

CHANGES IN FROG AND TOAD POPULATIONS OVER 30 YEARS IN NEW YORK STATE

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Abstract. Lack of historical data against which to measure population trends greatly hampers understanding the status of amphibians. In 2001–2002 we resurveyed a hitherto unexamined baseline of monitoring data established in 1973–1980 at some 300 sites in western, central, and northern New York State, USA, and contrasted population transitions with environmental conditions to identify correlates of population change in American toads (*Bufo americanus*), northern spring peepers (*Pseudacris crucifer*), western chorus frogs (*Pseudacris triseriata*), leopard frogs (*Rana pipiens*), and wood frogs (*Rana sylvatica*). At the regional level, loss of habitats along roadsides has been substantial (minimally 7–12% of sites), yet within remaining wetlands, populations of most anurans have not declined. At the local level, population disappearance was associated with elevated levels of acid deposition (in American toad, spring peeper, western chorus frog, and leopard frog), urban development (American toad and spring peeper), increased forest cover (western chorus frog), and high-intensity agriculture (spring peeper); whereas population persistence was associated with increased deciduous forest cover (American toad, spring peeper, and wood frog) and low-intensity agriculture (American toad and western chorus frog). Habitat configurations at surprisingly large spatial scales (5–10 km from surveyed populations) were most closely associated with transitions in local anuran populations, implying that large-scale extinction–recolonization dynamics influence population transitions, a result land managers should consider in conservation planning.

Key words: acid deposition; amphibians; anurans; frogs; habitat fragmentation; New York State, USA; population dynamics; population trends; toads; urbanization.

INTRODUCTION

Despite widespread expression of concern about amphibian declines, extensive baseline data against which to measure amphibian population change are largely unavailable anywhere in North America prior to 1990 (Houlahan et al. 2000). Amphibians have only recently risen to prominence as a subject for research; therefore, for most species, historical data on populations are typically anecdotal, sparse, or too outdated to inform debates over contemporary amphibian decline. In particular, characteristically wide population fluctuations (Anura) and secretive habits (Caudata) made research directed at estimating trends in regional populations unrewarding before the hypothesis of global amphibian decline needed to be evaluated (Wake 1991). Lack of standardization of survey methods also has hindered comparisons among sites and across studies (Alford and Richards 1999). Together, these circumstances severely limit not only our ability to measure regional population trends, but also to discriminate among mul-

tle proposed causes of amphibian population declines (Davidson et al. 2002).

One traditional method that can yield repeatable information on landscape-wide changes in species status is road surveys of spring calling anurans, in which all species audible from multiple stations are recorded (Zimmerman 1994). We recently examined such a baseline of monitoring data established some 25–30 years ago using standardized methods. From 1973 to 1980, one of us (F. W. Schueler, with the help of co-operating observers) conducted roadside surveys in a 700 × 100 km area of western, central, and northern New York State. During surveys, the occurrence of frogs and toads at some 300 sites were recorded. This monitoring baseline has not been previously reassessed.

Therefore, during 2001–2002 we resurveyed these sites and we report here changes in populations correlated with measurements of environmental conditions (geographical location, elevation, soil pH, acid and base deposition, and adjacent land cover). Resurveying these sites permitted us to: (1) characterize recent trends in frog and toad populations over a large region, and (2) evaluate several hypotheses about determinants of anuran population change.

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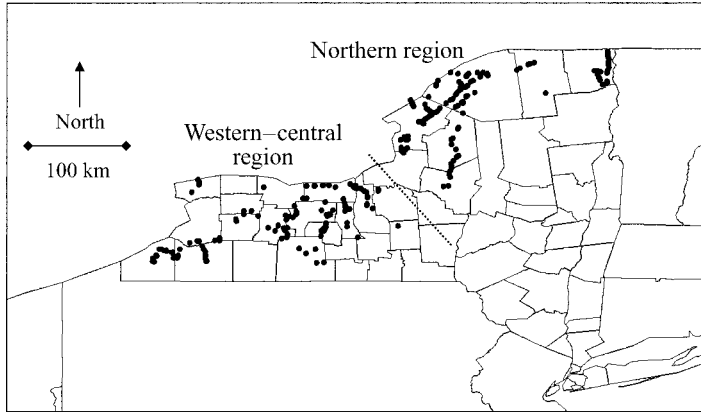


FIG. 1. Locations of 300 sites where anuran populations were surveyed in April–May in 1970–1980 (original baseline surveys) and 2001–2002 in western, central, and northern New York State, USA. Surveys consisted of roadside stops to detect the presence of calling anurans, by species.

MATERIALS AND METHODS

Site surveys: 1973–1980

Between 1973 and 1980, F. W. Schueler made or organized road surveys, during April and May, of calling frogs throughout northern New York State and Vermont in order to determine the range of *Pseudacris triseriata*. Within New York State, sites surveyed extended from the Buffalo area, east to Syracuse, north to Watertown, and east to the Lake Champlain Basin (Fig. 1). Because the goal of these surveys was to delimit the range of *P. triseriata*, calling by other species (especially *Pseudacris crucifer* and *Rana sylvatica*) was also recorded to indicate the presence of wetland habitat unoccupied by *P. triseriata*. Some surveys were diurnal (6%) or their time unrecorded (23%), with the remainder made at night, mostly between dusk and midnight. At each site, the observer stood by the roadside for 1–2 min and recorded all species that vocalized. The location of listening stations was recorded as direction and odometer distance (to the nearest tenth of a mile, or 160 m) from a landmark (typically a road intersection, or the center of a small settlement). In total, 784 records of calling anurans were obtained from 519 sites. Hereafter, these records are referred to as the “original” surveys. Of these, 11% of site surveys were made in 1973, 23% in 1974, 51% in 1975, 4% in 1976, and 11% in 1980.

