
NORTHEAST REGIONAL AND STATE TRENDS IN ANURAN OCCUPANCY FROM CALLING SURVEY DATA (2001–2011) FROM THE NORTH AMERICAN AMPHIBIAN MONITORING PROGRAM

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Abstract.—We present the first regional trends in anuran occupancy from North American Amphibian Monitoring Program (NAAMP) data from 11 northeastern states using 11 years of data. NAAMP is a long-term monitoring program where observers collect data at assigned random roadside routes using a calling survey technique. We assessed occupancy trends for 17 species. Eight species had regional trends whose 95% posterior interval did not include zero; of these seven were negative (*Anaxyrus fowleri*, *Acris crepitans*, *Pseudacris brachyphona*, *Pseudacris feriarum-kalmi* complex, *Lithobates palustris*, *Lithobates pipiens*, and *Lithobates sphenoccephalus*) and one was positive (*Hyla versicolor-chrysoscelis* complex). We also assessed state level trends for 103 species/state combinations; of these, 29 showed a decline and nine showed an increase in occupancy.

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

INTRODUCTION

The scientific community became concerned about amphibian declines as a global issue in the 1990s, though early reports were primarily anecdotal evidence (Blaustein and Wake 1990; Wake and Morowitz 1991; Phillips 1994; Drost and Fellers 1996). Quantitative evidence from long-term monitoring using standardized methods was needed (Pechmann et al. 1991). The North American Amphibian Monitoring Program (NAAMP) was established in response to this information gap (Weir and Mossman 2005).

The NAAMP survey design and goals are similar to the North American Breeding Bird Survey (BBS), a long-term monitoring program for birds begun in the 1960s that provides avian population trends used by the avian conservation community (Bystrack 1981; Robbins et al. 1986, 1989; Sauer et al. 2003; North American Bird Conservation Initiative 2009). The intent of NAAMP is to provide for frogs a long-term monitoring program that can assess population trends and be of conservation value in a manner similar to what BBS provides for birds and their conservation.

The NAAMP survey design is similar to BBS in that both are surveys conducted along random roadside routes with a series of listening sites from which volunteer observers collect observational data (Bystrack 1981; Robbins et al. 1986; Weir and Mossman 2005). Both surveys also have a broad geographic scope; NAAMP surveys are conducted in over 20 states mainly in states east of the Mississippi River or bordering it, and

BBS has even broader coverage. Both surveys rely on volunteer observers, and are managed by the U.S. Geological Survey (USGS) in cooperation with multiple state partners (and international cooperation in the case of BBS).

The surveys have their differences. The BBS observations are conducted during daylight hours and are based on sight and sound, with observers reporting the number of individual birds seen or heard at each listening site (Bystrack 1981; Robbins et al. 1986). The NAAMP surveys are conducted during evening hours when many frog species are most vocal; as such the survey relies solely on sound (Weir and Mossman 2005). The NAAMP observers report calling activity for each species using a 1–3 rating system as an index to abundance, rather than attempt to count individuals of each species.

Analyses of NAAMP data have been based mainly on observed presence-absence, because observed presence is regarded as unambiguous evidence of species presence (but see Discussion). In addition, methodologies exist (“occupancy models”) which allow for the simultaneous modeling of both occurrence probability and detection probability (MacKenzie et al. 2002, 2006). Previous analysis of NAAMP data provided individual state trends for anuran species (Weir et al. 2009), but this modeling framework did not allow for assessing regional trends in occupancy. For this paper, our objectives are to first develop an occupancy modeling framework that allows reporting regional trends, while also estimating trends for individual states within the region, and

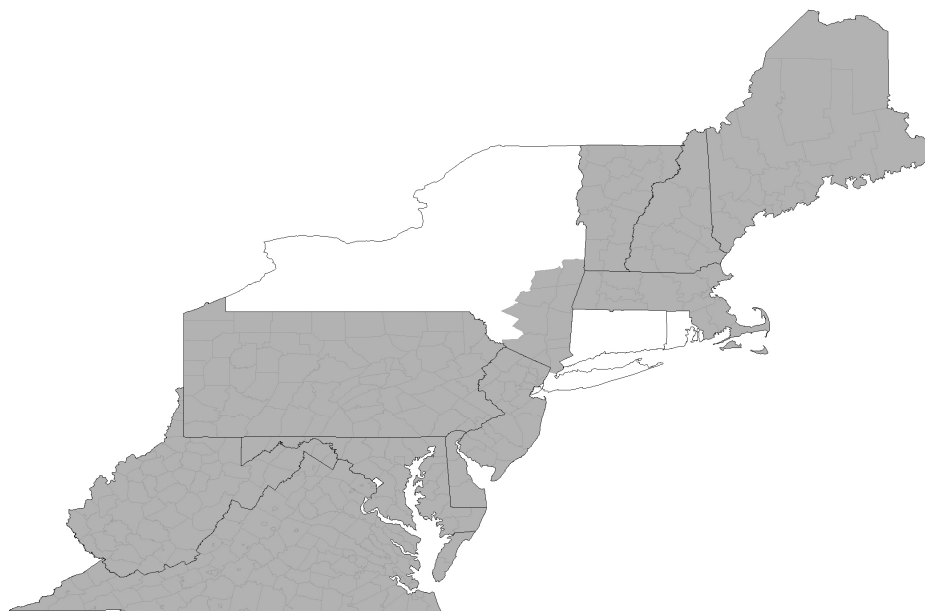


FIGURE 1. The 11 northeastern states (USA) in which NAAMP surveys were conducted (gray).

secondly to estimate trends of anuran species for the Northeast region as a whole, as well as separately for the individual states in the region.

MATERIALS AND METHODS

The NAAMP surveys were conducted along random roadside routes where observers identified species by their unique breeding vocalizations. Each route was composed of 10 sites spaced at least 0.8 km apart and routes were typically visited several times per year corresponding to the calling phenology of anurans for the state (Weir and Mossman 2005; Weir et al. 2009). At each site, observers listened for five minutes and then reported the species that were detected using a calling index to rate the level of calling activity from one to three, where one indicated individuals calling with no

overlap, two indicated intermediate level, and three indicated a full chorus (see Weir and Mossman 2005 for further protocol description). In addition, observers reported some environmental data (e.g., air temperature, time of the survey).

We used NAAMP data from 11 northeastern states: Delaware, Maine, Maryland, Massachusetts, New Jersey, New Hampshire, New York (limited to Hudson River region), Pennsylvania, Vermont, Virginia, and West Virginia (Fig. 1). Most states had 11 years of data (2001–2011; see Table 1). Beginning in 2006, observers were required to pass an online frog call identification quiz (USGS Frog Quiz, Available from <http://www.pwrc.usgs.gov/frogquiz> [Accessed 28 September 2012]). There were 349 routes with data collected during this time period. Typically, observers were asked to survey a route three to four times per year,

TABLE 1. Total number of surveys conducted and number of sites surveyed per year in each state. New York did not start surveying until 2008; Vermont did not conduct surveys in 2007.

State	Number of Surveys	Survey Year										
		2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Delaware	365	140	90	110	140	140	120	80	90	150	120	110
Maine	1097	500	470	420	530	470	310	320	230	200	250	310
Maryland	707	190	210	170	200	190	60	80	70	80	100	130
Massachusetts	529	150	170	130	100	140	100	190	160	130	170	120
New Hampshire	343	140	140	120	120	140	80	90	30	40	50	80
New Jersey*	676	90	70	480	350	400	240	250	240	230	210	300
New York	334	-	-	-	-	-	-	-	50	210	150	220
Pennsylvania	310	220	140	140	80	10	100	80	60	70	110	150
Vermont	124	70	60	40	40	30	40	-	40	30	80	50
Virginia	354	160	220	160	120	130	70	110	90	90	110	100
West Virginia	459	320	310	160	220	200	110	110	110	160	100	50
Total	5,298											

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

corresponding to the calling phenology of species in their state. Routes were surveyed more or less frequently, dependent on observer availability, the number of observers assigned to a given route, and the number of additional surveys conducted by observers. Routes that were surveyed ranged from a single survey in a year to a maximum of 18 surveys per year. For the Northeast in the 11-year period examined here, there were 5,298 surveys conducted. Since each route had 10 listening sites (referred to as “stops” in the NAAMP survey), this would result in 52,980 site visits if all 10 sites were visited on every survey. Occasionally a site was not surveyed (e.g., road block, weather deterioration), so the actual number of site visits was 52,604.

For each site visit an air temperature was recorded or estimated. For most surveys observers reported air temperature collected at the site (96% of site visits). In some cases, observers omitted air temperature at one or more sites on their route on the survey night. For any sites missing air temperature data, we used the average air temperature calculated using their provided readings (3% of site visits). In a few cases observers did not report air temperature for any sites on the route (1% of site visits); we estimated the air temperature at these sites using the nearest weather station for the survey date and time. We used Wunderground’s Weather History website (Available from <http://www.wunderground.com/history/> [Accessed 28 September 2012]) to find the town nearest to the route’s start point and estimated the air temperature by averaging the air temperature reported for the hour of the start and end of the survey.

Sunset time varies by date and location. We used R (Available from <http://www.r-project.org> [Accessed 28 September 2012]), an open source statistical software, with its maptools package to calculate sunset time using the survey date and the route’s start point, adjusted for Daylight Savings Time when necessary. Observers reported the time the survey started and ended for the route, and optionally reported start time at each site. If observers reported start time for a site visit we used it (70% of site visits), otherwise we estimated the site visit time based on the other times provided (30% of site visits) using a custom Java program. We converted site visit start times into minutes after sunset (site visit start time – sunset time). Although observers were instructed to start surveys 30 min after sunset or later, some site visits occurred prior to sunset (2% of site visits).

