

REGIONAL DYNAMICS OF WETLAND-BREEDING FROGS AND TOADS: TURNOVER AND SYNCHRONY

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Abstract. We used data from a statewide frog monitoring network to investigate population turnover and synchrony in eight wetland-breeding species. We found that subpopulations at many sites turn over frequently, with breeding choruses absent or undetectable in most years. Frequencies of detection across sites were significantly associated with the density of wetland patches (all species) and the areal extent of several terrestrial land cover categories (seven species) within 1 km. Intraspecific population fluctuations were statistically synchronized between survey sites separated by up to 50–100 km, but synchrony was not strong. Anuran abundances were significantly correlated with rainfall 1–4 years earlier, indicating that rainfall influences population fluctuations. However, population synchrony was much weaker than rainfall synchrony. Managers attempting to maintain amphibian populations regionally should focus on maintaining landscapes with high densities of wetlands and sufficient upland habitat resources. The dynamic nature of amphibian populations at individual wetlands is well known, and our results suggest that species distributions at the landscape level are similarly dynamic.

Key words: anuran; autocorrelation; frog; metapopulation; monitoring; rainfall synchrony; spatial synchrony; toad; turnover; wetland; Wisconsin.

INTRODUCTION

Many species have patchy distributions, but in landscapes where patches are anthropogenically altered and increasingly isolated there are often concerns about continued persistence. The influence of habitat fragmentation on species persistence hinges on the frequency of subpopulation turnover and the degree to which local subpopulations fluctuate in synchrony (Hanski et al. 1995, Akçakaya 2000). Turnover (i.e., extinctions and colonizations) of individual subpopulations occurs as the result of a combination of local and regional factors. Extinctions result from a variety of factors including insufficient reproduction/immigration, habitat succession or destruction, and catastrophic events. Colonization of unoccupied patches requires immigration from occupied patches. Thus, all other factors being equal, sites with more neighboring patches

of suitable habitat should be occupied more consistently and be colonized more rapidly following extinctions. Conversely, landscape conversion that reduces the density of habitat patches or impedes dispersal will increase extinction and reduce colonization probabilities (Hanski et al. 1995, Bolger et al. 1997, Gaona et al. 1998). Besides subpopulation extinction and colonization rates, the degree to which subpopulation dynamics are synchronized is also important (Akçakaya 2000). Regionally synchronized dynamics reduce the mean time to system-wide extinction, especially when the probability of subpopulation extinction is high (Harrison and Quinn 1989, Heino et al. 1997). In empirical studies, subpopulation fluctuations are often significantly synchronized (i.e., positively correlated) with synchrony declining with distance (Bjørnstad et al. 1999, Koenig 1999, Ranta et al. 1999).

Because wetland-breeding amphibians are patchily distributed and extinction/colonization dynamics have been documented for various species, their population biology and conservation are often discussed in the context of metapopulations (Marsh and Trenham 2001, Semlitsch 2002). However, population turnover in amphibians is poorly understood, and population synchrony has not been addressed previously for this group. For less mobile organisms such as amphibians, synchrony far beyond the scale of dispersal can result from either regionally correlated environmental parameters (Moran 1953) or wide-ranging predators (Petty et

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TABLE 1. Survey season, approximate length of larval period, and age at sexual maturity for Wisconsin frogs and toads in this study.

Scientific name	Common name	Time of survey	Larval period (wk) [†]	Age at maturity (yr) [‡]	Sites (N)
<i>Rana sylvatica</i>	wood frog	April	6–9	1–4	876
<i>Pseudacris triseriata</i>	chorus frog	April	8–10	1–2	955
<i>Pseudacris crucifer</i>	spring peeper	April	12–14	2	933
<i>Rana pipiens</i>	leopard frog	April	12–14	1–4	832
<i>Bufo americanus</i>	American toad	May–June	5–6	2–4	1112
<i>Hyla versicolor</i>	gray treefrog	May–June	8–10	2	1032
<i>Hyla chrysoscelis</i>	Cope's gray treefrog	May–June	8–10	1–2	456
<i>Rana clamitans</i>	green frog	July	52	2–3	1117

Notes: Entries for the rightmost ("Sites") column are the total numbers of survey sites where the species was detected at least once. Total Wisconsin Frog and Toad Survey sites = 1350.

[†] Larval periods from Oldfield and Moriarity (1994).

[‡] Years to maturity based on: *R. sylvatica*, Berven (1982), Sagor et al. (1998); *P. triseriata*, Smith (1987); *P. crucifer*, Lykens and Forester (1987); *R. pipiens*, Collins (1975); *B. americanus*, Kalb and Zug (1990), Acker et al. (1986); *H. versicolor*, Collins (1975); *H. chrysoscelis*, Duellman and Trueb (1994); *R. clamitans*, Shirose and Brooks (1995).

al. 2000). With respect to environmental factors, rainfall typically initiates breeding migrations and maintains wetlands through the period of larval development. In drier years, aggregations of breeding adults are often reduced or reproduction may fail completely (Semlitsch et al. 1996, Trenham et al. 2000). Thus, with rainfall patterns strongly autocorrelated over hundreds to thousands of kilometers (Koenig 2002), there is reason to suspect that pond-breeding amphibians might exhibit large-scale synchronized dynamics (Akçakaya 2000). However, because even nearby ponds often ex-

hibit divergent hydroperiods and predator communities (Rowe and Dunson 1995, Skelly et al. 1999, Trenham et al. 2001), dynamics may be less synchronous than rainfall.

