

Evaluating breeding and metamorph occupancy and vernal pool management effects for wood frogs using a hierarchical model

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Summary

1. World-wide declines in amphibian populations are often attributed to loss of habitat and exploitation; additionally, climate change may play an important role in future declines. Despite protection of habitat, amphibians relying on temporary habitats, such as vernal pools, may need active management to maintain their populations under forecasts of warming temperatures and more variable precipitation. However, few studies have examined the factors influencing where these species choose to breed (breeding occurrence) and the conditional likelihood of successful metamorphosis, while accounting for imperfect detection.

2. We developed an occupancy model and estimated parameters within a Bayesian framework to investigate the factors influencing probabilities of wood frog *Lithobates sylvatica* breeding and successful metamorphosis at Patuxent Research Refuge, Maryland, USA. Our objectives were to obtain estimates of breeding occurrence and metamorph occupancy and evaluate the success of current management actions.

3. The probabilities of wood frog breeding and successful metamorphosis varied by year and were positively related to the pond's typical hydroperiod length and annual precipitation. Contrary to our predictions, previous occupancy states had little effect on breeding and metamorph occupancy probabilities, which is likely to be due to high correlation of occupancy with hydroperiod length. Additionally, we did not observe a relationship between breeding occupancy probabilities and the spatial arrangement of pools. Although sample sizes were small, management actions resulted in an increase in both breeding and metamorph occupancy probabilities.

4. *Synthesis and applications.* We demonstrate that management actions targeting short-hydroperiod pools favourably influence both components of breeding success. However, continued monitoring is needed to determine whether managed pools remain suitable for wood frogs. With predicted changes in climate and a positive relationship between breeding occupancy and winter precipitation, a proactive focus on active management of vernal pools may provide a means to maintain wood frog populations in the future.

Key-words: Bayesian, habitat management, *Lithobates sylvatica*, presence, wetlands

Introduction

Declines in amphibian populations have been observed around the world in recent decades (Wake 1991; Stuart *et al.* 2004; Wake & Vredenburg 2008). Amphibians are now at greater peril than at any time in recent geological

history, with one-third of all amphibian species now considered threatened (Stuart *et al.* 2004). In the north-eastern region of the United States, climate change and continued urbanization are considered the primary threats to amphibian populations, especially those associated with seasonal or vernal pools (Calhoun & deMaynadier 2008).

With land development becoming an increasing threat to vernal pool habitat, federal lands may become isolated refuges of critical habitat for many amphibian species.

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Even in protected areas, climate change may reduce reproductive success, thereby jeopardizing the persistence of amphibian species that rely on vernal pools. The climate in the north-eastern United States has become warmer over the last 70 years, and droughts have become more frequent in the last two decades (Polsky *et al.* 2000). Climate models predict the warming trend to continue over the next century, with precipitation expected to become more variable (Polsky *et al.* 2000) and droughts more frequent (Burke, Brown & Christidis 2006; Meehl *et al.* 2007). These climate changes may result in vernal pools rarely holding water during the breeding season or having shortened hydroperiods. Pools with shorter hydroperiods could act as population sinks if adults lay eggs in pools containing water during the breeding season and the water evaporates before larvae are large enough to successfully metamorphose. If a large proportion of pools exhibit these characteristics and the frequency of reproductive failure increases, both local populations and metapopulations may be at risk for local extirpation.

Concerns about these potential declines have prompted several federal agencies in the North-east and Mid-Atlantic regions of the United States to begin programmes to locate and monitor vernal pools on protected lands (Van Meter, Bailey & Grant 2008). This research agrees with current literature suggesting that the distribution of many pond-breeding amphibian populations are dynamic and strongly dependent on the hydroperiod length of individual pools (Semlitsch, Scott & Pechmann 1988; Semlitsch & Wilbur 1988; Chelgren *et al.* 2006; Rothermel & Semlitsch 2006; Mattfeldt, Bailey & Grant 2009; Matthews *et al.* 2012; Zipkin, Grant & Fagan 2012). These habitats and the associated local amphibian population dynamics are related to environmental conditions (Berven 1990; Berven & Grudzien 1990; Church *et al.* 2007), which are likely to worsen in the future (Polsky *et al.* 2000).

