TRENDS IN ANURAN OCCUPANCY FROM NORTHEASTERN STATES OF THE NORTH AMERICAN AMPHIBIAN MONITORING PROGRAM

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Abstract.—We present the first multi-year occupancy trends from North American Amphibian Monitoring Program (NAAMP) data in 10 northeastern states using seven years of data (2001-2007). NAAMP uses a calling survey technique where observers listen for anuran vocalizations along assigned random roadside routes. We were able to assess occupancy trends in 10 northeastern states for 16 species and one species complex, for 94 species/state combinations. We found no significant trends for 64 species/state combinations. For the remaining 30 species/state combinations with significant trends, these split between declining and increasing trends. On a species-by-species basis, two species had declining trends, with significant trends in six states for *Pseudacris crucifer* and four states for *Bufo americanus*. The trends of *Rana catesbeiana* significantly increased in four states, but had no trend in the remaining states.

Key Words.—amphibian monitoring; calling survey; NAAMP; occupancy modeling; occupancy trends

INTRODUCTION

In the 1990s, the scientific community raised concern about global amphibian decline, though early reports used primarily anecdotal evidence (Blaustein and Wake 1990; Vial and Saylor 1993). A need for quantitative evidence from long-term investigations using standardized methods was recognized (Pechmann et al. 1991; Vial and Saylor 1993). This led to the formation of the North American Amphibian Monitoring Program (NAAMP) as a long-term monitoring program to assess population trends for calling amphibians (Weir et al. 2005).

NAAMP uses a survey technique where observers listen for anuran vocalizations and identify species by their unique calls. This takes advantage of the fact that most anuran species make unique breeding vocalizations, where males call to attract females. The use of frog call surveys to monitor amphibians was pioneered by the Wisconsin Frog and Toad Survey in the 1980s (Mossman and Hine 1984), and other locations in the 1990s including Iowa (Hemesath 1998), Ontario (Bishop et al. 1997), Missouri (Johnson 1998), Minnesota (Moriarty 1998), and Michigan (Genet and Sargent 2003).

NAAMP is a partnership among the United States Geological Survey (USGS) and various state partners using a common sampling design and survey protocol to collect data since 2001, and going back to 1997 with some variation in protocol (e.g., how long observers listen per site). The number of states participating in NAAMP has changed over the years, with 17 states contributing data in 2001 and 21 states by 2008.

One conducts NAAMP surveys along random roadside routes. By using random routes, rather than opportunistic sampling, NAAMP's sampling design allows one to draw inferences at a larger landscape scale, such as the statewide trends reported here. Advantages to adopting a roadside calling survey methodology include: (1) all sites are accessible; (2) no landowner permission is needed; (3) one can visit more sites per night; and (4) there is little risk of transmitting amphibian diseases among survey locations.

This paper describes an assessment framework to provide periodic reporting of occupancy trends from NAAMP data. Additionally, we report the first multi-year occupancy trends from seven years of NAAMP data for 10 northeastern states.

MATERIALS AND METHODS

We used NAAMP data from 10 states of the northeastern United States: Delaware, Maine, Maryland, Massachusetts, New Jersey, New Hampshire, Pennsylvania, Vermont, Virginia, and West Virginia. For nine states we used seven years of data (2001–2007); Vermont did not conduct surveys in 2007 and thus has a six-year dataset. Roadside routes are created from a random start point and direction of travel to make the surveys as spatially random as possible. Each route has 10 survey points, called stops, located at 0.8 km or more apart where wetland habitats are present (e.g., roadside ditch, vernal pool, pond, etc). NAAMP provides observers with route maps and driving directions. Occasionally a stop must be retired (e.g., safety issue). In such cases, the surveyor documents the stop

retirement in the NAAMP database, and a replacement stop is added to the route to retain 10 survey points. In analyses, the retired and replacement survey points occur as separate sites.

Participants survey routes three or four times per year during sampling periods that target early breeding through late-breeding anurans. Some routes may be surveyed more frequently. Routes are visited during the evening, starting 30 minutes after sunset or later; surveys should be completed by 0100. At the start and end of the survey, observers record wind conditions using the Beaufort wind scale, sky conditions, and air temperature. Observers are instructed to avoid sampling when winds are too strong (code four or above, which is ≥ 20.9 km/h) or when minimum air temperatures are not met. The minimum air temperature varies with sampling periods and ranges from 5.6°C to 12.8°C. At each stop, observers listen for five minutes and record every species of anuran heard using an amphibian calling index, a one-to-three scale to estimate abundance. At each stop, observers may record time, air temperature, and some other abiotic variables. (see Weir and Mossman (2005) for more details of the NAAMP protocol or visit the NAAMP website: http://www. pwrc.usgs.gov/naamp). For modeling purposes, we converted the data to observed presence or absence and thus converted the amphibian calling index values to zero for absence and one for presence.

We used the data from all sampling periods in a year as replicate samples to obtain information about detectability. However, because of distinct seasonal patterns in anuran calling behavior, which vary by species, we allowed for seasonal variation in detection probability as described in the statistical methods section below (Weir et al. 2005). An alternative to modeling seasonal variation in detection probability would be to truncate the data to produce a single period of constant detection probability. However, NAAMP does not provide sufficient replication to allow this approach as truncation would yield a single observation at each route in most states. Additionally, by including all data and explicitly modeling the detection process, we were able to adjust estimates of occupancy to account for false non-detections.

Starting in 2006, observers were required to pass an on-line frog call identification quiz for their data to be included in analyses. In addition to the quiz criteria, data were included in these analyses if sky and wind data were collected at the start and/or end of the survey night, air temperature was recorded at eight or more stops on the survey night, and the survey was completed in less than three hours. While the survey protocol instructs observers to initiate surveys 30 minutes after sunset or later, we included data in these analyses if surveys began as early as 30 minutes prior to sunset.

Sunset time varies with latitude and time of year. We calculated minutes after sunset as the time recorded by the observer minus the sunset time for the survey date at the approximate start location of the route. We used first stop's site coordinates, if available, or the randomly generated start point for calculating sunset time. We generated sunset time using a Java software package (K-Zone Computing. 2003. Sunrise/sunset calculator. Available from http://www.kevinboone.com/suntimes .html [Accessed 3 March 2009]) and adjusted for Daylight Savings Time as necessary. For some surveys, observers recorded start time at every stop. In other cases, observers recorded a start time and end time for the overall survey. If only start time and end time for the entire route were available, then we estimated the start time for individual stops by dividing the entire survey time equally among the 10 stop locations.