Occasionally a site or whole route must be retired (e.g., safety issue), but at any given time a route had 10 sites. In this dataset there are 3,528 unique sites. Of these, 128 sites were retired and replaced; in analyses these are treated as separate sites. All routes were considered to be within the species range for five species or species complexes with widespread distribution in the Northeast: *Hyla versicolor-chrysoscelis* complex,

Pseudacris crucifer, *Lithobates catesbeianus*, *Lithobates clamitans*, and *Lithobates palustris*. For the *H. versicolor-chrysoscelis* complex, we combined observational data reported as *Hyla versicolor*, *Hyla chrysoscelis*, or the species complex.

For species with more limited distributions, sites were considered to be within the species range if any portion of the route fell within generalized species range maps (Fig. 2). Only routes within the range were used in analyses for the remaining 12 species or species complex: *Anaxyrus americanus*, *Anaxyrus fowleri*, *Acris crepitans*, *Hyla andersonii*, *Hyla cinerea*, *Pseudacris brachyphona*, *Pseudacris feriarum-kalmi* complex, *Lithobates pipiens*, *Lithobates septentrionalis*, *Lithobates sphenoccephalus*, *Lithobates sylvaticus*, and *Lithobates virgatipes*. For the *P. feriarum-kalmi* complex, we combined observational data reported as *Pseudacris feriarum*, *Pseudacris kalmi*, or the species complex.

Model development.—We modeled detection probability and site occupancy using multi-season occupancy models (MacKenzie et al. 2003), implemented using a Bayesian analysis framework (Royle and Kéry 2007; Kéry and Schaub 2012, p. 436) in WinBUGS (Available from <http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml> [Accessed 28 September 2012]). These models accommodate explicit modeling of factors that influence both detection probability and site occupancy at the level of the NAAMP stop.

A number of factors are thought to influence detection probability (see Detection probability models below). To evaluate these factors, we considered logit models of the form:

$$\text{Eq (1)} \quad \text{logit}(p[i, j, t]) = \beta_0 + \sum_{k=1}^K \beta_k \cdot u_{k[i, j, t]}$$

where $u_{k[i, j, t]}$ is the value of (detection) covariate

$k = 1, 2, \dots, K$ for the observation collected at site i (a specific route/stop combination) and sampling occasion j within year t .

Because sampling occurred over 11 years, we accommodated explicit occupancy dynamics which allowed the occupancy status of sites ($z[i, t] = 1$ if site “ i ” is occupied in year t) to change from occupied to unoccupied and vice versa. The full model as described by MacKenzie et al. (2003) and Royle and Kéry (2007) accommodates both “extinction” (complement of local survival) and “colonization” parameters according to a Markovian model of the following form:

$$\text{Eq (2)} \quad z[i, t] \sim \text{Bernoulli}(\psi[i, t])$$

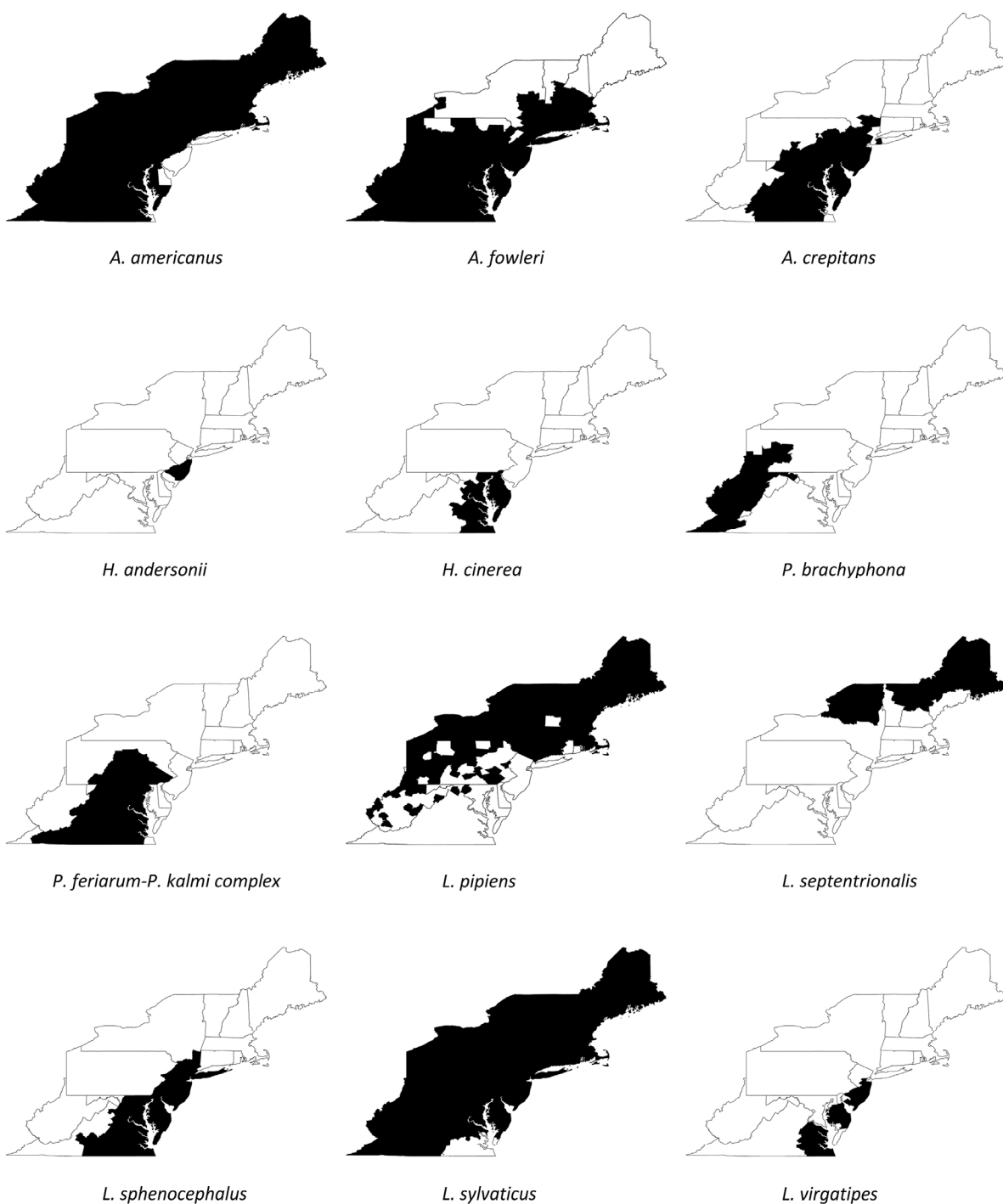


FIGURE 2. Northeastern distributions of the 12 species with limited distributions in the region. Black shading indicates areas considered within the range of each species. Range maps similar to Conant and Collins (1998) were created by modifying USGS National Amphibian Atlas (Available from <http://www.pwrc.usgs.gov/naa> [Accessed 28 September 2012]) county level distribution maps.

With

$$\text{Eq (3)} \quad \psi[i, t] = \phi(z[i, t-1]) + \gamma(1 - z[i, t-1])$$

Where ϕ = “local survival probability,” is the probability that a previously occupied site (i.e., at time $t-1$) remains

occupied at time t , and γ is the colonization probability; i.e., the probability that a site unoccupied at time $t-1$ becomes occupied at time t . In practice, ϕ and γ may both be year-specific. In our analysis, we wanted to allow geographic specificity in the occupancy dynamics parameters (at the level of the state) in which case a fully

TABLE 2. Posterior summaries (posterior mean, 2.5 and 97.5 percentiles) of regional occupancy trends (slope of the least-squares fit) for 17 anuran species or species complexes. Shown in bold text are the trends for which the 95% posterior interval does not include 0. The annual percent change was computed based on the estimated trend relative to the intercept under the linear trend model, and also using the geometric mean rate of change following Link and Sauer (1998). Species names are abbreviated in the table as follows: *A. americanus* (Aame), *A. fowleri* (Afow), *A. crepitans* (Acre), *H. andersonii* (Hand), *H. cinerea* (Hcin), *H. versicolor-chrysoscelis* complex (Hvcc), *P. brachyphona* (Pbra), *P. crucifer* (Pcru), *P. feriarum-kalmi* complex (Pfkc), *L. catesbeianus* (Lcat), *L. clamitans* (Lcla), *L. palustris* (Lpal), *L. pipiens* (Lpip), *L. septentrionalis* (Lsep), *L. sphenocephalus* (Lsph), *L. sylvaticus* (Lsyl), and *L. virgatipes* (Lvirl).

Species Code	Slope	2.5%	97.5%	Percent change linear trend	Percent change geometric mean
Aame	-0.00273	-0.00990	0.00343	-0.42635	-0.413152
Afow	-0.00940	-0.01556	-0.00284	-3.84337	-3.878157
Acre	-0.01170	-0.01847	-0.00558	-9.4525	-9.303738
Hand	-0.01164	-0.02681	0.00565	-4.34226	-4.096254
Hcin	0.00543	-0.00280	0.01417	1.959222	1.956803
Hvcc	0.00769	0.00306	0.01198	1.253375	1.620385
Pbra	-0.01131	-0.02174	-0.00103	-3.17322	-3.508903
Pcru	0.00114	-0.00091	0.00366	0.12513	0.1358696
Pfkc	-0.03234	-0.04066	-0.02456	-11.1835	-10.44718
Lcat	-0.00352	-0.00917	0.00094	-1.09386	-1.135277
Lcla	-0.00191	-0.00722	0.00233	-0.38481	-0.331859
Lpal	-0.00447	-0.00865	-0.00034	-2.27715	-2.429424
Lpip	-0.00941	-0.01761	-0.00132	-10.6265	-10.67778
Lsep	-0.00252	-0.01112	0.00757	-1.39488	-1.766831
Lsph	-0.00987	-0.01894	-0.00181	-3.9634	-4.468922
Lsyl	0.00214	-0.00488	0.00937	0.49102	0.5678909
Lvir	0.00046	-0.00697	0.00649	0.362883	-1.620976
Average				-2.82177	-2.929265

parameterized model would involve 110 ϕ parameters ([years -1] times states) and 110 γ parameters. To achieve a more economical model parameterization, we assumed only state-specific values of the parameters, and we adopted the autologistic formulation of the model described by Royle and Dorazio (2008, p. 311) in which $\psi[i, t]$ is modeled on the logit-scale according to:

Eq (4)

$$\text{logit}(\psi[i, t]) = a0(\text{state}[i]) + a1(\text{state}[i]) * z[i, t - 1]$$

where, under this parameterization, the local survival rate for state s is $\text{logit}^{-1}(a0[s] + a1[s])$ and the local colonization rate for state s is $\text{logit}^{-1}(a0[s])$.