The influence of pool- and habitat-specific factors on the abundance and occupancy of vernal pool amphibians is well studied (Pechmann *et al.* 2001; DiMauro & Hunter 2002; Petranka, Kennedy & Murray 2003; Petranka, Smith & Scott 2004; Vasconcelos & Calhoun 2006; Petranka *et al.* 2007). However, few have accounted for imperfect detection, potentially underestimating abundance, occupancy and/or the influence of certain variables on these metrics (but see Church 2008; Mattfeldt, Bailey & Grant 2009; Zipkin, Grant & Fagan 2012). Additionally, many studies cite precipitation as an important factor influencing breeding and successful metamorphosis of vernal pool amphibian species (e.g. Berven 1990; DiMauro & Hunter 2002; Calhoun *et al.* 2003; Baldwin, Calhoun & deMaynadier 2006; Petranka *et al.* 2007), yet none have explicitly tested the effects of precipitation on amphibian population or occupancy dynamics.

Warming temperatures and more variable precipitation associated with projected climate change may necessitate active management of vernal pools, but despite much research, there remains significant uncertainty in the

response of amphibian populations to manipulation or creation of these habitats (Pechmann *et al.* 2001; Lichko & Calhoun 2003; Vasconcelos & Calhoun 2006; Shoo *et al.* 2011). We chose to focus our study on the wood frog *Lithobates sylvatica* because it relies on small, temporary, predator-free vernal pools for breeding (Berven 1982, 1990; Hopey & Petranka 1994; Lichko & Calhoun 2003) and is widely spread across North America (Martof & Humphries 1959; Lannoo 2005). A short lifespan and propensity for annual breeding mean that changes in occupancy due to environmental changes and/or management actions should be readily apparent.

Occupancy models that account for imperfect detection (MacKenzie *et al.* 2002, 2003, 2006) are often used in metapopulation studies (Martin *et al.* 2009, 2010; MacKenzie *et al.* 2011) and large-scale monitoring programmes (e.g. Muths *et al.* 2005; O'Connell *et al.* 2006; Collier *et al.* 2010). These models have also been implemented within a hierarchical framework, which allows for the separation of the observation model and the ecological process model while including both sources of uncertainty in estimates of variance pertaining to parameters of interest (Royle & Kéry 2007; Royle & Dorazio 2008). In addition, many studies using occupancy models are interested both in the species occurrence at sampled sites (finite-sample occupancy) and in making inference to a larger study area (unconditional occupancy probability). While both maximum likelihood and Bayesian approaches yield estimates of unconditional occupancy probability, a Bayesian framework offers a straightforward way of estimating finite-sample occupancy and its associated precision (Royle & Kéry 2007). We developed an occupancy model within a Bayesian framework to investigate the factors influencing occupancy probabilities of wood frog breeding and successful metamorphosis at Patuxent Research Refuge (PRR), Maryland, USA. Our objectives were to obtain estimates of breeding and metamorphosis occupancy and evaluate the success of current management actions.

Materials and methods

OCCUPANCY SURVEYS

Patuxent Research Refuge covers 5,280 ha and is located in central Maryland, USA; approximately 75% of the refuge is deciduous forest. Vernal pools were located at PRR using a dual-frame sampling design (see Van Meter, Bailey & Grant 2008), which allowed investigators to locate pools from both an area and a list sample frame. The area frame includes all possible sampling units within the area of interest, while the list frame consists of sampling units with known locations. In the case of Van Meter, Bailey & Grant (2008), the locations of some vernal pools were obtained from aerial photographs (i.e. list frame), and the remainder were found by randomly sampling from the area frame. Up to four occupancy surveys were conducted each year consisting of visual encounter and dip net surveys. Two visual encounter surveys involving multiple independent observers were

used to detect egg masses in early spring (generally early March), and two dip net surveys were conducted in late May to early June to target late-stage tadpoles, which were assumed to indicate successful metamorphosis (Mattfeldt, Bailey & Grant 2009). Surveys were conducted at 53 vernal pools at PRR from 2006–2010.