Statistical methods.—The basis of our modeling approach was the multi-season occupancy model described by Mackenzie et al. (2003). This model contains components that represent the underlying ecological process governing occupancy of "sites" (taken here to be NAAMP stops) and imperfect observation of that process. We defined $z(i,t)$ to be the binary occupancy status of site (or sample location) "i" during breeding season (year) "t". Thus, $z(i,t) = 1$ for an occupied site, and $z(i,t) = 0$ otherwise. The objects of inference are summaries of these occupancy state variables or parameters of an underlying model describing variation in occupancy states (described below). In practice, we cannot observe occupancy state perfectly because even if a species occupies a site, it may not be actively calling during the brief sample or it may be present in such low numbers that individuals are undetectable. Thus, we obtain observations y_{ijt} for samples $j = 1, 2,…, J$ of site i during season t. We note that replicate samples are required in order to obtain information about detection probability. In particular, we assume that the observations y_{ijt} are independent Bernoulli trials with parameter p_{it} (detection probability), which may depend on site- or season-specific covariates.

A number of variables affect the likelihood that an observer detects a species in an occupied site. We used three covariates in this analysis: minutes after sunset, Julian calendar day, and air temperature. We modeled these covariates as linear effects on the logit-transformed detection probability (as in logistic regression). In a previous study conducted with NAAMP data in Maryland, these detection factors were included in the best model for seven or more of 10 species included in the study (Weir et al. 2005). Because previous work has shown that detection probability may reach a peak at a particular temperature or date, we looked at two levels of inclusion for each of these covariates; linear and quadratic. Thus, 27 possible covariate combinations

were possible. We fit the model if there was at least one detection for a given species/state combination in each survey year. For each species/state combination, we used the detection model that resulted in the lowest Akaike's Information Criterion (AIC) to estimate the occupancy trend.

A paucity of literature exploring trend assessment as an inferential goal in occupancy studies exists. One approach, presented by MacKenzie et al. (2003), projects forward in time from the estimated initial probability of occupancy using the estimated rates of colonization and extinction as:

$$\hat{\psi}_t = \hat{\psi}_{t-1}(1 - \hat{\epsilon}_{t-1}) + (1 - \hat{\psi}_{t-1})\hat{\gamma}_{t-1}$$

where $\hat{\psi}_t$ is the estimated probability of occupancy in year t for a typical site in the population (E[z(i,t)] where the average is over sites), $\hat{\epsilon}_{t-1}$ is the estimated probability that an occupied site at time t-1 becomes unoccupied at time t (i.e., "local extinction probability"), and $\hat{\gamma}_{t-1}$ is the estimated probability that an unoccupied site at time t-1 becomes occupied at time t. This method yields unbiased estimates of annual occupancy if the model is correct, but is data hungry and highly parameterized because it requires estimation of the rates of colonization and extinction for each year, even though these rates are likely to be related over time. For the seven years of NAAMP data, 14 parameters are required to describe the occupancy dynamics, with still more parameters needed for the detection process, as described below. The large number of parameters is problematic for species with few detections or when few sites were sampled and results in imprecise estimates. In general, we refer to the temporal ensemble of year-specific parameters ψ_t as the trajectory (Link and Sauer 1997) to distinguish these quantities from specific parametric descriptions of trend such as linear or other polynomial functions.

An obvious way to reduce the model size, thereby improving the precision of estimates, is to assume a common colonization rate (γ) and extinction rate (ϵ) govern the occupancy dynamics over the entire study period. Then, these single rates insert directly into the above projection equation to estimate occupancy rate over time. Although this direct use of the reduced model would improve precision, this extreme reduction has its own difficulties. Namely, the resulting estimated occupancy trajectory is constrained, perhaps artificially, to follow a strict geometric pattern (i.e., strictly linear on the log-scale). This false restriction might strongly bias estimates of occupancy. Thus, we have a variance-bias trade-off and must find an adequate estimation procedure that does not suffer inordinately from either highly variable estimates or bias.

As a compromise, we restricted our attention to the estimation of the unobserved occupancy dynamics at the sampled sites rather than in the entire hypothetical super-population of sites from which the samples were drawn, and thus focus on estimating the proportion of sampled sites that are occupied in any given year. To accomplish this, we use the above, reduced model with common colonization and extinction rates along with hidden Markov model smoothing to obtain an estimate of site-specific probability of occupancy. To be specific, let z(i,t) be the unobserved occupancy status for site i at time t. Then we use smoothing to construct an estimator $\widehat{\psi_t|Y}$, where Y represents the observational data, whose expectation is given by

$$E[\widehat{\psi_t|Y}] = Prob(z(i,t) = 1 \mid$$

observed data at site i is sampled). This sample estimator differs from $\hat{\psi}_t$ above, whose expectation is given by

$$E[\hat{\psi}_t] = Prob(z(i,t) = 1).$$

In words, $\widehat{\psi_t|Y}$, our smoothing-based estimator of the trajectory, estimates the proportion of sample sites that are occupied in each year, whereas the projection-based estimator ($\hat{\psi}_t$) estimates the occupancy rate for the entire population of hypothetical sites from which our sample was selected. Note that if, as desired, the sampled sites are a representative sample of the entire population of sites, and the model adequately describes the trajectory, then these two estimators have the same expectation. In this situation, the two estimates of trajectory would only differ in their uncertainty. However, in a situation like ours, where a model of constant dynamics perhaps fails to capture the true pattern, $\widehat{\psi_t|Y}$ will be a better estimator of sample trajectory than $\widehat{\psi_t}$ simply because the estimate of the smoothed trajectory $\widehat{\psi_t|Y}$ is not constrained to precisely follow the model, but is strongly informed by the sample data combined with the model. In this way, although $\widehat{\psi_t|Y}$ is based on a more parsimonious model because it uses the constant-dynamics model to attain statistical stability, it also yields a more flexible estimate of the trajectory than $\widehat{\psi_t}$ with the same model.

For estimating the trajectory based on $\widehat{\psi_t|Y}$, we exploit the fact that the colonization-extinction model is a special case of the general class of statistical models called hidden Markov models (HMMs). HMMs are well studied in statistical (Cappé et al. 2005) and engineering (Ephraim and Merhav 2002) literature, with a wealth of estimation tools available. We use smoothing, a popular estimation method for HMMs (Cappé et al. 2005). Smoothing is a statistical technique that estimates the

TABLE 1. The number of sites (and routes) by year in 10 northeastern states surveyed for calling amphibians for the North American Amphibian Monitoring Program.

