Monitoring multiple species: Estimating state variables and exploring the efficacy of a monitoring program

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ABSTRACT

Monitoring programs have the potential to identify population declines and differentiate among the possible cause(s) of these declines. Recent criticisms regarding the design of monitoring programs have highlighted a failure to clearly state objectives and to address detectability and spatial sampling issues. Here, we incorporate these criticisms to design an efficient monitoring program whose goals are to determine environmental factors which influence the current distribution and measure change in distributions over time for a suite of amphibians. In designing the study we (1) specified a priori factors that may relate to occupancy, extinction, and colonization probabilities and (2) used the data collected (incorporating detectability) to address our scientific questions and adjust our sampling protocols. Our results highlight the role of wetland hydroperiod and other local covariates in the probability of amphibian occupancy. There was a change in overall occupancy probabilities for most species over the first three years of monitoring. Most colonization and extinction estimates were constant over time (years) and space (among wetlands), with one notable exception: local extinction probabilities for *Rana clamitans* were lower for wetlands with longer hydroperiods. We used information from the target system to generate scenarios of population change and gauge the ability of the current sampling to meet monitoring goals. Our results highlight the limitations of the current sampling design, emphasizing the need for long-term efforts, with periodic re-evaluation of the program in a framework that can inform management decisions.

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1. Introduction

A major challenge for scientist and land managers is monitoring biological diversity to assess the state of populations of conservation concern and evaluate management policies. Several large-scale monitoring programs have been initiated throughout the world to meet this challenge (e.g. US Breeding Bird Survey (Robbins et al., 1986), US National Resource Inventory (Olsen et al., 1999), Swiss Biodiversity Monitoring Program (Weber et al., 2004), various programs in the tropics (Danielsen et al., 2003a,b)). Multiple-species monitoring approaches have the potential to yield data on the changes in occurrence for a large number of species, or change in community composition, across time and space (Manley, 2004). However, current concerns focus on the need for monitoring programs that are guided by a priori hypotheses (Nichols and Williams, 2006), and account for important sources of error, including imperfect detection of target species (Yoccoz et al., 2001; Kéry and Schmid, 2004). Monitoring programs should provide data to differentiate among factors influencing population or distributional change, and not merely describe a population or species trend.

Many managers may understand the need to incorporate conservation oriented science into monitoring programs, but there are few published examples to emulate (but see Nichols et al., 1995; Karanth et al., 2004). Here, we use our experience with designing, implementing, analyzing and adapting a monitoring program during its first three years to illustrate key items that should be considered during the early phases of a monitoring program. We illustrate the approach with a practical example involving a suite of wetland-breeding amphibians on protected land embedded within an urban landscape. The concepts underlying our monitoring design are general and can be easily modified to fit a variety of taxa or systems. Key components include (1) careful a priori consideration of the biological system and factors that may contribute to change in that system, (2) probabilistic selection of sample units and a sampling design that incorporates potential detection probability differences and (3) early analysis of data to allow adjustment of monitoring protocols or goals.

Our focus on wetland-breeding amphibians was generated by a concern over recent global amphibian declines. Among the factors thought to contribute to amphibian population declines, habitat loss or alteration is generally considered to be a leading cause (Cushman, 2006); however, even populations in protected areas have undergone declines (Corn and Fogleman, 1984; Fellers and Drost, 1993; Halliday, 2005). In particular, smaller protected areas within urbanized landscapes may be more susceptible to outside activities (Stottlemyer, 1987; Schonewald-Cox and Buechner, 1992; Taylor and Knight, 2003). Of primary interest in our system is the alteration and degradation of wetlands, which are crucial breeding, foraging, or hibernating habitat for frogs and some salamanders. For example, urbanization may alter the hydroperiod of a wetland and thereby may change which amphibian species occupy a given wetland (Snodgrass et al., 2000; Rubbo and Kiesecker, 2005), or an increase in water conductivity (often associated with urbanization/impervious surfaces and salt; Kaushal et al., 2005) may decrease amphibian presence or embryonic survivorship (Glooschenko et al., 1992; Turtle, 2000, Karraker et al., 2008).

The U.S. National Park Service (NPS) has recently devoted a great deal of effort on developing monitoring programs for a subset of vital resources (http://science.nature.nps.gov/im/). Many of the NPS lands in the eastern U.S. are small, isolated areas. NPS biologists and managers are particularly concerned about amphibian populations within national park units in and around the Washington DC metropolitan area (National Park Service, 2006). Accordingly, we initiated a monitoring program at a single park for a suite of wetland-breeding amphibians. The program's goals are to explore a priori hypotheses about environmental factors which may (1) influence initial amphibian distribution (i.e. the probability that a wetland is occupied by target species during the first year of monitoring), and (2) contribute to changes in occupancy (ψ) over time via two processes: local wetland colonization (γ) and extinction (ε). Notice that annual estimates of occupancy and estimates of change in species distributions over time (i.e., trends in occupancy) are natural outcomes of this approach.

In addition to hydroperiod and conductivity, we hypothesize that several environmental factors may influence the probability of an amphibian species occupying and persisting in a wetland including: flooding, wetland area, canopy cover and aquatic vegetation. Flooding by the river may wash out amphibian eggs and larvae, and potentially introduce aquatic predators (Dorcas et al., 2006). Larger wetlands may have longer hydroperiods and are larger targets for dispersing amphibians (Seale, 1982; Brooks and Hayashi, 2002; Armstrong, 2005). Closed canopy conditions may reduce larval survivorship for some species (Skelly et al., 1999), and aquatic vegetation may provide protection from predators or serve as an oviposition site (Sredl and Collins, 1992; Egan and Paton, 2004; Kopp et al., 2006).

Based on our sample frame and a priori biological hypotheses, we used probabilistic sampling to select monitoring sites and repeatedly sampled these sites to collect information suitable for estimating the detection probability for each of our target amphibian species, taking into account the asynchrony in amphibian breeding phenology. Most surveys are unlikely to detect all species present during a sampling event, resulting in false–negative errors that can affect the bias and precision of occupancy estimates (MacKenzie et al., 2006). By visiting each sample site multiple times and/or using multiple independent observers, the probability of detection can be estimated and incorporated to provide unbiased estimates of occupancy probability (MacKenzie et al., 2006).

Finally, we used information from our first three years of surveys to simulate future population change scenarios for two of the amphibian species likely to be sensitive to urbanization (*Ambystoma maculatum* and *Notophthalmus viridescens*; Rubbo and Kiesecker, 2005). We examined the ability of our monitoring program to detect a large change (50%) in occupancy over a short (5 years) time period using various sampling designs. These scenarios are of interest to park managers (Shawn Carter, *personal communication*), giving them early feedback and setting realistic expectations for the monitoring program, potentially leading to adjustments in the monitoring effort and duration, or re-evaluation of the program's goals.

2. Study area

We sampled wetlands in the Chesapeake & Ohio Canal National Historical Park (CHOH), Maryland, USA (38° 59′N, 77° 14′W), located within the urbanized Washington DC metropolitan area. CHOH is adjacent to the Potomac River, and the park includes a historically active canal running parallel to the river (Fig. 1). Our study was conducted in the southern section of the park known as the Potomac Gorge Region.

3. Methods

3.1. Sampling design and field methods

Our sample frame consisted of all known wetlands which are isolated and less than 0.4 ha in the Potomac Gorge region of CHOH. These constraints are based primarily on sampling logistics (i.e., we could not effectively sample a wetland that was very large or define a wetland that was not isolated).
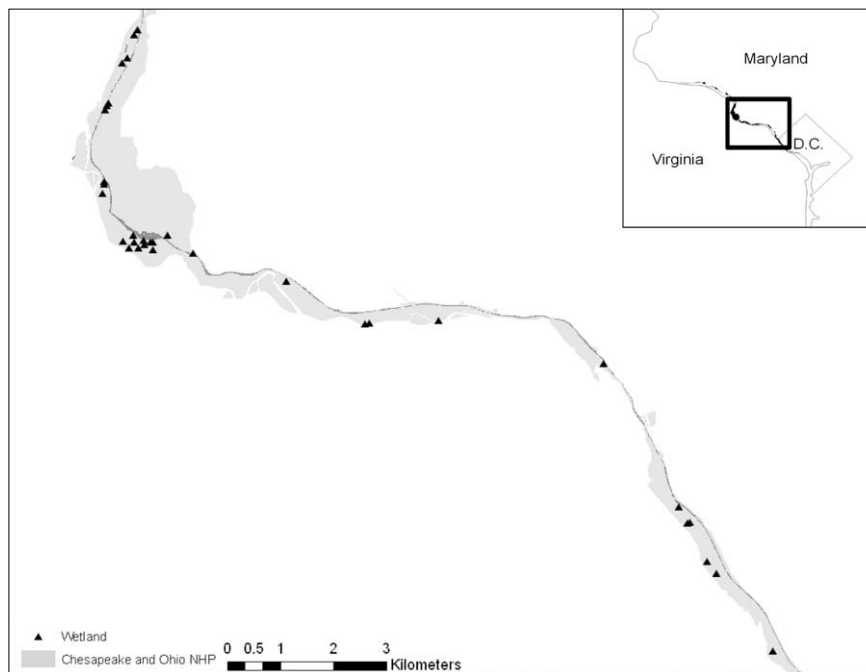
Fig. 1 – Location of 33 wetlands surveyed for amphibians in the Chesapeake and Ohio National Historic Park (2005–2007).