Based on life-history knowledge for this species, we modelled wood frog breeding occupancy at time t as a function of the observed breeding occupancy state at time $t-1$ and the observed metamorph occupancy state at time $t-2$ (Berven 1990). Biologically, this structure acknowledges that breeding female wood frogs at time t likely represent surviving breeders from the previous year ($t-1$), first-time female breeders from the metamorph cohort at time $t-2$ or a mixture of both. Logistically, we are confident that the observed occupancy states represent the true occupancy status because of high detection probabilities for both life stages and multiple surveys (minimum overall detection probability, $p^* = 1 - (1 - p)^2 > 0.99$). To implement this higher-order Markov model, data from 2006–2007 were used as covariates, yielding breeding and metamorph occupancy estimates for 2008–2010 only.

Pool characteristics, such as hydroperiod length and spatial arrangement, were recorded for each pool. All surveyed pools were ephemeral, and hydroperiod length was determined by the average time of year when the pond usually dried: short-hydroperiod pools rarely retained water through early June, medium-hydroperiod pools retained water through early June in wet years, and long-hydroperiod pools retained water through early June in most years. In this region, wood frogs typically breed in late February to early March, and tadpoles metamorphose in late May to early June. Pools were categorized as either clustered or isolated: clusters of two to six pools generally included pools within 20 m of another, and isolated pools were >300 m from the nearest known pool. We also included precipitation data from the weather station in Laurel, Maryland, as covariates explaining variation in occupancy estimates. We modelled the probabilities of breeding occurrence and successful metamorphosis as a function of the average precipitation (cm) per month for the 5 months prior to egg laying (October–February; range: 6.41–11.54 cm month⁻¹) and the average precipitation per month for the 3 months during larval development (March–May; range: 10.71–14.91 cm month⁻¹), respectively.

Few short-hydroperiod pools supported breeding or retained water long enough for metamorphosis; therefore, we focused our management experiment on these pools. Four short-hydroperiod pools were managed after metamorphosis (July) in 2009 to test whether hydroperiod length could be extended to increase the probability of metamorphosis. We intended to lengthen the hydroperiod just enough to ensure successful metamorphosis but not so long as to create permanent pools, which could result in the colonization of predators, such as green frogs *Rana clamitans* or fish. Management consisted of installing an ethylene-propylene-diene monomer (EPDM) rubber liner to reduce water loss through seepage and evapotranspiration.

Wood frog populations have been shown to be positively correlated with deeper pools with long, yet still temporary, hydroperiods (Calhoun *et al.* 2003; Petranka, Kennedy & Murray 2003; Babbitt 2005; Baldwin, Calhoun & deMaynadier 2006). Therefore, we expected wood frog breeding occupancy rates to increase with hydroperiod length. Additionally, we expected breeding and metamorph occupancy rates to increase with precipitation, as more precipitation is likely to provide more

breeding habitat and extend hydroperiods through metamorphosis (Brooks 2004). Clustered pools were also expected to have higher breeding occupancy rates due to more potential sources of dispersing juvenile frogs from nearby pools, although isolated occupied pools tend to have larger breeding populations (Baldwin, Calhoun & deMaynadier 2006). Likewise, we predicted that metamorph occupancy rates would be positively related to hydroperiod length and higher following management because of the higher probability that those pools would retain water through metamorphosis.

STATISTICAL ANALYSIS

The observations from the occupancy surveys were summarized as the encounter histories y_{ij} , where y_{ij} is the number of occasions on which eggs or tadpoles were observed for pool/year combination i and stage j (eggs: $j = 1$, tadpoles: $j = 2$). We assumed that y_{ij} was distributed binomially when pool i was truly occupied by wood frogs in state j (i.e. $z_{ij} = 1$)

$$y_{ij} \sim \begin{cases} \text{Bin}(T_{ij}, p_j), & z_{ij} = 1 \\ 0, & z_{ij} = 0 \end{cases}, \quad \text{eqn 1}$$

where T_{ij} is the number of sampling occasions conducted at pool i during stage j , and p_j is the conditional, stage-specific detection probability. The true occupancy state for breeding wood frogs, z_{i1} , is described by

$$z_{i1} \sim \text{Bern}(\psi_{i1}), \quad \text{eqn 2}$$

where ψ_{i1} is the probability of wood frog breeding (i.e. egg masses). Because a pool can only be occupied by tadpoles if eggs are present, we modelled metamorph occupancy, ψ_{i2} , conditional on the site supporting breeding, as

$$z_{i2} \sim \begin{cases} \text{Bern}(\psi_{i2}), & z_{i1} = 1 \\ 0, & z_{i1} = 0 \end{cases}. \quad \text{eqn 3}$$

