressed as a percentage of the number laid in year 1 (first census). Format and values are as in Fig. 3.

populations within clusters, particularly for *R. sylvatica*. The fact that *A. maculatum* showed greater synchrony (mean correlation coefficient = 0.32) than *R. sylvatica* (0.06) for populations in the same geographic isolate is also consistent with our observations of greater habitat shifting by *R. sylvatica*. In general, population synchrony tended to be lower for contrasts of *A. maculatum* populations or geographic isolates where major perturbations from beaver activity or other factors occurred, with probability values exceeding or approaching significance (Table 2). In contrast, *R. sylvatica* populations and geographic isolates tended to change asynchronously, regardless of the degree of disturbance.

We examined relationships between pond distance and annual synchrony in population change for all pair-

wise comparisons of local pond populations within parks. We examined distance relationships for geographic isolates at two scales: within parks and for all geographic isolates across the region. For *A. maculatum* the population synchrony decreased with the distance between geographic isolates at both park and regional scales, but was independent of distance for paired pond populations (Table 3). For *R. sylvatica*, population synchrony was independent of distance for all contrasts.

Turnover rates

Local turnover for *A. maculatum* (i.e., absence of masses in ponds where masses were present the previous year) occurred for 3 of 31 ponds during the study

TABLE 1. Degree of synchrony in annual changes in relative population size of two amphibian species for different spatial and demographic groupings.

Paired contrast in same park†	<i>Ambystoma maculatum</i>			<i>Rana sylvatica</i>		
	<i>N</i>	Mean (SE)	<i>P</i>	<i>N</i>	Mean (SE)	<i>P</i>
In same isolate (87 m)	21	0.32 (0.12)	0.06	18	0.06 (0.12)	0.38
In different isolate (8.3 km)	81	0.26 (0.05)	< 0.0001	55	0.09 (0.06)	0.15
Between isolates (9.7 km)	20	0.54 (0.06)	0.001	14	0.19 (0.12)	0.12

Notes: The number of pairings (*N*) and observed mean (with 1 SE in parentheses) for correlation coefficients are presented. Pairings are for ponds in the same isolate, ponds in different isolates, or for entire isolates ("between isolates"). *P* values are from randomization tests and are based on the proportion of 1000 randomly generated correlation coefficients that exceeded the mean for each group.

† Mean distance between paired groups is given in parenthesis.

and averaged 1.69 + 0.95% (mean ± 1 SE) annually. At two sites adults bred the year following an absence. The third pond was a very shallow site that underwent progressive filling with *Sphagnum* moss over the duration of the study. Adults failed to use this site in 3 of 10 years. At a larger spatial scale, none of the 16 *A. maculatum* geographic isolates experienced a turnover (masses present every year). Local-pond turnover was higher for *R. sylvatica* (annual rate = 7.38 + 2.02%) and 12 of 26 pond populations failed to utilize local ponds for one or more years. As with *A. maculatum*, no geographic isolate experienced a turnover. Annual turnover rates increased significantly for *R. sylvatica* from 1994 through 2002 (regression analysis: *P* = 0.01, *r*² = 0.60, slope = 1.72), but not for *A. maculatum* (*P* = 0.09, *r*² = 0.35, slope = 0.61). The respective number of egg masses laid annually in ponds with vs. without turnovers was 86 + 14 egg masses vs. 23 + 16 egg masses (mean + 1 SE) for *A. maculatum* and 226 + 54 vs. 26 + 14 egg masses for *R. sylvatica*. Sample sizes for *A. maculatum* turnovers were too small for meaningful statistical comparisons; however,

means differed significantly for *R. sylvatica* (*t* test: *P* = 0.005).

DISCUSSION

This study documents long-term population dynamics of a relatively large number of amphibian populations over a broad geographic region and provides novel insights into population synchrony at different spatial scales. The most important findings that are relevant to both monitoring programs and amphibian-management issues are that: (1) breeding habitats are dynamic and, even in protected parks, are subject to strong biotic perturbations, (2) behavioral switching is common at very fine scales and may strongly compromise demographic independence, and (3) clusters of local ponds may lack metapopulation structure. We discuss these in detail below.