Our sample frame consisted of 169 wetlands from which we selected a random sub-sample of 33 wetlands.

The 33 wetlands were visited on four occasions from March–July for three years (2005–2007; 12 visits over the study duration). Two detection methods were used to document the presence of amphibian species during these visits: visual encounter or dip-net surveys. Visual encounter surveys were conducted early in the year to target amphibian eggs and breeding adults whereas dip-net surveys were used later in the season to target larval amphibians. During each visit, surveys were conducted by two independent observers (a modification of the independent double-observer approach of Nichols et al., 2000). Observers began their surveys at opposite sides of a wetland site and walked around the perimeter of the pond in the same direction, separately recording detections of all life stages of encountered amphibian species. In

this manner each observer was the first person to survey half of the wetland, and we maximized the time between the first observer and the second observer surveying the same part of the wetland.

During each visit to a wetland, we measured covariates that relate to our a priori hypotheses with respect to amphibian occupancy (Tables 1 and 2), as well as variables that may influence amphibian detection (maximum water depth and the water temperature at the edge of the wetland). We used GIS (ArcMap9, Environmental Systems Research Institute, Redlands, CA) to construct a relative flood potential index by combining distance and slope from the river: lower index values indicate wetlands that were more likely to flood. These calculated flood index values corresponded well to the flooding events we observed during the study.

Table 1 – The explanation, mean, minimum and maximum value for covariates used to model initial occupancy (2005). All of the values are from the initial survey year (2005), with the exception of Hydroperiod. Hydroperiod, flood, cond, and canopy were standardized in our analysis.

Covariate	Explanations	Mean	Minimum	Maximum	±1SD
Hydroperiod	Average hydroperiod score over 3 years. The score designates the month that the wetland dried. (1 = April; 2 = May; 3 = June; 4 = July; 5 = water present thru July)	4.0	1.7	5	1.2
Area	Minimum wetland area (minimum length × minimum width; hectares)	0.05	0.001	0.247	0.05
Flood	Slope * distance from river (low values indicate likely to flood)	23	0	159	29
Cond	Maximum wetland conductivity (μs)	314	32	946	254
Veg	Presence of Aquatic vegetation (1 = >15% aquatic vegetation present; 0 < 15% aquatic vegetation present)	0.27	0	1	0.45
Canopy	Percent canopy cover over the entire wetland	71	6	99	27

Table 2 – Expected a priori relationships (positive or negative) between the habitat covariates (Table 1) and species-specific occupancy probabilities. These expected relationships are based on previous studies and our own hypotheses.

Covariate	Expected relationship with occupancy	Species relationship expected for	Source
Hydroperiod	+	All	Shoop (1974)
			Skelly et al. (1999)
			Babbitt et al. (2003)
Area	+	All	Seale (1982)
			Armstrong (2005)
			Werner et al. (2007)
Flood[a]	+	All	Dorcas et al. (2006)
Cond	−	All	Glooschenko et al. (1992)
			Turtle (2000)
Veg	+	*N. viridescens*	Egan and Paton (2004)
		P. crucifer	Van Buskirk (2005)
		R. catesbeiana	Kopp et al. (2006)
		R. clamitans	Mazerolle et al. (2005)
Canopy	−	*Bufo* spp.	
		P. crucifer	Skelly et al. (1999)
		R. clamitans	

a Lower flood values represent wetlands that are more likely to flood.

3.2. Analysis

We used multi-season occupancy models to estimate initial occupancy probabilities (ψ_{2005}) for each species, as well as colonization (γ) and extinction probabilities (ε) between years (MacKenzie et al., 2003, 2006). Annual occupancy probability estimates were derived from these parameters. Occupancy models account for imperfect detection, and provide unbiased estimates of occupancy probability and associated rate parameters (colonization and extinction probabilities). To apply these models, detection histories are compiled for each species at each wetland site. Example detection histories from this study include the following history from a single wetland over the three years:

11010000 11000000 110000––

where "1" represents detection of the target species during a single observer's survey, and "0" represents non-detection. In this example, both observers detected the target species on the first visit during the first year (represented by the first two values: "11"). During the second visit, only the second observer detected the species (represented by the interior '01'), and neither observer detected the species during the third and fourth visit of the first year. During the second year, both observers detected the species on the first visit, but the species was not detected on subsequent visits. This same pattern of detections was repeated in the third year, but the site was dry on the fourth visit. Missing values, denoted as '–', represent a wetland that was dry, flooded or not visited. There were eight detection/nondetection occasions per year (two observers surveyed each wetland during four visits).

We hypothesized that initial amphibian occupancy would be related to several local habitat variables (Table 2). The influence of the percent canopy cover and aquatic vegetation on the probability of occupancy was expected to vary by species: for *Bufo* spp., *Pseudacris crucifer*, and *Rana clamitans* we expected a negative relationship between occupancy probability and the percent canopy cover, and for the other species we expected no relationship between occupancy probability and canopy cover (Skelly et al., 1999). The relationship (positive or negative) between occupancy probability and the other covariates was expected to be consistent among species (although the magnitude of the relationship may vary by species; Table 2).

Using these hypotheses we defined a candidate set of models for each of the eight amphibian species (Appendix A). We considered the hydroperiod and area of a wetland to be factors of primary importance influencing amphibian occupancy probabilities. Flood index, conductivity, aquatic vegetation, and canopy cover were considered secondary factors. Our candidate model set was designed to compare the relative importance of the variable within each set of factors (primary or secondary), and not between these sets.

Since the occupancy state of wetlands may change over time, we investigated the influence of a subset of our collected covariates on colonization and extinction probabilities. We expected larger wetlands to have a higher probability of colonization for *Ambystoma maculatum*, as larger wetlands are a larger target, and may be more likely to intercept dispersing adults (Whitehead and Jones, 1969; Haddad and Baum, 1999). We expected wetlands with a shorter hydroperiod to have a higher probability of extinction for *A. maculatum*, *P. crucifer*, *R. catesbeiana*, *R. clamitans* and *R. sylvatica*. In addition, we investigated whether colonization or extinction probabilities were zero (i.e., testing whether occupancy was static from 2005–2007), varied by year, or were constant among years.

Finally, we modeled detection probability (*p*) as a function of water temperature (linear or quadratic), maximum water depth, or visit (year was considered an additive effect in this case). Water temperature is likely to influence the probability of detection through its influence on amphibian activity, egg hatching, and larval development, and may serve as a surrogate for breeding phenology. Water depth may hamper observers' ability to see or capture amphibians in deeper wetlands. Lastly, including models with visit-specific detection

probabilities allowed us to investigate and incorporate potential detection differences within and among years and between our two different detection methods (visual encounter and dip-net surveys). Previous analyses have suggested that aquatic vegetation and the skill level of the observer did not influence detection probabilities (Grant et al., 2005; Bailey et al., 2006).

Analyses were performed using program PRESENCE (Hines and MacKenzie, 2004) and Program MARK (White and Burnham, 1999). These programs use Akaike's Information Criterion (AIC) to rank models and calculate Akaike weights (w; Burnham and Anderson, 2002). We evaluated the relative importance of the covariates for each species by summing the AIC weights for all models in the model set where variable j occurred ($w_+(j)$; Burnham and Anderson, 2002).

3.3.   Exploring sampling design trade-offs

Using data from our monitoring, we explored sampling design trade-offs under a common monitoring objective: to detect a specified level of change in species distributions (Bailey et al., 2007). We chose two species (A. maculatum and N. viridescens) that are likely to be sensitive to urbanization, but whose response may vary due to their different initial occupancy probabilities in the Potomac Gorge region, habitat requirements, known dispersal distances, and extinction and colonization probabilities (Shoop, 1974; Healy, 1975; Gill, 1978; Gibbs, 1998; Rubbo and Kiesecker, 2005).

We explored the ability of different sampling designs to detect a specified change in amphibian occupancy by generating up to four different change scenarios (Table 3). The first two scenarios depict a 50% decline in occupancy over five years. This level of decline was generated using the species initial occupancy estimates (ψ_{2005}) with either: (scenario 1) constant extinction and colonization probabilities (i.e., rate parameters), or (scenario 2) rate parameters that fluctuated between 'good' (higher colonization and lower extinction probabilities) and 'bad' years (lower colonization and higher extinction probabilities; Table 3). A third scenario depicts a 50% increase in occupancy over five years assuming constant rate parameters, and the final scenario represents distribution change among occupied wetlands but stable overall occupancy probability (Table 3). We attempted to tailor these scenarios to our biological system; for example, our multi-season analysis for A. maculatum showed higher occupancy probabilities for wetlands that retained water through at least two survey seasons. Accordingly, we considered two groups of sites in generating our change scenarios for this species: wetlands with long or short hydroperiods, with an approximately equal number of wetlands in each group. For N. viridescens we only examined scenario 1, since the initial analysis revealed low occupancy probabilities ($\psi_{2005} = 0.15$) and constant rate parameters. For each of the four scenarios, we examined the ability of four sample designs to detect change in the amphibian distributions. These four sampling designs were created by varying the number of sampled wetland sites (35 or 70) and the frequency of surveys (annually or alternate years). Surveying 35 wetlands annually represents the original and current level of monitoring effort.