Site resurveys: 2001–2002

We repeated surveys during 2001 and 2002 of as many of the original survey sites as we could confidently relocate. To maximize comparability between surveys, we confined counts to the same period (April and May) as the original surveys had been conducted. To relocate the survey sites, we used the original site descriptions to scout out survey sites during the daylight and then secured geographical coordinates for those sites that we could confidently identify ($n = 300$ sites). Site coordinates were determined with hand-held global positioning system receivers accurate to ± 20 m. Subsequent audio surveys involved remaining at a wet-

land's edge between dusk and midnight for 5 min and recording all species heard calling during each 1-min interval to ensure that data could be extracted that were comparable with the original counts (1–2 min) as well as with counts being conducted elsewhere with other protocols. To minimize any year-specific bias in geographical coverage, we assembled survey sites into proximal sets of 10–15 sites to form survey routes, and then randomly choose routes each year for surveying. In neither the original, nor contemporary surveys, were counts made under extreme conditions of freezing temperatures, wind, or vehicular noise. All survey data are currently archived with the New York State Department of Environmental Conservation as part of the New York State Amphibian and Reptile Atlas Project (*available online*).⁴

Trends in occurrence

To evaluate population change for each species, we compared presence vs. absence at each sampling site between the two survey periods (1973–1980 vs. 2001–2002) using McNemar's tests (Zar 1984) owing to the paired nature of the sampling design (before/after) and dichotomous nature of the survey data (present/absent). Analyses were made for the five species whose chorusing period broadly overlapped the survey period (April and May) and that were detected at ≥ 10 sites: American toads (*Bufo americanus*), northern spring peepers (*Pseudacris crucifer*), western chorus frogs (*Pseudacris triseriata*), leopard frogs (*Rana pipiens*), and wood frogs (*Rana sylvatica*). To examine the spatial scale at which population processes might be operating in each species, we determined for all possible pairs of populations whether population transitions were the same ($= 1$) or different ($= 0$) and then averaged these values within various classes of between-site distances (0.0–1.0, 1.1–10.0, 10.1–100.0, and 100.1–999.9 km). Ambient temperature is a major driver of amphibian activity (Beebe 1995), so we also

⁴ <http://www.dec.state.ny.us/website/dfwmr/wildlife/herp/>

TABLE 1. Characteristics of frog survey sites that were destroyed vs. persisted between 1970 and 2000, in western, central, and northern New York, USA (values are means \pm SE).

Variable	Destroyed ($n = 23$)	Persisted ($n = 300$)	$F_{1, 297}$	P
Pasture (%)	34.2 \pm 4.4	37.1 \pm 1.1	0.43	0.5127
Row crops (%)	10.3 \pm 2.0	11.5 \pm 0.5	0.33	0.5646
Developed land (%)	9.8 \pm 3.6	2.9 \pm 0.4	14.95	0.0001
Cultivated grasses (%)	1.5 \pm 0.6	0.5 \pm 0.1	6.28	0.0097
Deciduous forest (%)	29.1 \pm 3.3	28.8 \pm 0.9	0.01	0.9328
Evergreen forest (%)	0.8 \pm 0.3	1.4 \pm 0.1	0.91	0.3402
Mixed forest (%)	9.0 \pm 1.6	10.7 \pm 0.5	0.69	0.4063
Water (%)	2.3 \pm 1.5	2.0 \pm 0.4	0.03	0.8563
Marsh (%)	0.1 \pm 0.04	0.4 \pm 0.1	0.59	0.4437
Swamp (%)	2.4 \pm 1.0	4.0 \pm 0.5	0.73	0.3938

Note: All variables were measured within a circle of radius 1 km centered on the survey site; n is the number of survey sites.

contrasted it between survey periods to determine weather climatic conditions were similar between surveys. To do so, we determined average maximum daily temperatures at Syracuse, a location central to the region surveyed, during the original and contemporary surveys (data source is the National Oceanic and Atmospheric Agency's Northeast Regional Climate Center; *available online*).⁵ We used the number of observations of vocalizing frogs made each month to weight the contribution that each monthly temperature value made to average temperature (and its variance) for the two survey periods and contrasted means using an independent sample t test (Zar 1984).

Environmental correlates of population transitions

Geographical location, elevation, soil pH, acid and base deposition, and adjacent land cover at each survey location were recorded and linked to anuran survey data. Survey site elevation was determined from U.S. Geological Survey topographical maps. Composition of the surrounding landscape at four spatial scales (circular areas with radii of 0.5, 1.0, 5.0, and 10.0 km extending from each site surveyed) was estimated from the National Land Cover Dataset (*available online*).⁶ This data set integrates 1992 Landsat thematic mapper imagery and supplemental data to produce 21 categories of land cover information at a 30-m resolution (Vogelmann et al. 1998). The pH of the top 5 cm of soil at each survey site was obtained from STATSGO, a database of soil properties compiled by the Natural Resources Conservation Service (USDA-NRCS 1994). Estimated levels of atmospheric acid and base deposition at each site were obtained from Hames et al. (2002) who used data on mean deposition of inorganic ions collected between 1984 and 1999 at sites throughout the United States by the National Atmospheric Deposition Program's National Trend Network (Lamb and Bowersox 2000). From these data, Hames et al. (2002) derived two relative scales that reflected overall acid

and base deposition, respectively, at sites monitored and then spatially interpolated these data across the region, from which we obtained point estimates of acid and base deposition for each of our survey sites.

We contrasted environmental conditions among sites where each species underwent the four possible classes of population transitions between survey periods: remained absent, appeared, disappeared, or remained present. Comparisons were made with a univariate analysis of variance procedure appropriate to the unbalanced nature of the survey design (PROC GLM; SAS Institute 1989). Only population transition classes with ≥ 5 observations for each species were included in the analysis. Estimates of land cover are presented for the particular spatial scale (within a circle of radius 0.5, 1.0, 5.0, or 10.0 km from survey site) that provided the best discrimination among population transition classes based on overall model fit as reflected by the magnitude of the model adjusted R^2 . All land cover data, initially measured and presented in the *Results* as proportions, were arc-sin transformed prior to analysis. Results from statistical tests yielding $\alpha \leq 0.05$ were interpreted.