Detection probability models.—We considered models that allowed detection probability to vary in response to: (1) minutes from sunset; (2) day-of-year; (3) temperature; (4) latitude; and (5) latitude interacting with day-of-year. Covariates were modeled according to Eq. (1). Each of factors 1–4 were considered to be quadratic terms which allows for a distinct optimum in detection probability as a function of the covariate (Weir et al. 2005). In addition, because we expect the optimum to vary geographically, we included an interaction of each of the covariates with latitude.

Model selection.—We used the model indicator variable approach of Kuo and Mallick (1998) to identify

the best model (see also Royle and Dorazio 2008, p.109 for an example involving occupancy models). This approach allows calculation of posterior probabilities for each model.

Trend estimation.—To characterize state-level trends, we computed $N[s, t] =$ “the number of occupied sites” by summing of the occupancy state variables ($z(i, t)$) for all NAAMP stops within each state “ s ”, and for each year “ t ”. This was converted to proportion of occupied sites by dividing by the number of stops in each state. We define this time-series of $N[s, t]$ values to be the “trajectory” (note: the term “trend” is usually used in the context of a scalar summary of change over time).

We summarized this trajectory using a linear least-squares fit (Weir et al. 2009) to the posterior samples of the trajectory $N[s, t]$ for $t = 1, 2, \dots, 11$. We refer to the slope of the least-squares fit as the trend. This calculation was done by post-processing the MCMC output in R (the R script is provided in Appendix 1) using the R function `lsfit()`. For each state we report both the set of estimated $N[s, t]$ values and the trend (the linear fit; see results). If the 95% posterior confidence interval for the least-squares trend did not include zero, then we conclude a positive or negative trend in occupancy.

To compute the regional trend, we computed the sum of $N[s, t]$ over all the states, creating the regional trajectory $N[t] = \sum_s N[s, t]$. The regional trend was computed by a least-squares fit to the time-series of $N[t]$ values. We computed the percent annual change from

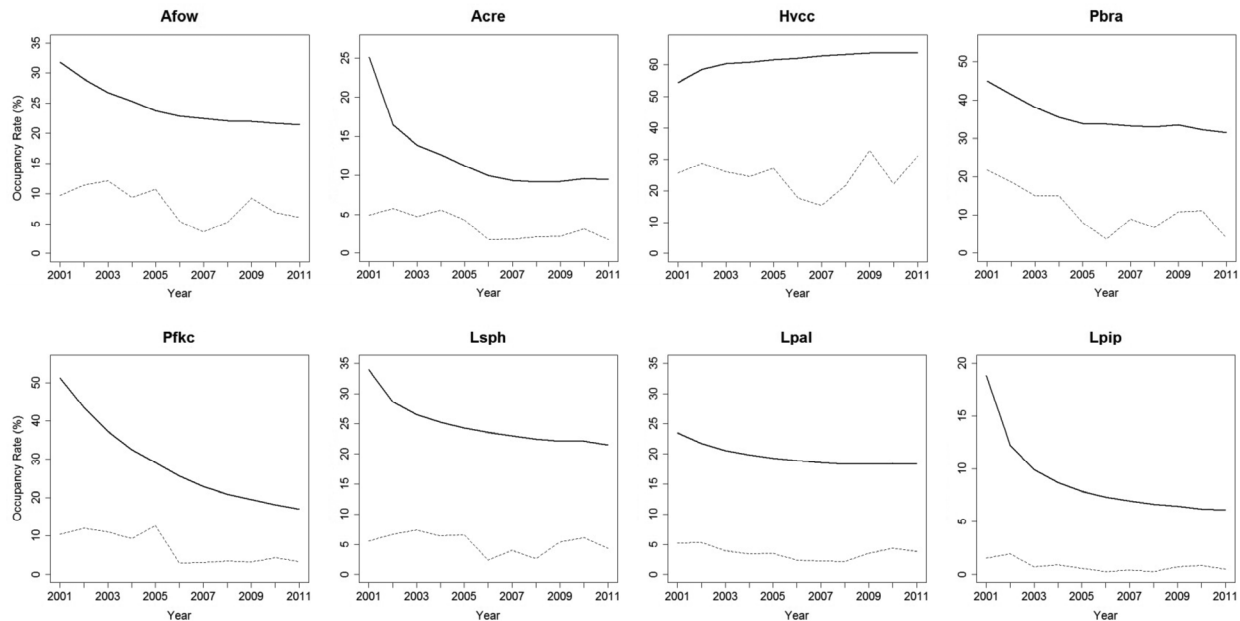


FIGURE 3. Annual estimates of occupancy for eight species with negative trends (95% posterior interval did not contain zero). Black line is the estimated occupancy rate, while the dotted line is the observed occupancy. The eight species or species complexes are: *A. fowleri* (Afow), *A. crepitans* (Acre), *H. versicolor-chrysoscelis* complex (Hvcc), *P. brachyphona* (Pbra), *P. feriarum-kalmi* complex (Pfkcc), *L. palustris* (Lpal), *L. pipiens* (Lpip), and *L. sphenoccephalus* (Lsph).

these summary results using two methods. For method 1, we used the slope from the linear trend model divided by the intercept of the model. For method 2, we computed the geometric mean rate of change following Link and Sauer (1998) which is currently a standard method of trend reporting for the North American Breeding Bird Survey. This summary is:

$$\text{Eq (5)} \quad \% \text{ annual change} = \left(\frac{N[11]}{N[1]} \right)^{\frac{1}{10}}$$

Model fitting.—We used the package WinBUGS to fit the models for each species adopting code from Kéry and Schaub (2012, p. 436). We used the R statistical software, and the R2WinBUGS package to carry-out MCMC using WinBUGS (see Appendix 1 for R script). We obtained posterior samples from 3 Markov chains run for 4,000 iterations with a burn-in phase of 2,000 iterations, making it a total of 6,000 iterations, and initiated with random starting values. We assessed convergence of the model parameters using the Rhat statistic (Brooks and Gelman 1998) for the monitored values of $N[s,t]$. The average Rhat values (averaged over $N[s,t]$ values) were less than 1.2 for all species, which indicated satisfactory convergence of the Markov chains.

RESULTS

We report Northeast regional occupancy trends for 17 species (Table 2); the top 10 models for each species are shown in Appendix 2. The average linear trend of our

regional trends for all species was -2.82% , and the average rate of change (geometric mean) of our regional trends for all species was -2.93% . Eight species had trends whose 95% posterior intervals did not include zero (we refer to these as “significant” even though this is not strictly the conventional meaning of that term; Fig. 3; Table 2). Seven species show decreasing trends (*A. fowleri*, *A. crepitans*, *P. brachyphona*, *P. feriarum-kalmi* complex, *L. palustris*, *L. pipiens*, and *L. sphenoccephalus*) and one exhibited an increasing trend (*H. versicolor-chrysoscelis* complex).

We also determined occupancy trends at the state level (Table 3). We were able to assess trends for 103 species/state combinations. Of these, 29 species/state combinations showed a significant declining trend in occupancy, whereas nine species/state combinations showed a significant increasing occupancy trend (Table 3; Fig. 4).

For toads, the regional result was significant decline for one species, *A. fowleri*. At the state level *A. americanus* showed significant decline in two states (Maine and Massachusetts) and *A. fowleri* in one (Maryland). For treefrogs and their allies, *A. crepitans* showed significant declines in two states (Maryland and Virginia) as well as regionally. One state, Delaware, showed a significant increasing trend for *H. cinerea*. The *H. versicolor-chrysoscelis* complex showed a significant increasing trend regionally and in three states (Delaware, Maryland, and West Virginia), but two states (New Hampshire and Pennsylvania) showed significant decreasing trends. *Pseudacris brachyphona* showed a regional decline, though no state trends were significant.

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TABLE 3 (PART 1). Posterior summaries (posterior mean, 2.5 and 97.5 percentiles) of occupancy trends for species/state combinations. In bold are the 38 species/state combinations for which the 95% interval of the trend did not include zero. Cells with dashes are states within the species range, but with fewer than 50 species detections so we considered as data insufficient. Cells colored gray are states outside of the species range. Species names are abbreviated as follows: *A. americanus* (Aame), *A. fowleri* (Afow), *A. crepitans* (Acre), *H. andersonii* (Hand), *H. cinerea* (Hcin), *H. versicolor-chrysoscelis* complex (Hvcc), *P. brachyphona* (Pbra), *P. crucifer* (Pcru), *P. feriarum-kalmi* complex (Pfkce), *L. catesbeianus* (Lcat), *L. clamitans* (Lcla), *L. palustris* (Lpal), *L. pipiens* (Lpip), *L. septentrionalis* (Lsep), *L. sphenoccephalus* (Lsph), *L. sylvaticus* (Lsyl), and *L. virgatipes* (Lvtr).