To determine whether the sample design affected the ability to detect our specified change(s) in amphibian distributions, we used a likelihood ratio test (LRT) to approximate power (Burnham et al., 1987:214-217). In each case the scenarios described above (Table 3) were considered the "true" generating model, or the alternative hypothesis (H$_a$), and the null hypothesis was represented by models representing no change in occupancy or its related rate parameters (H$_o$: time-constant occupancy and/or rate parameters). We approximated power (assuming either $\alpha = 0.05$ or $\alpha = 0.10$) by using the resulting chi-square statistic from the LRT as the noncentrality parameter, λ, and calculating power from a non-central chi-squared distribution (Burnham et al., 1987; Devineau et al., 2006; Bailey et al., 2007). All data generation was performed using program GENPRES (Bailey et al., 2007) and LRTs were performed using the Program MARK (White and Burnham, 1999).

4.   Results

We detected 13 amphibian species in all years of this study: A. maculatum, A. opacum, Bufo americanus, Bufo fowleri, Hemidactylium scutatum, Hyla chrysoscelis/versicolor, N. viridescens, Pseudacris crucifer, Rana catesbeiana, Rana clamitans, Rana palustris, Rana sphenocephala, and Rana sylvatica. B. americanus and B. fowleri tadpoles are very similar in appearance and were treated as the Bufo spp. complex. A. opacum, Hemidactylium scutatum, Hyla chrysoscelis/versicolor, and R. sphenocephala were rarely observed and did not have sufficient detections for formal multi-season occupancy analysis, thus we report results for eight species or species complexes. It is common for multi-species monitoring programs not to sample rare species well (Yoccoz et al., 2001; Sauer et al., 2003; Manley et al., 2004).

Model selection results suggest that detection probabilities varied with water temperature or visit for all species except N. viridescens (Appendix B). R. catesbeiana, R. clamitans and R. palustris all showed a quadratic relationship between water temperature and detection probability, but optimal detection temperature varied among species (Fig. 2, Appendix B). Detection probabilities for A. maculatum, P. crucifer, and R. sylvatica varied by visit and year (Table 4, Appendix B). For example, A. maculatum detection probabilities were highest during the first visit each year when this species' egg masses are conspicuous; however, detection probabilities were lower in 2006, relative to 2005 and 2007 (Fig. 3).

Initial occupancy estimates varied among species ranging from 0.09 ± 0.09 ($\hat{\psi}_{2005} \pm 1$SE) for N. viridescens to 0.86 ± 0.15 for R. palustris (Table 5). All covariates influenced initial occupancy estimates for one or more of the eight species, especially wetland hydroperiod (w_+(hydroperiod) > 0.7 for all species except Bufo spp. for which hydroperiod was excluded a priori; Table 4, Appendices A and B). Here, we report results for those covariates included in models with Akaike weights > 0.10 (Table 4, Appendix B).

A priori, wetland hydroperiod and area were considered primary factors likely to influence occupancy probabilities for seven amphibian species. Among these primary factors, hydroperiod had the most influence on initial occupancy probabilities for all of the species, except R. sylvatica (i.e., hydroperiod was relatively more important than wetland area based on

Table 3 – Parameter values used to generate four scenarios of change in amphibian distributions over a 5 year period and the approximate power to detect the distributional change in amphibian populations. Scenarios involve either constant colonization and extinction probabilities ($\gamma(.)$, and $\varepsilon(.)$), a repeating cycle of one good year ($\gamma_{good}, \varepsilon_{good}$) followed by two bad years (γ_{bad}, ε_{bad}), or time-specific colonization and extinction probabilities ($\gamma(t)$, $\varepsilon(t)$). For *Ambystoma maculatum* we modeled two groups of wetlands: Long hydroperiod and Short hydroperiod. Sampling designs differ in the frequency and number of wetlands (sites) sampled. Power is approximated using methods described by Burnham et al. (1987) involving a noncentral chi-square statistic from a likelihood ratio test.

Ambystoma maculatum
Scenario 1: 50% decline in occupancy assuming $\gamma(.)$, and $\varepsilon(.)$
A. Parameters used to generate decline

	$\gamma(.)$	$\varepsilon(.)$	ψ_1	Resulting year-specific estimates ψ_2	ψ_3	ψ_4	ψ_5
Long Hydroperiod	0.10	0.35	0.55	0.4	0.32	0.28	0.25
Short Hydroperiod	0.05	0.90	0.05	0.05	0.05	0.05	0.05
Overall			0.34	0.25	0.21	0.18	0.16

B. Approximate power to detect decline

Sampling Frequency	Number of Sites	χ^2	df	power (α 0.05)	power (α 0.10)
Every year	35	5.1	6	34%	47%
Alternating year	35	4.7	6	32%	44%
Every year	70	10.0	6	64%	76%
Alternating year	70	9.5	6	62%	73%

Scenario 2: 50% decline in occupancy assuming γ_{good}, ε_{good} and ε_{bad}, γ_{bad}
A. Parameters used to generate decline

	γ_{good}	γ_{bad}	ε_{good}	ε_{bad}	ψ_1	Resulting year-specific estimates ψ_2	ψ_3	ψ_4	ψ_5
Long Hydroperiod	0.15	0.05	0.20	0.55	0.55	0.51	0.25	0.15	0.25
Short Hydroperiod	0.05	0.03	0.70	0.95	0.05	0.06	0.03	0.03	0.06
Overall					0.34	0.31	0.16	0.10	0.17

B. Approximate power to detect decline

Sampling frequency	Number of sites	χ^2	df	Power (α 0.05)	Power (α 0.10)
Every year	35	11.5	6	72%	81%
Alternating year	35	6.2	6	42%	55%
Every year	70	23.1	6	97%	99%
Alternating year	70	12.5	6	76%	84%

Scenario 3: 50% increase in occupancy assuming $\gamma(.)$, and $\varepsilon(.)$
A. Parameters used to generate increase

	$\gamma(.)$	$\varepsilon(.)$	ψ_1	Resulting year-specific estimates ψ_2	ψ_3	ψ_4	ψ_5
Long Hydroperiod	0.4	0.1	0.55	0.68	0.74	0.77	0.78
Short Hydroperiod	0.1	0.7	0.05	0.11	0.12	0.12	0.13
Overall			0.34	0.43	0.47	0.49	0.50

B. Approximate power to detect increase

Sampling frequency	Number of sites	χ^2	df	Power (α 0.05)	Power (α 0.10)
Every year	35	4.1	6	28%	39%
Every year	70	8.2	6	54%	66%

Scenario 4: Detecting change in distribution assuming $\psi_1 = \psi_5$, $\gamma(t)$, $\varepsilon(t)$
A. Parameters used to generate change

	γ_{good}	γ_{bad}	ε_{good}	ε_{bad}	ψ_1	Resulting year-specific estimates ψ_2	ψ_3	ψ_4	ψ_5
Long Hydroperiod	0.25	0.05	0.1	0.3	0.55	0.61	0.44	0.34	0.47
Short Hydroperiod	0.10	0.05	0.05	0.85	0.05	0.14	0.06	0.06	0.15
Overall					0.34	0.41	0.28	0.22	0.33

Table 3 – (continued)

B. Approximate power to detect change in distribution

Sampling frequency	Number of sites	χ^2	df	Power ($\acute{\alpha}$ 0.05)	Power ($\acute{\alpha}$ 0.10)
Every year	35	7.8	6	52%	64%
Alternating year	35	1.4	6	11%	19%
Every year	70	15.5	6	86%	92%
Alternating year	70	2.7	6	19%	29%

Notophthalmus viridescens
Scenario 1: 50% decline in occupancy assuming $\gamma(.)$, and $\varepsilon(.)$
A. Parameters used to generate decline — Resulting year-specific estimates

$\gamma_{(.)}$	$\varepsilon_{(.)}$	ψ_1	ψ_2	ψ_3	ψ_4	ψ_5
0.05	0.60	0.15	0.10	0.09	0.08	0.08

B. Approximate power to detect decline

Sampling frequency	Number of sites	χ^2	df	Power ($\acute{\alpha}$ 0.05)	Power ($\acute{\alpha}$ 0.10)
Every year	35	1.3	3	14%	22%
Alternating year	35	1.2	3	13%	21%
Every year	70	2.6	3	24%	35%
Alternating year	70	2.4	3	22%	33%

summed Akaike weights; Table 4, Appendix B). Species preferred longer hydroperiods (Fig. 4) and larger wetlands (Table 4, Appendix B).