State	Survey Year						
	2001	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**
Delaware	130 (13)	90 (9)	110 (11)	140 (14)	140 (14)	120 (12)	80 (8)
Maine	498 (50)	456 (46)	402 (41)	516 (52)	459 (46)	299 (30)	300 (30)
Maryland	190 (19)	210 (21)	169 (17)	200 (20)	182 (19)	60 (6)	80 (8)
Massachusetts	150 (15)	170 (17)	130 (13)	100 (10)	137 (14)	100 (10)	190 (19)
New Hampshire	140 (14)	139 (14)	120 (12)	120 (12)	140 (14)	60 (6)	70 (7)
New Jersey*	90 (9)	60 (6)	478 (48)	342 (35)	386 (39)	240 (24)	256 (26)
Pennsylvania	220 (22)	140 (14)	140 (14)	78 (8)	10 (1)	100 (10)	80 (8)
Vermont	70 (7)	60 (6)	40 (4)	40 (4)	30 (3)	40 (4)	0
Virginia	170 (17)	219 (22)	160 (16)	120 (12)	130 (13)	70 (7)	100 (10)
West Virginia	310 (31)	268 (27)	150 (15)	200 (20)	200 (20)	110 (11)	109 (11)

*In 2003, New Jersey increased the number of routes in the state.

underlying time series of unobserved state probabilities in HMMs (Ephraim and Merhav 2002; Cappé et al. 2005). In the context of the colonization-extinction model, each site is treated as an independent realization of a HMM for which the smoothed trajectories $\psi_{it}|Y = Prob(Z_{it} = 1 \mid Y_{i,1,\cdot}, Y_{i,2,\cdot}, \cdots, Y_{i,T,\cdot}, \theta)$ were obtained using the method in Appendix 1, where θ are the model parameters, $Y_{i,t,\cdot}$ is the set of observations for site i at time t, and $Z_{i,t}$ is the latent true occupancy state for site i at time t. We use maximum likelihood estimates of the model parameters in the smoothing computation to yield an estimate of this probability, $\widehat{\psi_{it}|Y}$, a site-specific smoothed trajectory. We then averaged the site-specific smoothed trajectories over all of the sites to obtain an overall estimate the proportion of sites occupied at each time, by $\widehat{\psi_t|Y} = M^{-1}\sum_i \widehat{\psi_{it}|Y}$, where M is the number of sites in the sample. These numbers formed the estimated sample-wide trajectory that we used in the next stage of the analysis to compute trend. Unlike the projection method, these smoothed trajectories are not restricted to the particular pattern dictated by the fitted model. By conditioning on the data, these smoothed trajectories estimate $E[Z_{it}|Y_i]$, which is necessarily closer to Z_{it} for the sample at hand than the projection method, which estimates $E[Z_{it}]$ because we have conditioned on additional information. Thus, smoothing provides a way to use the simpler, less parameterized model, yet estimate a sample trend that reveals more complex patterns. See Discussion for more details on the inferential implications of choosing our smoothing method.

Then, to estimate trend, the rate of change in occupancy over time, we fit a linear regression model through this smoothed trajectory. To account for the non-independence of these time series data, we used the bootstrap (Efron and Tibshirani 1993) to estimate the correlation structure within this trend. We computed

100 bootstrap iterations for each species/state. We used generalized least squares, also known as the Aitken model, to estimate the linear slope of the trend, accounting for the estimated correlation structure (Monahan 2008). We tested for the significance of the trend slope using t-tests. Because we dealt with a short time series (seven years) with substantial temporal correlation, we lowered the significance bar to $\alpha = 0.1$ from the standard $\alpha = 0.05$.

We fit the colonization-extinction model by maximizing the likelihood given by Mackenzie et al. (2003). We did all computations with the open source statistical computing environment, R (R Project for Statistical Computing. Available from http://www.r-project.org [Accessed 3 March 2009]), and its extension package unmarked (Fiske. 2009. unmarked: An R Package for the Analysis of Wildlife Survey Data. Available from http://r-forge.r-project.org/projects/unmarked/ [Accessed 3 March 2009]).

RESULTS

The number of routes surveyed varied by state and year, though most states had fewer routes surveyed during 2006–2007 than other years (Table 1). Twenty-nine anuran species or species complexes occur within the 10 states; all were detected at least once during NAAMP surveys. For 12 species, we did not have enough data to assess trends; most of these species have distributions restricted to southern Virginia for our study area. We report occupancy trends for the remaining 16 species (*Acris crepitans, Bufo americanus, B. fowleri, Hyla chrysoscelis, H. cinerea, H. versicolor, Pseudacris brachyphona, P. crucifer, Rana catesbeiana, R. clamitans, R. palustris, R. pipiens, R. septentrionalis, R. sphenocephala, R. sylvatica, and R. virgatipes*) and the *Pseudacris feriarum* species complex (*P. feriarum, P.*
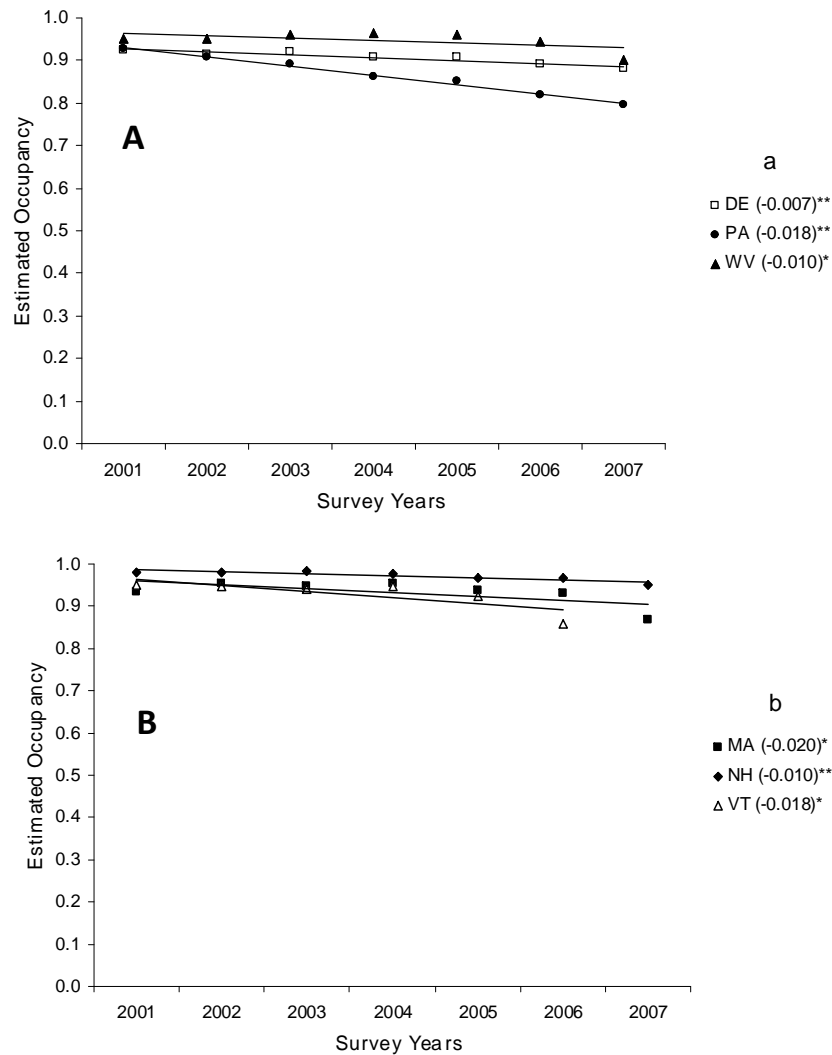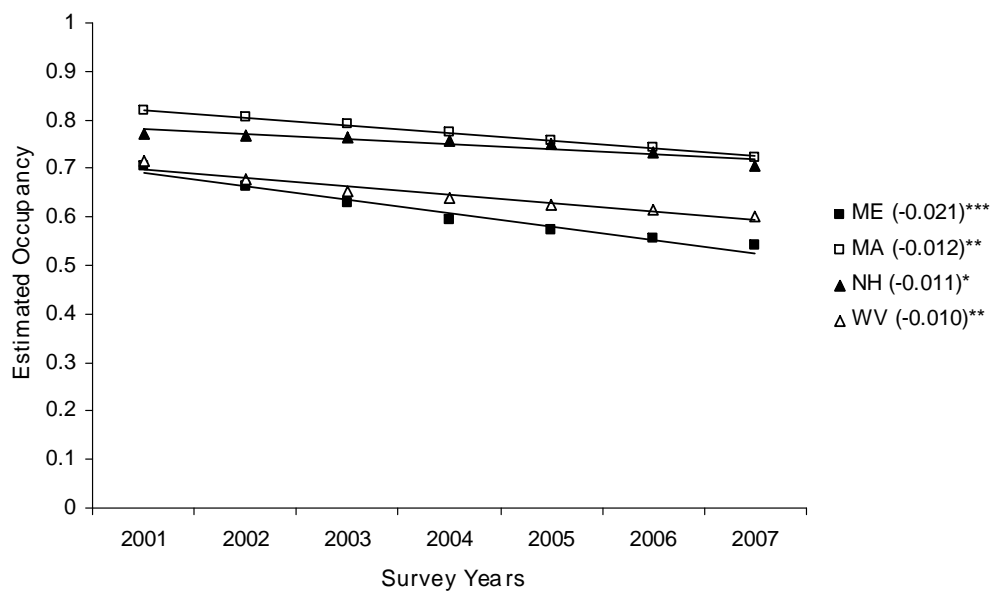
FIGURE 1. Estimated occupancy trends for *Pseudacris crucifer* in six states of the northeastern United States from 2001–2007. Trends (A) shown for Delaware (DE), Pennsylvania (PA), and West Virginia (WV) and (B) for Massachusetts (MA), New Hampshire (NH), and Vermont (VT). Overall trend in parentheses with asterisks indicating significance level (*p < 0.1, ** p < 0.05, *** p < 0.01). Vermont did not survey in 2007.