RESULTS

Comparison of surveys

Of the 519 sites originally surveyed, we definitively relocated 323 sites (62%). Of these, 23 (7% of all sites relocated or 12% of sites not relocated) had evidently been destroyed (primarily by filling or ditching). Sites destroyed were surrounded by more developed lands and by more cultivated grasses than sites that persisted (Table 1). Notably, extent of agricultural land was comparable near sites that were destroyed vs. that persisted.

Ambient temperatures were comparable between survey periods. Mean temperature across all months during which surveys were made was 9.35°C \pm 0.18°C (mean \pm SE) during 1973–1980 and 9.61°C \pm 0.16°C during 2001–2002; mean temperatures did not differ ($t = 1.11$, $df = 923$, $P = 0.268$) between survey periods. Phenological patterns of species detection (Fig. 2) were

⁵ (<http://met-www.cit.cornell.edu/>)

⁶ (<http://landcover.usgs.gov/>)

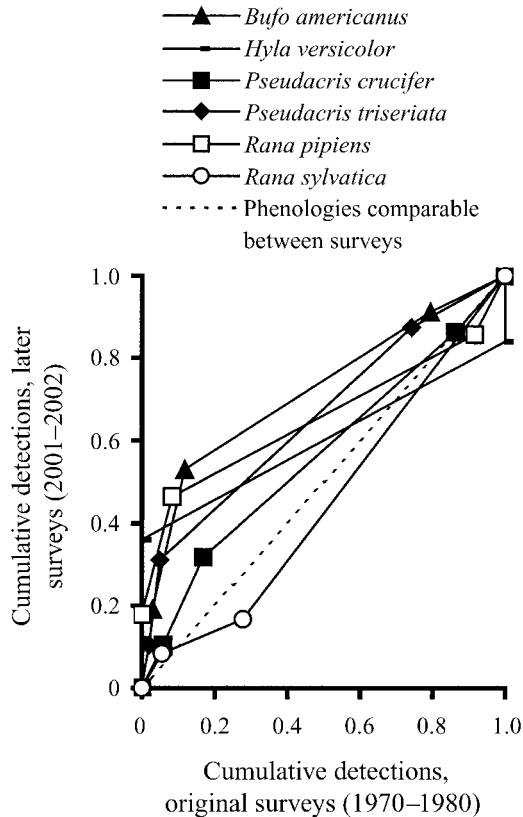


FIG. 2. Comparison of phenology of anuran calling activity during the original (1973–1980) and later (2001–2002) surveys. Consecutive points represent the cumulative fraction of total detections obtained for a particular species by Julian dates 100–110, 111–120, 121–130, 131–140, and 141–150 (100 = 10 April). Identical phenologies of species detections would be represented by the straight (dashed) line.

also broadly comparable between survey periods, although somewhat more advanced seasonally during 2001–2002 than during the original surveys for all species, except the wood frog.

Trends in frog and toad populations

Trends in anuran populations were estimated based on a comparison of frog and toad occurrence during the initial surveys (1–2 min listening interval/site) vs. the more recent surveys (2-min listening interval/site) across the 300 sites extant in both survey periods (Table 2). These analyses indicated that American toad occurrence increased region-wide, particularly in the western–central region. Spring peeper occurrence also increased in both sub-regions and region-wide. Western chorus frog occurrence was stable region-wide, a pattern that subsumed an increase in occurrence in the west-central sub-region and a strong decrease in occurrence in the northern sub-region. Leopard frog occurrence increased modestly region-wide, a trend not detectable in either sub-region likely due to low sample sizes. Wood frog occurrence was stable region-wide.

Because some original surveys were made during daylight hours (6%) or did not have survey times precisely recorded (23%), we repeated the trend analyses excluding such sites ($n = 216$ sites with definitive nighttime counts). This reanalysis only substantially affected trend estimates for the western chorus frog, which became negative (disappearances = 32% of sites, appearances = 19%, $P = 0.001$) region-wide. Similarly, length of survey interval influenced probability of detection, although not substantially: 90% of occupied sites were so classified by two minutes for spring peeper, American toad, and leopard frog and by three minutes for western chorus frog and wood frog (Fig. 3). Reanalyzing the 2001–2002 survey data based on one-minute (rather than two-minute) listening interval yielded trends in occurrence comparable to those reported in Table 2, with the exception that the region-wide trend in occurrence of western chorus frogs became negative (disappearances = 25% of sites, appearances = 16%, $P = 0.013$).

Environmental correlates of population transitions

American toads.—In comparison to sites where American toad populations were absent or disappeared, sites where populations persisted or appeared were at higher elevations in the western and southern portions of the region and in areas with more pasture, more deciduous and mixed forest, less evergreen forest, less developed land, and lower levels of acid and base deposition (Table 3). The spatial scale providing the strongest habitat-based discrimination among population transitions of toads was 5–10 km from the survey site (Table 3). Relative similarity of population transitions was maximized at a spatial scale of 1.1–10.0 km (Fig. 4).

Northern spring peeper.—In comparison to sites where spring peeper populations were absent or disappeared, sites where populations that persisted or appeared were more southerly and westerly and occurred at higher elevations, on less acid soils, and in areas with less row crops, less developed land, less cultivated grasses, less evergreen forest, more mixed forest, less open water, and less marsh (Table 4). Relationships with swamps were ambiguous (Table 4). The spatial scale providing the strongest habitat-based discrimination among population transition types of spring peepers was 1–5 km for open land uses and 10 km for forests (Table 4). Relative similarity of population transitions was maximized at a spatial scale of 0.0–1.0 km (Fig. 4).