Among the secondary factors we considered for *A. maculatum* and *R. sylvatica* (flood and water conductivity), flood had a positive relationship with the occupancy probabilities and seemed especially important for *A. maculatum* (w_+(flood) = 0.99 and 0.54 for *A. maculatum* and *R. sylvatica*; respectively). For *R. sylvatica* there was also moderate support for a negative relationship between conductivity and the occupancy probability (w_+(conductivity) = 0.42 and 0.01 for *R. sylvatica* and *A. maculatum*; respectively). We expected percent canopy cover to influence initial occupancy probabilities for *P. crucifer* and *R. clamitans* and this was indeed the case (w_+(canopy) = 0.92 for *P. crucifer* and 0.99 for *R. clamitans*); however, contrary to our a priori predictions *P. crucifer* and *R. clamitans* had a higher probability of occupying wetlands with a higher percent of canopy cover (Tables 2 and 4, Appendix B). Our exploration
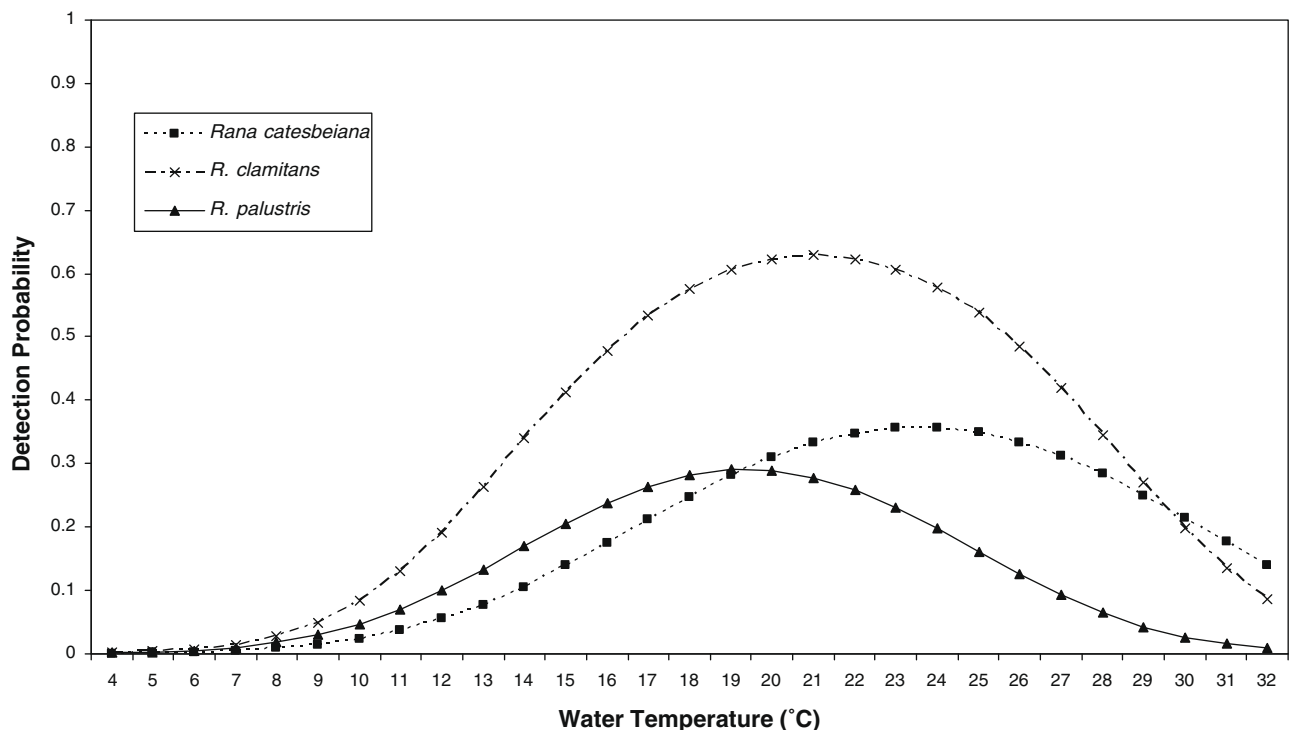

Fig. 2 – The relationship between the detection probability of three amphibian species (*Rana catesbeiana*, *R. clamitans* and *R. palustris*) and water temperature at wetlands in the Chesapeake and Ohio NHP.

Table 4 – Summary of model selection statistics for models ($w > 0.1$) for a subset of amphibian species at Chesapeake and Ohio NHP wetlands from 2005–2007. ΔAIC is the difference in AIC value for a particular model when compared with the top ranked model; w is the AIC model weight; K is the number of parameters. Refer to Table 1 for explanations of the covariates. Values are the estimates of the slopes for each covariate. Hydroperiod is abbreviated as Hydro in this table. The detection covariates are defined as: wtemp (water temperature/10(°C)), wtemp² ((water temperature/10)² (°C)), and visit + yr (sampling visit with an additive year effect). We indicate when colonization or extinction estimates were modeled as zero in the following manner: $\gamma1 = 0$ where colonization between 2005 and 2006 equals zero and $\gamma2 = 0$ where colonization between 2006 and 2007 equals zero. Additional species and model results can be found in Appendix B.

Model	ΔAIC	w	K	Occupancy					Extinction	Colonization
				Hydro	Area	Flood	Cond	Canopy	Hydro	Area
Ambystoma maculatum										
ψ(Hydro, area, flood), $\gamma(\gamma2 = 0)$, $\varepsilon(\varepsilon1 = 0)$, p(visit + yr)	0.00	0.36	12	3.14	17.98	5.04				
ψ(Hydro, flood), $\gamma(\gamma2 = 0)$, $\varepsilon(\varepsilon1 = 0)$, p(visit + yr)	0.45	0.29	11	3.02		3.95				
ψ(Hydro, area, flood), $\gamma(\gamma1 = area, \gamma2 = 0)$, $\varepsilon(\varepsilon1 = 0)$, p(visit + yr)	1.37	0.18	13	3.14	17.98	5.04				
ψ(Hydro, flood), $\gamma(\gamma1 = area, \gamma2 = 0)$, $\varepsilon(\varepsilon1 = 0)$, p(visit + yr)	1.82	0.15	12	3.02		3.95				−8.99
Pseudacris crucifer										
ψ(Hydro, canopy), $\gamma(.)$, $\varepsilon(.)$, p(visit + yr)	0.00	0.42	11	3.44				3.83		
ψ(Hydro, area,canopy), $\gamma(.)$, $\varepsilon(.)$, p(visit + yr)	1.50	0.20	12	3.35	7.57			4.39		
ψ(Hydro, canopy),$\gamma(.)$, ε(Hydro), p(visit + yr)	1.98	0.16	12	3.44				3.83	−0.43	
Rana clamitans										
ψ(Hydro, canopy), $\gamma(.)$, ε(hydro), p(wtemp, wtemp²)	0.00	0.78	9	7.01				3.79	−2.48	
ψ(Hydro, canopy), $\gamma(.)$,$\varepsilon(.)$, p(wtemp, wtemp²)	2.61	0.21	8	7.01				3.79		
Rana sylvatica										
ψ(Hydro, area, flood), $\gamma(.)$, $\varepsilon(.)$, p(visit + yr)	0.00	0.28	12	1.59	34.28	2.90				
ψ(Hydro, area, cond), $\gamma(.)$, $\varepsilon(.)$,p(visit + yr)	1.48	0.13	12	0.98	19.33		−1.83			
ψ(Area, cond),$\gamma(.)$,$\varepsilon(.)$, p(visit + yr)	1.86	0.11	11		26.68		−1.98			
ψ(Hydro, area, flood),$\gamma(.)$, ε(hydro), p(visit + yr)	1.93	0.11	13	1.57	33.87	2.86			−0.44	
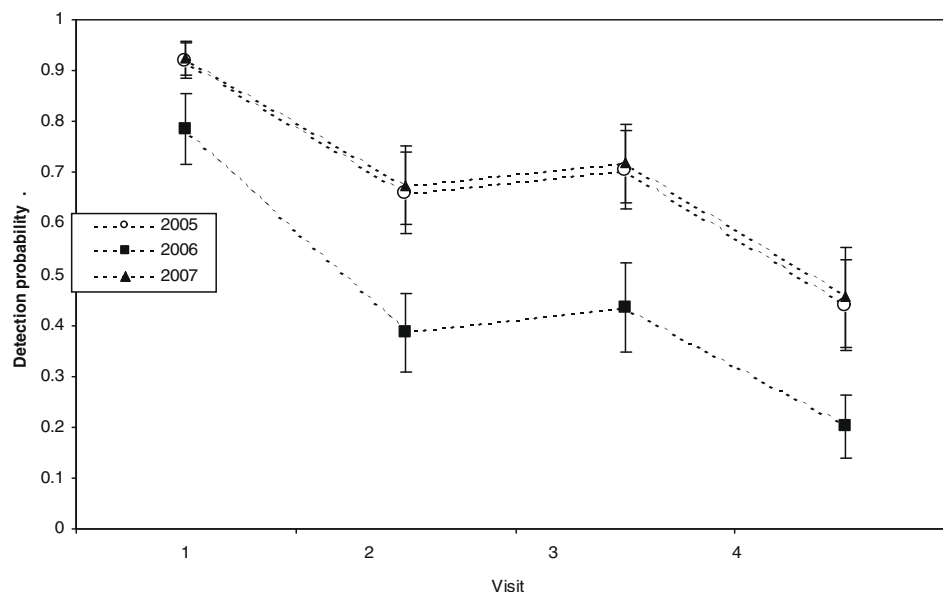
Fig. 3 – Visit specific detection probability estimates for *Ambystoma maculatum*. Wetlands were visited four times (March–July) each year.

of secondary factors for the remaining species revealed that *R. catesbeiana* had a higher occupancy probability in wetlands with less than 15% of the wetland having aquatic vegetation (Appendix B). For *Bufo* spp*., N. viridescens*, and *R. palustris*, there was much model uncertainty, suggesting no clear relationship between initial occupancy probabilities and any of

Table 5 – Model-averaged estimates and unconditional standard errors for year-specific occupancy, extinction and colonization probabilities for eight amphibian species found in the Chesapeake and Ohio NHP. Models with Akaike weights >0.02 were used to calculate the model-averaged estimates (Appendix B). For models containing covariates, parameters were estimated using the mean of the covariate among wetlands, except for the 'veg' covariate where parameter values are given for ponds with <15% aquatic vegetation.