Here we use data from the statewide Wisconsin Frog and Toad Survey to investigate turnover and synchrony in eight species of wetland-breeding anurans. Based on prior theoretical and empirical studies, we predicted that turnover should be common and that there should be a significant association between turnover at sites and habitat in the surrounding landscape. In particular, sites with greater densities of wetland patches and fewer barriers to movement should be occupied in more years. We also measured the degree to which fluctuations in subpopulations are statistically synchronized across different spatial scales, and tested for positive correlation with rainfall. Finally, we discuss the implications of these results for the maintenance of amphibian populations in fragmented landscapes and the design and interpretation of amphibian monitoring programs.

METHODS

Data from the Wisconsin Frog and Toad Survey (WFTS), spanning the years 1981–1998, were used for the analyses. The eight anuran species that occurred at enough sites to be considered were *Bufo americanus*, *Hyla chrysoscelis*, *Hyla versicolor*, *Pseudacris crucifer*, *Pseudacris triseriata*, *Rana clamitans*, *Rana pipiens*, and *Rana sylvatica* (Table 1). All of these species breed and develop from egg through metamorphosis in aquatic habitats.

Below is a summary of the survey methods; for complete details see Mossman et al. (1998). Volunteers collected data along 135 survey routes. Each route had 10 fixed listening stops (hereafter referred to as "sites") located near one or more wetlands (Fig. 1). Because Wisconsin anurans breed at different times, routes were run one night each during early spring (1–28 April), late spring (20 May–5 June), and summer

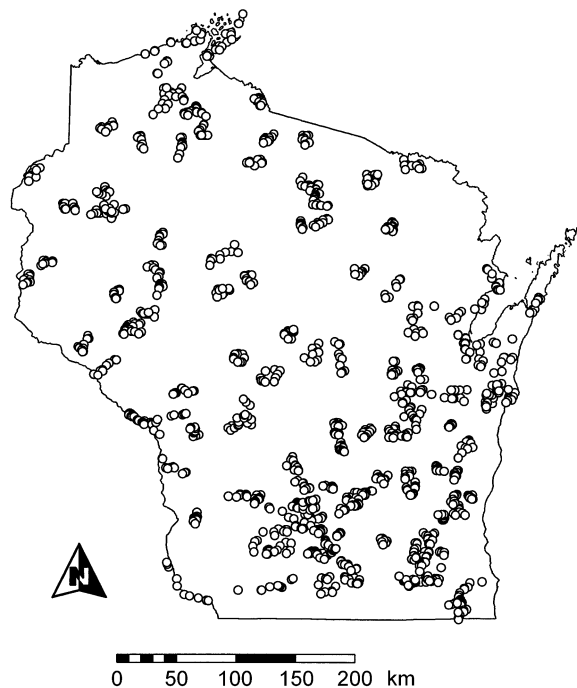


FIG. 1. Map of Wisconsin with the location of the 1350 Wisconsin Frog and Toad Survey (WFTS) sampling sites (circles) along 135 routes.

TABLE 2. Habitat variables summarized for the area within 1 km of each Wisconsin Frog and Toad Survey site.

Type and code	Habitat variable (units)	Mean (range)
Location		
UTME	East coordinates (m)	...
UTMN	North coordinates (m)	...
Terrestrial		
PAVE	length of paved roads (km)	5.6 (0.5–27.8)
DEV	residential or industrial (%)	2.1 (0–65.9)
CULT	cultivated or pasture (%)	42.2 (0–98.1)
FORS	forest or shrub covered (%)	34.5 (0.4–99.3)
GHRB	grassland or herbaceous (%)	2.2 (0.69–9.0)
Aquatic		
OWP	small lakes and ponds (no.)	0.38 (0–7.0)
EMP	emergent wetland patches (no.)	1.51 (0–11.0)
SSP	scrub or shrub wetland patches (no.)	1.01 (0–10.0)
FORP	forested wetland patches (no.)	0.33 (0–5.0)

Notes: For PAVE, DEV, and GHRB, the variable was log transformed prior to habitat analyses. Code sources are as follows: PAVE, U.S. Census Bureau (1995 [TIGER Classes A1–A4, A6, and A7]); DEV, U.S. Geological Survey (1986 [LULC Codes 21–23]); CULT, U.S. Geological Survey (1986 [LULC Codes 61, 81–85]); FORS, U.S. Geological Survey (1986 [LULC Codes 41–43, 51–53]); GHRB, U.S. Geological Survey (1986 [LULC Code 71]); OWP, Wisconsin Department of Natural Resources (1984–1996 [Wetland Classes A, W (modifier H)]); EMP, Wisconsin Department of Natural Resources (1984–1996 [Wetland Class E]); SSP, Wisconsin Department of Natural Resources (1984–1996 [Wetland Class S]); FORP, Wisconsin Department of Natural Resources (1984–1996 [Wetland Class T]).

(1–15 July). Surveys were conducted only when air and water temperatures exceeded established minimums and wind was minimal. During each site visit the volunteers evaluated the relative intensity of the calls of all anuran species heard over a 5-min period. Call intensities were recorded as zero if no calls were heard, one if non-overlapping calls were heard, two if calls overlapped but individuals could be distinguished, or three if calls were overlapping and continuous.