kalmi, and *P. triseriata*; Appendix 2). We were able to evaluate 94 species/state combinations. Fifteen species/state combinations exhibited significant positive trends (p ≤ 0.10) with 12 at a ≥ 1% annual rate of change. The majority of these significant increases were for Ranids (Appendix 2). Fifteen species/state combinations showed significant negative trends (p ≤ 0.10) with 13 at a ≥ 1% annual rate of change. We found no significant trend for 64 species/state combinations.

We looked for species showing consistent trends in decline or increase, where three or more states had a statistically significant trend of the same direction. Two species, *P. crucifer* and *B. americanus*, showed a pattern of declining trends, with six states for *P. crucifer* (Fig. 1a and 1b) and four states for *B. americanus* (Fig. 2). Another two species, *R. catesbeiana* and *R. sphenocephala*, showed a pattern of increasing trends, with four states for *R. catesbeiana* (Fig. 3) and three states for *R. sphenocephala* (Fig. 4). Two species, *R. clamitans* (Fig. 5) and *H. versicolor*, exhibited mixed trend results where statistically significant trends of both directions were found. In addition, there were four species (*B. fowleri*, *R. palustris*, *R. sylvatica*, and *R. virgatipes*) that had at least one state with a significant trend. There were no significant trends for six species (*A. crepitans*, *H. chrysoscelis*, *H. cinerea*, *P. brachyphona*, *R. pipiens*, and *R. septentrionalis*).

FIGURE 2. Estimated occupancy trends for *Bufo americanus* in four states of the northeastern United States from 2001–2007. Trends shown for Maine (ME), Massachusetts (MA), New Hampshire (NH), and West Virginia (WV). Overall trend in parentheses with asterisks indicating significance level (*$P < 0.1$, ** $P < 0.05$, *** $P < 0.01$).

DISCUSSION

This paper presents the first multi-year assessment of occupancy trends for anurans from NAAMP data. There are no comparable reports in the literature describing trends for anurans in the northeastern United States. Existing studies tend to be for a few localities (Daszak et al. 2005; Brander et al. 2007), resampling of historical sites (Gibbs et al. 2005) or for a single state or province in other regions of North America (Mossman et al. 1998; de Solla et al. 2006). Additionally, the time series for these studies is earlier (late 1990s or early 2000s) than our dataset.

Pseudacris crucifer showed a downward trend in all states and were significant for six states. Despite these declines, this species still has very high occupancy rates and continues to be common. Initial occupancy rates were ≥ 90% in every state. Such high levels of occupancy leave little room for site colonization as so few sites are unoccupied. Finding a downward trend becomes more likely because occupancy rates can only remain stable or decrease. Elsewhere for *P. crucifer*, Mossman et al. (1998) found similar trends in Wisconsin between 1984–1994, showing this species to be abundant but experiencing a small but significant decline. In contrast, Gibbs et al. (2005) found *P. crucifer* to be increasing in New York when they revisited 300 sites in 2001–2002 that had been surveyed in 1973–1980.

Bufo americanus showed a downward trend in eight of 10 states. Trends were significant for four of the eight states. These four states had initial occupancy rates ranging between 70–81%. In comparison, this species was stable to increasing in Wisconsin during 1984–1994 comparing the 2001–2002 surveys with data from 1973–1980 (Gibbs et al. 2005).

Rana catesbeiana showed significant increasing trends for four states (Delaware, New Jersey, Virginia, and West Virginia). The Wisconsin study was unable to assess trends for *R. catesbeiana*, as the species is not state-wide in its distribution and was irregularly sampled (Mossman et al. 1998). There were four significant trends for *Rana clamitans*; two states had increasing trends (Massachusetts and West Virginia) while two had decreasing trends (Maine and Maryland). Mossman et al. (1998) found this species to be stable from 1984–1994 in Wisconsin. Gibbs et al. (2005) did not examine trends for either species in New York.