Species Code	Delaware			Maine			Maryland		
	slope	2.5%	97.5%	slope	2.5%	97.5%	slope	2.5%	97.5%
Aame	0.0058	-0.0061	0.0173	-0.0162	-0.0239	-0.0088	-0.0031	-0.0133	0.0071
Afow	-0.0056	-0.0132	0.0022				-0.0332	-0.0420	-0.0241
Acre	0.0031	-0.0038	0.0094				-0.0388	-0.0555	-0.0241
Hand									
Hcin	0.0125	0.0044	0.0211				0.0026	-0.0065	0.0125
Hvcc	0.0342	0.0247	0.0432	0.0036	-0.0013	0.0082	0.0100	0.0016	0.0182
Pbra							-	-	-
Pcru	0.0069	0.0021	0.0116	-0.0027	-0.0042	-0.0011	0.0017	-0.0019	0.0047
Pfkce	-0.0332	-0.0500	-0.0182				-0.0285	-0.0385	-0.0182
Lcat	0.0033	-0.0055	0.0116	-0.0073	-0.0149	-0.0001	-0.0281	-0.0353	-0.0210
Lcla	-0.001	-0.010	0.0070	-0.0039	-0.0096	0.0013	-0.0170	-0.0241	-0.0097
Lpal	-0.0013	-0.0120	0.0098	0.0113	0.0029	0.0195	-0.0147	-0.0230	-0.0063
Lpip				-0.018	-0.030	-0.005	-	-	-
Lsep				-0.0031	-0.0128	0.0082			
Lsph	0.0135	-0.0006	0.0279				-0.0087	-0.0213	0.0040
Lsyl	0.0053	-0.0061	0.0153	-0.0054	-0.0104	-0.0005	-0.0026	-0.0125	0.0079
Lvir	-	-	-				-	-	-

Pseudacris crucifer had significant trends in three states, with Delaware showing an increase while Maine and Pennsylvania showed a decrease; the regional trend was positive but not significant for this species. The *P. feriarum-kalmi* complex had significant decreasing trends regionally and in five states (Delaware, Maryland, New Jersey, Virginia, and West Virginia). There were no significant trends for *H. andersonii*.

For ranids, *L. catesbeianus* had six significant results with five states showing declining trends (Maine, Maryland, Massachusetts, New Hampshire, and Virginia) and one state (West Virginia) showing an increasing trend. Three states (Maryland, Massachusetts, and Virginia) had declining trends for *L. clamitans*. For *L. palustris*, the regional trend showed significant decline and three states had declining trends (Maryland, New York, and Virginia) while Maine showed an increasing trend. *Lithobates pipiens* showed a significant decline regionally and in Maine. *Lithobates sphenoccephalus* showed significant declines in two states (New Jersey and Virginia) as well as regionally. For *L. sylvaticus*, Maine had a decreasing trend while two states (New Hampshire and Pennsylvania) had an

increasing trend. Two ranids, *L. septentrionalis* and *L. virgatipes*, had no significant trends.

DISCUSSION

Our study indicated that, on average, the probability of occurrence for anurans in the Northeast declined over the past decade. Furthermore, five of the seven species or species complexes we found to have regional significant decline are considered severe or high concern for northeastern regional responsibility by Northeast Partners in Amphibian and Reptile Conservation (NEPARC 2010). The NEPARC rating considers two factors: the number of northeastern states with the species included in its Wildlife Action Plans, and whether the Northeast comprises over 50% of the species distribution. The greatest concern rating by NEPARC is severe concern; two species in our study (*P. brachyphona* and *L. virgatipes*) received this rating. Of these, we found *P. brachyphona* to have a significant negative regional trend. High concern is the next level on the NEPARC rating scale with four anurans receiving this rating: *A. crepitans*, *A. fowleri*, *L. pipiens*, and *P.*

TABLE 3 (PART 2). Posterior summaries (posterior mean, 2.5 and 97.5 percentiles) of occupancy trends for species/state combinations. In bold are the 38 species/state combinations for which the 95% interval of the trend did not include zero. Cells with dashes are states within the species range, but with fewer than 50 species detections so we considered as data insufficient. Cells colored gray are states outside of the species range. Species names are abbreviated as follows: *A. americanus* (Aame), *A. fowleri* (Afow), *A. crepitans* (Acre), *H. andersonii* (Hand), *H. cinerea* (Hcin), *H. versicolor-chrysoscelis* complex (Hvcc), *P. brachyphona* (Pbra), *P. crucifer* (Pcru), *P. feriarum-kalmi* complex (Pfkce), *L. catesbeianus* (Lcat), *L. clamitans* (Lcla), *L. palustris* (Lpal), *L. pipiens* (Lpip), *L. septentrionalis* (Lsep), *L. sphenoccephalus* (Lsph), *L. sylvaticus* (Lsyl), and *L. virgatipes* (Lviri).

Species Code	Massachusetts			New Hampshire			New Jersey		
	slope	2.5%	97.5%	slope	2.5%	97.5%	slope	2.5%	97.5%
Aame	-0.0196	-0.0311	-0.0081	0.0050	-0.0091	0.0180	0.0092	-0.0073	0.0268
Afow	-	-	-	-	-	-	-0.003	-0.015	0.010
Acre							-0.0019	-0.0118	0.0053
Hand							-0.0116	-0.0268	0.0057
Hcin									
Hvcc	-0.0011	-0.0106	0.0079	-0.0116	-0.0229	-0.0009	0.0017	-0.0073	0.0109
Pbra									
Pcru	-0.0033	-0.0082	0.0017	-0.0027	-0.0078	0.0014	0.0055	-0.0002	0.0113
Pfkce							-0.0365	-0.0538	-0.0228
Lcat	-0.0118	-0.0197	-0.0041	-0.0181	-0.0290	-0.0071	-0.0003	-0.0083	0.0079
Lcla	-0.0078	-0.0155	-0.0006	-0.0013	-0.0114	0.0086	-0.0052	-0.0137	0.0035
Lpal	-0.0019	-0.0071	0.0030	-0.0031	-0.0135	0.0079	0.0016	-0.0056	0.0085
Lpip	-	-	-	-	-	-			
Lsep				-0.0008	-0.0067	0.0031			
Lsph							-0.0114	-0.0239	-0.0001
Lsyl	-0.0010	-0.0129	0.0113	0.0150	0.0042	0.0258	0.0009	-0.0104	0.0123
Lviri							0.0056	-0.0028	0.0144

kalmi. In our study *P. kalmi* is included within the *P. feriarum-kalmi* complex, and we found a significant negative trend regionally for these four species or species complexes. Thus, further research and conservation efforts may be warranted for the five species with significant negative regional trends and a NEPARC rating of high or severe concern.

Adams et al. (2013) found U.S. amphibian occupancy declined 3.7% annually from 2002 to 2011. Limiting the Adams et al. species to those considered least concern by the International Union for Conservation of Nature (IUCN) showed a mean annual trend of -2.7%. Of the 17 species or species complexes in our study 16 are considered least concern by IUCN (Available from <http://www.iucn.org/> [Accessed 21 June 2013]), with the only exception being *Hyla andersonii* that is listed as near threatened. The Adams et al. (2013) analysis included salamanders and anurans, was national in focus, but sites were largely restricted to federal protected lands. In contrast, our study is limited to anurans of the northeastern United States with study sites largely not in protected areas but rather located on random roadside routes. With Adams et al.'s area of inference being federally protected lands and this study's sample frame

being lands near roads, taken together it is suggestive that, at least for the northeastern United States, the declines may encompass the larger landscape as a whole. Also notable, Adams et al. (2013) and this study suggest declines are occurring in amphibian species previously thought to be of little conservation concern.

Our current analysis is a Bayesian analog of the likelihood method used in Weir et al. (2009) for estimating occupancy trajectories from NAAMP data. The main distinction is that using Bayesian analysis by Markov chain Monte Carlo method (MCMC), we can obtain posterior samples of the latent occupancy variables directly, whereas using likelihood methods the maximum likelihood estimates (MLEs) had to be used in a secondary smoothing step to provide estimates of the trajectory for each route, which then had to be combined to form a regional estimate.

In the last decade, it has become more common to account for imperfect detection in ecological studies (MacKenzie et al. 2002; Mazerolle et al. 2007). Recognizing that it is typically not possible to detect every individual or species during a survey of a site (false negative), there are now many statistical approaches to address non-detection (MacKenzie et al.

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TABLE 3 (PART 3). Posterior summaries (posterior mean, 2.5 and 97.5 percentiles) of occupancy trends for species/state combinations. In bold are the 38 species/state combinations for which the 95% interval of the trend did not include zero. Cells with dashes are states within the species range, but with fewer than 50 species detections so we considered as data insufficient. Cells colored gray are states outside of the species range. Species names are abbreviated as follows: *A. americanus* (Aame), *A. fowleri* (Afow), *A. crepitans* (Acre), *H. andersonii* (Hand), *H. cinerea* (Hcin), *H. versicolor-chrysoscelis* complex (Hvcc), *P. brachyphona* (Pbra), *P. crucifer* (Pcru), *P. feriarum-kalmi* complex (Pfkc), *L. catesbeianus* (Lcat), *L. clamitans* (Lcla), *L. palustris* (Lpal), *L. pipiens* (Lpip), *L. septentrionalis* (Lsep), *L. sphenocephalus* (Lsph), *L. sylvaticus* (Lsyl), and *L. virgatipes* (Lvir).