Breeding-habitat dynamics, behavioral switching, and breeding-site fidelity

Within a cluster of local ponds, resident populations experienced a dynamic environment in which predation risk, degree of pond filling, seasonal habitat duration, and the number and arrangement of breeding sites var-

TABLE 2. Comparisons of degree of amphibian population synchrony for paired contrasts within parks.

Paired contrast, by species	Site perturbation†				<i>P</i> ‡
	No		Yes		
	Mean CC	<i>N</i>	Mean CC	<i>N</i>	
<i>Ambystoma maculatum</i>					
In same isolate	0.62	8	0.14	13	0.01
In different isolate	0.37	30	0.20	51	0.13
Between isolates	0.66	8	0.46	12	0.10
<i>Rana sylvatica</i>					
In same isolate	0.04	7	0.07	11	0.91
In different isolate	0.12	23	0.07	32	0.70
Between isolates	0.22	8	0.14	6	0.73

† Values under site perturbation are the means (*N* = sample size) for correlation coefficients, CC; larger values indicate greater positive synchrony. "No" indicates pairs where a major site perturbation was never documented; "Yes" indicates pairings where one or both pair members experienced major perturbations, primarily from beaver activity.

‡ Probability values (*P*) are for randomization tests.

TABLE 3. Summary statistics for demographic autocorrelation analysis.

Population group, by species†	<i>N</i> ‡	Correlation coefficient	<i>P</i> §
<i>Ambystoma maculatum</i>			
Ponds within parks	102	-0.007	0.63
Isolates within parks	20	-0.634	0.02
All isolates	112	-0.17	<0.0001
<i>Rana sylvatica</i>			
Ponds within parks	73	0.054	0.64
Isolates within parks	14	-0.27	0.53
All isolates	73	0.10	0.09

† Relationships were examined for all pond populations within parks (maximum distance between ponds = 26.9 km), all geographic isolates within parks (maximum distance between isolates = 26.9 km), and all geographic isolates (regional trends; maximum distance = 465 km).

‡ Number of paired comparisons.

§ *P* values are for Mantel tests and indicate whether correlation coefficients deviate significantly from zero.

ied with time. A fundamental behavioral question that relates to demographic independence is the scale at which pond-breeding amphibians perceived their environment. That is, Do amphibians view clusters of local ponds as habitat patches that can be assessed for quality and exploited optimally? Or, Is a single pond and surrounding terrestrial habitat the general universe for an individual animal? A growing body of evidence suggests that at very small scales local ponds are perceived more as habitat patches than as entire habitats. Experimental studies indicate that breeding adults assess habitat quality prior to ovipositing and actively avoid ponds or natural pools that are of low quality to future offspring (Resetarits and Wilbur 1989, Kats and Sih 1992, Hopey and Petranka 1994, Petranka et al. 1994, Spieler and Linsenmair 1997). Numerous studies have also documented the rapid colonization of new ponds by amphibians (e.g., Lehtinen and Galatowitsch 2001, Pechmann et al. 2001, Stevens et al. 2002), suggesting that adults often treat ponds in their vicinity as habitat patches and rapidly exploit high-quality patches that become available. Marsh (2001) concluded that behavioral responses were more important than demographic responses in explaining the use of experimental ponds between years. Our observations suggest that habitat switching is commonplace when local breeding ponds are in close proximity and disturbance occurs from beaver activity, fish invasions, or human activities. At this scale many amphibians may choose breeding sites opportunistically and shift from one site to another depending on predator loads or disturbance history.

Geographic scale appears to strongly influence site philopatry. Berven and Grudzien (1990) and Gill (1978) reported strong site philopatry in adult *Rana sylvatica* and eastern newts (*Notophthalmus viridescens*) for ponds that were mostly >1 km apart. However, Hopey and Petranka (1994) found that adult *R. sylvatica* completely avoided ovipositing in ponds with fish when fish-free experimental ponds were in close proximity (<6 m apart). Our study of clusters of local ponds was conducted at a fine scale (mean distance between neighboring ponds = 87 m), and both field observations and data on population synchrony indicate that site philopatry was weak within clusters.