Occupancy and population trends are related, but not necessarily the same. Occupancy trends measure change in the number of sites occupied, while population trends measure change in number of individuals. For a species that assembles in large breeding congregations, the site remains occupied until the population size is reduced to zero. For such species, a large change in population size occurs before a change in occupancy is detected (Royle 2004). Occupancy-based assessments may be relatively inefficient compared to abundance-based trend assessments (Dorazio 2007). However, counting numbers of individual anurans during calling surveys is not feasible, but NAAMP observers rate each species using an amphibian calling index (1–3 scale). Rather
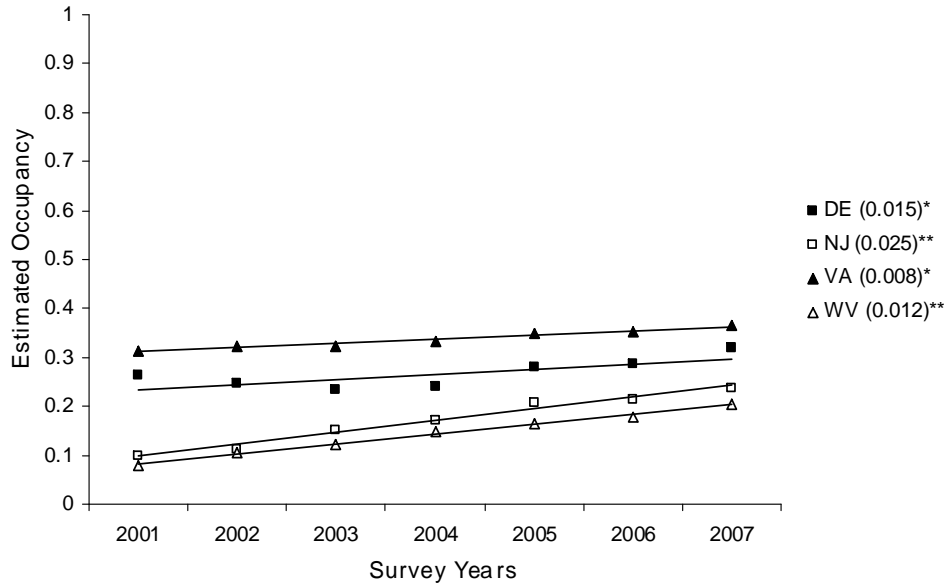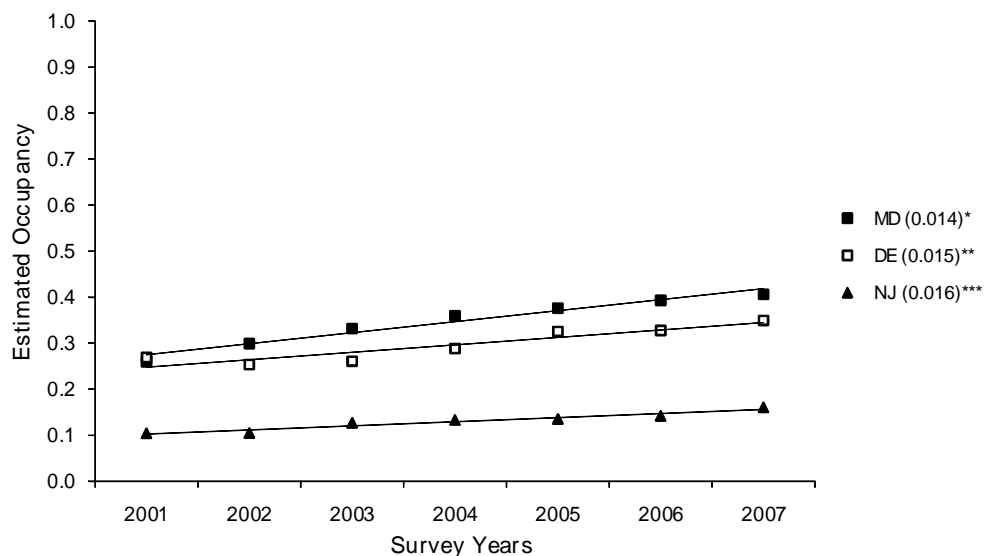
FIGURE 3. Estimated occupancy trends for *Rana catesbeiana* in four states of the northeastern United States from 2001–2007. Trends shown for Delaware (DE), New Jersey (NJ), Virginia (VA), and West Virginia (WV). Overall trend in parentheses with asterisks indicating significance level (*$P < 0.1$, ** $P < 0.05$, *** $P < 0.01$).

than truncate the data to presence-absence it may be possible to develop models for the observed index data (e.g., Royle 2004; Royle and Link 2005). Multi-state occupancy models are inherently "parameter hungry," however, and for most species there is relatively limited information about state transitions and detectability for the higher index values. Thus, for most species and even in relatively small geographic regions, the simple binary occupancy models are relatively stable from a statistical point of view. We note that Mossman et al. (1998) developed simple regression models using amphibian calling index data, but that approach did not account for the "repeated measures" nature of the data (that is, sample locations are repeatedly sampled during a year, and across years). As this is a major feature of the survey design, we believe that it should be addressed explicitly in the modeling framework, which was one objective of our work.

More research to assess the relationship between population size and amphibian calling index is needed because the relationship is likely different among species. Two studies (Corn et al. 2000; Nelson and Graves 2004) have examined this relationship using mark-recapture to estimate anuran population size while also conducting calling surveys using a calling index. Nelson and Graves (2004) found a positive relationship between population size and amphibian calling index for *R. clamitans* in Michigan. Corn et al. (2000) found call surveys able to estimate relative abundance for *P. maculata* in Colorado, but had difficulty detecting rare or irregularly calling species, *R. pipiens* and *Spea*

bombifons, respectively. Shirose et al. (1997) found a significant linear relationship between call counts and chorus size for *B. fowleri* and *R. catesbeiana*.

A concern with volunteer-based programs is whether the volunteers are adequately prepared to collect survey data. A scientific peer review of NAAMP in 2002 (unpublished report) recommended that NAAMP create an online frog-call identification test for volunteers. Based on this recommendation, the Frog Quiz (www.pwrc.usgs.gov/frogquiz) was developed, and as of 2006, observers are required to pass the quiz for their data to be included in USGS analyses. Several studies have shown that observers tend to have higher agreement on presence-absence of species than on the assignment of the call index values (Bishop et al. 1997; Shirose et al. 1997; Genet and Sargent 2003). Bishop et al. (1997) found observers agreed on presence-absence of species 76% to 92% of the time, but call index values agreement ranged from 56% to 83%. Shirose et al. (1997) compared novice, intermediate, and expert observers and found the groups agreed 93–96% on species presence-absence while call index agreement (when exclude agreement on absences) ranged from 46–83%. Genet and Sargent (2003) evaluated observer frog call identification using 12 audio tracks on compact disk. Correct identification of species ranged from 60% for *B. fowleri* up to 98% for *R. clamitans* and *R. catesbeiana*. False negatives (failure to detect species that is present) ranged from 1.6% for *R. clamitans* to 40% for *B. fowleri*. False positives (reporting a species as present that is not) were generally lower and ranged from 0.8% for *R.*

FIGURE 4. Estimated occupancy trends for *Rana sphenocephala* in three states of the northeastern United States from 2001–2007. Trends shown for Delaware (DE), Maryland (MD), and New Jersey (NJ). Overall trend in parentheses with asterisks indicating significance level (*$P < 0.1$, ** $P < 0.05$, *** $P < 0.01$).

catesbeiana to 9.9% for *H. versicolor*. The standard occupancy models, such as were used in our work, account for so-called "false negative" errors. Extension of the models to accommodate false positives is possible (Royle and Link 2006) but such models pose a number of conceptual and technical problems that impede their practical application.