Both occupancy probabilities were thought to be functions of covariates relating to pool hydroperiod length (i.e. short, medium, long), precipitation and management action, and spatial arrangement (i.e. clustered, isolated) and previous occupancy states were considered for breeding occupancy ψ_{i1} only. Therefore, we deterministically modelled ψ_{ij} as a function of these covariates, such that

$$\text{logit}(\psi_{i1}) = \mathbf{x}'_{i1} \boldsymbol{\beta} \quad \text{eqn 4}$$

and

$$\text{logit}(\psi_{i2}) = \mathbf{x}'_{i2} \boldsymbol{\alpha}, \quad \text{eqn 5}$$

where \mathbf{x}'_{i1} and \mathbf{x}'_{i2} are covariate vectors, and $\boldsymbol{\beta}$ and $\boldsymbol{\alpha}$ are regression coefficient vectors.

We took a Bayesian approach to estimate model parameters using Markov Chain Monte Carlo (MCMC) simulation implemented in R statistical computing environment (R Development Core Team 2012; see Appendix S1 in Supporting Information). We obtained 50 000 MCMC samples and used a burn-in period of 25 000 iterations. We used vague prior distributions for all estimated parameters:

$$p_j \sim \text{Beta}(1, 1) \quad \text{eqn 6}$$

and

$$\alpha, \beta \sim \text{Norm}(0, 100). \quad \text{eqn 7}$$

Due to some non-conjugacy in the model specification, a hybrid MCMC algorithm was constructed using both Gibbs and Metropolis–Hastings updates (see Gelman & Hill 2007). Where conjugate full-conditional distributions were analytically tractable, they were calculated for p_j and z_{ij} , and Gibbs sampling was used. In this case, detection probabilities were sampled from a beta full-conditional distribution

$$p_j \sim \text{Beta}\left(\sum_{\text{all } z_{ij}=1} y_{ij} + \eta_{pj}, \sum_{\text{all } z_{ij}=1} (T_{ij} - y_{ij}) + \omega_{pj}\right), \quad \text{eqn 8}$$

where η_{pj} and ω_{pj} are the parameters from the prior distribution on p_j (i.e. $\eta_{pj} = \omega_{pj} = 1$). The true occupancy states, z_{ij} , for all sites where $y_{i1} = 0$ (with an ambiguous occupancy status) were sampled from a Bernoulli full-conditional distribution with probability $\tilde{\psi}_{ij}$, where

$$\tilde{\psi}_{i1} = \frac{(1 - p_1)^{T_{i1}} \psi_{i1} \psi_{i2}^{z_{i2}} (1 - \psi_{i2})^{1 - z_{i2}}}{(1 - p_1)^{T_{i1}} \psi_{i1} \psi_{i2}^{z_{i2}} (1 - \psi_{i2})^{1 - z_{i2}} + 1 - \psi_{i1}}, \quad \text{eqn 9}$$

and, for all sites where $z_{i1} = 1$ and $y_{i2} = 0$,

$$\tilde{\psi}_{i2} = \frac{(1 - p_2)^{T_{i2}} \psi_{i2}}{(1 - p_2)^{T_{i2}} \psi_{i2} + 1 - \psi_{i2}}. \quad \text{eqn 10}$$

In order to determine when the algorithm had converged, we used two chains and computed the Gelman–Rubin convergence statistic, which was <1.1 for all model parameters in our case (Gelman & Rubin 1992; Brooks & Gelman 1998). The Bayesian P -value for the model, based on the mean squared error ($P = 0.63$), did not indicate any lack of fit in terms of dispersion.