Western chorus frog.—In comparison to sites where populations were absent or disappeared, sites where western chorus frog populations persisted or appeared tended to be more southerly and westerly, on less acid soils and in areas with more pasture, less cultivated grasses, and less forest of all types (Table 5). Relationships with elevation and extent of marsh and swamp were ambiguous. Spatial scale providing the

TABLE 2. Changes in anuran populations in New York State between 1970–1980 and 2001–2002.

Species	Population change (transitions, %)				<i>P</i>	Trend
	Absent	Disappeared	Appeared	Persisted		
<i>Bufo americanus</i>						
Northern	77.1	11.1	11.7	0.0	1.000	stable
Western–central	57.6	6.6	32.0	3.6	0.001	increase
Region-wide	68.2	9.0	21.1	1.6	0.002	increase
<i>Hyla versicolor</i>						
Northern	89.5	0.0	10.5	0.0	0.001	increase
Western–central	93.4	0.7	5.8	0.0	0.045	increase
Region-wide	91.3	0.4	8.4	0.0	0.001	increase
<i>Pseudacris crucifer</i>						
Northern	14.2	22.2	37.6	25.9	0.014	increase
Western–central	10.9	10.2	36.5	42.3	0.001	increase
Region-wide	12.7	16.7	37.1	33.4	0.001	increase
<i>Pseudacris triseriata</i>						
Northern	41.9	34.6	12.9	10.5	0.001	decrease
Western–central	49.6	14.6	30.6	5.1	0.007	increase
Region-wide	45.4	25.4	21.1	8.0	0.308	stable
<i>Rana pipiens</i>						
Northern	85.8	4.3	9.8	0.0	0.095	stable
Western–central	87.6	3.6	8.7	0.0	0.145	stable
Region-wide	86.6	4.0	9.3	0.0	0.017	increase
<i>Rana sylvatica</i>						
Northern	93.2	5.6	1.2	0.0	0.070	stable
Western–central	86.1	6.6	7.3	0.0	0.887	stable
Region-wide	90.0	6.0	4.0	0.0	0.361	stable

Notes: In total, 300 sites were surveyed: 162 in western and central New York and 138 in northern New York (see Fig. 1), during April and May of each survey period. *P* is the probability of populations disappearing and appearing with comparable frequency, based on McNemar's test.

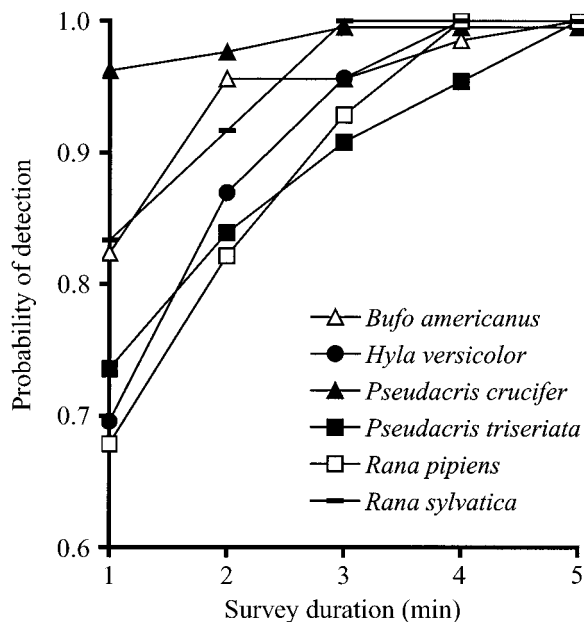


FIG. 3. Cumulative fraction of sites classified as occupied by a particular species in relation to duration of survey at a site.

strongest habitat-based discrimination among population transitions of western chorus frogs was 5–10 km (Table 5). Relative similarity of population transitions was maximized at a spatial scale of 0.0–1.0 km (Fig. 4).

Leopard frog.—In comparison to sites where populations were absent or disappeared, sites where leopard frog populations appeared were at lower elevations, on less acid soils, and surrounded by more open water, more marsh, less swamp, and an intermediate extent of pasture (Table 6). Spatial scale providing the strongest habitat-based discrimination among population transitions of leopard frogs varied from 1–10 km (Table 6). Relative similarity of population transitions was maximized at a spatial scale of 1.1–10.0 km (Fig. 4).

Wood frog.—In comparison to sites where populations were absent or disappeared, sites where wood frog populations appeared were in more westerly and southerly locations, at higher elevations, had less pasture, more deciduous and mixed forest, and less evergreen forest, and more swamp (Table 7). The spatial scale providing the strongest habitat-based discrimination among population transitions of wood frogs varied from 1 to 10 km (Table 7). Relative similarity of population transitions was maximized at a spatial scale of 1.1–10.0 km (Fig. 4).

TABLE 3. Relationship between environmental conditions and changes in populations of American toads (*Bufo americanus*) between 1970 and 2000 in western, central, and northern New York (values are means \pm SE).