NAAMP surveys are conducted along roadside routes. This approach has advantages (e.g., sites are accessible, no landowner permission needed, able to visit more sites per night, no risk of transmitting amphibian diseases among sites) and potential disadvantages (i.e., road effects). Roads may have direct and indirect impacts on individual amphibians through such processes as road
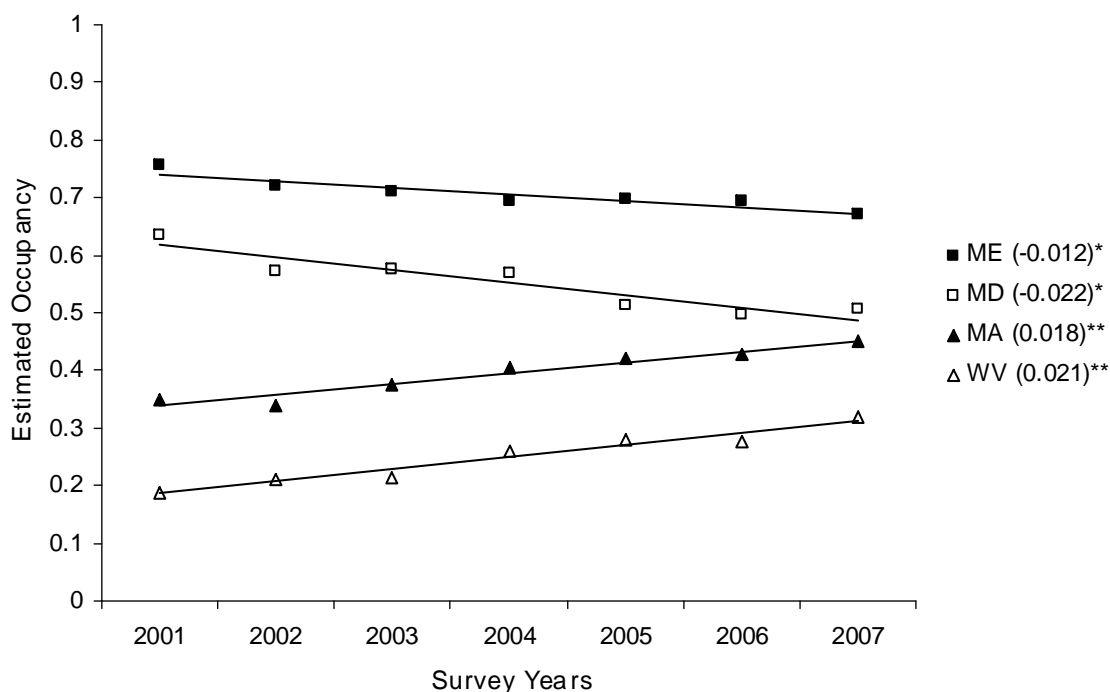
FIGURE 5. Estimated occupancy trends for *Rana clamitans* in four states of the northeastern United States from 2001–2007. Trends shown for Maine (ME), Maryland (MD), Massachusetts (MA), and West Virginia (WV). Overall trend in parentheses with asterisks indicating significance level (*$P < 0.1$, **$P < 0.05$, ***$P < 0.01$).

mortality and chemical run-off (see Andrews et al. 2008). Impacts on amphibian populations are hard to assess. How far from the road is included in NAAMP's sampling effort varies depending on the species (i.e., quiet versus loud calling species) and sound degradation due to topography, vegetation, and other factors (Gerhardt and Huber 2002). Research to document audible distances for various species and environmental factors would be relevant to NAAMP to understand better how much of the surrounding landscape is encompassed by the survey. Another consideration is whether habitat change along roadsides is representative of habitat change in the larger landscape, as differences could bias species detected and associated trends. Studies examining habitat change near and far from roads have been done for the Breeding Bird Survey (BBS), which provides avian population trends using a similar network of roadside routes (Peterjohn 1994). Keller and Scallan (1999) found rates of increase in urban cover were greater along Maryland roads compared to the larger landscape, while in Ohio this change was not significant. For all habitat types comparing habitat near and far from roads, Keller and Scallan (1999) found the direction of change was the same. Other studies have found little to no effect (Bart et al. 1995; McNulty et al. 2008). Similar studies for NAAMP are warranted. Thus, a number of factors related to the roadside aspect of the survey complicate interpretation of NAAMP data and its relationship to the larger landscape.

The difficulty in assessing declines in species with very low occupancy rates and increases in species with very high occupancy rates must be emphasized. This problem is due to the general statistical fact that small effects are more difficult to detect than large ones, given the same sampling effort. Thus, in general, the power to detect changes in occupancy depends strongly on the true occupancy rate. An important future contribution would be a comprehensive power analysis to characterize this power curve for a range of occupancy rates. Thus, some species with low occupancy rates may be in decline, although we could not find sufficient evidence. As we collect more data in future years, our power to detect such declines will improve.

Our smoothing method differs from the projection method of MacKenzie et al (2003). The projection method estimates the latent time series of latent occupancy rates for a hypothetical infinite population from which the sampled sites were taken. In contrast, smoothing refines this estimate by conditioning on the observed sites in the sample. The decision to use the projection method or smoothing to estimate trend should be determined by the application. For monitoring programs such as NAAMP, where the same sites are visited annually, interest might lie in the rate of occupancy change at those particular sites. In this scenario, smoothing is preferred. Smoothing would also be favorable if generalizing from the sample of sites to a theoretically much larger population of sites is questionable, such as when the sampled sites make up a substantial proportion of the total sites of interest. A benefit of conditioning on our sample is that the smoothing trend estimates are more precise than those from the projection method. To maximize our power to detect trends, we chose the finite-sample based smoothing trend estimator.