Results

The number of pools supporting wood frog breeding and metamorphosis (finite occupancy rates, $\psi^{(fs)}$; Royle & Kéry 2007) varied from year to year (Table 1), although there was little uncertainty pertaining to the annual estimates due to high detection probabilities (Tables 1 and 2). Breeding occupancy probability was highest in 2010 and lower in 2008 and 2009, showing a positive relationship with precipitation amounts (Fig. 1, Table 3), and the same pattern occurred with successful metamorphosis. Conditional metamorphosis occupancy rates were higher in 2008 and 2009, corresponding to higher amounts of spring precipitation (Fig. 2).

The probability a pool supported wood frog breeding increased with hydroperiod length (Table 3 and Fig. 1), and all long-hydroperiod pools supported breeding in every year. Contrary to our expectations, clustered pools had a lower breeding occupancy rate than isolated pools, although not significantly, and all managed pools

Table 1. Posterior means for the number of sampled vernal pools supporting wood frog breeding and successful metamorphosis (53 total sampled pools) and the finite occupancy rates ($\psi_j^{(fs)}$, where j is the life-history stage) at Patuxent Research Refuge, Maryland, USA. There was very little uncertainty in the credible intervals, and the upper and lower bounds were the same integer value as the mean. Therefore, we omitted the credible intervals around the mean from the table. This high precision was due to high detection probabilities ($p^* = 1 - (1 - p)^2 > 0.99$) resulting in essentially a census of vernal pool occupancy status

Year	Breeding		Metamorphosis	
	Mean	$\psi_1^{(fs)}$	Mean	$\psi_2^{(fs)}$
2008	14.0	0.264	9.0	0.170
2009	14.0	0.264	9.0	0.170
2010	26.0	0.491	7.0	0.132

Table 2. Posterior means and 95% credible intervals for detection probability of wood frog egg masses ($j = 1$) and late-stage tadpoles ($j = 2$) at Patuxent Research Refuge, Maryland, USA

Stage (j)	Mean	95% CI
Egg mass ($j = 1$)	0.945	(0.896, 0.980)
Late-stage tadpole ($j = 2$)	0.962	(0.897, 0.995)

supported breeding. The probability of metamorphosis also increased with hydroperiod length. Management actions successfully extended the hydroperiod length, such that approximately one of the four managed pools produced post-metamorphic wood frogs, resulting in $\tilde{\psi}_{i2}$ values intermediate to those of natural short- and medium-hydroperiod pools. Previous occupancy states had little influence on either occupancy probability (Table 3). We expected both covariates to have a positive influence on breeding probability, yet the 95% credible intervals of the coefficients for both breeding and metamorphosis occupancy in previous time steps included zero.

Discussion

While several studies provide a temporal snapshot of differences in counts of amphibians between natural and artificial or manipulated pools (Pechmann *et al.* 2001; DiMauro & Hunter 2002; Vasconcelos & Calhoun 2006), few studies have explicitly estimated occupancy rates for both breeding and successful metamorphosis in response to anthropogenic change over time (Petranka, Kennedy & Murray 2003; Petranka *et al.* 2007), and none have accounted for imperfect detection. We present estimates of the effect of precipitation on wood frog occupancy rates, and we provide some evidence of a positive effect of vernal pool management on breeding and late-stage tadpole occupancy probabilities, although our sample size is small and further research is needed.

The high annual variability in occupancy rates of wood frogs was not surprising, since complete reproductive failure