We used GIS data from several sources to characterize terrestrial and aquatic habitat within 1 km of each WFTS site (Table 2). This buffer represents a reasonable approximation of the mean distances moved by amphibians in mark–recapture studies, and thus encompasses a large portion of the wetland and terrestrial habitats utilized by anurans at each site (Marsh and Trenham 2001). We categorized terrestrial habitat as developed, cultivated, forest/shrub, or grass/herbaceous based on land use and land cover maps (scale = 1:100 000; U.S. Geological Survey 1986) and determined the area in each category. We determined the total length of paved road using the TIGER maps (U.S. Census Bureau 1995). Aquatic habitat characterizations were based on the Wisconsin Wetland Inventory maps (scale = 1:24 000; Wisconsin Department of Natural Resources 1984–1996). For each site, we determined the total number of open water, emergent wetland, forested wetland, and scrub-shrub wetland patches within the 1-km buffer. We downloaded monthly rainfall totals ($N = 281$ weather stations) and mean temperatures ($N = 31$ weather stations) for sites throughout Wisconsin from the National Climate Data Center (available online).⁷

For our analyses of each species, we used only data from the survey period that coincided with its peak of calling activity (Table 1). To evaluate turnover we used data from sites surveyed in all 10 years from 1989 to 1998, including for each species only sites where it was detected at least once. For each site we determined the number of years that each species was detected. Then as an indication of time to recolonization, for sites with absences in at least two years, we calculated the mean length of gaps in detection (Koenig 2001).

In any analysis of presence–absence data, some absences are failures in detection and not strict absences. In a recent analysis, Crouch and Paton (2002) found that 5-min surveys missed species that were known to be present in $\leq 20\%$ of surveys, while 10-min surveys resulted in $\leq 10\%$ false absences. For 5-min surveys, their Fig. 4 predicts false-absence rates of 20% for *B. americanus*, 15% for *R. clamitans*, 10% for *R. sylvatica* and *H. versicolor*, and 5% for *P. crucifer*. Thus, in our analyses higher rates of absence in the WFTS data will be interpreted as support for true turnover. However, because many amphibians are long lived and may skip breeding in some years, even a true absence of calling in one or more years may not represent an extinction (Marsh and Trenham 2001). For the remainder of this paper, when we refer to unoccupied sites or years when frogs were absent, we recognize that in some cases frogs may have been present.

To further establish the veracity of the WFTS data for our purposes, we compared our 1992–1994 results with those of a Canadian study conducted in these years and encompassing many of the same species (Hecnar and M'Closkey 1996). In addition to auditory surveys,

⁷ URL: <http://www.ncdc.noaa.gov>.

they sampled for embryonic, larval, and transformed amphibians over several visits annually, presumably increasing detection probabilities. Following Hecnar and M'Closkey (1996), for each species we calculated "gains" and "losses" as follows: gains = number of new detections in year $n + 1$ /number detections in year n ; losses = number of shifts to nondetection in year $n + 1$ /number of detections in year n .

We used stepwise forward-addition multiple linear regression to test for association between turnover at sites (years detected and length of gaps in detection) and habitat within 1 km. Log transformations were used to normalize the variance in several of the habitat parameters (Table 2). Analyses were performed using both the output of a principal components analysis of the habitat variables, and the habitat variables directly. Both produced qualitatively identical results; for ease of interpretation the latter are presented. To accommodate for potential spatial autocorrelation among the landscape variables considered, we also included the x and y map coordinates of each site in the pool of independent variables (Augustin et al. 2001). Due to incomplete wetland maps, 462 of the 1350 sites had $\geq 5\%$ missing data and were not included in the habitat analyses.

We analyzed spatial autocorrelation using the modified Mantel correlogram approach to determine the statistical extent of synchrony (Koenig and Knops 1998). This process required several steps for each species (or season, for weather data). First, we detrended each time series, obtaining residuals by regressing year on call intensity for each species/site combination in order to eliminate long-term trends that can inflate synchrony estimates. This allowed us to focus on short-term, year-to-year fluctuations. We also constructed detrended time series of rainfall totals and monthly temperatures for each weather station during each of the anuran survey intervals (April, May/June, July) and the entire "summer" (April to August). In all cases we confirmed the normal distribution of the residuals prior to further analysis.

Next, for all pairs of sites with at least eight years of overlapping surveys between 1981 and 1998 we calculated the Pearson correlation coefficient (r) between the two detrended call intensity time series (i.e., autocorrelation) and the Euclidean distance between the two sites. We then tested for significantly positive correlations (i.e., synchrony) within discrete distance classes using randomization trials (Koenig and Knops 1998). For these analyses we set the minimum distance class so that there were at least 50 independent pairs of sites per randomization run; larger distance classes were spaced evenly to allow comparisons across broad spatial scales. Within each distance class, subsets of up to 100 independent correlations were randomly selected from the total pool of pairwise comparisons such that each site was included no more than once per trial. We limited randomization subsets to 100 correlations

to maintain power at a consistent level across species and distance classes. We generated 1000 such subsets for each distance class, checking each to ensure that it had not been previously used. For each randomly assembled subset we calculated the mean r and counted the number of negative and positive r values. Statistical significance was determined based on the fraction of subsets where the number of positive r values was greater than the number of negative r values. For example, if there were more positive r values in 960 of the 1000 subsets, $P = 0.04$. To approximate the absolute magnitude of correlation for each distance class we also calculated the mean of the mean r values over all subsets.

Due to the methods of the WFTS, it was not possible to compare correlations from pairs of sites within routes to correlations from pairs of sites on different routes. This is because in a given year the sites within a route are all surveyed on the same night, with similar weather, and by the same observer. However, sites on different routes are usually surveyed on different nights, with different weather, and by different observers, so correlations are likely to be lower even if actual densities are identical. Thus, we calculated spatial autocorrelation for all possible pairs of sites on the same route, and all possible pairs of sites on different routes, separately.