Species Code	New York			Pennsylvania			Vermont		
	slope	2.5%	97.5%	slope	2.5%	97.5%	slope	2.5%	97.5%
Aame	0.0147	-0.0353	0.0523	-0.0016	-0.0152	0.0119	-0.0055	-0.0269	0.0156
Afow	-	-	-	-	-	-	-	-	-
Acre	-	-	-	-	-	-			
Hand									
Hcin									
Hvcc									
Hvcc	0.0252	-0.0084	0.0584	-0.0100	-0.0175	-0.0029	0.0030	-0.0101	0.0180
Pbra				-	-	-			
Pcru	0.0075	-0.0052	0.0385	-0.0052	-0.0101	-0.0004	-0.0024	-0.0090	0.0043
Pfkc				-	-	-			
Lcat	0.0129	-0.0475	0.0501	-0.0008	-0.0092	0.0085	0.0084	-0.0054	0.0214
Lcla	0.0336	-0.0280	0.0668	-0.0041	-0.0128	0.0043	-0.0087	-0.0238	0.0059
Lpal	-0.0453	-0.0733	-0.0017	-0.0036	-0.0125	0.0052	-	-	-
Lpip	-	-	-	-	-	-	-	-	-
Lsep							-	-	-
Lsph	-	-	-	-0.0013	-0.0091	0.0035			
Lsyl	-0.0100	-0.0624	0.0384	0.0159	0.0044	0.0272	-0.0058	-0.0253	0.0126
Lvir									
	Virginia			West Virginia					
	slope	2.5%	97.5%	slope	2.5%	97.5%			
Aame	0.0013	-0.0145	0.0155	0.0031	-0.0088	0.0160			
Afow	-0.0067	-0.0169	0.0040	-0.0060	-0.0129	0.0008			
Acre	-0.0228	-0.0367	-0.0093	-	-	-			
Hand									
Hcin							-0.0006	-0.0216	0.0222
Hvcc	0.0070	-0.0029	0.0162	0.0269	0.0156	0.0377			
Pbra	-	-	-	-0.0129	-0.0261	0.0003			
Pcru	0.0020	-0.0032	0.0065	0.0027	-0.0018	0.0068			
Pfkc	-0.0466	-0.0589	-0.0337	-0.0213	-0.0336	-0.0067			
Lcat	-0.0093	-0.0175	-0.0008	0.0071	0.0004	0.0137			
Lcla	-0.0115	-0.0223	-0.0016	0.0055	-0.0027	0.0136			
Lpal	-0.0183	-0.0295	-0.0053	-0.0008	-0.0045	0.0029			
Lpip				-	-	-			
Lsep									
Lsph	-0.0217	-0.0423	-0.0033						
Lsyl	-	-	-	0.0146	-0.0009	0.0302			
Lvir	-	-	-						

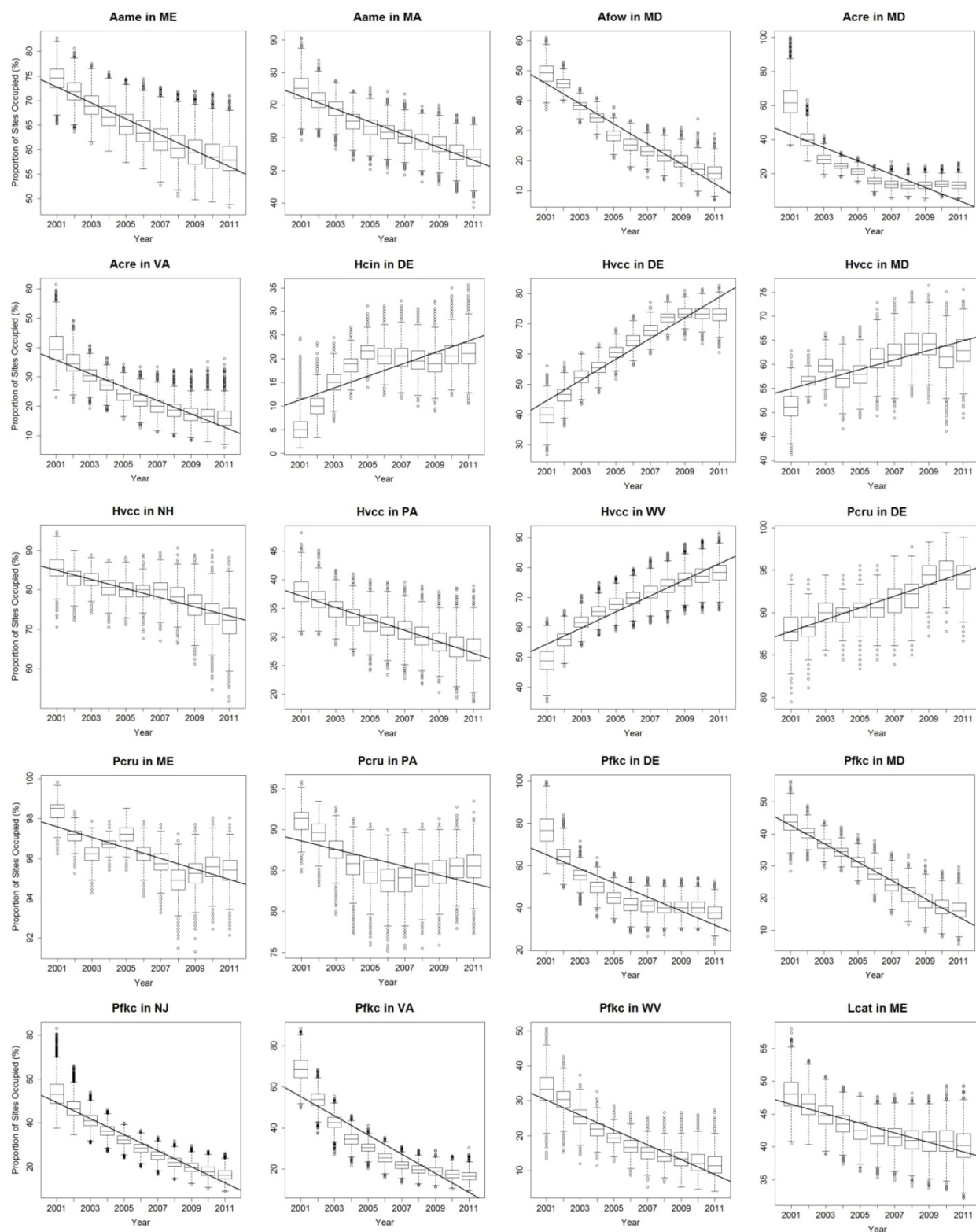


FIGURE 4 (PART 1). Occupancy trend graphs for 38 species/state combinations with significant trends. Black line is posterior mean of least squares trend. The box plots depict the posterior distribution of occupied sites for each year. The three horizontal lines of the box plots represent quantiles (25%, 50%, and 75% of the distribution), the smaller horizontal lines are 2.5% and 97.5%, and circles are extreme values. Species names are abbreviated as follows: *A. americanus* (Aame), *A. fowleri* (Afow), *A. crepitans* (Acre), *H. cinerea* (Hcin), *H. versicolor-chrysoscelis* complex (Hvcc), *P. crucifer* (Pcru), *P. feriarum-kalmi* complex (Pfkci), *L. catesbeianus* (Lcat), *L. clamitans* (Lcla), *L. palustris* (Lpal), *L. pipiens* (Lpip), *L. sphenoccephalus* (Lsph), and *L. sylvaticus* (Lsyl). States are abbreviated as: Delaware (DE), Maine (ME), Maryland (MD), Massachusetts (MA), New Hampshire (NH), New Jersey (NJ), New York (NY), Pennsylvania (PA), Vermont (VT), Virginia (VA), and West Virginia (WV).

