DISSERTATION

MANAGING VERNAL POOL HABITATS ON FEDERAL LANDS: MAINTAINING OBLIGATE AMPHIBIAN SPECIES

Submitted by

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ABSTRACT

MANAGING VERNAL POOL HABITATS ON FEDERAL LANDS: MAINTAINING OBLIGATE AMPHIBIAN SPECIES

Substantial declines in global biodiversity have occurred over the past century, with the current amphibian crisis being arguably the most visible conservation issue in the past two decades. Amphibians are now at greater peril than at any time in recent geological history, with one-third of all amphibian species now considered threatened. Despite the severity and multitude of threats that amphibians face, they remain among the least studied vertebrate taxa, both globally and within the U.S. While many questions remain as to why some amphibian populations continue to decline, even more uncertainty exists about what management strategies should be implemented to reverse, halt, or prevent future declining trends. Additionally, there are many studies investigating the influences of variables on larval growth and survival, but few have examined the impacts of these conditions on post-metamorphic performance, despite acknowledging the importance of these life history stages on population growth. My dissertation focused on a metapopulation of wood frogs (Lithobates sylvatica) and addressed several ecological and management objectives. First, I developed sensitivity metrics to determine the parameters that are most influential on successful wood frog reproduction (metamorphosis). I then developed a dynamic occupancy model to investigate the variables that influence breeding and successful metamorphosis probabilities of wood frogs. I used the resulting parameter estimates from that analysis to define ecological thresholds that could be used to guide management decisions. Finally, I investigate the influence of natal pool characteristics and larval traits on juvenile survival, dispersal, age-specific breeding probabilities of wood frogs, as well as the variables influencing adult survival, using multistate mark-recapture models.

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My objective in Chapter 1 was to develop equilibrium occupancy expressions and their associated sensitivity metrics for dynamic multistate occupancy models. Recently, multistate occupancy models have been developed to investigate dynamic systems involving more than one occupied state, including reproductive states, relative abundance states and joint habitatoccupancy states. However, the influence of transition rates on the relative distribution among occupancy states at equilibrium had not been examined (but see Miller 2012). To illustrate my approach I used two examples that represent common multistate occupancy systems. The first example involves a three-state dynamic model involving occupied states with and without successful reproduction (California spotted owl) and the second involves a novel way of using a multistate occupancy approach to accommodate second-order Markov processes (wood frog breeding and metamorphosis). I found that when equilibrium occupancy rates are low, sensitivity to parameters related to colonization is high, while sensitivity to persistence parameters is greater when equilibrium occupancy rates are high. Sensitivities can also provide guidance for managers when estimates of transition probabilities are not available. Because management will typically invoke changes in the transition rates, sensitivity analyses can provide valuable information about the potential influence of different actions and when it may be prudent to shift the focus of management among the various dynamic rates.

The next portion of my dissertation focused on developing a framework for determining optimal management decisions for a metapopulation of wood frogs. First, in Chapter 2, I developed an occupancy model within a Bayesian framework to investigate the factors influencing probabilities of wood frog breeding and successful metamorphosis. I applied this model to a wood frog metapopulation at Patuxent Research Refuge, Maryland, USA, to evaluate the success of current management actions. Importantly, the resulting posterior probability

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distributions from this analysis can be used to predict metapopulation viability and ecological thresholds and estimate the occupancy of sampled pools in response to management. I found that 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 my predictions, previous occupancy states had little effect on breeding and metamorph occupancy probabilities, which is likely due to high correlation of occupancy with hydroperiod length. Additionally, I did not observe a relationship between breeding occupancy probabilities and the spatial arrangement of pools. Though sample sizes were small, management actions targeting short-hydroperiod pools favorably influence both breeding and metamorph occupancy probabilities. Still, 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 into the future.

In Chapter 3, I use the results from Chapter 2 to perform population viability analyses (PVA) using a dynamic occupancy model to evaluate potential ecological thresholds for two wood frog metapopulations that represent two extremes of population size and health – one population is large and stable, while the other is small and declining. I then discuss how these ecological thresholds could be incorporated into an adaptive resource management framework. I projected wood frog populations for scenarios involving different numbers of pools using occupancy estimates of breeding and successful metamorphosis from two different study areas to evaluate the probability of quasi-extinction and the proportion of vernal pools producing metamorphs. Results from PVAs were similar for both study areas, suggesting that \geq 50 pools are required to ensure long-term persistence with approximately 16% of pools producing

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metamorphs in stable populations. I demonstrate one way to incorporate the results of the PVA into a utility function that balances the trade-offs between ecological and financial objectives, which can be used within an adaptive resource management framework for making optimal, transparent decisions. My approach provides a framework for using a standard method (i.e., PVA) and available information to inform a formal decision process in order to determine optimal and timely management policies.