Our formulation of a model for assessing population trends has a number of technical limitations. First, the state by species analysis requires many parameters, leading to relatively imprecise inferences for many state/species combinations. We believe that the data can be unified into a single hierarchical model in order to provide composite estimates of group or community summaries and improved precision of individual species estimates (Link 1999; Sauer and Link 2002; Russell et al. 2009). Second, we regarded NAAMP stops as spatial replicates so the occupancy process was assumed to be independent across stops. The fact that stops are nested within routes may induce a spatial dependence structure that could influence the precision of trend estimates. Finally, as noted above, we did not use the ordinal amphibian calling index data; but we developed some extensions of the multi-state models described in Royle (2004) and Royle and Link (2005) for open "multi-season" situations. However, these extensions use highly parameterized models and we have not yet developed an effective reduced-parameter version of those models.

As NAAMP continues to collect data in these and other states, occupancy trends can be assessed for additional partnering states and updated for these northeastern states. Thus, NAAMP has the ability to provide the conservation community with status and trend information for calling amphibians, supplying information to fill a current gap in our knowledge. As climate change and other factors influence our environment in the coming decades, NAAMP's long-term monitoring of calling amphibians will become an even more important resource to the scientific and conservation community.

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APPENDIX 1. Computational details for estimating site-specific trajectories.

Computationally, we implemented smoothing using the forward-backward algorithm, which is efficiently comprised of a forward pass and a backward pass through the data (e.g., Rabiner 1989; Cappé et al. 2005). In the forward pass, the forward variables are defined as:

$$\alpha_{i,t}(1) = Prob(Y_{i,1,\cdot}, Y_{i,2,\cdot}, \cdots, Y_{i,t,\cdot}, Z_{i,t} = 1 \mid \hat{\theta})$$

and

$$\alpha_{i,t}(0) = Prob(Y_{i,1,\cdot}, Y_{i,2,\cdot}, \cdots, Y_{i,t,\cdot}, Z_{i,t} = 0 \mid \hat{\theta})$$

where $Y_{i,t,\cdot}$ is the set of observations for site i at time t, and $\hat{\theta}$ is the set of parameter estimates, and $Z_{i,t}$ is the latent true occupancy state for site i at time t. The forward variables are computed in a recursive pass through the data for site i as follows. First, the algorithm is initialized with $\alpha_{i,1}(1) = \psi_1 Prob(Y_{i,1,\cdot} | Z_{i,t} = 1, \hat{\theta})$ and $\alpha_{i,1}(0) = (1 - \hat{\psi}_1) Prob(Y_{i,1,\cdot} | Z_{i,t} = 0, \hat{\theta})$. Note that $Prob(Y_{i,t,\cdot} | Z_{i,t} = 1, \hat{\theta})$ and $Prob(Y_{i,t,\cdot} | Z_{i,t} = 0, \hat{\theta})$ are computed using the fitted detection model as described by MacKenzie et al. (2003). Then subsequent forward variables are recursively computed using the following equations:

$$\alpha_{i,t+1}(1) = (\alpha_{i,t}(0)\hat{\gamma} + \alpha_{i,t}(1)(1 - \hat{\epsilon}))Prob(Y_{i,1,\cdot} | Z_{i,t} = 1, \hat{\theta})$$

$$\alpha_{i,t+1}(0) = (\alpha_{i,t}(0)(1 - \hat{\gamma}) + \alpha_{i,t}(1)\hat{\epsilon})Prob(Y_{i,1,\cdot} | Z_{i,t} = 0, \hat{\theta})$$

for $t = 2, 3, \ldots, T$.

In the next step, we compute the backward variables defined as:

$$\beta_{i,t}(1) = Prob(Y_{i,t+1,\cdot}, Y_{i,t+2,\cdot}, \cdots, Y_{i,T,\cdot} | Z_{i,t} = 1, \hat{\theta}) \text{ and}$$

$$\beta_{i,t}(0) = Prob(Y_{i,t+1,\cdot}, Y_{i,t+2,\cdot}, \cdots, Y_{i,T,\cdot} | Z_{i,t} = 0, \hat{\theta}).$$

To compute these backwards variables, we first initialize them at the final time step with $\beta_{i,T}(1) = \beta_{i,T}(0) = 1$. Note that this choice of initialization values is arbitrary, the only requirement being that they are all equal for the final year, as any scaling will cancel. Then we move recursively in a backwards pass through time:

$$\beta_{i,t}(1) = \epsilon Prob(Y_{i,t+1,\cdot} | Z_{i,t} = 0, \hat{\theta})\beta_{i,t+1}(0) + (1 - \epsilon)Prob(Y_{i,t+1,\cdot} | Z_{i,t} = 1, \hat{\theta})\beta_{i,t+1}(1)$$

and

$$\beta_{i,t}(0) = (1 - \gamma)Prob(Y_{i,t+1,\cdot} | Z_{i,t} = 0, \hat{\theta})\beta_{i,t+1}(0) + \gamma Prob(Y_{i,t+1,\cdot} | Z_{i,t} = 1, \hat{\theta})\beta_{i,t+1}(1)$$

for $t = T - 1, T - 2, \ldots, 1$.

Finally, the smoothed trend for site i is computed by combining the forward and backward variables:

$$\psi_{it} | Y = Prob(Z_{it} = 1 | Y_{i,1,\cdot}, Y_{i,2,\cdot}, \cdots, Y_{i,T,\cdot}) = \frac{\alpha_{i,t}(1)\beta_{i,t}(1)}{\alpha_{i,t}(0)\beta_{i,t}(0) + \alpha_{i,t}(1)\beta_{i,t}(1)}$$

for $t = 1, 2, \ldots, T$.

APPENDIX 2. Occupancy trends from generalized least squares trend analysis, where n is the number of sites surveyed in the state, significance level (* is $P < 0.1$, ** is $P < 0.05$, and *** is $P < 0.01$).