Variable	Scale	Absent (n = 204)	Disappeared (n = 26)	Appeared (n = 63)	Persisted (n = 5)	$F_{3, 295}$	P
Latitude ($^{\circ}$)	point	43.7 \pm 0.06	43.5 \pm 0.1	43.3 \pm 0.08	42.6 \pm 0.1	5.23	0.0001
Longitude ($^{\circ}$)	point	76.1 \pm 0.1	76.4 \pm 0.2	76.7 \pm 0.1	77.8 \pm 0.3	3.95	0.0009
Elevation (m)	point	207.8 \pm 9.1	231.7 \pm 26.7	241.0 \pm 16.3	388.8 \pm 67.0	3.93	0.0091
Acid deposition \dagger	point	1.7 \pm 0.02	2.0 \pm 0.07	1.5 \pm 0.03	1.5 \pm 0.1	10.37	0.0001
Base deposition \dagger	point	0.3 \pm 0.04	0.8 \pm 0.1	0.3 \pm 0.05	0.1 \pm 0.1	6.97	0.0002
Soil pH	point	5.8 \pm 0.05	5.8 \pm 0.09	5.9 \pm 0.06	5.8 \pm 0.2	0.74	0.5301
Pasture (%)	10	30.3 \pm 0.8	31.2 \pm 2.1	34.8 \pm 1.0	27.4 \pm 4.3	2.57	0.0548
Row crops (%)	1	11.5 \pm 0.7	7.9 \pm 1.2	12.8 \pm 1.1	9.7 \pm 2.4	1.59	0.1909
Developed land (%)	10	2.4 \pm 0.1	2.2 \pm 0.5	1.2 \pm 0.1	0.8 \pm 0.1	4.4	0.0048
Cultivated grasses (%)	1	0.5 \pm 0.1	1.0 \pm 0.5	0.5 \pm 0.2	0.0 \pm 0.0	0.75	0.5216
Deciduous forest (%)	5	28.9 \pm 0.7	34.4 \pm 1.7	32.7 \pm 1.5	38.9 \pm 6.4	4.35	0.0051
Evergreen forest (%)	10	2.6 \pm 0.2	2.1 \pm 0.3	1.2 \pm 0.2	1.0 \pm 0.1	3.49	0.0161
Mixed forest (%)	10	14.4 \pm 0.5	15.8 \pm 1.5	10.6 \pm 0.9	17.4 \pm 3.6	4.77	0.0029
Water (%)	5	3.5 \pm 0.5	1.4 \pm 0.5	2.2 \pm 0.4	0.5 \pm 0.2	1.54	0.2036
Marsh (%)	10	0.3 \pm 0.04	0.1 \pm 0.03	0.2 \pm 0.03	0.1 \pm 0.1	2.23	0.1029
Swamp (%)	1	4.6 \pm 0.7	4.0 \pm 1.2	1.8 \pm 0.4	1.8 \pm 1.3	1.75	0.1564

Note: Scale refers to scale of measurement, that is, the length (km) of radius of a circle centered on the survey site within which land use was measured, and was that which yielded the greatest separation among population trends; n is the number of survey sites.

\dagger Increasing values reflect increasing levels of deposition (see *Methods; Environmental correlates of population transitions*; Hames et al. 2002).

DISCUSSION

Our analysis of trends in species occurrence was based on surveys of roadside wetland sites that had remained extant between 1970 and 2001. An unknown,

yet potentially substantial, fraction of sites originally surveyed likely were destroyed between surveys. Surveyed wetlands were classified as destroyed only if precise directions lead us to a site that also exhibited clear evidence of being a former wetland (e.g., a playing field fringed by *Typha*). We confidently relocated 62% of the original survey sites upon which we could make a determination of wetland status. Therefore, we suspect that wetland destruction was much greater than the minimum 7% of original sites we have reported. This unknown component of habitat loss cannot be readily accounted for in the analysis of population trends. Aggregate wetland loss has been estimated at circa 60% in New York State (New York State Office of Parks, Recreation and Historic Preservation 1988). Thus, we conclude that populations of five frog and toad species occurring within roadside wetlands in western, central, and northern New York have likely declined in the region over the last 30 years due to habitat loss, yet have largely remained stable in the wetland habitat that remains.

Our amphibian monitoring study is unusual in that it is well replicated at the regional scale, largely consistent in methodology, and spans several decades (Alford and Richards 1999). Our surveys suggest that only northern populations of western chorus frogs evidently have undergone substantial declines in the study region in recent decades (see also Schueler 1999). Weather conditions, as indexed by ambient temperatures, were comparable between surveys, suggesting survey results were not skewed by year-specific, climate-related bias in calling activity. Other unknown bias associated with methodology may exist (e.g., associated with modest shifts detected in calling phenology [Fig. 2]), yet personnel in common between the original and later sur-

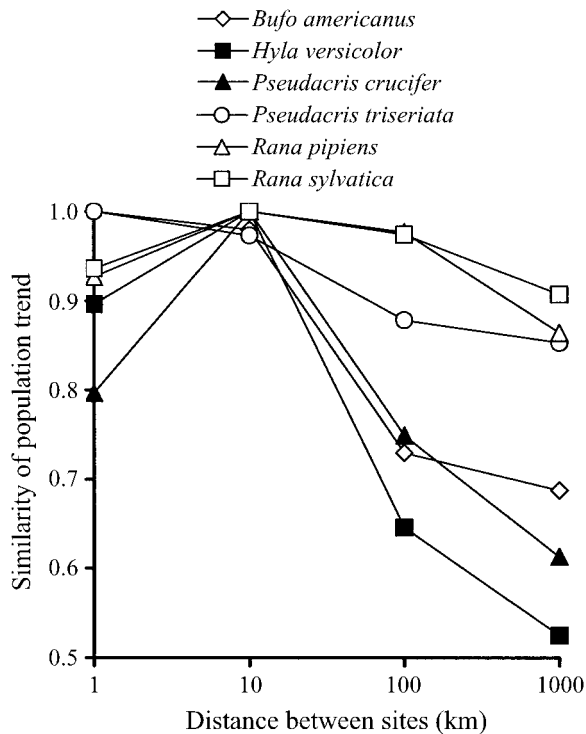


FIG. 4. Similarity of transitions in anuran populations over 30 years in western and northern New York State in relation to distance between sites. Similarity values are relative to the maximum value observed for each species.

TABLE 4. Relationship between environmental conditions and changes in populations of spring peepers (*Pseudacris crucifer*) between 1970 and 2000 in western, central, and northern New York (values are means \pm SE).