Species	$\hat{\psi}_{2005}$ (SE)	$\hat{\psi}_{2006}$ (SE)	$\hat{\psi}_{2007}$ (SE)	$\hat{\varepsilon}$ (SE)	$\hat{\gamma}$ (SE)
Ambystoma maculatum	0.10 (0.09)	0.25 (0.11)	0.23 (0.10)	0.08[b] (0.08)	0.17[c] (0.09)
Bufo spp.	0.55 (0.10)	0.56 (0.10)	0.56 (0.12)	0.13 (0.11)	0.18 (0.10)
Notophthalmus viridescens[a]	0.09 (0.09)	0.09 (0.07)	0.09 (0.07)	0.23 (0.14)	0.02 (0.02)
Pseudacris crucifer[a]	0.10 (0.14)	0.23 (0.09)	0.27 (0.10)	0.48 (0.17)	0.20 (0.09)
Rana catesbeiana	0.48 (0.18)	0.44 (0.20)	0.63 (0.17)	0.45[c] (0.35)	0.34 (0.13)
Rana clamitans	0.79 (0.22)	0.37 (0.20)	0.24 (0.17)	0.56 (0.24)	0.13 (0.10)
Rana palustris[a]	0.86 (0.15)	0.67 (0.15)	0.55 (0.16)	0.21 (0.12)	0.08 (0.06)
Rana sylvatica	0.28 (0.14)	0.27 (0.11)	0.26 (0.10)	0.19 (0.11)	0.05 (0.05)

a Species was only detected at wetlands that remain wet through July, thus parameter values are reported for wetlands with a hydroperiod covariate = 5.
b Probabilities reported for 2006–2007 only.
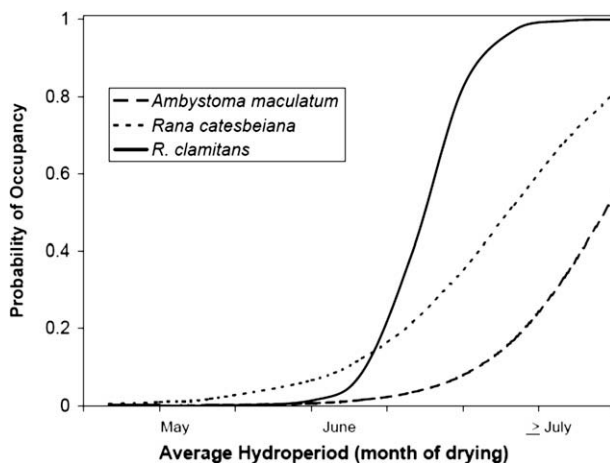c Probabilities reported for 2005–2006 only.

Fig. 4 – The relationship between the average hydroperiod of a wetland and the probability of occupancy by *Ambystoma maculatum*, *Rana catesbeiana*, and *R. clamitans*. Estimation of the occupancy probability is based on the top model which had Akaike weights of *w* = 0.36 for *Ambystoma maculatum*, *w* = 0.29 for *Rana catesbeiana*, and *w* = 0.78 for *R. clamitans*. Refer to Appendix B for unconditional standard errors and confidence intervals.

our collected covariates; for these species we present the results of our analysis in Appendix B but refrain from detailed interpretation. It is important to note that the influence of the covariates on occupancy probabilities should be considered in the context of the covariate's range observed at CHOH (Table 1).

The occupancy state changed among sites for most species (estimates of colonization or extinction were not zero; Table 5), indicating that some sites were colonized and others failed to support breeding and/or foraging activity (i.e., went locally "extinct"). Model selection results suggested that colonization and extinction probabilities were often constant among wetlands and years, but were usually greater than zero. Time or year-specific rate parameters were favored for two species, *A. maculatum* and *R. catesbeiana*, but our a priori factor (wetland area) was not important in estimates of local colonization (Appendix B). Wetlands that were prone to drying had a higher extinction probability for *R. clamitans* (Table 4, Appendix B).

4.1. Sampling design trade-offs

Under the current level of monitoring effort, there is little ability to detect a 50% decline in occupancy probabilities over 5 years for *N. viridescens* (Table 3). The approximated power increases when twice as many sites are sampled, but our results suggest that it is unreasonable to expect the current monitoring program to detect a 'significant' decline in this species over 5 years. It is important to note however, that the estimates of change and year-specific occupancy are still unbiased, but precision may be poor for these estimates.

The ability to detect change in occupancy probabilities for *A. maculatum* is much better, with relatively high approximations of power to detect declines that are induced by temporally changing colonization and extinction probabilities (Table 3, Scenario 2). Both the sampling frequency and the

number of sampled sites influence power approximates for this species, but the influence varies among change scenarios.

5. Discussion

Uncertainty and concern for biological systems throughout the world have resulted in a general call for baseline and monitoring information (e.g., Storfer, 2003). Reviews of existing monitoring programs suggest these programs could be more efficient and effective (Yoccoz et al., 2001; Nichols and Williams, 2006; Field et al., 2007). These criticisms are common, but published examples of monitoring programs that address these issues are uncommon (but see Nichols et al., 1995; Karanth et al., 2004). Here, we emphasize what we consider to be key components for a successful monitoring program: clearly defined objectives and a priori hypotheses, sampling methods that address spatial variation and detectability, and early analysis of data to allow adjustment of monitoring protocols or goals. Our objective was to examine factors likely to influence the distribution of a suite of amphibian species. We developed a series of a priori hypotheses regarding the factors likely to influence amphibian distributions, and designed a monitoring program that allows us to differentiate among our hypotheses. Biological and logistical criteria were considered and our design included carefully defining a sample frame within the area of interest. We then selected sample sites using a probabilistic method and sampled those sites in a manner that allowed us to estimate and adjust for detection probability differences across time, space and species.

Our focus on occupancy and its rate parameters (extinction and colonization) allowed us to sample a moderate proportion of the sample frame (∼20%) and investigate factors which may influence changes in amphibian population distributions in this region. Furthermore, important factors in the distribution of these species among wetland sites were revealed because we did not rely upon only naïve or implicit estimates of occupancy (MacKenzie et al., 2006). Specifically, we found that hydroperiod may be a limiting factor in the distribution of nearly all of the species, and may influence changes in amphibian population distributions. Hydroperiod is one of the primary wetland-level characteristics associated with amphibian presence and species richness (Skelly et al., 1999; Babbitt et al., 2003; Church, 2008). Our analyses indicate this pattern also holds for pond-breeding amphibians found in CHOH, and in all cases, the influence was positive. For example, A. maculatum had a higher probability of occupancy in wetlands with a sufficient hydroperiod for larval development (water through June; Petranka, 1998). Recall that occurrence of any life history phase is included in our analysis, thus non-permanent pools may be occupied by juvenile or adults of R. clamitans and R. catesbeiana, though these pools are unlikely to support reproduction. The hydroperiod of a wetland may vary due to environmental stochasticity or changes outside of the park which may not be under the control of park resource managers (e.g., watershed modifications or water diversion); however, at CHOH managers are able to control the canal water levels, which were observed to influence the hydroperiod of some of the sampled wetlands.

In addition to hydroperiod, wetland area and flooding potential also influenced occupancy probabilities for some species. This is the only study we know of that demonstrates the negative influence that flooding may have on the probability of occupancy for A. maculatum and R. sylvatica (but see observational evidence of Dorcas et al., 2006). Flooding by the Potomac River decreases occupancy probabilities for these species, which migrate to breeding ponds during the spring when flooding may occur, possibly washing out amphibian eggs, larvae or tadpoles, and disrupting migrating adults. The remaining covariates we explored influenced the occupancy probabilities for some species (e.g. percentage canopy cover for P. crucifer and R. clamitans), but the relationships were not consistent among species, nor were the relationships consistent with our a priori hypotheses.

Using only implicit estimates of occupancy would mask changes in the distribution of amphibian species among wetlands. Moreover, we found that detection probabilities varied within and among years, underscoring the importance of estimating and modeling detection probability to provide unbiased estimates of occupancy, colonization and extinction probabilities for each species. In the three years of wetland surveys there was a change in overall occupancy probabilities for most species; however Bufo spp., N. viridescens, and R. sylvatica had relatively constant estimates of occupancy (Table 5). All species experienced some annual turnover, indicating that the same sites are not occupied each year. Though most rate parameter estimates were constant over time (years) and space (among wetlands, Appendix B), there was one notable exception: local extinction probabilities for R. clamitans were lower for wetlands with longer hydroperiods. It is important to note that these results are based on only two estimates of the rate parameters, and future data may reveal more information on the factors influencing turnover in local wetland occupancy.