State	Species	n	Change in occupancy/year	std error	p value	Significance level
Delaware	*Acris crepitans*	170	0.004	0.003	0.256	
Maryland	*Acris crepitans*	210	0	0.011	0.99	
New Jersey	*Acris crepitans*	566	0.004	0.003	0.298	
Virginia	*Acris crepitans*	319	-0.004	0.002	0.167	
Delaware	*Bufo americanus*	170	-0.001	0.006	0.833	
Maine	*Bufo americanus*	610	-0.021	0.005	0.005	***
Maryland	*Bufo americanus*	210	-0.007	0.009	0.483	
Massachusetts	*Bufo americanus*	280	-0.012	0.004	0.024	**
New Hampshire	*Bufo americanus*	170	-0.011	0.005	0.078	*
New Jersey	*Bufo americanus*	566	0.005	0.006	0.391	
Pennsylvania	*Bufo americanus*	220	-0.011	0.008	0.25	
Vermont	*Bufo americanus*	100	0.011	0.011	0.354	
Virginia	*Bufo americanus*	319	-0.002	0.006	0.684	
West Virginia	*Bufo americanus*	388	-0.01	0.003	0.03	**
Delaware	*Bufo fowleri*	170	-0.009	0.002	0.007	***
Maryland	*Bufo fowleri*	210	-0.01	0.007	0.211	
New Jersey	*Bufo fowleri*	566	0.016	0.011	0.228	
Virginia	*Bufo fowleri*	319	0.008	0.005	0.215	
West Virginia	*Bufo fowleri*	388	-0.002	0.003	0.53	
Delaware	*Hyla chrysoscelis*	170	0.004	0.012	0.745	
Maryland	*Hyla chrysoscelis*	210	0.004	0.004	0.302	
Virginia	*Hyla chrysoscelis*	319	0.005	0.003	0.113	
West Virginia	*Hyla chrysoscelis*	388	0.001	0.001	0.193	
Maryland	*Hyla cinerea*	210	0.008	0.009	0.389	
Virginia	*Hyla cinerea*	319	0.008	0.007	0.331	
Delaware	*Hyla versicolor*	170	0	0.006	0.98	
Maine	*Hyla versicolor*	610	-0.012	0.003	0.012	**
Maryland	*Hyla versicolor*	210	-0.007	0.008	0.434	
Massachusetts	*Hyla versicolor*	280	-0.006	0.007	0.482	
New Hampshire	*Hyla versicolor*	170	-0.019	0.005	0.009	***
New Jersey	*Hyla versicolor*	566	-0.003	0.01	0.79	
Vermont	*Hyla versicolor*	100	-0.008	0.007	0.324	
Virginia	*Hyla versicolor*	319	0.008	0.002	0.015	**
West Virginia	*Hyla versicolor*	388	0.012	0.007	0.149	
West Virginia	*Pseudacris brachyphona*	388	-0.001	0.003	0.784	
Delaware	*Pseudacris crucifer*	170	-0.007	0.002	0.027	**
Maine	*Pseudacris crucifer*	610	-0.004	0.002	0.109	
Maryland	*Pseudacris crucifer*	210	-0.004	0.003	0.288	
Massachusetts	*Pseudacris crucifer*	280	-0.02	0.009	0.073	*
New Hampshire	*Pseudacris crucifer*	170	-0.01	0.003	0.011	**
New Jersey	*Pseudacris crucifer*	566	-0.012	0.007	0.132	
Pennsylvania	*Pseudacris crucifer*	220	-0.018	0.005	0.016	**
Vermont	*Pseudacris crucifer*	100	-0.018	0.007	0.056	*
Virginia	*Pseudacris crucifer*	319	-0.006	0.003	0.135	
West Virginia	*Pseudacris crucifer*	388	-0.01	0.004	0.069	*
Delaware	*Pseudacris feriarum* complex	170	-0.008	0.006	0.198	
Maryland	*Pseudacris feriarum* complex	210	0.009	0.004	0.065	*
New Jersey	*Pseudacris feriarum* complex	566	0.007	0.007	0.395	
Virginia	*Pseudacris feriarum* complex	319	-0.007	0.005	0.249	
West Virginia	*Pseudacris feriarum* complex	388	0.009	0.005	0.164	
Delaware	*Rana catesbeiana*	170	0.015	0.006	0.065	*
Maine	*Rana catesbeiana*	610	0.006	0.006	0.337	
Maryland	*Rana catesbeiana*	210	-0.006	0.006	0.352	
Massachusetts	*Rana catesbeiana*	280	0.01	0.006	0.158	
New Hampshire	*Rana catesbeiana*	170	-0.001	0.005	0.871	
New Jersey	*Rana catesbeiana*	566	0.025	0.008	0.031	**
Pennsylvania	*Rana catesbeiana*	220	0.012	0.01	0.254	
Vermont	*Rana catesbeiana*	100	0.006	0.004	0.252	
Virginia	*Rana catesbeiana*	319	0.008	0.004	0.08	*
West Virginia	*Rana catesbeiana*	388	0.012	0.004	0.04	**
Delaware	*Rana clamitans*	170	-0.004	0.007	0.612	
Maine	*Rana clamitans*	610	-0.012	0.005	0.06	*

Maryland	*Rana clamitans*	210	-0.022	0.009	0.065	*
Massachusetts	*Rana clamitans*	280	0.018	0.005	0.02	**
New Hampshire	*Rana clamitans*	170	-0.006	0.004	0.199	
New Jersey	*Rana clamitans*	566	0.016	0.011	0.209	
Pennsylvania	*Rana clamitans*	220	0.001	0.004	0.8	
Vermont	*Rana clamitans*	100	0.007	0.016	0.677	
Virginia	*Rana clamitans*	319	0.001	0.003	0.682	
West Virginia	*Rana clamitans*	388	0.021	0.008	0.043	**
Delaware	*Rana palustris*	170	0.018	0.005	0.019	**
Maine	*Rana palustris*	610	0.011	0.006	0.135	
Maryland	*Rana palustris*	210	0.004	0.008	0.625	
Massachusetts	*Rana palustris*	280	0.003	0.002	0.166	
New Hampshire	*Rana palustris*	170	0.006	0.006	0.334	
New Jersey	*Rana palustris*	566	0.01	0.005	0.104	
Pennsylvania	*Rana palustris*	220	0.013	0.011	0.305	
Virginia	*Rana palustris*	319	-0.001	0.002	0.679	
Maine	*Rana pipiens*	610	0.001	0.003	0.823	
Maine	*Rana septentrionalis*	610	0	0.002	0.892	
Delaware	*Rana sphenocephala*	170	0.015	0.006	0.047	**
Maryland	*Rana sphenocephala*	210	0.014	0.005	0.05	*
New Jersey	*Rana sphenocephala*	566	0.016	0.003	0.002	***
Virginia	*Rana sphenocephala*	319	0.001	0.003	0.811	
Delaware	*Rana sylvatica*	170	0.017	0.006	0.034	**
Maine	*Rana sylvatica*	610	-0.01	0.006	0.166	
Maryland	*Rana sylvatica*	210	0.027	0.01	0.036	**
Massachusetts	*Rana sylvatica*	280	0.007	0.014	0.656	
New Hampshire	*Rana sylvatica*	170	-0.003	0.003	0.321	
New Jersey	*Rana sylvatica*	566	-0.003	0.005	0.55	
Pennsylvania	*Rana sylvatica*	220	0.012	0.006	0.113	
Vermont	*Rana sylvatica*	100	0	0.001	0.94	
West Virginia	*Rana sylvatica*	388	0.017	0.013	0.244	
New Jersey	*Rana virgatipes*	566	0.018	0.005	0.017	**

Errata: The captions for Figures 2, 3, 4, and 5 were corrected at the author's request on 2 January 2009. The original captions mistakenly contained references to Vermont that were not correct.