Variable	Scale	Absent (n = 38)	Disappeared (n = 50)	Appeared (n = 100)	Persisted (n = 111)	$F_{3, 295}$	P
Latitude (°)	point	43.7 \pm 0.2	43.8 \pm 0.1	43.7 \pm 0.07	43.2 \pm 0.09	7.11	0.0001
Longitude (°)	point	76.0 \pm 0.2	75.7 \pm 0.3	76.1 \pm 0.1	76.9 \pm 0.2	9.20	0.0001
Elevation (m)	point	193.2 \pm 16.3	181.9 \pm 19.1	196.7 \pm 10.1	274.7 \pm 15.2	9.34	0.0001
Acid deposition†	point	1.6 \pm 0.05	1.8 \pm 0.07	1.6 \pm 0.03	1.7 \pm 0.03	2.02	0.1112
Base deposition†	point	0.2 \pm 0.08	0.4 \pm 0.1	0.3 \pm 0.04	0.4 \pm 0.05	0.84	0.4730
Soil pH	point	5.7 \pm 0.07	5.6 \pm 0.08	5.9 \pm 0.06	6.0 \pm 0.08	2.9	0.0351
Pasture (%)	1	39.7 \pm 3.4	32.1 \pm 3.0	39.1 \pm 1.7	35.3 \pm 1.8	1.98	0.1164
Row crops (%)	10	12.0 \pm 1.4	11.2 \pm 0.7	10.3 \pm 0.7	8.2 \pm 0.4	4.47	0.0004
Developed land (%)	1	5.1 \pm 1.4	6.6 \pm 2.1	2.2 \pm 0.4	2.4 \pm 0.5	4.27	0.0057
Cultivated grasses (%)	1	1.3 \pm 0.5	0.7 \pm 0.3	0.4 \pm 0.1	0.3 \pm 0.09	2.68	0.0469
Deciduous forest (%)	1	23.8 \pm 2.1	28.8 \pm 2.2	30.0 \pm 1.4	29.5 \pm 1.6	1.57	0.1968
Evergreen forest (%)	10	2.2 \pm 0.4	3.5 \pm 0.6	2.1 \pm 0.2	1.7 \pm 0.2	3.58	0.0143
Mixed forest (%)	10	10.7 \pm 1.0	12.8 \pm 0.7	11.2 \pm 0.6	18.4 \pm 0.8	20.82	0.0001
Water (%)	10	6.7 \pm 1.3	5.8 \pm 1.0	6.1 \pm 0.7	2.8 \pm 0.4	5.20	0.0006
Marsh (%)	5	0.7 \pm 0.2	0.4 \pm 0.1	0.2 \pm 0.04	0.2 \pm 0.04	4.78	0.0029
Swamp (%)	1	1.3 \pm 0.3	6.4 \pm 1.8	2.6 \pm 0.5	5.1 \pm 1.0	4.08	0.0073

Note: Scale refers to scale of measurement, that is, the length (km) of radius of a circle centered on the survey site within which land use was measured, and was that which yielded the greatest separation among population trends; n is the number of survey sites.

† Increasing values reflect increasing levels of deposition (see *Methods; Environmental correlates of population transitions*; Hames et al. 2002).

veys in our study fostered comparability of survey results. The single-visit sampling approach that we used clearly would yield a high rate of failed detections (e.g., Kéry 2002, MacKenzie et al. 2002). One result would be inflated estimates of rates of population turnover. Because this bias was equally present in both surveys, however, estimates of trend are expected to be valid if conservative.

Hecnar and M'Closkey (1996) have emphasized the importance of distinguishing factors that negatively affect a species at the local scale from patterns of persistence at the regional scale in order to determine spe-

cies status. In our study, despite evident regional stability in populations of the species surveyed, patterns of population transitions yielded insights into the environmental factors and their associated spatial scale that may be affecting local population dynamics. For example, American toads and spring peepers both were less persistent in areas surrounded by residential or commercial land uses (developed lands) or lawns (cultivated grasses). Whether this relationship is associated with a loss of breeding ponds, habitats for adults, or both, is not clear. Such negative affects of urban land uses on amphibians have been reported previously

TABLE 5. Relationship between environmental conditions and changes in populations of western chorus frogs (*Pseudacris triseriata*) between 1970 and 2000 in western, central, and northern New York (values are means \pm SE).

Variable	Scale	Absent (n = 136)	Disappeared (n = 76)	Appeared (n = 63)	Persisted (n = 24)	$F_{3, 295}$	P
Latitude (°)	point	43.4 \pm 0.07	43.9 \pm 0.1	43.3 \pm 0.1	43.9 \pm 0.2	7.86	0.0001
Longitude (°)	point	76.2 \pm 0.1	75.8 \pm 0.2	76.9 \pm 0.2	76.1 \pm 0.3	6.15	0.0001
Elevation (m)	point	231.4 \pm 10.8	180.0 \pm 14.6	253.8 \pm 18.0	191.7 \pm 27.0	4.47	0.0043
Acid deposition†	point	1.6 \pm 0.03	1.7 \pm 0.05	1.6 \pm 0.03	1.6 \pm 0.05	1.89	0.1310
Base deposition†	point	0.4 \pm 0.04	0.4 \pm 0.07	0.3 \pm 0.04	0.2 \pm 0.08	1.15	0.3280
Soil pH	point	5.7 \pm 0.07	5.9 \pm 0.05	5.9 \pm 0.06	5.9 \pm 0.1	2.55	0.0461
Pasture (%)	5	32.1 \pm 1.1	35.1 \pm 1.7	33.2 \pm 1.8	39.6 \pm 2.3	2.38	0.0496
Row crops (%)	10	9.9 \pm 0.5	10.9 \pm 0.7	10.0 \pm 0.8	7.3 \pm 1.3	1.87	0.1354
Developed land (%)	10	2.3 \pm 0.2	2.4 \pm 0.3	1.7 \pm 0.2	1.2 \pm 0.1	2.22	0.0858
Cultivated grasses (%)	10	0.5 \pm 0.05	0.3 \pm 0.05	0.4 \pm 0.05	0.2 \pm 0.04	4.75	0.0030
Deciduous forest (%)	5	33.3 \pm 0.9	25.9 \pm 1.0	30.2 \pm 1.4	28.6 \pm 1.9	7.90	0.0001
Evergreen forest (%)	10	2.8 \pm 0.3	2.1 \pm 0.2	1.7 \pm 0.3	1.1 \pm 0.2	3.01	0.0306
Mixed forest (%)	10	12.5 \pm 0.6	13.8 \pm 0.7	15.8 \pm 1.3	15.9 \pm 1.1	3.11	0.0267
Water (%)	10	4.4 \pm 0.5	6.0 \pm 0.9	5.7 \pm 1.0	3.8 \pm 1.1	1.24	0.2942
Marsh (%)	10	0.2 \pm 0.03	0.5 \pm 0.08	0.2 \pm 0.04	0.2 \pm 0.1	5.50	0.0017
Swamp (%)	10	3.2 \pm 0.2	4.2 \pm 0.4	2.5 \pm 0.3	4.6 \pm 0.8	3.72	0.0180