Although our monitoring program was primarily designed to address scientific questions regarding environmental factors believed to influence amphibian distributions, many management agencies want to use monitoring data to detect species declines. Thus, we evaluated the ability of our monitoring program to detect a specified level of change in distribution over a 5 year period, a realistic time period to evaluate expectations for this monitoring program. Our results indicate that the approximate power to detect a change in occupancy varied by species, the number of wetlands sampled, and the frequency of sampling. For example, for the more common species (A. maculatum) the power to detect a 50% decline in occupancy over five years was higher than for the less common species (N. viridescens). For species with a low occupancy probability, such as N. viridescens, our results and those of others (MacKenzie and Royle, 2005) suggest sampling designs that maximize the number of wetlands sampled to increase parameter precision and power. If rate parameters vary among years, as is evident for some species in our study (Table 4), an annual sampling frequency has tremendous advantage (Table 3). Under the current annual sampling frequency, it will be difficult to detect a "statistically significant" change in occupancy for rare species and it will likely require >5 years to 'detect' changes in amphibian distributions. These results highlight the limitations of the current sampling design and emphasize the need for long-term efforts or re-evaluation of monitoring

expectations. However, we reemphasize that if model assumptions are met, the estimates of change in occupancy for these species will be unbiased, but time-dependent occupancy models may not be the most parsimonious given the limited number of occupied wetlands and years of sampling.

Interestingly, our findings leave managers in a difficult dilemma should they decide that active management is required to conserve or maintain amphibian populations residing within park boundaries. The environmental factors that most influenced amphibian occupancy (hydroperiod, wetland area, and flooding potential) are the most difficult to control and variations in these factors are likely to increase under most climate change scenarios (e.g. Polsky et al., 2000). Factors that would be easier to manipulate (canopy cover and aquatic vegetation) appeared to have relatively little impact on occupancy probabilities in our system. Moreover, the current monitoring program may not be capable of detecting rather large declines in a short period of time, suggesting that managers should be leery of waiting until 'significant declines' are detected before initiating conservation efforts (Nichols and Williams, 2006). An alternative might be to consider and test possible management actions before species are imperiled, and base management decisions on desired management objectives by casting the problem in a decision making framework (Nichols and Williams, 2006). As shown here, monitoring plays a vital role in estimating the status of the system, and has a future role in discriminating among competing models representing the systems response to management actions (Nichols and Williams, 2006).

Appendix A

Occupancy structure of the candidate model set for each amphibian species. See Table 1 for covariate definitions. Primary factors are the covariates we expected to have a strong influence on the probability of occupancy for most species. Secondary factors are covariates that were hypothesized to have less influence on occupancy probabilities.

Species	Primary factors		Secondary factors			
	Hydroperiod	Area	Flood	Cond	Veg	Canopy
Ambystoma maculatum	x		x			
	x			x		
		x	x			
		x		x		
	x	x	x			
	x	x		x		
	x					
		x				
	x	x				
			x			
				x		
Bufo spp.						x[a]
			x			x[a]
				x		x[a]
			x			
				x		
Notophthalmus viridescens	x		x			
	x			x		
	x				x	
		x	x			
		x		x		
		x			x	
	x	x	x			
	x	x		x		
	x	x			x	
	x					
		x				
	x	x				

Appendix A– *continued*

Species	Primary factors		Secondary factors			
	Hydroperiod	Area	Flood	Cond	Veg	Canopy
			x			
				x		
					x	
Pseudacris crucifer	x		x			
	x			x		
	x				x	
	x					x
		x	x			
		x		x		
		x			x	
		x				x
	x	x	x			
	x	x		x		
	x	x			x	
	x	x				x
	x					
		x				
	x	x				
			x			
				x		
					x	
						x
Rana catesbeiana	x		x			
	x			x		
	x				x	
		x	x			
		x		x		
		x			x	
	x	x	x			
	x	x		x		
	x	x			x	
	x					
		x				
	x	x				
			x			
				x		
					x	
Rana clamitans	x		x			
	x			x		
	x				x	
	x					x
		x	x			
		x		x		
		x			x	
		x				x
	x	x	x			
	x	x		x		
	x	x			x	
		x				x
	x					
		x				
	x	x				
			x			
				x		
					x	
						x

Appendix A – *continued*

Species	Primary factors		Secondary factors			
	Hydroperiod	Area	Flood	Cond	Veg	Canopy
Rana palustris	x		x			
	x			x		
		x	x			
		x		x		
	x	x	x			
	x	x		x		
	x					
		x				
	x	x				
			x			
				x		
Rana sylvatica	x		x			
	x			x		
		x	x			
		x		x		
	x	x	x			
	x	x		x		
	x					
		x				
	x	x				
			x			
				x		

a For *Bufo* spp. Canopy was considered the primary factor.

Appendix B

Summary of model selection statistics for models (ΔAIC < 8) for amphibian data collected at Chesapeake and Ohio NHP wetlands from 2005–2007. ΔAIC is the difference in AIC value for a particular model when compared with the top ranked model; w is the AIC model weight; K is the number of parameters; $-2 l$ is twice the negative log-likelihood value. Refer to Table 1 for explanations of the covariates. Hydroperiod is abbreviated as Hydro in this table. The detection covariates are defined as: wtemp (water temperature/10(°C)), wtemp^2 ((water temperature/10)^2 (°C)), and visit + yr (sampling visit with an additive year effect). We indicate when colonization or extinction estimates were modeled as zero in the following manner: $\gamma 1 = 0$ where colonization between 2005 and 2006 equals zero and $\gamma 2 = 0$ where colonization between 2006 and 2007 equals zero.

Model	ΔAIC	w	K	$-2 l$	Occupancy						Extinction	Colonization
					Hydro	Area	Flood	Cond	Veg	Canopy	Hydro	Area
Ambystoma maculatum												
ψ(hydro, area, flood), $\gamma(\gamma 2 = 0)$, $\varepsilon(\varepsilon 1 = 0)$, p(visit + yr)	0.00	0.36	12	296.36	3.14	17.98	5.04					
ψ(hydro, flood), $\gamma(\gamma 2 = 0)$, $\varepsilon(\varepsilon 1 = 0)$, p(visit + yr)	0.45	0.29	11	298.81	3.02		3.95					
ψ(hydro, area, flood), $\gamma(\gamma 1 = \text{area}, \gamma 2 = 0)$, $\varepsilon(\varepsilon 1 = 0)$, p(visit + yr)	1.37	0.18	13	295.73	3.14	17.98	5.04					
ψ(hydro, flood), $\gamma(\gamma 1 = \text{area}, \gamma 2 = 0)$, $\varepsilon(\varepsilon 1 = 0)$, p(visit + yr)	1.82	0.15	12	298.18	3.02		3.95					−8.99
$\psi(.), \gamma(.), \varepsilon(.), p(.)$	57.5	0.00	4	369.9								
Model average estimate					3.08	17.98	4.56					−8.99
Unconditional SE					1.52	11.78	1.80					13.08
95% CI					(0.11, 6.05)	(−5.10, 41.07)	(1.04, 8.08)					(−34.63, 16.66)

Appendix B – *continued*

Model	ΔAIC	w	K	−2l	Occupancy						Extinction	Colonization
					Hydro	Area	Flood	Cond	Veg	Canopy	Hydro	Area
Bufo spp.												
$\psi(.)$, $\gamma(.)$, $\varepsilon(.)$, p(wtemp, wtemp^2)	0.00	0.37	6	331.14								
ψ(flood), $\gamma(.)$, $\varepsilon(.)$, p(wtemp, wtemp^2)	1.51	0.17	7	330.65			0.28					
ψ(canopy) $\gamma(.)$, $\varepsilon(.)$, p(wtemp, wtemp^2)	1.57	0.17	7	330.71						0.25		
ψ(cond), $\gamma(.)$, $\varepsilon(.)$, p(wtemp, zwtemp^2)	1.79	0.15	7	330.93				−0.21				
ψ(canopy, flood), $\gamma(.)$, $\varepsilon(.)$, p(wtemp, wtemp^2)	3.33	0.07	8	330.47			0.21			0.17		
ψ(canopy, cond), $\gamma(.)$, $\varepsilon(.)$, p(wtemp, wtemp^2)	3.53	0.06	8	330.67				−0.10		0.21		
$\psi(.)$, $\gamma(.)$, $\varepsilon(.)$, $p(.)$	3.94	0.05	4	339.08								
Model average estimate							0.26	−0.18		0.22		
Unconditional SE							0.44	0.47		0.39		
95% CI							(−0.60, 1.12)	(−1.10, 0.74)		(−0.55, 0.99)		
Notophthalmus viridescens												
ψ(Veg), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	0.00	0.49	5	184.00					2.88			
ψ(area, Veg), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	1.42	0.24	6	183.42		7.91			2.89			
ψ(hydro, area, cond), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	2.33	0.15	7	182.33	81.82	−1.01		−0.70				
$\psi(.)$, $\gamma(.)$, $\varepsilon(.)$, $p(.)$	5.18	0.04	4	191.18				−0.79				
ψ(cond), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	5.77	0.03	5	189.77								
ψ(area), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	6.44	0.02	5	190.44		7.10						
ψ(flood), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	6.78	0.02	5	190.78			0.26					
ψ(area, cond), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	6.98	0.01	6	188.98		8.28		−0.85				
ψ(area, flood), $\gamma(.)$, $\varepsilon(.)$, $p(.)$	7.75	0.01	6	189.75		8.82	0.36					
Model average estimate					81.82	4.80	0.30	−0.73	2.88			
Unconditional SE					2.49	10.82	0.41	0.80	1.23			
95% CI					(76.9, 86.7)	(−16.40, 26.00)	(−0.50, 1.10)	(−2.29, 0.83)	(0.47, 5.30)			
Pseudacris crucifer												
ψ(hydro, canopy), $\gamma(.)$, $\varepsilon(.)$, p(visit + yr)	0.00	0.42	11	189.94	3.44					3.83		
ψ(hydro, area, canopy), $\gamma(.)$, $\varepsilon(.)$, p(visit + yr)	1.50	0.20	12	189.44	3.35	7.57				4.39		
ψ(hydro, canopy), $\gamma(.)$, ε(hydro), p(visit + yr)	1.98	0.16	12	189.92	3.44					3.83	−0.43	
ψ(hydro, area, canopy), $\gamma(.)$, ε(hydro), p(visit + yr)	3.48	0.07	13	189.42	3.35	7.57				4.39	−0.43	
ψ(area, canopy), $\gamma(.)$, $\varepsilon(.)$, p(visit + yr)	5.52	0.03	11	195.46		14.21				4.06		
ψ(canopy), $\gamma(.)$, $\varepsilon(.)$, p(visit + yr)	5.67	0.02	10	197.61						3.04		
ψ(hydro, cond), $\gamma(.)$, $\varepsilon(.)$, p(visit + yr)	6.76	0.01	11	196.70	2.17			−2.11				
ψ(area, canopy), $\gamma(.)$, ε(hydro), p(visit + yr)	7.48	0.01	12	195.42		14.19				4.05	−0.46	
ψ(canopy), $\gamma(.)$, ε(hydro), p(visit + yr)	7.63	0.01	11	197.57						3.04	−0.47	