It is possible that apparently synchronized fluctuations may result simply from more frogs calling in years with more rain, rather than from actual population fluctuations. In order to test this alternative, we calculated cross correlations between the detrended call intensities and overlapping rainfall time series. We included only pairs of WFTS and weather station sites separated by >25 km and with at least eight years of overlapping data. For each species we used calling intensities and rainfall totals from only the month(s) when that species calls most actively (Table 1). We then used randomization trials to test for significantly positive correlations, and calculated mean correlation values and P values in the same way that we did for the frog spatial autocorrelation analyses. Finally, we evaluated correlations between call intensities and rainfall one, two, three, and four years earlier. Calculations were performed using rainfall totals during the respective survey month(s) and for the entire summer (April through August).

RESULTS

The landscapes within 1 km of the Wisconsin Frog and Toad Survey (WFTS) sites ranged from almost completely agricultural to completely forested (Table 2). Residential and industrial development generally encompassed small areas. Overall, the dominant land uses were agricultural, with a mean of 42.2% in cultivated or pasture categories. Most habitat variables were not strongly correlated. Correlation among pairs of habitat variables only exceeded 0.40 in two cases: PAVE and DEV ($r = 0.83$), and CULT and FORS (r

= -0.75). In our analyses of landscape correlates of turnover, PAVE but not DEV was included in the pool of potential explanatory variables. The species considered in our analyses were widespread in the state, detected at least once from 34% (*H. chrysoscelis*) to 83% (*R. clamitans*) of the WFTS sites (Table 1).

Considering subpopulation turnover at sites surveyed every year from 1989 to 1998, frogs were absent in at least one of those years from 50% (*P. crucifer*) to 99% (*B. americanus*) of the sites (Fig. 2). At many sites, frogs were detected in only 1–3 out of 10 years (range: from 12% for *P. crucifer* to 46% for *H. chrysoscelis*). For all five species for which we could predict false-absence rates based on Crouch and Paton (2002), the observed absence rates were from 2.3 to 4.4 times higher (Table 3), making observer error alone an unlikely explanation for the observed detection frequencies. Also, the proportions of WFTS sites gaining and losing each species annually between 1992 and 1994 were high and similar to the results of Hecnar and M'Closkey (1996; our Table 4). For each species, the number of years detected was positively associated with the regional density of one or more of the wetland patch types (Table 3). Frequency of detection was also significantly associated with the amount of grassland/herbaceous or forest/shrub cover in the surrounding uplands for five species. The amount of paved roads and cultivated/pasture land were each significantly associated with occupancy for two species, but in each case one association was negative and one was positive (Table 3). Gaps in detection of from one to nine years were observed for all species. For four species, gaps in detection were shorter at sites with higher densities of wetland patches within 1 km. Nonwetland habitat parameters were significantly associated with the length of gaps for just two species (Table 3).

Calling intensities were significantly but not strongly synchronous both within and between survey routes. When considering only pairs of sites from within the same survey routes, synchrony was highly significant for all eight species (Table 5). However, even at distances <2 km, synchrony was not particularly strong, with mean correlations from 0.23 for *R. clamitans* to 0.51 for *H. versicolor* (mean $r = 0.35$; Table 5). Considering among-route synchrony, neither *R. pipiens* nor *H. chrysoscelis* showed evidence of significant synchrony within any distance class (Table 5). For the remaining six species, mean correlations were positive within all distance classes, and statistically significant synchrony extended to differing spatial scales. Among early-spring breeders (*R. sylvatica*, *P. triseriata*, and *P. crucifer*), significant synchrony was limited to sites <10 km apart, while in *B. americanus*, *H. versicolor*, and *R. clamitans* significant synchrony extended to sites separated by >10 km. In general, species that were significantly synchronous over greater distances were the ones present at more sites statewide (Table 1; $r_s = 0.94$, $P < 0.001$, $N = 8$). However, even more so than within routes, synchrony

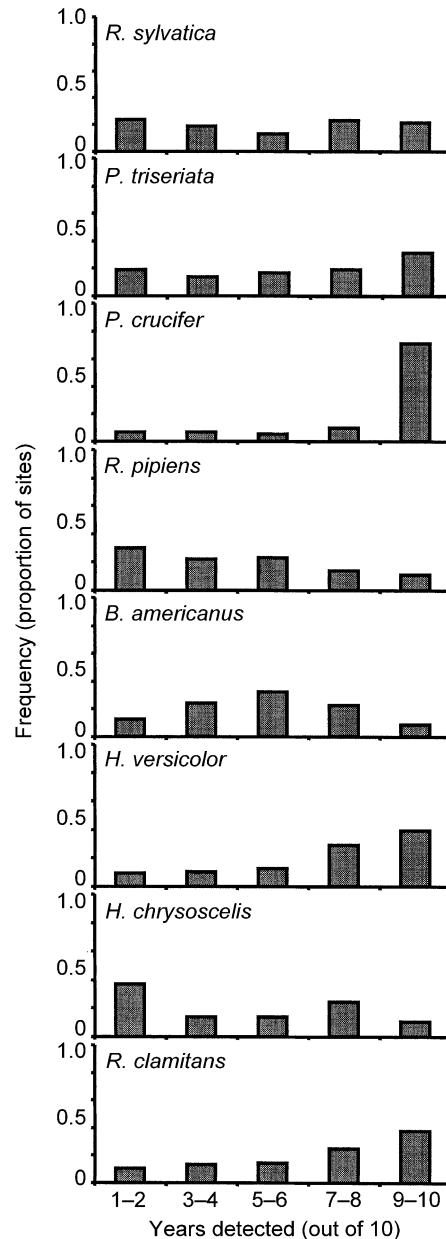


FIG. 2. Frequency of detection at Wisconsin Frog and Toad Survey (WFTS) sites surveyed every year from 1989 to 1998. For each species, only sites with at least one detection were included in this assessment. For means ± 1 SD, see Table 3.

was not strong within any distance category (all mean $r < 0.20$). In contrast, rainfall totals and mean temperatures were highly synchronized even between sites >100 km apart (Table 6).