Note: Scale refers to scale of measurement, that is, the length (km) of radius of a circle centered on the survey site within which land use was measured, and was that which yielded the greatest separation among population trends; n is the number of survey sites.

† Increasing values reflect increasing levels of deposition (see *Methods; Environmental correlates of population transitions*; Hames et al. 2002).

TABLE 6. Relationship between environmental conditions and changes in populations of leopard frogs (*Rana pipiens*) between 1970 and 2000 in western, central, and northern New York (values are means \pm SE).

Variable	Scale	Absent (<i>n</i> = 259)	Disappeared (<i>n</i> = 12)	Appeared (<i>n</i> = 28)	<i>F</i> _{2, 296}	<i>P</i>
Latitude (°)	point	43.5 \pm 0.05	43.7 \pm 0.3	43.8 \pm 0.1	1.75	0.1745
Longitude (°)	point	76.3 \pm 0.1	75.9 \pm 0.5	76.1 \pm 0.3	0.43	0.6465
Elevation (m)	point	226.0 \pm 8.1	230.5 \pm 58.6	158.4 \pm 19.4	3.34	0.0167
Acid deposition†	point	1.7 \pm 0.02	1.6 \pm 0.1	1.6 \pm 0.06	1.24	0.2902
Base deposition†	point	0.4 \pm 0.03	0.1 \pm 0.1	0.2 \pm 0.09	2.40	0.0972
Soil pH	point	5.8 \pm 0.04	5.2 \pm 0.5	5.9 \pm 0.1	4.74	0.0094
Pasture (%)	1	37.9 \pm 1.1	23.3 \pm 2.9	32.2 \pm 4.3	4.06	0.0182
Row crops (%)	1	11.4 \pm 0.5	13.6 \pm 2.9	10.7 \pm 2.2	0.36	0.6981
Developed land (%)	1	3.7 \pm 0.6	7.0 \pm 5.0	2.4 \pm 0.9	0.78	0.4604
Cultivated grasses (%)	1	0.5 \pm 0.1	1.4 \pm 1.2	0.6 \pm 0.4	1.3	0.2748
Deciduous forest (%)	10	30.6 \pm 0.6	33.7 \pm 3.7	29.8 \pm 2.2	0.62	0.5394
Evergreen forest (%)	1	1.2 \pm 0.2	2.9 \pm 1.4	0.8 \pm 0.2	1.51	0.2232
Mixed forest (%)	1	8.9 \pm 0.5	11.9 \pm 2.2	11.6 \pm 2.1	1.49	0.2261
Water (%)	10	4.6 \pm 0.4	6.2 \pm 2.4	8.6 \pm 2.0	4.23	0.0155
Marsh (%)	1	0.2 \pm 0.04	0.5 \pm 0.5	1.5 \pm 0.9	6.48	0.0018
Swamp (%)	5	3.6 \pm 0.3	7.1 \pm 2.2	2.6 \pm 0.4	3.72	0.0254

Note: Scale refers to scale of measurement, that is, the length (km) of radius of a circle centered on the survey site within which land use was measured, and was that which yielded the greatest separation among population trends; *n* is the number of survey sites.

† Increasing values reflect increasing levels of deposition (see *Methods; Environmental correlates of population transitions*; Hames et al. 2002).

(Findlay and Houlihan 1997, Knutson et al. 1999) and are likely related to conversion of natural to unsuitable habitats, as well as disruption of movement by anthropogenic barriers such as roads.

Notably, there was little negative association between population transitions and extent of agriculture in any of the five species studied (Table 1). Moreover, positive associations with extent of pasture were evident in America toads and western chorus frogs. Only spring peepers indicated a negative association with extent of row crops. Thus, low intensity agriculture, quite widespread in the region studied, as it has been

practiced over the last 30 years, is not evidently associated with ongoing declines of amphibians in the region. Studies by Knutson et al. (1999) in the mid-western United States yielded a similar conclusion, although other researchers have concluded that agriculture, particularly intensive mono-cropping with heavy application of agrochemicals, is associated with local extinctions (e.g., Davidson et al. 2002) and declines in amphibian diversity (Bonin et al. 1997).

Strong, positive associations between amphibians and forest are frequently reported in the literature (e.g., Laan and Verboom 1990, Findlay and Houlihan 1997,

TABLE 7. Relationship between environmental conditions and changes in populations of wood frogs (*Rana sylvatica*) between 1970 and 2000 in western, central, and northern New York (values are means \pm SE).