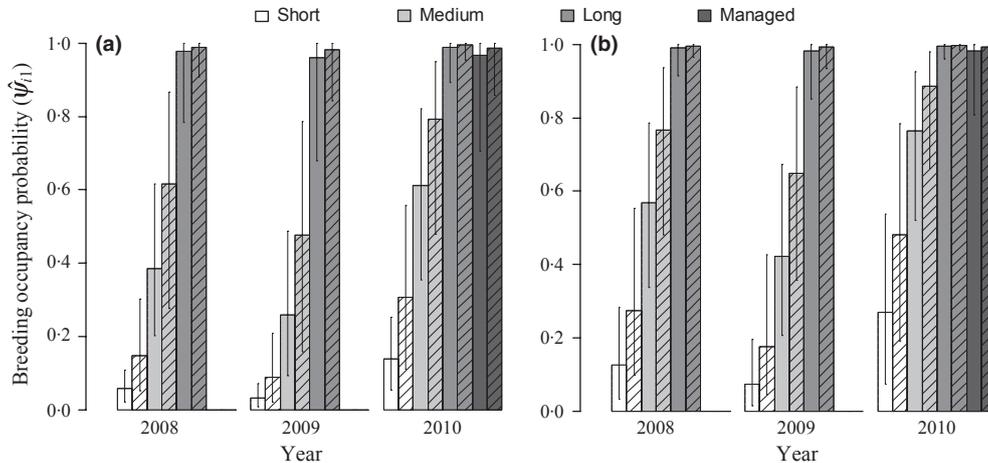


Fig. 1. Probability of occupancy for breeding wood frogs ($\hat{\psi}_{11}$) in vernal pools at Patuxent Research Refuge, Maryland, USA. Because metamorph occupancy status in $t-2$ had little effect on breeding occupancy probability, we report only the estimates of $\hat{\psi}_{11}$ for pools that supported breeding in $t-1$ (a) and those that did not support breeding in $t-1$ (b). Error bars represent 95% credible intervals, unhatched bars represent clustered pools, and hatched bars represent isolated pools. Management occurred in 2009 post-metamorphosis; therefore, estimates for managed pools are only available for 2010.

Table 3. Posterior means and 95% credible intervals for covariate coefficients explaining variation in occupancy probability of wood frog breeding ($j = 1$) and successful metamorphosis, given breeding occurred ($j = 2$), at Patuxent Research Refuge, Maryland, USA. The intercept represents a short-hydroperiod, isolated, unmanaged pool that did not support breeding in $t-1$ or metamorphosis in $t-2$

Stage (j)	Covariate	Coefficient mean	95% CI
Egg mass ($j = 1$)	Intercept	-4.46	(-6.99, -2.13)
	Medium hydroperiod	2.41	(1.31, 3.60)
	Long hydroperiod	10.61	(4.32, 23.54)
	Clustered	-1.05	(-2.22, 0.09)
	Winter precipitation*	0.31	(0.08, 0.55)
	Management	10.38	(2.61, 23.95)
	Breeding occupancy ($t-1$)	0.76	(-0.37, 1.86)
	Metamorph occupancy ($t-2$)	0.11	(-1.81, 2.11)
Late-stage tadpole ($j = 2$)	Intercept	-9.45	(-15.47, -3.97)
	Medium hydroperiod	3.26	(0.98, 6.18)
	Long hydroperiod	3.60	(1.32, 6.54)
	Spring precipitation†	0.51	(0.15, 0.91)
	Management	2.40	(-1.58, 6.13)

*Winter precipitation was measured as the mean amount (cm) of precipitation/month from the 5 months prior to breeding (i.e. October–February).

†Spring precipitation was measured as the mean amount (cm) of precipitation/month from the 3 months between breeding and metamorphosis (i.e. March–May).

at pools is not uncommon and can influence future breeding population sizes (Berven 1995), potentially resulting in local extinction. Annual variation in breeding and successful metamorphosis was most obvious in short- and medium-hydroperiod pools; pools with longer hydroperiods consistently support breeding, allow for successful metamorphosis and are likely to protect both the local population and metapopulation from extinction (Berven 1990, 1995; Berven & Grudzien 1990). Our results, and those from other studies (Berven 1990, 1995), provide evidence that the higher annual variability in the short- and medium-hydroperiod pools is a function of annual and seasonal variation in precipitation amounts, which may explain the negative correlation between $\hat{\psi}_{11}$ and $\hat{\psi}_{12}$

across years. Winter precipitation contributes to the abundance of suitable habitat available to breeding adults, but once eggs are laid, a pool’s hydrological characteristics together with spring precipitation influence the annual hydroperiod (Brooks 2004) and determine the probability tadpoles survive until metamorphosis.