For the six species showing evidence of synchrony in interrout comparisons, calling intensities were significantly positively correlated with rainfall totals both during the months when these species call most actively (five of six species) and over the course of the entire

TABLE 3. Results of stepwise multiple linear regression analyses testing for association between site occupancy and landscape habitat variables (see Table 2).

Species	Number of years detected			Length of gaps in detection		
	Years detected (<i>N</i> sites)	Associated landscape variables	<i>R</i> ²	Mean length (<i>N</i> sites)	Associated landscape variables	<i>R</i> ²
<i>R. sylvatica</i>	5.6 ± 3.0 (121)	FORP+***; UTMN+***; UTME+**; GHRB-*; PAVE+**	0.39	2.3 ± 1.8 (92)	UTMN-***; EMP-***; UTME-*	0.23
<i>P. triseriata</i>	6.1 ± 3.1 (148)	CULT+***; EMP+*; FORP-*	0.15	2.7 ± 1.9 (99)	...	
<i>P. crucifer</i>	8.3 ± 2.7 (159)	FORS+***; SSP+*	0.19	2.6 ± 1.9 (44)	UTMN-***	0.19
<i>R. pipiens</i>	4.4 ± 2.6 (125)	EMP+**; UTME+*	0.10	3.1 ± 2.1 (111)	UTME-*; OPENP-*	0.10
<i>B. americanus</i>	5.1 ± 2.2 (172)	OPENP+***; GHRB-***; UTMN+**; FORS-*; PAVE-*	0.20	1.9 ± 1.2 (157)	OPENP-*	0.03
<i>H. versicolor</i>	7.4 ± 2.4 (139)	UTME-***; SSP+***; CULT-*; FORP-**	0.30	1.5 ± 0.9 (83)	CULT+***; GHRB+*	0.11
<i>H. chrysoscelis</i>	4.5 ± 3.1 (70)	SSP+***; GHRB+***; UTMN+***; FORP-*	0.44	3.8 ± 2.5 (63)	UTMN-***; GHRB-***; EMP-***; FORS+*; SSP-*	0.41
<i>R. clamitans</i>	6.6 ± 2.8 (121)	GHRB-***; OPENP+*	0.14	2.0 ± 1.6 (83)	UTME+**	0.08

Notes: Independent variable codes are listed in order of entry into the multiple regression model, and trailing symbols (+/-) indicate the direction of the relationship with the associated *P* values. Years detected and mean length are means (±1 SD) for these turnover metrics; *N* sites = number of sites included in each analysis; *R*² is the adjusted *R* square value for the final model. The numbers of sites in the two analyses differ because only sites with detections in 1–8 out of 10 years were used in the analysis of gaps.

* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

summer (four of six species; Table 7). Two results suggest that call indices indicate population size and not just current environmental conditions. First, the call indices for these six species were more strongly correlated with rainfall totals one to four years earlier than with rainfall in the current year, suggesting that current environmental conditions were not the primary cause of the observed synchrony (Table 7). Second, the time lags producing the strongest correlations between each species and rainfall totals were also positively corre-

lated with the mean reported times to maturity for these species (*r*_s = 0.87, *P* = 0.05; Fig. 3).

DISCUSSION

Turnover and synchrony

Our analyses reveal two important features of the regional distributions and dynamics of frogs and toads in Wisconsin. First, although each of these species occurred at most sites (Table 1), in many years populations were not detected at these known suitable sites (Fig. 2). Absences were sufficiently common in the Wisconsin Frog and Toad Survey (WFTS) data set that it is unlikely that false absences alone could produce these gaps (Crouch and Paton 2002); turnover in occupancy is a natural part of the dynamics of these systems. Second, the dynamics of even nearby subpopulations are not strongly correlated, especially when compared with the strong regional synchrony of rainfall. Although the highly dynamic nature of amphibian populations at single sites is well known (Berven 1990, Semlitsch et al. 1996), our analyses add to a growing body of data suggesting that the regional distributions of many amphibians may be similarly dynamic, with frequent extinctions and colonizations in wetland breeding habitats (Hecnar and M'Closkey 1996, Skelly et al. 1999).

TABLE 4. Mean species-specific gains and losses at Wisconsin Frog and Toad Survey sites surveyed in 1992–1994.

Species	Gains	Losses
<i>R. sylvatica</i>	0.25 (0.44)	0.22 (0.31)
<i>P. triseriata</i>	0.19 (0.19)	0.26 (0.10)
<i>P. crucifer</i>	0.06 (0.23)	0.08 (0.04)
<i>R. pipiens</i>	0.32 (0.21)	0.28 (0.35)
<i>B. americanus</i>	0.33 (0.34)	0.32 (0.26)
<i>H. versicolor</i>	0.16 (0.10)	0.25 (0.24)
<i>H. chrysoscelis</i>	0.29 (···)	0.21 (···)
<i>R. clamitans</i>	0.17 (0.07)	0.16 (0.14)
Total mean	0.20 (0.22)	0.22 (0.22)
Paired <i>t</i> test	-0.22; NS	0.07; NS

Note: We tested the similarity between mean gains and losses in the Wisconsin Frog and Toad Survey and Hecnar and M'Closkey (1996) using paired *t* tests. Gains and losses observed by Hecnar and M'Closkey (1996) and calculated from their Fig. 5 are shown in parentheses.