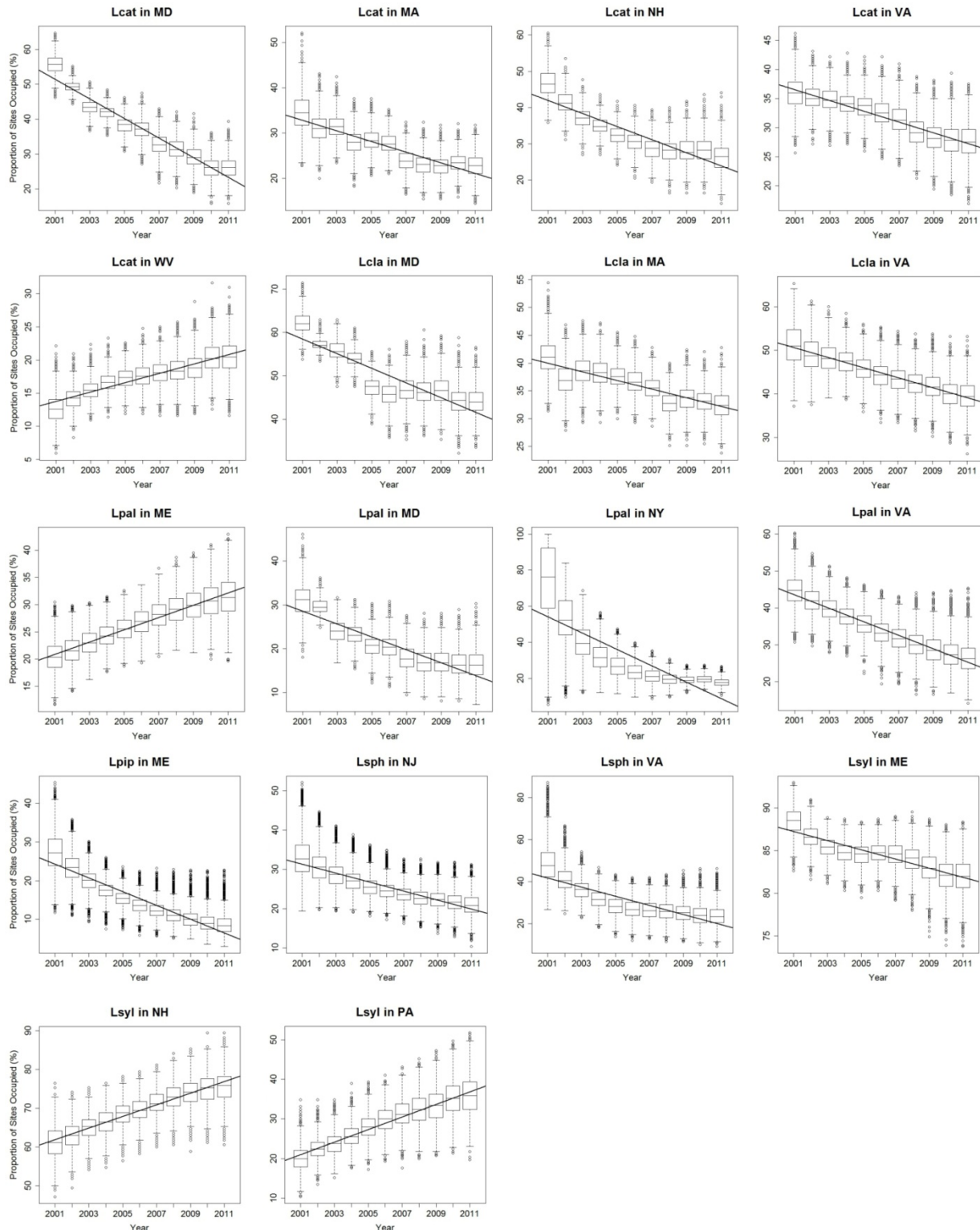


FIGURE 4 (PART 2). Occupancy trend graphs for 38 species/state combinations with significant trends. Black line is posterior mean of least squares trend. The box plots depict the posterior distribution of occupied sites for each year. The three horizontal lines of the box plots represent quantiles (25%, 50%, and 75% of the distribution), the smaller horizontal lines are 2.5% and 97.5%, and circles are extreme values. Species names are abbreviated as follows: *A. americanus* (Aame), *A. fowleri* (Afo), *A. crepitans* (Acre), *H. cinerea* (Hcin), *H. versicolor-chrysoscelis* complex (Hvcc), *P. crucifer* (Pcr), *P. feriarum-kalmi* complex (Pfk), *L. catesbeianus* (Lcat), *L. clamitans* (Lcla), *L. palustris* (Lpal), *L. pipiens* (Lpip), *L. sphenoccephalus* (Lsph), and *L. sylvaticus* (Lslyl). States are abbreviated as: Delaware (DE), Maine (ME), Maryland (MD), Massachusetts (MA), New Hampshire (NH), New Jersey (NJ), New York (NY), Pennsylvania (PA), Vermont (VT), Virginia (VA), and West Virginia (WV).

2006; Royle and Dorazio 2008). False positive errors, when individuals or species are absent but reported as detected, have often been ignored or assumed unimportant; but this is changing (Royle and Link 2006; Yoshizaki et al. 2009; McClintock et al. 2010a). Since the early days of anuran calling surveys, research has examined observer ability and variation (Shirose et al. 1997; Genet and Sargent 2003; Lotz and Allen 2007; Pierce and Gutzwiller 2007). During field experiments simulating calling surveys, such that true calling activity is known, recent studies have shown that both false negative and false positive errors occur in auditory surveys of birds (Simons et al. 2007) and amphibians (McClintock et al. 2010b; Miller et al. 2012). Miller et al. (2012) found that USGS frog quiz scores were a good predictor of observer error rates. Thus, observer frog quiz results, in addition to screening out unqualified observers, could be incorporated into future analyses to account for differences in observer detection for NAAMP surveys. Our current approach to NAAMP analyses accounts for false negatives. Accounting for false positive errors by incorporating the frog quiz into the modeling framework and determining how to handle data from years prior to the quiz should be the focus of future work. It is well-known (Royle and Link 2006; Miller et al. 2011) that false positive errors produces bias in estimation of occupancy rate. The bias is expected to be relatively more severe for lower occupancy rates and therefore we expect trend estimates to be biased toward 0 in the presence of false positive errors. As such, we expect that the number of significant (both positive and negative) trends is understated. In this paper we report state and regional occupancy trends using an 11-year dataset from Northeast NAAMP states for 17 anuran species. With continuing data collection in these and other participating states, NAAMP will be able to provide the conservation community with much needed information on the status of frogs and toads. In the coming decades, NAAMP's long-term dataset will be an important resource to the conservation and scientific community.

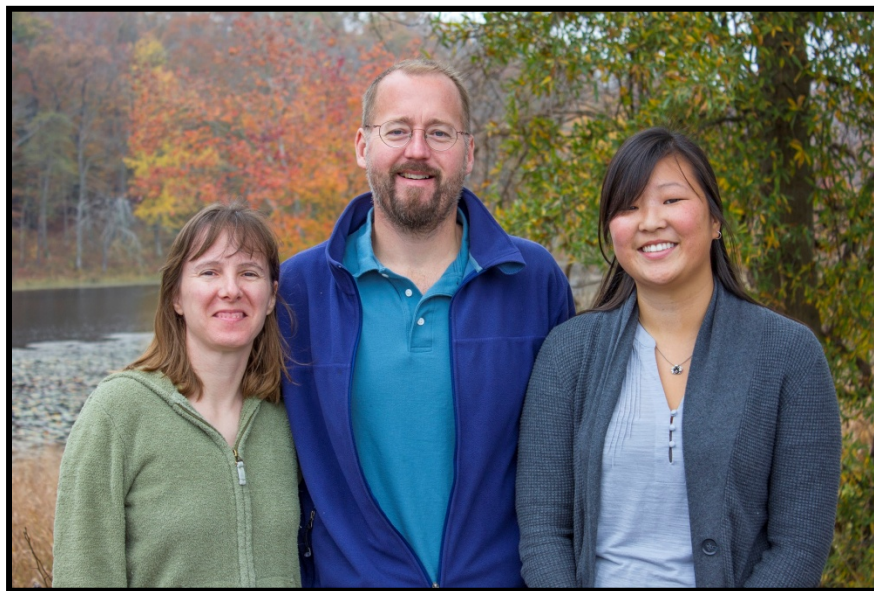
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20 Aug. 2014. Errata: Author added to author line, Appendix 2 replaced with new correct version.



LINDA WEIR (left) is a Wildlife Biologist at USGS Patuxent Wildlife Research Center in Laurel, Maryland. She is the USGS coordinator of the North American Amphibian Monitoring Program. Linda received her bachelor's degree in Zoology from the State University of New York, College at Oswego (SUNY Oswego) and her master's degree in Sustainable Development and Conservation Biology from the University of Maryland.

ANDY ROYLE (center) is a Research Statistician with USGS Patuxent Wildlife Research Center engaged in the development of statistical methods and analytic tools for animal demographic modeling, statistical inference, and sampling wildlife populations and communities. Andy is a co-author of *Hierarchical Modeling and Inference in Ecology*, as well as numerous scientific papers. He has been with USGS since 2004. Previously he worked as a statistician (1998–2004) for the U.S. Fish and Wildlife Service in the Migratory Bird Management Office and as a visiting scientist in the Geophysical Statistics Project at the National Center for Atmospheric Research in Boulder, Colorado. He has a Ph.D. in Statistics (1996) from North Carolina State University and a B.S. in Fisheries and Wildlife (1990) from Michigan State University.

KIMBERLY GAZENSKI (right) is a contractor for IAP World Services at the USGS Patuxent Wildlife Research Center. In 2011, she received a B.S. in Integrated Science and Technology concentrating in Environment and Biosystems from James Madison University in Harrisonburg, Virginia. During college she worked as a Stream Monitoring Intern for the Watershed Management Division of the Montgomery County Department of Environmental Protection in Maryland. After graduating, Kimberly worked as a student contractor and currently works as an IAP contractor at USGS Patuxent Wildlife Research Center where she helps manage route maps for the North American Amphibian Monitoring Program. During this time she also worked on various project using R for spatial and statistical analyses. (Photographed by Kinard Boone).

OSWALDO VILLENA (not pictured) is a student contractor for the USGS Patuxent Wildlife Research Center where he is working for the North American Amphibian Monitoring Program. In 2010, he received a M.S. in Environmental Sciences from Towson University, Maryland. Currently he is in his last year of his PhD in the Marine Estuarine & Environmental Science Program at the University of Maryland College Park. His research is focused on how tire leachate is affecting aquatic organisms.

APPENDIX 1. R/WinBUGS script used to model range-wide Spring Peeper data.

```
####NE NAAMP Analysis for Spring Peepers####
#load R2WinBUGS Package
library("R2WinBUGS")

#read in Spring Peeper data
y.orig<-read.table("Pcru.csv",na.strings=c("NULL","NA"), sep=",", header=TRUE)

#subset just the data
y<-y.orig
y<- y[,3:200]
y<- as.matrix(y)

#read in State for each route
state<-read.table("routes_states.csv", na.strings=c("NULL","NA"), sep=",", header=TRUE)
state<-state[,3]
state<-as.numeric(factor(state))

#set number of sites, year, and repetitions
nsite<-dim(y)[1]
nyear<-11
nrep<-18

#read in Julian date data
julian<- read.table("juliandate.csv", na.strings=c("NULL","NA"),sep=",",header=TRUE)
juldate<- julian[,3:200]
juldate<- as.matrix(juldate)

#read in air temperature data
airtemp<- read.table("airtemp.csv", na.strings=c("NULL","NA"),sep=",",header=TRUE)
airtemp<- airtemp[,3:200]
airtemp<- as.matrix(airtemp)

#Read in minutes after sunset data
minutes<- read.table("MinAfterSunset.csv", na.strings=c("NULL","NA"),sep=",",header=TRUE)
minutes<- minutes[,3:200]
minutes<- as.matrix(minutes)

#read in startpoints coordinates
library(plyr)
startpoints<- read.table("Startpoints.csv", na.strings=c("NULL","NA"),sep=",",header=TRUE)

#join based on routenumber
startcoords<-join(y.orig, startpoints, by=intersect(names(y.orig), names(startpoints)))

#subset lat lons
lat<- startcoords[,201]

#create datelat covariate
datelat<- array(NA, dim=c(nsite,198))
date2lat<- array(NA, dim=c(nsite,198))

for(i in 1:nsite){
  for(v in 1:198){
    datelat[i,v] <- juldate[i,v]*lat[i]
    date2lat[i,v]<- juldate[i,v]*juldate[i,v]*lat[i]
  }
}

#normalize coordinates
mean.lat<-mean(lat, na.rm=TRUE)
sd.lat<-sd(lat)
lat<-(lat-mean.lat)/sd.lat
```