We were unable to directly measure movements between ponds by marking animals. However, evidence of habitat switching following the creation of new ponds or degradation of existing ponds suggests that the majority of animals may abandon their natal or home ponds in response to site perturbations. In the three detailed examples that we presented, the majority of *R. sylvatica* in local geographic isolates utilized new beaver ponds or created wetlands within 1–2 years of their formation. Similarly, an estimated 63% of female *Ambystoma maculatum* in a geographic isolate oviposited in a new beaver pond immediately after its formation. Given that females in Appalachian populations

of these species appear to require more than two years to reach sexual maturity (Berven 1982, Petranka 1998), animals that bred in new ponds at BLRI (Blue Ridge Parkway) and CUGA (Cumberland Gap National Historical Park) were either first-time breeders that did not return to their natal ponds or repeat breeders that moved from their historical breeding ponds. Regardless, the data indicate wholesale shifts in breeding populations between local breeding sites.

Population synchrony as a tool for detecting levels of demographic independence

Spatial synchrony in population fluctuations has been documented in a wide array of organisms, including insects, plants, birds, and mammals (e.g., Ims and Steen 1990, Hanski and Woiwood 1992, Swetnam and Lynch 1993, Paradis et al. 2000, Driskell et al. 2001). Researchers have identified several factors that may contribute to synchrony, including the Moran effect, dispersal of large numbers of juveniles from a source population to surrounding smaller populations, or the effects of wide-ranging predators that feed on patches of prey (Moran 1953, Ranta et al. 1998, Ims and Andreassen 2000, Ripa 2000, Greenman and Benton 2001). These factors interact and operate at different spatial scales, and their relative importance is often difficult to ascertain.

We expected population synchrony to decrease with the distance between paired populations because similarity of microtopography, elevation, breeding dates, and associated weather events (the Moran effect) decreases with geographic distance. In addition the probability of small populations simultaneously receiving large numbers of emigrating juveniles from a large source pond diminishes with distance. In reality, synchrony between paired pond populations within parks was not significantly associated with geographic distance for either species. Synchrony between paired populations within geographic isolates (mean distance = 87 m apart) was approximately the same as that of paired ponds in different isolates (mean = 8.34 km apart), and was lower on average than that between paired geographic isolates that have high demographic independence. These patterns suggest that inter-pond movements occurred at sufficiently high levels within geographic isolates to counteract positive synchronization associated with dispersal and the Moran effect. The synchrony data are consistent with our field observations of numerous instances of local habitat shifting, suggesting that contrasts of levels of synchrony within vs. between geographic isolates may be a useful tool for detecting lack of demographic independence in other amphibian species.

Our field observations indicate that *A. maculatum* also engages in habitat shifting at the local level, but to a lesser extent than *R. sylvatica*. Local synchrony in *A. maculatum* was relatively high between pairs within the same geographic isolate in the absence of site per-

turbations, but was markedly reduced where perturbations were documented. Synchrony was also lower between pond pairs within the same geographic isolate than between pairs of isolates that were more geographically isolated. Ongoing studies of fine-scale genetic variation (Tim King, *personal communication*) will help clarify the degree of site fidelity that this species exhibits at the local level.

Demographic independence, metapopulation structure, and turnover rates

Although pond-breeding amphibians often have been characterized as having metapopulation structure, the extent to which this occurs is a function of spatial organization and the distance between breeding sites. Metapopulation structure does not occur under two general conditions in the absence of major barriers: (1) where the distance between neighboring groups is greater than the dispersal capabilities of a species, and (2) where the distance between groups is so small that neighboring groups lack a significant degree of genetic and demographic independence due to high rates of intergroup dispersal (Harrison 1991, McCullough 1996). In the first case local-pond populations clearly qualify as basic monitoring units for documenting population trends. In the latter case, the groups are best treated as subpopulations of a single monitoring unit (local population) since the dynamics of subpopulations may largely reflect lack of breeding-site fidelity rather than true demographic changes in response to environmental stressors.

The extent to which local-pond populations of amphibians exhibit metapopulation organization is poorly resolved (Marsh and Trenham 2001). Trenham et al. (2001) examined organization of *Ambystoma californiense* populations in California where adjoining ponds were an average of 300 m apart. They concluded that interpond dispersal was so high that extinction events would be rare and genetic independence would be unlikely at the local level. Although spatial autocorrelation of demographic parameters such as age and mass distributions provided some evidence of demographic independence, the subpopulations did not appear to be organized as classic metapopulations (McCullough 1996).