TABLE 5. Results of spatial autocorrelation analyses for Wisconsin anurans.

Species	Mean correlation, by distance classes (km)					
	Within route pairs		Between route pairs			
	<2	<10	<10	10-<25	25-<50	50-<100
<i>R. sylvatica</i>	0.40***	0.36***	0.18**	0.11	0.07	0.05
<i>P. triseriata</i>	0.29***	0.22***	0.08*	0.06	0.04	0.03
<i>P. crucifer</i>	0.33***	0.25***	0.15**	0.07	0.05	0.05
<i>R. pipiens</i>	0.27***	0.22***	-0.02	0.01	0.02	0.00
<i>B. americanus</i>	0.45***	0.42***	0.17***	0.07	0.08	0.09*
<i>H. versicolor</i>	0.51***	0.42***	0.09*	0.14**	0.07	0.03
<i>H. chrysoscelis</i>	0.34***	0.37***	-0.08	0.03	0.04	0.02
<i>R. clamitans</i>	0.23***	0.22***	0.11***	0.06	0.07*	0.05

Notes: "Within route" tests included only correlations between pairs of sites on the same route; "between route" tests included only correlations between pairs on different routes. For each species, mean *r* values from the randomization trials are reported for each distance category.

* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

As predicted, frequencies of detection were higher, and gaps in detection were shorter, at sites with greater densities of wetland patches within 1 km (Table 3). These results, plus the correlation of call indices with rainfall in earlier years (Table 7), and the association between ages to breeding and the lags producing the strongest correlations (Fig. 3), support the assumption that variation in call indices represent changing population densities and not just responses to current weather or observation error. While we cannot differentiate between undetectably small and extinct subpopulations, the similarity between the frequency of gains and losses found here and in the intensive surveys of Hecnar and M'Closkey (1996) suggests that many of the gaps are real (Table 4).

Why is turnover common? Because temporary wetlands commonly dry before tadpoles reach metamorphosis, repeated reproductive failures in marginal habitat or during droughts may explain many local extinctions (Semlitsch et al. 1996, Skelly 1996). Also, a variety of studies indicate that significant fractions of juvenile anurans disperse from their natal ponds to breed at sites up to several kilometers away, providing potential colonists of unoccupied sites (Marsh and Trenham 2001). Because a single calling male is all that is needed to score a site as occupied, even sites incapable of supporting tadpoles to metamorphosis

(i.e., sink habitats) may be occupied intermittently if located within dispersal distance of productive habitats (Sjögren-Gulve 1994, Edenham 1996).

Although our regression analyses supported the hypothesis that landscape habitat parameters influence turnover, these models generally explained <40% of the variance in detection frequency and the length of gaps (Table 3). Low predictive power may result from the imprecise nature of the calling survey data and the GIS-derived habitat parameters. Also, and more interesting from a biological perspective, the absence of local data on the wetlands at which these frogs were actually calling likely contributes. In-wetland features, such as the presence of fish or water chemistry, have been shown to strongly influence site occupancy and local diversity (Fisher and Shaffer 1996, Hecnar and M'Closkey 1998). Unfortunately, because the frogs heard at a given WFTS site may be calling from more than one wetland, we could not analyze the relationship between turnover and specific breeding site characteristics. Nonetheless, the consistent positive relationship between occupancy and wetland densities within 1 km supports immigration as a key contributor to the observed dynamics of these systems. Regardless of the cause or causes of turnover, the pattern observed here emphasizes the dynamic nature of anuran populations across the landscape.

TABLE 6. Analyses of spatial autocorrelation for 281 rainfall stations and 31 temperature stations across Wisconsin, USA.

Time of survey	Distance between weather stations (km)						
	Rainfall totals					Mean temperatures	
	<25	25-<50	50-<75	75-<100	100-<250	<100	100-<250
April	0.87	0.83	0.78	0.72	0.54	0.97	0.96
May/June	0.88	0.83	0.78	0.72	0.57	0.94	0.93
July	0.74	0.64	0.53	0.44	0.25	0.95	0.93
April-August	0.81	0.79	0.73	0.68	0.54	0.90	0.87

Notes: For each of the time periods, the mean *r* value from the randomization trials is reported for each distance category. All *P* < 0.001.

TABLE 7. Correlation between call intensity and rainfall totals at sites <25 km apart.

Species	Breeding season rain (time lag years)					Total summer rain (time lag years)			
	0	1	2	3	4	1	2	3	4
<i>R. sylvatica</i>	0.02	0.09*	0.12**	0.06	-0.06	0.03	0.08*	0.04	0.02
<i>P. triseriata</i>	0.05	0.06*	0.04	-0.04	-0.01	0.02	0.05	0.00	-0.04
<i>P. crucifer</i>	0.06	-0.04	0.00	-0.01	-0.01	0.02	0.09*	0.01	-0.05
<i>B. americanus</i>	0.01	-0.04	0.03	-0.02	0.08**	-0.03	0.06*	0.00	0.10**
<i>H. versicolor</i>	0.03	-0.03	0.09***	-0.06	-0.04	-0.05	0.08*	-0.01	-0.02
<i>R. clamitans</i>	0.06*	0.04	-0.01	-0.08	0.07*	0.04	0.00	0.03	0.05

Notes: Values reported are mean *r* values from randomization trials. For each species, analyses were performed using rainfall during the month(s) in which that species was surveyed (breeding season) and for April through August (total summer). Correlations were calculated between the anuran call intensities and rainfall from zero to four years earlier to test for current and delayed effects.

* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

Recently there has been considerable interest in synchronized subpopulation dynamics and the implications for the persistence of metapopulations (Koenig 1999, Akçakaya 2000). Our analyses show that Wisconsin anurans exhibit significantly synchronized dynamics. However, over even short distances subpopulations do not appear to be strongly synchronized. For sites separated by <2 km, mean correlations exceeded 0.50 for only one species, and this was for within-route correlations, which for methodological reasons are biased towards higher correlations. Although calling surveys do not provide the most accurate population estimates, data from other pond-breeding amphibian studies reveal similar levels of synchrony: in five studies where subpopulation sizes were estimated directly by mark-recapture or counts of egg masses, mean levels of synchrony ranged from 0.27 to 0.64 and correlations between adjacent populations were frequently

negative (Table 8). Given that even nearby breeding habitats can have very different hydroperiods, predator and competitor communities, and surrounding vegetation (Skelly et al. 1999, Trenham et al. 2001), it is not surprising that subpopulation dynamics are considerably less synchronous than rainfall.

Synchronized subpopulation dynamics make metapopulations more vulnerable to system-wide extinction, especially when patch extinction probabilities are relatively high (Harrison and Quinn 1989, Akçakaya 2000). Based on the high frequency of species gains and losses at survey sites (Table 4) and weakly synchronized dynamics, regional extinction probabilities for isolated anuran metapopulations such as urban parks may be somewhat higher than if dynamics were completely independent. However, recent work by Matter (2001) suggests that the relationship between synchrony and metapopulation extinction probability is less straightforward when simulations are made more realistic by varying carrying capacity and dispersal probability with patch size. Given the low levels of synchrony and widespread nature of the species considered here, the general threat of synchronized extinctions for Wisconsin anurans is probably less pressing than that of wetland destruction and general habitat degradation (Halley et al. 1996, Marsh and Trenham 2001).

Akçakaya (2000) recently advocated improving metapopulation viability models by including realistic levels of population synchrony. Unfortunately, for most endangered species it is unlikely that data on spatial synchrony exist. Akçakaya (2000) suggested that if no species-specific synchrony data are available, rainfall synchrony could be used as a surrogate. Although this may be reasonable in some cases, our analyses indicate that such an approach would grossly overestimate the degree to which subpopulations of Wisconsin anurans fluctuate in synchrony. In related experiments, Benton et al. (2001) also found that even given completely synchronized environmental perturbations, population synchrony averaged only 0.60.

Because the species in this study are not necessarily equally detectable (Crouch and Paton 2002), meaning-

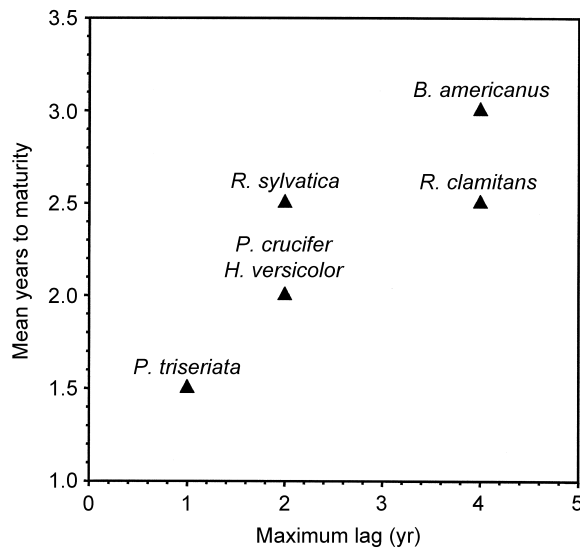


FIG. 3. For the six synchronized species, the time lag producing the strongest mean correlation between rainfall and call indices (Table 7) is plotted against age at sexual maturity (the midpoint of the range of published values; Table 1). Spearman rank order correlation: $r_s = 0.87$, $P = 0.05$.

TABLE 8. Mean correlation (r) calculated from estimated numbers of breeding adults at breeding ponds. Also reported are the number of ponds used to estimate r , the maximum distance separating ponds, the number of years with population estimates, and population estimation methods.

Species	r (range)	Ponds (N)	Distance (km)	Years (no.)	Method [†]	Source
Frogs						
<i>Rana sylvatica</i>	0.64 (−0.02–0.96)	5	2	7	A	Berven and Grudzien (1990)
<i>Rana temporaria</i>	0.27 (0.00–0.52)	3	11	23	B	Meyer et al. (1998) [‡]
<i>Bufo calamita</i>	0.33 (−0.25–0.95)	4	<1	6	B	Sinsch (1992) [§]
Salamanders						
<i>Notophthalmus viridescens</i>	0.32 (−0.47–0.97)	5	2	6	A	Gill et al. (1983) [§]
<i>Ambystoma californiense</i>	0.54 (−0.28–0.98)	8	2	3	C	Trenham et al. (2001)

[†] A = mark–recapture of males and females; B = egg mass counts; C = mark–recapture of males.

[‡] Data from “main” breeding season used.