Previous occupancy states did not have strong effects on breeding occupancy probabilities ($\hat{\psi}_{11}$), contrary to our prediction of positive influences. We believed that if a pool supported breeding in $t-1$, there was a higher probability that some females would return to breed in t . Similarly, we thought that pools that supported metamorphosis in $t-2$ would have higher breeding occupancy probabilities in t due to first-time breeding females

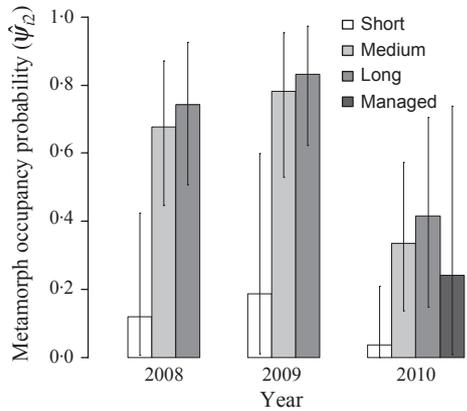


Fig. 2. Probability of occupancy for metamorphic (given breeding occurred) wood frogs ($\hat{\psi}_{12}$) in vernal pools at Patuxent Research Refuge, Maryland, USA. Error bars represent 95% credible intervals. Management occurred in 2009 post-metamorphosis; therefore, estimates for managed pools are only available for 2010.

(Berven 1990). The lack of influence of these covariates is likely due to high correlation between hydroperiod length and occupancy status. Short-hydroperiod pools rarely supported breeding, let alone metamorphosis, and the probability that a pool supported both increased with hydroperiod length. Similarly, Zipkin, Grant & Fagan (2012) found that a model including only habitat covariates, including hydroperiod length, performed as well as one including past occupancy states to predict amphibian occupancy. Therefore, we believe that much of the variation in occupancy probabilities was accounted for by including hydroperiod covariates in the model. We fit an *a posteriori* model without the hydroperiod covariate, which resulted in past occupancy states having a much greater influence on breeding occupancy probability.

Higher breeding occupancy probabilities ($\hat{\psi}_{11}$) in isolated pools were consistent with other studies that found larger populations at isolated pools (Calhoun *et al.* 2003; Petranks, Smith & Scott 2004; Baldwin, Calhoun & deMaynadier 2006), although the effect of the spatial arrangement in our study was not significant (Table 3). Isolated pools likely draw in more individuals because there are fewer nearby breeding sites, potentially increasing breeding occupancy probability.

High detection probabilities suggest that a census of wood frog breeding and metamorph occupancy may be possible at PRR, especially with ≥ 2 surveys for a given life stage (i.e. $p^* > 0.99$; Table 2). However, detection probabilities may not be as high in other systems (Church 2008; Mattfeldt, Bailey & Grant 2009), and an optimal survey design should be determined on a case-by-case basis. A census or methods that result in a very high detection probability result in little to no variance in finite occupancy estimates ($\hat{\psi}^{(fs)}$) because there is little uncertainty in the occupancy status of surveyed pools, and occupancy rates are not extrapolated to unsurveyed pools. The occupancy estimates reported in Figure 1 provide inference for