We found strong evidence that local perturbations may cause marked shifts in habitat use. For *R. sylvatica*, population synchrony within geographic isolates was weak regardless of the level of local disturbance. This suggests that even under relatively stable conditions, interpond movements are occurring at high rates. Emerging fine-scale genetic studies of *R. sylvatica* are consistent with this interpretation. Newman and Squire (2001) and Squire and Newman (2002) examined microsatellite variation of *R. sylvatica* at spatial scales that are similar to those of this study. With a few exceptions, pond populations in close proximity (<1 km) showed strikingly similar allelic frequencies, which

suggests high rates of movement between populations. Mark-recapture data from these studies are consistent with this interpretation, with 40% of recaptures of breeding adults reflecting interpond movements. Berven and Grudzien (1990) reported that ~18% of juveniles dispersed to non-natal ponds, even though most ponds were >1 km apart. Our data on habitat switching and population synchrony, together with emerging data on fine-scale genetic variation, provide no support for the hypothesis that pond populations of *R. sylvatica* that are <400 m apart are organized as metapopulations. These are perhaps better treated as constituting an essentially panmictic population.

Population bottlenecks and extinctions/colonization events can influence both community diversity and genetic substructuring within species. The rates at which these occur are strongly influenced by spatial scale and the criteria used to define a population. Local-pond turnovers of *R. sylvatica* were often associated with habitat shifting in conjunction with physical pond deterioration or the invasion of fish. For example, adults appeared to abandon two unmaintained beaver ponds in BLRI after the sites became more shallow (mean depth <10 cm) following partial failure of dams. Most ponds that suffered local turnovers were relatively small habitats that supported small numbers of breeding adults. These appeared to serve as marginal breeding habitats within clusters of local ponds.

In our study 62% of local-pond populations of *R. sylvatica* experienced turnovers (i.e., failed to utilize local ponds for one or more years), compared to 0% of geographic isolates. Thus, local populations of *R. sylvatica* could be characterized as being either highly resistant to local turnover (extinction) or highly prone to local turnover depending on whether individuals utilizing local clusters of ponds are treated as a single panmictic population, or as an array of populations with metapopulation organization.

Researchers often have documented high extinction and recolonization rates for pond-breeding amphibians (reviewed by Marsh and Trenham [2001]), but have done so by treating each pond as a local population. In reality, many of these "populations" may be only subpopulations of local, extinction-resistant populations that are essentially panmictic. As in our case, many perceived turnovers may simply reflect animals engaging in opportunistic, wholesale shifting between ponds in response to patch dynamics. The distinction is not trivial because loss of a subpopulation vs. an entire geographic isolate can have fundamentally different consequences with respect to genetic substructuring and the loss of genetic diversity within species. We suggest that population turnover rates for amphibians need to be reexamined within this context.

Hecnar and M'Closkey (1997) presented one of the few studies to examine the spatial scale of turnover events. They found that 25% of local-pond populations of the green frog (*Rana clamitans*) in Canada suffered

turnovers over the course of three breeding seasons, while no turnovers occurred for entire watersheds where ponds were separated by an average distance of 1.5 km. Skelly et al. (1999) also reported relatively high local turnover rates for species that were monitored in 37 ponds from 1988–1992 on a 540-ha reserve in Michigan (USA). However, none of 14 species that were monitored disappeared from the reserve during the five-year survey. These data are consistent with our own in demonstrating markedly different turnover rates over relatively narrow spatial scales, and very low turnover rates above the level of the local-pond population.