[§] Population values extracted from figures.

ful interspecific comparison of turnover metrics and synchrony are impossible. However, one pattern unbiased by differential species detectability is the concordance between age at maturity and the time lags producing the strongest correlation with rainfall. Whereas most estimates of demographic parameters are based on at most a few local populations, these results provide a long-term regional evaluation of the predominant time to maturity. Of the species analyzed here, the population biology of *R. sylvatica* has been studied in the most detail. Berven (1982) found most breeding males to be one year old in lowland Maryland and three years old in the mountains of Virginia, while Sagor et al. (1998) found similar numbers of 2-yr-old and 3-yr-old males in a lowland population in Quebec. Assuming that most individuals breed only once (Berven 1990), our results suggest that a 2-yr delay is most common in Wisconsin *R. sylvatica* (Table 7). For Wisconsin *B. americanus* our results suggest that males generally require four years to reach maturity. This contrasts with two skeletochronological studies of age structure in *B. americanus* where 2-yr-old and 3-yr-old males predominated at localities in Illinois and Virginia, respectively (Acker et al. 1986, Kalb and Zug 1990). Consistent with other studies, Wisconsin *P. triseriata* appear to mature at one year and *P. crucifer* at two years (Lykens and Forester 1987, Smith 1987). Not unexpectedly, we also found some indication that in some species, populations in southern Wisconsin mature earlier than in the north (*P. Trenham, unpublished data*).

Management and monitoring

One of our more striking findings is the consistent positive association between local wetland densities and frequencies of detection. The influence of wetland isolation on site occupancy and turnover in amphibians has been repeatedly documented (Marsh and Trenham 2001). This pattern is generally interpreted as resulting from an increased probability of rescue or recolonization in areas with higher densities of nearby wetlands, and thus more potential sources of dispersers. Because local extinctions appear to occur frequently,

maintaining sufficient densities of wetland habitats in the landscape to allow for recolonization should be a primary goal for managers (Semlitsch 2002). However, amphibians also require sufficient upland habitat, as is suggested in our analyses by the significant associations between nonwetland habitat parameters and site occupancies (Table 3). Although, wetland-breeding amphibians have often been described as natural metapopulations, where wetland habitat patches are nested in homogeneous upland “matrix” habitat (reviewed in Semlitsch 2000, 2002, Marsh and Trenham 2001), recent studies have repeatedly demonstrated that the quantity and spatial arrangement of both upland and wetland habitats influence the distributions and dynamics of pond-breeding amphibians (Sjögren-Gulve and Ray 1996, Hecnar and M'Closkey 1998, Pope et al. 2000, Guerry and Hunter 2002).

Agriculture and roads are common upland habitat modifications that have been shown to adversely impact amphibian populations in other studies (Fahrig et al. 1995, Carr and Fahrig 2001, Findlay et al. 2001, Davidson et al. 2002, Guerry and Hunter 2002). Our analyses only revealed significant negative associations between these features and two species (agriculture: *H. versicolor*; roads: *B. americanus*). Relative to agricultural effects, our results are consistent with the findings of Knutson et al. (1999) and Lehtinen et al. (1999) of no demonstrable effects on amphibian diversity in Wisconsin and Minnesota, USA, wetlands, respectively. Fahrig et al. (1995) found that higher traffic densities were associated with reduced breeding choruses and smaller numbers of frogs and toads encountered along roads, and Lehtinen et al. (1999) found lower diversity in landscapes with more roads. The absence of strong effects of agriculture or roads in our analyses may be due to our consideration of occupancy rather than abundance. Clearly, in some regions both of these land uses negatively impact amphibians, and more detailed work to understand their implications for regional population persistence is warranted.

Overall, our results support the prior conclusions of other authors regarding the management of landscapes

for viable amphibian populations. Protecting the wetland breeding habitats on which these species depend is critical (Semlitsch 2002), and higher densities of wetlands will promote less frequent turnover. Conservation strategies should work to promote landscapes with high densities of diverse wetland types and less disturbed upland habitats (Knutson et al. 1999, Semlitsch 2002).

Call surveys are now used to track the distribution and abundance of frog populations in many regions of the United States and Canada (Mossman et al. 1998). Where population fluctuations are strongly correlated over large distances, it might be possible to reduce monitoring coverage without losing critical information. However, since no strong large-scale synchrony exists in Wisconsin anuran dynamics, the current monitoring design would appear to be necessary to encompass regional variability (Koenig 2001). *Rana pipiens* and *Hyla chrysoscelis* showed no indication of synchrony in interroute comparisons. Because the intraroute comparisons for these species exhibited the expected positive correlations, similar to the other species we analyzed, we suspect that observer differences in interpreting call intensities or highly condition-sensitive calling activity for these species obscures correlations between routes (Sauer et al. 1994). Regardless of the cause, these results emphasize that interpretations of monitoring data must strongly consider the methods by which the data were collected. Crouch and Paton (2002) illustrate many of the critical issues to be considered in designing and interpreting frog call surveys, ranging from setting the length of the listening period to differential detectability of species.

In conclusion, the significant associations between the Wisconsin Frog and Toad Survey (WFTS) call data and habitat, rainfall, and demography indicate that these data do reflect changes in amphibian population sizes and not just current climatic conditions or observer error. However, because call indices were also positively correlated with rainfall during the current breeding season, it might be possible to develop models to remove the effect of current weather from call indices and increase the power to detect population declines and other patterns. Although most monitoring programs are initiated as a means to detect regional declines or monitor pests, this is another example of the utility of these data sets especially in the investigation of large-scale ecological patterns and processes (Beard et al. 1999).

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