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```
#normalize minutes after sunset
mean.min<-mean(minutes, na.rm=TRUE)
sd.min<-sd(minutes[!is.na(minutes)])
minutes<-(minutes-mean.min)/sd.min

#normalize Julian date
mean.date<- mean(juldate, na.rm=TRUE)
sd.date<- sd(juldate[!is.na(juldate)])
date<-(juldate-mean.date)/sd.date

#normalize temperature
mean.temp<-mean(airtemp, na.rm=TRUE)
sd.temp<- sd(airtemp[!is.na(airtemp)])
airtemp<-(airtemp-mean.temp)/sd.temp

#normalize datelat
mean.datelat<-mean(datelat, na.rm=TRUE)
sd.datelat<- sd(datelat[!is.na(datelat)])
datelat<- (datelat-mean.datelat)/sd.datelat

#normalize date2lat
mean.date2lat<-mean(date2lat, na.rm=TRUE)
sd.date2lat<- sd(date2lat[!is.na(date2lat)])
date2lat<- (date2lat-mean.date2lat)/sd.date2lat

# MCMC settings
ni <- 4000
nt <- 1
nb <- 2000
nc <- 3

Zst<-matrix(rbinom(nyear*nsite,1,0.5),ncol=nyear,nrow=nsite)

##Create 3D matrix for species data
y->ytmp
y=array(dim=c(nsite,nrep,nyear))
for(t in 1:nyear){
  y[,t]=ytmp[,((t-1)*18+(1:18))]
}

##Create 3D Matrix for covariate data
date <- array(date, dim=c(nsite,nrep,nyear))
airtemp<- array(airtemp, dim=c(nsite,nrep,nyear))
minutes<- array(minutes,dim=c(nsite,nrep,nyear))
datelat <- array(datelat, dim=c(nsite,nrep,nyear))
date2lat <- array(date2lat, dim=c(nsite,nrep,nyear))

#to make sure all covariates have the same # of NA's
airtemp[is.na(date) != is.na(airtemp)] <- 0
minutes[is.na(date) != is.na(minutes)] <- 0

#check # of NA's
##species should have 608807, covariates should have 608440
#Species should ALWAYS have more NA's because of skipped stops
sum(is.na(y))
sum(is.na(date))
sum(is.na(airtemp))
sum(is.na(minutes))
sum(is.na(lat))

#create table of number of reps for each route for each year
nanum<-ifelse(is.na(y) == TRUE, 0, 1)
X2001<- rowSums(nanum[,1])
X2002<- rowSums(nanum[,2])
X2003<- rowSums(nanum[,3])
X2004<- rowSums(nanum[,4])
X2005<- rowSums(nanum[,5])
X2006<- rowSums(nanum[,6])
X2007<- rowSums(nanum[,7])
X2008<- rowSums(nanum[,8])
X2009<- rowSums(nanum[,9])
X2010<- rowSums(nanum[,10])
X2011<- rowSums(nanum[,11])
```


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```
nrep<- matrix(c(X2001,X2002,X2003,X2004,X2005,X2006,X2007,X2008,X2009,X2010,X2011), ncol=11,nrow=dim(y)[1])

pst<-rep(0,nyear)

#Bundle data
data <- list ("y","nsite","nrep","nyear","state","date","airtemp","minutes","lat","datelat","date2lat")

#####Set starting values for parameters
p<- c(0.3023,0.2863,0.3700,0.3114, 0.3231, 0.3287, 0.2233, 0.4296, 0.4194, 0.3020, 0.3742)

b.a<- 1.0254
b.a2<- -0.3848
b.d<- 2.2858
b.d2<- -1.5479
b.m<- 0.0531
b.m2<- -0.0402
b.l<- -0.0280
b.l2<- 0.0658
b.dl<- 1.0822
b.d2l<- -0.6495

#inital values
inits <- function()
  list (p0=p,z=Zst,a1=matrix(rnorm(nyear-1),nrow=11,ncol=(nyear-1),byrow=TRUE),
        a2=0,a3=0,a4=0,a5=0,a6=0,a7=0,beta.a=b.a,beta.a2=b.a2,beta.d=b.d,beta.d2=b.d2,
        beta.m=b.m,beta.m2=b.m2,beta.l=b.l,beta.l2=b.l2, beta.datelat=b.dl,
        beta.date2lat=b.d2l,mod=rep(1,10) )

#Specify model in BUGS language
sink("occ-cov_modelselection.txt")
cat("
model {

#Specify Priors
for(t in 1:nyear){
p0[t] ~ dunif(0,1)
logitp[t]<- log(p0[t]/(1-p0[t]))
beta.d ~ dnorm(0,.1)
beta.a ~ dnorm(0,.1)
beta.m ~ dnorm(0,.1)
beta.d2 ~ dnorm(0,.1)
beta.a2 ~ dnorm(0,.1)
beta.m2 ~ dnorm(0,.1)
beta.l ~ dnorm(0,.1)
beta.l2 ~ dnorm(0,.1)
beta.datelat ~ dnorm(0,.1)
beta.date2lat ~ dnorm(0,.1)

for(s in 1:11){
a0[s] ~ dnorm(0,.1)
logitpsi[s] ~ dnorm(0,.1)
logit(psi[s])<-logitpsi[s]
for(t in 1:(nyear-1)){
  a1[s,t]~dnorm(0,.1)
}
}

a2~dnorm(0,.1)
a3~dnorm(0,.1)
a4~dnorm(0,.1)
a5~dnorm(0,.1)
a6~dnorm(0,.1)
a7~dnorm(0,.1)
for(m in 1:10){
mod[m] ~ dbern(.5)
}

#State model
for(i in 1:nsite){
  z[i,1]~dbern(psi[state[i]])
}
```

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```

for(t in 2:nyear){
  logit(muZ[i,t])<- a0[state[i]] + a1[state[i],1]*z[i,t-1]
  z[i,t]~dbern(muZ[i,t])
}
}

#Observation model
for (t in 1:nyear){
  for(i in 1:nsite){
    for(j in 1:(nrep[i,t])){
      logit(p[i,j,t])<- logitp[t] + beta.d*date[i,j,t]*mod[1] + beta.a*airtemp[i,j,t]*mod[3]
      + beta.m*minutes[i,j,t]*mod[5] + beta.m2*pow(minutes[i,j,t],2)*mod[5]*mod[6]
      + beta.a2*pow(airtemp[i,j,t],2)*mod[4]*mod[3] + beta.d2*pow(date[i,j,t],2)*mod[1]*mod[2]
      + beta.l*lat[i]*mod[7] + beta.l2*pow(lat[i],2)*mod[7]*mod[8]
      + beta.datelat*date[i,j,t]*mod[1]*mod[7]*mod[9] +
      beta.date2lat*date2lat[i,j,t]*mod[1]*mod[2]*mod[7]*mod[10]

      Py[i,j,t]<- z[i,t]*p[i,j,t]
      y[i,j,t] ~ dbern(Py[i,j,t])    }
    }
  }

  for(i in 1:nsite){
    for(s in 1:11){
      X[i,s]<-equals(state[i],s)
    }
  }

  for(s in 1:11){
    for (t in 1:nyear){
      N[s,t]<- inprod(z[t],X[s])
    }
  }
  },fill = TRUE)
sink()

#Parameters monitored
parameters <- c("logitp","a0","a1","a2","a3","a4","a5","a6","a7","beta.d","beta.a",
               "beta.m","N","beta.d2","beta.a2","beta.m2","beta.l","beta.l2","beta.datelat", "beta.date2lat","mod")