Appendix B – *continued*

Model	ΔAIC	w	K	$-2l$	Occupancy Hydro	Area	Flood	Cond	Veg	Canopy	Extinction Hydro	Colonization Area
$\psi(.)$, $\gamma(.)$, $\varepsilon(.)$, $p(.)$	56.7	0.00	4	260.66								
Model average estimate					3.39	8.35		−2.11		3.97	−0.43	
Unconditional SE					1.95	11.02		1.21		2.05	2.65	
95% CI					(−0.44, 7.22)	(−13.24, 29.94)		(−4.48, 0.26)		(−0.04, 7.99)	(−5.62, 4.75)	
Rana catesbeiana												
ψ(hydro, veg), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	0.00	0.30	8	343.99	2.45				−2.42			
ψ(hydro, veg), $\gamma(.)$, $\varepsilon(\varepsilon1 = $ hydro, $\varepsilon2 = 0)$, p(wtemp, wtemp^2)	1.05	0.18	9	343.04	2.37				−2.37		−4.10	
ψ(hydro, area, Veg), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	2.00	0.11	9	343.99	2.47	−0.40			−2.43			
ψ(hydro), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	2.54	0.08	7	348.53	1.61							
ψ(hydro, area, veg) $\gamma(.)$, $\varepsilon(\varepsilon1 = $ hydro, $\varepsilon2 = 0)$, p(wtemp, wtemp^2)	3.05	0.07	10	343.04	2.36	0.20			−2.36		−4.11	
ψ(hydro), $\gamma(.)$, $\varepsilon(\varepsilon1 = $ hydro, $\varepsilon2 = 0)$, p(wtemp, wtemp^2)	3.49	0.05	8	347.48	1.56						−5.58	
ψ(hydro, flood), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	3.64	0.05	8	347.63	1.57		−0.42					
ψ(hydro, area), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	4.44	0.03	8	348.43	1.49	3.03						
ψ(hydro, cond), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	4.54	0.03	8	348.53	1.61			0.00				
ψ(hydro, cond), $\gamma(.)$, $\varepsilon(\varepsilon1 = $ hydro, $\varepsilon2 = 0)$, p(wtemp, wtemp^2)	5.49	0.02	9	347.48	1.55			−0.02			−5.58	
ψ(hydro, area, flood), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	5.63	0.02	9	347.62	1.54	0.91	−0.41					
ψ(hydro, area, cond) $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	6.44	0.01	9	348.43	1.48	3.07		−0.02				
ψ(area), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	6.57	0.01	7	352.56		12.47						
ψ(flood), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	7.47	0.01	7	353.46			−0.51					
ψ(area, veg), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	7.56	0.01	8	351.55		13.49			−0.96			
ψ(veg), $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	7.82	0.01	7	353.81					−0.85			
ψ(area, flood) $\gamma(.)$, $\varepsilon(\varepsilon2 = 0)$, p(wtemp, wtemp^2)	7.94	0.01	8	351.93		11.06	−0.36					
ψ(veg), $\gamma(.)$, $\varepsilon(\varepsilon1 = $ hydro, $\varepsilon2 = 0)$, p(wtemp, wtemp^2)	7.97	0.01	8	351.96					−0.93		−5.17	
$\psi(.)$, $\gamma(.)$, $\varepsilon(.)$, p(.)	64.8	0.00	4	416.80								
Model average estimate					2.15	1.59	−0.42	−0.01	−2.36		−4.45	
Unconditional SE					1.07	11.02	0.51	0.58	1.30		9.59	
95% CI					(0.06, 4.24)	(−20.01, 23.19)	(−1.42, 0.57)	(−1.15, 1.12)	(−4.90, 0.18)		(−23.25, 14.36)	
Rana clamitans												
ψ(hydro, canopy), $\gamma(.)$, ε(hydro), p(wtemp, wtemp^2)	0.00	0.78	9	472.24	7.01					3.79	−2.48	
ψ(hydro, canopy), $\gamma(.)$, $\varepsilon(.)$, p(wtemp, wtemp^2)	2.61	0.21	8	476.85	7.01					3.79		
$\psi(.)$, $\gamma(.)$, $\varepsilon(.)$, p(.)	95.6	0.00	4	580.44								

Appendix B – *continued*

Model	ΔAIC	w	K	−2l	Occupancy						Extinction	Colonization
					Hydro	Area	Flood	Cond	Veg	Canopy	Hydro	Area
Model average estimate					7.01					3.79	−2.48	
Unconditional SE					3.39					1.82	1.27	
95% CI					(0.37, 13.65)					(0.23, 7.36)	(−4.96, 0.00)	
Rana palustris												
ψ(hydro, area, flood), γ(.), ε(.), p(wtemp, wtemp^2)	0.00	1.00	9	273.67	187.49	−0.97	4.25					
ψ(.), γ(.), ε(.), p(.)	21.88	0.00	4	305.55								
Model average estimate					187.49	−0.97	4.25					
Unconditional SE					2.12	17.11	2.10					
95% CI					(183.3, 191.6)	(−34.51, 32.56)	(0.13, 8.37)					
Rana sylvatica												
ψ(hydro, area, flood), γ(.), ε(.), p(visit + yr)	0.00	0.28	12	354.91	1.59	34.28	2.90					
ψ(hydro, area, cond), γ(.), ε(.), p(visit + yr)	1.48	0.13	12	356.39	0.98	19.33		−1.83				
ψ(area, cond), γ(.), ε(.), p(visit + yr)	1.86	0.11	11	358.77		26.68		−1.98				
ψ(hydro, area, flood), γ(.), ε(hydro), p(visit + yr)	1.93	0.11	13	354.84	1.57	33.87	2.86				−0.44	
ψ(area, flood), γ(.), ε(.), p(visit + yr)	2.46	0.08	11	359.37		36.48	1.65					
ψ(hydro, cond), γ(.), ε(.), p(visit + yr)	3.37	0.05	11	360.28	1.44			−1.40				
ψ(hydro, area, cond), γ(.), ε(hydro), p(visit + yr)	3.39	0.05	13	356.30	0.97	19.31		−1.83			−0.49	
ψ(area, cond), γ(.), ε(hydro), p(visit + yr)	3.72	0.04	12	358.63		26.53		−1.98			−0.59	
ψ(area, flood), γ(.), ε(hydro), p(visit + yr)	4.30	0.03	12	359.21		36.42	1.66				−0.60	
ψ(hydro, flood), γ(.), ε(.), p(visit + yr)	4.49	0.03	11	361.40	1.76		1.50					
ψ(hydro, cond), γ(.), ε(hydro), p(visit + yr)	5.27	0.02	12	360.18	1.43			−1.40			−0.50	
ψ(hydro, area), γ(.), ε(.), p(visit + yr)	5.92	0.01	11	362.83	0.94	17.64						
ψ(hydro, flood), γ(.), ε(hydro), p(visit + yr)	6.39	0.01	12	361.30	1.75		1.50				−0.49	
ψ(area), γ(.), ε(.), p(visit + yr)	6.84	0.01	10	365.75		25.77						
ψ(hydro), γ(.), ε(.), p(visit + yr)	7.07	0.01	10	365.98	1.39							
ψ(hydro, area), γ(.), ε(hydro), p(visit + yr)	7.82	0.01	12	362.73	0.94	17.63					−0.50	
ψ(.), γ(.), ε(.), p(.)	53.10	0.00	4	373.92								
Model average estimate					1.40	29.51	2.52	−1.81			−0.50	
Unconditional SE					1.00	19.75	2.03	0.96			1.41	
95% CI					(−0.56, 3.36)	(−9.20, 68.21)	(−1.46, 6.50)	(−3.69, 0.07)			(−3.26, 2.27)	

Note: *Rana palustris* was only detected in wetlands with an average hydroperiod >4.7.

for descriptive purposes only and does not imply endorsement by the US Government.