Variable	Scale	Absent (<i>n</i> = 270)	Disappeared (<i>n</i> = 18)	Appeared (<i>n</i> = 12)	<i>F</i> _{2, 296}	<i>P</i>
Latitude (°)	point	43.6 \pm 0.05	43.6 \pm 0.2	42.6 \pm 0.1	8.55	0.0001
Longitude (°)	point	76.2 \pm 0.09	76.0 \pm 0.6	78.1 \pm 0.4	7.85	0.0001
Elevation (m)	point	211.9 \pm 7.7	217.0 \pm 35.6	402.1 \pm 38.9	12.59	0.0001
Acid deposition†	point	1.7 \pm 0.02	1.5 \pm 0.08	1.8 \pm 0.06	2.06	0.1290
Base deposition†	point	0.4 \pm 0.03	0.1 \pm 0.1	0.6 \pm 0.08	2.81	0.0617
Soil pH	point	5.8 \pm 0.04	5.5 \pm 0.1	5.8 \pm 0.1	1.48	0.2294
Pasture (%)	10	32.0 \pm 0.7	24.7 \pm 2.8	26.2 \pm 2.4	4.51	0.0118
Row crops (%)	1	11.0 \pm 0.6	15.9 \pm 3.8	8.0 \pm 2.4	2.13	0.1209
Developed land (%)	10	2.1 \pm 0.1	3.1 \pm 0.6	0.6 \pm 0.1	3.87	0.0209
Cultivated grasses (%)	10	0.4 \pm 0.03	0.6 \pm 0.1	0.2 \pm 0.03	2.11	0.1229
Deciduous forest (%)	10	30.4 \pm 0.6	28.8 \pm 1.5	40.4 \pm 3.5	5.95	0.0029
Evergreen forest (%)	5	1.8 \pm 0.1	6.7 \pm 1.9	1.5 \pm 0.5	19.02	0.0001
Mixed forest (%)	10	13.5 \pm 0.4	15.4 \pm 1.7	18.9 \pm 2.6	3.04	0.0495
Water (%)	10	5.1 \pm 0.4	5.9 \pm 1.8	0.7 \pm 0.2	2.35	0.0972
Marsh (%)	1	0.3 \pm 0.09	1.3 \pm 0.9	0.1 \pm 0.07	2.04	0.0542
Swamp (%)	1	3.4 \pm 0.4	6.6 \pm 3.0	11.1 \pm 4.6	5.47	0.0046

Note: Scale refers to scale of measurement, that is, the length (km) of radius of a circle centered on the survey site within which land use was measured, and was that which yielded the greatest separation among population trends; *n* is the number of survey sites.

† Increasing values reflect increasing levels of deposition (see *Methods; Environmental correlates of population transitions*; Hames et al. 2002).

Knutson et al. 1999); our study is no exception. Frog and toad species responding positively to extent of deciduous and mixed forest cover included American toads, spring peepers, and wood frogs. An important caveat is that responses to extent of coniferous forests were largely negative, as was the case for American toads, spring peepers, and wood frogs. Western chorus frog responded negatively to increasingly extent of forest of all types. Western chorus frog is associated with early successional stages (grasslands and brushy areas) and forest succession may be occurring to the detriment of this species. Notably, forest cover in New York State has increased over the last 20 years by some 3% (Cantrell 2002). We conclude that the ongoing expansion of the mostly deciduous native forests of New York State (Zipperer et al. 1990) will benefit many frogs and toads species, except the western chorus frog. Any trend toward plantation-style forestry in the state, which already is extensive and is primarily based on conifers, would be to the detriment of most species (see also Waldick et al. 1999), given the negative associations between many species and extent of coniferous forests.

Geographical patterns of population change in several species are consistent with acid deposition (Dunson et al. 1992) being an important cause of change in local populations and possibly regional populations in some species. Population persistence in four of five species (American toad, spring peeper, western chorus frog, and leopard frog) was associated with lower levels of acid deposition or higher soil pH. The region sampled extended across a strong gradient in acid deposition, which generally increases in an easterly direction (Hames et al. 2002). Thus, the frequent association of population persistence or appearance with more westerly and southerly locations in many species may also reflect an interaction with patterns of acid deposition.

One somewhat surprising result was the spatial scale at which population processes in many of the anurans studied likely were operating. Where land uses varied among classes of population transitions (Tables 3–7), the spatial scale at which the difference was maximized was disproportionately at the largest scale measured, that is, 0% of comparisons in which population transition/land use differences were maximized occurred at 0.5 km, 19% at 1.0 km, 22% at 5.0 km, and 58% at 10.0 km. In some species, such as the diminutive western chorus frog, the best discrimination among land uses and population transition classes occurred only at spatial scales of 5–10 km from surveyed sites. Moreover, in four of five species (spring peeper, American toad, leopard frog, and wood frog) population transitions were most similar among sites separated by distances of 1.1–10.0 km (with the remaining two species, western chorus frog and spring peeper, at ≤ 1 km; Fig. 2). Houlahan and Findlay (2003) also observed that land use change at surprisingly large spatial scales, i.e.,

2–3 km, influenced variation in amphibian species communities.

So-called “Moran effects” (Moran 1953) are the most likely cause of the spatial autocorrelation in population transitions observed. Moran effects are caused by density-independent factors (e.g., weather; Koenig 2002) that are correlated across populations and synchronize local population dynamics. We expect local variation in patterns of rainfall and hence breeding pool availability (especially for species, such as western chorus frogs, dependent on temporary pools) drive the spatial autocorrelations we observed in population transitions (Fig. 2). Whatever the case, most amphibian researchers assume that metapopulation processes in anurans occur within areas of radius 1 km and tailor the spatial scale their measurement of the environment accordingly (e.g., Knutson et al. 1999, Carr and Fahrig 2001), yet our study and that of Houlahan and Findlay (2003) suggest that habitat changes and environmental processes at far greater scales influence on population dynamics.

As emphasized by Semlitsch et al. (1996) and Skelly et al. (1999), pond-breeding frogs have fluctuating breeding populations with high annual rates of local extinctions. For such species, persistence is particularly contingent on periodic recolonization from adjacent, extant subpopulations (Sjögren 1991, Green 2003). Although habitat conditions directly adjacent to breeding areas are clearly vital to managing amphibian populations (Semlitsch 2000), our study implies that land managers should consider that planning efforts may need to occur at substantial spatial scales in order to ensure the long-term persistence of frog and toad populations.

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