Population monitoring

Population monitoring can be used to address an array of questions in conservation biology, and researchers must choose the appropriate demographic units and temporal and spatial scales to achieve specific goals. Monitoring programs should be based on clearly formulated questions and detailed planning that will achieve goals. A primary goal of many amphibian-monitoring programs is to document population trends, particularly with regard to delineating temporal and spatial patterns of regional or global amphibian decline (Houlahan et al. 2000, Davidson et al. 2002). Because the number of populations that can be monitored is limited, researchers should select populations or other demographic units for monitoring that provide relatively independent measures of responses to environmental stressors. Unfortunately, a fundamental lack of understanding of the degree of demographic independence of pond populations at fine scales has hampered the extent to which this basic feature can be incorporated into monitoring designs. In our study we monitored 31 ponds, but only 16 units (geographic isolates) were considered to have high levels of demographic independence.

Identifying the basic demographic unit for monitoring population trends is essential because this will influence the number of units that can be monitored across the landscape, estimates of detrended variation, and the statistical power of detecting population trends (Thomas 1997, Gibbs et al. 1998). For example, if individuals using clusters of local ponds in close proximity are treated as a single monitoring unit, then selecting several independent monitoring units with small numbers of ponds may better achieve goals than selecting a single unit containing many ponds. The criteria used to define a local population also affects other aspects that are relevant to conservation biology such as estimates of extinction/colonization rates, the extent to which a species exhibits metapopulation organization, and the degree of regional synchrony in population trends. Depending on the specific goals of a monitoring program, researchers may want to select individual ponds or a cluster of local ponds as the basic monitoring unit.

Genetic analysis is a powerful tool for understanding population organization in pond-breeding amphibians. Although very few fine-scale studies have been conducted on amphibians, emerging data suggest that clusters of local-pond populations within a few hundred meters lack genetic and demographic independence unless separated by major barriers to dispersal (Newman and Squire 2001). Genetic data alone cannot fully demonstrate that genetic uniformity in neighboring-pond populations is due to high levels of gene flow since other mechanisms can produce a similar pattern (Newman and Squire 2001). However, when coupled with information of local extinction/colonization events and habitat switching, the collective evidence provides a strong argument that pond populations in close proximity (<100–400 m apart) are better treated as a single local population.

From a logistical standpoint, treating a cluster of local ponds as a single monitoring unit for assessing population trends is practical given the dynamics of pond habitats and statistical noise generated via local habitat shifting. Beavers are keystone species that can alter the number, size, and spatial arrangement of clusters. Monitoring only one or two populations within a local cluster may not provide meaningful measures of overall population trends if the number of local ponds is in a constant state of flux. Statistical noise may be so large when using data for individual-pond populations that a decade or more may be required to detect true population trends (Pechmann et al. 1991, Blaustein et al. 1993, Pechmann and Wilbur 1994, Meyer et al. 1998). Although use of a cluster of local ponds as the basic monitoring unit may reduce sample size and increase effort, using pooled data from all subpopulations within a cluster should markedly reduce non-trend variation and increase statistical power for detecting trends. Consequently, there are both conceptual and logistical reasons for treating all pond populations within a few hundred meters of each other as a single monitoring unit for assessing population trends.

Monitoring programs that rely on landscape analysis often involve resampling sites where there are historical collection records, categorizing species as being present or absent based on survey data, then assessing trends at different spatial scales (e.g., Lannoo et al. 1994). Other approaches such as long-term call survey data (e.g., Mossman et al. 1998) combine elements of both population-trend and landscape analysis. A primary limitation of landscape analysis is that adequate null models have not been developed to predict population losses that are expected due to ecological succession (e.g., Pounds et al. 1997, Skelly et al. 1999) or stochastic events (e.g., Sjögren 1991, Hecnar and M'Closkey 1996, 1997, Skelly et al. 1999). As with trend analysis, defining what constitutes the basic monitoring unit will influence the data analysis and conclusions that are drawn (e.g., turnover rates and the degree of spatial synchrony across the landscape).

Establishing criteria for defining the basic monitoring unit will help standardize the interpretation of data and improve the efficiency of monitoring programs for pond-breeding amphibians, regardless of whether trend or landscape approaches are used. As a conservative benchmark for programs whose primary goal is to monitor population trends, we suggest that local-pond populations of *A. maculatum* and *R. sylvatica* be treated as subpopulations of a single local population when nearest neighbors are <100 and 200 m apart, respectively. We encourage additional studies that will provide more refined estimates of where the boundary lies between a local population and metapopulation organization in these and other pond-breeding amphibians.

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