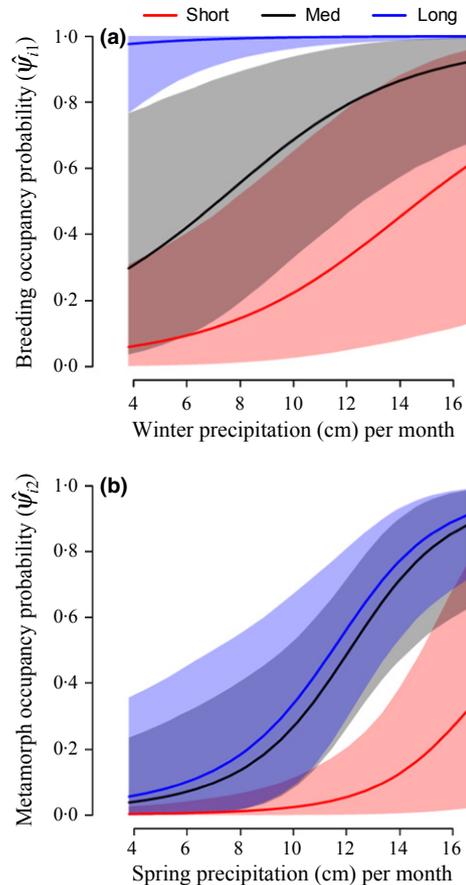


Fig. 3. The relationship between wood frog (a) breeding occupancy probability, $\hat{\psi}_{11}$, and average monthly winter precipitation (Oct–Feb) and (b) metamorph occupancy probability, $\hat{\psi}_{12}$, and average monthly spring precipitation (March–May) for vernal pools at Patuxent Research Refuge, Maryland, USA. We show breeding occupancy probability for unmanaged pools that supported breeding in $t-1$ and metamorphosis in $t-2$ and metamorph occupancy probabilities for unmanaged pools. Mean estimates are shown with heavy lines and their 95% credible intervals in shaded areas.

the entire population of pools at PRR (estimated to be 2,272 pools (SE=663); Van Meter, Bailey & Grant 2008) and have appropriately larger variances than the finite occupancy rates (Table 1). The sampled pools were randomly selected from the available pools at PRR, and therefore, the distribution of hydroperiod lengths among the sampled pools should be representative of all pools at PRR. The use of each occupancy metric ($\hat{\psi}$ and $\hat{\psi}^{(fs)}$) is dependent on the state variable of interest and associated management decisions.

The positive relationships between winter precipitation and breeding occupancy (Fig. 3a) and spring precipitation and metamorph occupancy (Fig. 3b) suggest that management may become necessary if future climate projections are realized. Temperatures are expected to increase and precipitation become more variable (Polsky *et al.* 2000), potentially leading to shorter hydroperiod lengths and increased probabilities of reproductive failure at some

sites. Management may increase the overall finite occupancy rate by increasing the breeding occupancy rate and, thus, have an effect on the reproductive success of wood frogs (Green, Bailey & Nichols 2011). Other species, such as spotted salamanders *Ambystoma maculatum* and Eastern spadefoot toads *Scaphiopus holbrookii*, also prefer vernal pools for breeding and may benefit from similar management strategies.

Our results provide some insight into potential increases in metamorph occupancy from the management of vernal pools; however, we only have 1 year of post-management data to include in our analysis and cannot determine whether any negative effects may occur in subsequent years (see Pechmann *et al.* 2001; Petranka, Kennedy & Murray 2003; Vasconcelos & Calhoun 2006). The goal of the management experiment was to increase the hydroperiod length of pools and, therefore, increase the probability of metamorphosis (ψ_{i2}) and the long-term probability of breeding (ψ_{i1}). Wood frogs utilized managed pools for breeding in the 1st year after management occurred, and the conditional probability of metamorphosis was comparable with unmanaged pools with longer hydroperiods, suggesting that deepening and installing liners in poorly performing pools may benefit overall occupancy rates. However, we observed the colonization and successful breeding by predators (i.e. green frogs) in managed pools at the beginning of the 2nd year after installing liners. Our management action may have inadvertently led to hydroperiods that are too long (permanent), and future data collection and analysis are necessary to assess the effects of this hydrological change on wood frog occupancy probabilities. Despite the possible permanency of the managed pools, we still believe that our approach has merit. There are many variables that determine hydroperiod length of vernal pools, including depth, canopy cover, soil characteristics and surrounding vegetation (Biebighauser 2007), and trial and error may be necessary to find the combination of factors resulting in the desired hydroperiod length.

Occupancy surveys are often used to determine the status of populations with multiple surveys occurring across a breeding season (Muths *et al.* 2005). Our model can easily be adopted by programmes that are already collecting detection data on various life-history stages to determine local influences on occupancy of these species, as well as informing the management of vernal pools. Our results suggest that some management actions may be useful for maintaining amphibian populations under future climate scenarios, and a formal adaptive management framework should be developed to incorporate these results into a decision policy for managers that includes other objectives (e.g. other species) and constraints (e.g. cost; Williams, Szaro & Shapiro 2007).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Description of the hierarchical Bayesian analysis.