#Call WinBUGS from R
out_ms_Peru<- bugs (data, inits, parameters, "occ-cov_modelselection.txt", n.thin=nt,n.chains=nc, n.burnin=nb,n.iter=ni,debug=TRUE)

```

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APPENDIX 2. For each of the 17 species the top 10 models (in terms of posterior probability) are reported below. These variables include Julian date, air temperature, minutes after sunset, latitude, date-latitude interaction, and the quadratic versions of each (denoted by superscript). A value of 1 in the table indicates that the variable is in the model, and a value of 0 indicates it is not. Species names are abbreviated in the table as follows: *A. americanus* (Aame), *A. fowleri* (Afow), *A. crepitans* (Acre), *H. andersonii* (Hand), *H. cinerea* (Hcin), *H. versicolor-chrysoscelis* complex (Hvcc), *P. brachyphona* (Pbra), *P. crucifer* (Pcru), *P. feriarum-kalmi* complex (Pfkc), *L. catesbeianus* (Lcat), *L. clamitans* (Lcla), *L. palustris* (Lpal), *L. pipiens* (Lpip), *L. septentrionalis* (Lsep), *L. sphenoccephalus* (Lsph), *L. sylvaticus* (Lsyl), and *L. virgatipes* (Lvtr).

Species code	Date	Date ²	Airtemp	Airtemp ²	Minutes	Minutes ²	Latitude	Latitude ²	Date-Lat	Date2-Lat	Posterior Probability
Aame	1	1	1	0	1	1	0	0	0	0	0.8192
	1	1	1	1	1	1	0	0	0	0	0.1778
	1	1	1	0	1	1	1	0	0	0	0.0030
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
Afow	0	1	1	1	1	0	1	1	0	0	0.3375
	1	1	1	1	1	1	1	1	0	0	0.3317
	0	1	1	1	1	0	0	0	0	0	0.3292
	1	1	1	1	1	1	1	1	0	1	0.0017
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
Acre	0	1	1	1	1	0	1	1	0	0	0.3023
	0	1	1	1	1	0	0	0	0	0	0.3005
	1	1	1	1	0	0	0	0	0	0	0.2355
	1	0	1	1	0	0	0	0	0	0	0.0823
	1	1	1	1	1	0	0	0	0	0	0.0342
	1	1	0	0	1	0	0	0	0	0	0.0170
	1	1	0	0	0	0	0	0	0	0	0.0085
	1	1	1	0	1	0	0	0	0	0	0.0072
	1	1	1	0	0	0	0	0	0	0	0.0035
	0	1	1	1	1	0	1	0	0	0	0.0025
Hand	1	1	0	0	0	1	0	0	0	0	0.2983
	1	1	0	0	1	1	0	0	0	0	0.1965
	1	1	0	0	0	1	1	0	1	0	0.0965
	1	1	0	0	0	1	1	1	1	0	0.0778
	1	1	0	0	0	1	1	0	1	1	0.0505

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	1	1	0	0	0	1	1	1	1	1	0.0455
	1	0	0	0	0	1	0	0	0	0	0.0413
	1	1	0	0	0	1	1	0	0	0	0.0360
	1	1	0	0	0	1	1	1	0	0	0.0305
	1	1	0	0	1	1	1	1	0	0	0.0220
Hcin	1	1	0	0	0	1	1	0	1	0	0.2242
	1	1	0	0	0	1	1	1	1	0	0.2032
	1	1	0	0	0	1	1	1	0	0	0.1697
	1	1	0	0	0	1	0	0	0	0	0.1513
	1	1	0	0	0	1	1	0	0	0	0.1215
	1	1	0	0	0	1	1	1	0	1	0.0555
	1	1	0	0	0	1	1	0	1	1	0.0132
	1	1	0	0	0	1	1	1	1	1	0.0115
	1	1	0	0	1	1	1	0	1	0	0.0093
	1	1	0	0	1	1	1	1	1	0	0.0092
Hvcc	1	1	1	1	1	1	1	1	0	0	0.6365
	1	1	1	1	1	1	1	1	1	0	0.3033
	1	1	1	0	1	1	1	1	1	0	0.0397
	1	1	1	1	1	1	1	1	0	1	0.0128
	1	1	1	1	1	1	1	1	1	1	0.0028
	1	1	0	0	1	1	1	1	1	0	0.0020
	1	1	1	0	1	1	1	1	1	1	0.0015
	1	1	1	0	1	1	1	1	0	0	0.0013
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
Pbra	1	1	0	0	1	1	1	0	0	0	0.3325
	1	1	0	0	1	1	1	0	1	0	0.2807
	1	1	0	0	1	1	1	1	0	1	0.1800
	1	1	0	0	1	1	1	1	1	1	0.0630
	1	1	0	0	1	1	1	1	0	0	0.0593
	1	1	0	0	1	1	1	0	0	1	0.0455
	1	1	0	0	1	1	1	1	1	0	0.0310
	1	1	1	0	1	1	1	0	0	0	0.0077
	1	1	0	0	0	1	1	0	0	1	0.0002
	1	1	1	0	1	1	1	0	1	0	0.0002
Pcru	1	1	1	0	1	1	1	1	0	0	0.5642
	1	1	0	0	1	1	1	1	0	0	0.4092
	1	1	1	0	1	1	1	1	0	1	0.0153
	1	1	0	0	1	1	1	1	0	1	0.0058
	1	1	0	0	1	1	1	1	1	0	0.0025
	1	1	1	0	1	1	1	1	1	0	0.0017
	1	1	1	1	1	1	1	1	0	0	0.0013

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	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
	---	---	---	---	---	---	---	---	---	---	---
Pfk	1	1	0	0	0	1	0	0	0	0	0.4888
	1	1	0	0	0	0	0	0	0	0	0.3038
	1	0	0	0	0	0	0	0	0	0	0.1372
	1	0	0	0	0	1	0	0	0	0	0.0300
	1	1	0	0	1	1	0	0	0	0	0.0100
	1	1	0	0	0	0	1	0	0	0	0.0078
	1	1	0	0	0	1	1	0	0	0	0.0075
	1	0	0	0	0	0	1	0	0	0	0.0045
	1	1	1	0	0	1	0	0	0	0	0.0033
	1	1	0	0	1	0	0	0	0	0	0.0027
Lcat	1	1	1	0	1	1	1	0	1	0	0.6153
	1	1	1	0	1	1	1	0	0	0	0.1338
	1	1	1	0	1	1	1	0	1	1	0.1215
	1	1	1	0	1	1	1	1	1	0	0.0878
	1	1	1	0	1	1	1	1	0	0	0.0247
	1	1	1	0	1	1	1	1	1	1	0.0065
	1	1	1	1	1	1	1	0	1	0	0.0057
	1	1	1	0	1	1	1	0	0	1	0.0033
	1	1	1	1	1	1	1	1	1	0	0.0012
	1	1	1	1	1	1	1	0	1	1	0.0002
Lcla	1	1	0	0	0	1	1	0	1	1	0.1558
	1	1	0	0	0	0	1	0	1	1	0.1553
	1	1	0	1	0	0	1	0	1	1	0.1553
	1	1	0	1	0	1	1	0	1	1	0.1552
	1	1	0	1	0	0	0	0	1	1	0.0122
	1	1	0	1	0	0	0	1	1	0	0.0115
	1	1	0	1	0	0	0	0	0	1	0.0113
	1	1	0	0	0	0	0	0	1	1	0.0112
	1	1	0	1	0	1	0	1	1	0	0.0112
	1	1	0	1	0	1	0	0	0	1	0.0107
Lpal	1	1	0	0	0	1	1	0	1	1	0.1558
	1	1	0	0	0	0	1	0	1	1	0.1553
	1	1	0	1	0	0	1	0	1	1	0.1553
	1	1	0	1	0	1	1	0	1	1	0.1552
	0	0	0	0	0	0	1	0	0	0	0.0282
	0	0	0	0	0	0	1	1	0	0	0.0263
	1	1	0	1	0	0	0	0	1	1	0.0122
	1	1	0	0	0	0	0	0	1	1	0.0112
	1	1	0	1	0	1	0	1	1	0	0.0112

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	1	1	0	1	0	1	0	0	0	1	0.0107
	1	0	0	0	0	1	0	0	0	0	0.3420
	1	0	0	0	0	1	1	1	0	0	0.3073
	1	0	0	0	0	1	1	0	0	1	0.1375
	1	0	0	0	0	1	1	1	1	0	0.0747
Lpip	1	0	0	0	0	1	1	1	0	1	0.0542
	1	0	0	0	0	1	1	0	0	0	0.0228
	1	0	0	0	0	1	1	1	1	1	0.0153
	1	0	0	0	0	1	1	0	1	1	0.0087
	1	0	0	0	0	1	1	0	1	0	0.0070
	1	1	0	0	0	1	0	0	0	0	0.0068
	1	1	1	0	1	0	1	1	0	1	0.1110
	1	1	1	0	1	0	1	0	0	0	0.1043
	1	1	1	0	0	1	1	1	0	1	0.0608
	1	1	1	0	0	0	1	1	0	1	0.0560
Lsep	1	1	1	0	1	0	1	1	0	0	0.0520
	1	1	1	0	0	0	1	0	0	0	0.0442
	1	1	1	0	0	1	1	0	0	0	0.0408
	1	1	1	0	1	0	1	0	1	0	0.0295
	1	1	1	1	1	0	1	0	0	0	0.0218
	1	1	1	1	1	0	1	0	1	0	0.0215
	1	0	1	0	0	1	1	0	1	0	0.2773
	1	0	1	1	0	1	1	0	0	0	0.2368
	1	0	0	0	0	1	1	0	1	0	0.1015
	1	0	1	1	0	1	1	0	1	0	0.0738
Lsph	1	0	1	0	0	1	1	0	0	0	0.0645
	1	0	1	0	0	1	1	1	1	0	0.0622
	1	0	1	0	0	1	1	0	1	1	0.0445
	1	1	0	0	1	1	1	0	1	0	0.0412
	1	0	0	0	0	1	1	1	1	0	0.0218
	1	0	1	1	0	1	1	1	0	0	0.0198
	1	1	1	0	1	0	1	1	0	1	0.2488
	1	1	1	0	0	0	1	1	0	1	0.1892
	1	1	1	0	0	1	1	1	0	1	0.1753
	1	1	1	0	1	0	1	0	0	0	0.084
Lsyl	1	1	1	0	0	0	1	0	0	0	0.0778
	1	1	1	0	0	1	1	0	0	0	0.074
	1	1	1	0	1	0	1	1	0	0	0.0255
	1	1	1	0	0	1	1	1	0	0	0.0247
	1	1	1	0	0	0	1	1	0	0	0.0233
	1	1	1	1	1	0	1	1	0	1	0.0167
Lvir	1	0	0	0	0	1	0	0	0	0	0.2618

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1	1	0	0	1	1	0	0	0	0	0.2170
1	1	1	0	1	1	0	0	0	0	0.1843
1	0	1	0	0	1	0	0	0	0	0.1780
1	1	1	1	1	1	0	0	0	0	0.0620
1	1	0	0	0	1	0	0	0	0	0.0430
1	1	1	0	0	1	0	0	0	0	0.0385
1	0	1	1	0	1	0	0	0	0	0.0082
1	1	0	0	1	1	1	1	1	0	0.0022
1	1	1	0	1	1	1	1	1	0	0.0017