REFERENCES

Armstrong, D.P., 2005. Integrating the metapopulation and habitat paradigms for understanding broad-scale declines of species. Conservation Biology 19, 1402–1410.

Babbitt, K.J., Baber, M.J., Tarr, T.L., 2003. Patterns of larval amphibian distribution along a wetland hydroperiod gradient. Canadian Journal of Zoology 81, 1539–1552.

Bailey, L.L., Grant, E. H.C., Mattfeldt, S. D., 2006. Amphibian Monitoring Protocol Revision 1.2. National Park Service Technical Report.

Bailey, L.L., Hines, J.E., Nichols, J.D., MacKenzie, D.I., 2007. Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. Ecological Applications 17, 281–290.

Brooks, R.T., Hayashi, M., 2002. Depth-area-volume and hydroperiod relationships of ephemeral (vernal) forest pools in southern New England. Wetlands 22, 247–255.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. 2nd ed.. Springer-Verlag, New York, USA.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., Pollock, K.P., 1987. Design and analysis of methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph 5, 1–437.

Church, D.R., 2008. Role of current versus historical hydrology in amphibian species turnover within local pond communities. Copeia 1, 115–125.

Corn, P.S., Fogleman, J.C., 1984. Extinction of montane populations of the northern Leopard Frog (*Rana pipiens*) in Colorado. Journal of Herpetology 18, 147–152.

Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation 128, 231–240.

Danielsen, F., Mendoza, M.M., Alviola, P., Balete, D.S., Enghoff, M., Poulsen, M.K., Jensen, A.E., 2003a. Biodiversity monitoring in developing countries: what are we trying to achieve? Oryx 37, 407–409.

Danielsen, F., Mendoza, M.M., Tagtag, A., Alviola, P., Balete, D.S., Enghoff, M., Poulsen, M.K., Jensen, A.E., 2003b. On participatory biodiversity monitoring and its applicability – a reply to Yoccoz et al. and Rodríguez. Oryx 37, 412.

Devineau, O., Choquet, R., Lebreton, J., 2006. Planning capture–recapture studies: straightforward precision, bias, and power calculations. Wildlife Society Bulletin 34, 1028–1035.

Dorcas, M.E., Price, S.J., Vaughan, G.E., 2006. Amphibians and reptiles of the great falls bypassed reaches in South Carolina. Journal of the North Carolina Academy of Science 121, 1–9.

Egan, R.S., Paton, P.W.C., 2004. Within-pond parameters affecting oviposition by wood frogs and spotted salamanders. Wetlands 24, 1–13.

Fellers, G.M., Drost, C.A., 1993. Disappearance of the cascades frog *Rana cascadae* at the southern end of its range, California, USA. Biological Conservation 65, 177–181.

Field, S.A., O'Conner, P.J., Tyre, A.J., Possingham, H.P., 2007. Making monitoring meaningful. Austral Ecology 32, 485–491.

Gibbs, J.P., 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13, 263–268.

Glooschenko, V., Weller, W.F., Smith, P.G.R., Alvo, R., Archbold, J.H.G., 1992. Amphibian distribution with respect to pond water chemistry near Sudbury, Ontario. Canadian Journal of Fisheries and Aquatic Sciences 49 (Suppl. 1), 114–121.

Gill, D.E., 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs 48, 145–166.

Grant, E.H.C., Jung, R.E., Nichols, J.D., Hines, J.E., 2005. Double-observer approach to estimating egg mass abundance of pool-breeding amphibians. Wetlands Ecology and Management 13, 305–320.

Haddad, N.M., Baum, K.A., 1999. An experimental test of corridor effects on butterfly densities. Ecological Applications 9, 623–633.

Halliday, T., 2005. Diverse phenomena influencing amphibian population declines. In: Lannoo, Michael (Ed.), Amphibian Declines: The Conservation Status of United States Species. University of California Press, Berkeley, California, pp. 3–16.

Healy, W.R., 1975. Terrestrial activity and home range in efts of *Notophthalmus viridescens*. American Midland Naturalist 93, 131–138.

Hines, J.E., MacKenzie, D.I., 2004. PRESENCE, version 2.0. (<http://www.mbr-pwrc.usgs.gov/software.html>).

Karraker, N.E., Gibbs, J.P., Vonesh, J.R., 2008. Impacts of road deicing salt on the demography of vernal pool-breeding amphibians. Ecological Applications 18, 724–734.

Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., Hines, J.E., 2004. Tigers and their prey: predicting carnivore densities from prey abundance. Proceedings of the National Academy of Sciences of the United States of America 101, 4854–4858.

Kaushal, S.S., Groffman, P.M., Likens, G.E., Belt, K.T., Stack, W.P., Kelly, V.R., Band, L.E., Fisher, G.T., 2005. Increased salinization of fresh water in the Northeastern United States. Proceedings of the National Academy of Sciences of the United States of America 102, 13517–13520.

Kéry, M., Schmid, H., 2004. Monitoring programs need to take into account imperfect species detectability. Basic and Applied Ecology 5, 65–73.

Kopp, K., Wachlevski, M., Eterovick, P.C., 2006. Environmental complexity reduces tadpole predation by water bugs. Canadian Journal of Zoology 84, 136–140.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutsen, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84, 2200–2207.

MacKenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42, 1105–1114.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, New York, USA.

Manley, P.N., Zielinski, W.J., Schlesinger, M.D., Mori, S.R., 2004. Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. Ecological Applications 14, 296–310.

Mazerolle, M.J., Desrochers, A., Rochefort, L., 2005. Landscape characteristics influence pond occupancy by frogs after accounting for detectability. Ecological Applications 15, 824–834.

National Park Service, 2006. A Conceptual Basis for Natural Resource Monitoring. National Park Service Publication.

Nichols, J.D., Johnson, F.A., Williams, B.K., 1995. Managing North American waterfowl in the face of uncertainty. Annual Review of Ecology and Systematic 26, 177–199.

Nichols, J.D., Hines, J.E., Sauer, J.R., Fallon, F., Fallon, J., Heglund, P.J., 2000. A double-observer approach for estimating detection probability and abundance from avian point counts. Auk 117, 393–408.

Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. Trends in Ecology and Evolution 21, 668–673.

Olsen, A.R., Sedransk, J., Edwards, D., Gotway, C.A., Liggett, W., Rathbun, S., Reckhow, K.H., Young, L.J., 1999. Statistical issues for monitoring ecological and natural resources in the United States. Environmental Monitoring and Assessment 54, 1–45.

Petranka, J.W., 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC, USA.

Polsky, C., Allard, J., Currit, N., Yarnal, B., 2000. The Mid-Atlantic region and its climate: past, present, and future. Climate Research 14, 161–173.

Robbins, C.S., Bystrak, D., Geissler, P.H., 1986. The Breeding Bird Survey: Its First Fifteen Years, 1965–1979. U S Fish and Wildlife Service Resource Publication.

Rubbo, M.J., Kiesecker, J.M., 2005. Amphibian breeding distribution in an urbanized landscape. Conservation Biology 19, 504–511.

Sauer, J.R., Fallon, J.E., Johnson, R., 2003. Use of North American breeding bird survey data to estimate population change for bird conservation regions. The Journal of Wildlife Management 67, 372–389.

Schonewald-Cox, C., Buechner, M., 1992. Park protection and public roads. In: Fiedler, P., Jain, S. (Eds.), Conservation Biology: The Theory and Practice of Nature Conservation, Preservation and Management. Chapman and Hall, NY, USA, pp. 373–395.

Seale, D.B., 1982. Physical factors influencing oviposition by the wood frog, *Rana sylvatica*, in Pennsylvania. Copeia 1982, 627–635.

Shoop, C.R., 1974. Yearly variation in larval survival of *Ambystoma maculatum*. Ecology 55, 440–444.

Skelly, D.K., Werner, E.E., Cortwright, S.A., 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80, 2326–2337.

Snodgrass, J.W., Komoroski, M.J., Bryan, A.L., Burger, J., 2000. Relationship among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulation. Conservation Biology 14, 414–419.

Sredl, M.J., Collins, J.P., 1992. The interaction of predation, competition, and habitat complexity in structuring an amphibian community. Copeia 1992, 607–614.

Storfer, A., 2003. Amphibian declines: future directions. Diversity and Distributions 9, 151–163.

Stottlemyer, R., 1987. External threats to ecosystems of National Parks. Environmental Management 11, 87–89.

Taylor, A.R., Knight, R.L., 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological Applications 13, 951–963.

Turtle, S.L., 2000. Embryonic survivorship of spotted salamander (*Ambystoma maculatum*) in roadside and woodland vernal pools in southeastern New Hampshire. Journal of Herpetology 34, 60–67.

Van Buskirk, J., 2005. Local and landscape influence on amphibian occurrence and abundance. Ecology 86, 1936–1947.

Weber, D., Hintermann, U., Zangger, A., 2004. Scale and trends in species richness: considerations for monitoring biological diversity for political purposes. Global Ecology and Biogeography 13, 97–104.

Werner, E.E., Yurewicz, K.L., Skelly, D.K., Relyea, R.A., 2007. Turnover in an amphibian metacommunity: the role of local and regional factors. Oikos 116, 1713–1725.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, 120–139.

Whitehead, D.R., Jones, C.E., 1969. Small islands and the equilibrium theory of insular biogeography. Evolution 23, 171–179.

Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space and time. Trends in Ecology and Evolution 16, 446–453.