My final chapter shifts from landscape-level inquiry to factors influencing local, population-level demographics. Many studies have investigated the factors influencing growth and survival of amphibian larval stages and assumed that certain characteristics result in longterm advantages in survival and breeding. Unfortunately, few studies have investigated whether these characteristics actually influence the post-metamorphic vital rates that most influence population growth rates. In Chapter 4, I used multistate mark-recapture models to investigate the influences of natal-pool and metamorph characteristics on wood frog population dynamics at Patuxent National Research Refuge, Maryland, USA. Estimates of annual juvenile apparent survival among ponds ranged from 0.01 (SE = 0.05) to 0.48 (SE = 0.07) and were negatively related to conductivity within natal pools. Apparent survival probabilities for adults during the non-breeding season (mid-March-mid-February) were similar but less variable (range: 0.20 -0.45); survival probabilities were lower for females and negatively related to mean monthly precipitation during the same period. Survival of adults during the breeding season was generally very high, and most estimates were near 1.0. Estimates of recruitment and dispersal probabilities indicated that males mature earlier than females, and a small percentage of each sex disperses to breed at ponds other than their natal pool. Using modern analytical methods, I provide the first robust estimates of post-metamorphic vital rates of wood frogs that allow for variation in capture

probabilities across time and space. I found little evidence for an effect of traits of recent metamorphs on juvenile survival, suggesting that wood frogs may be able to overcome initial disadvantages to have similar post-metamorphic performance. My results, combined with the large collection of knowledge on pre-metamorphic vital rates, provide a more complete picture of factors influencing wood frog population dynamics.

My dissertation provides information on little studied components of the wood frog life history and population dynamics at both the landscape and local population levels. I provide the first estimates of breeding and successful metamorphosis occupancy probabilities and the factors influencing them through the use of occupancy models. I found that precipitation and hydroperiod had positive effects on both the probability of breeding and successful metamorphosis, suggesting that future changes in climate may have detrimental impacts on wood frog occupancy rates. I also provide the first robust estimates of post-metamorphic survival, dispersal, and breeding probabilities for a wild wood frog population. I identify important factors influencing these parameters and provide evidence to support more recent hypotheses that natal pool characteristics may not have as large an effect on post-metamorphic survival as previously thought. In addition to addressing some shortcomings and gaps in previous research on amphibian populations, I provide evidence for the positive effects of one management action on wood frog occupancy rates. There is a great amount of uncertainty about how climate change may affect pond-breeding amphibians, but I describe a framework to guide management decisions that may mitigate these potential effects while allowing for the incorporation of new information as it is collected.

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CHAPTER 1: EXPLORING SENSITIVITY OF A MULTISTATE OCCUPANCY MODEL TO INFORM MANAGEMENT DECISIONS¹

Dynamic occupancy models are often used to investigate questions regarding the processes that influence patch occupancy and are prominent in the fields of population and community ecology and conservation biology. Recently, multistate occupancy models have been developed to investigate dynamic systems involving more than one occupied state, including reproductive states, relative abundance states and joint habitat-occupancy states. Despite the increased interest in multistate occupancy models, sensitivities of the equilibrium state distribution to changes in transition rates have not been examined.

I developed equilibrium occupancy expressions and their associated sensitivity metrics for dynamic multistate occupancy models. To illustrate my approach I used two examples that represent common multistate occupancy systems. The first example involves a three-state dynamic model involving occupied states with and without successful reproduction (California spotted owl *Strix occidentalis occidentalis*) and the second involves a novel way of using a multistate occupancy approach to accommodate second-order Markov processes (wood frog *Lithobates sylvatica* breeding and metamorphosis).

In many ways, multistate sensitivity metrics behave in similar ways as standard occupancy sensitivities. When equilibrium occupancy rates are low, sensitivity to parameters related to colonization is high, while sensitivity to persistence parameters is greater when equilibrium occupancy rates are high. Sensitivities can also provide guidance for managers when estimates of transition probabilities are not available.

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Multistate models provide practitioners a flexible framework to define multiple, distinct occupied states and the ability to choose which state, or combination of states, is most relevant to questions and decisions about their own systems. In addition to standard multistate occupancy models, I provide an example of how a second-order Markov process can be modified to fit a multistate framework. Assuming the system is near equilibrium, my sensitivity analyses illustrate how to investigate the sensitivity of the system-specific equilibrium state(s) to dynamic transition rates. Because management will typically act on these transition rates, sensitivity analyses can provide valuable information about the potential influence of different actions and when it may be prudent to shift the focus of management among the various dynamic rates.

INTRODUCTION

Occupancy models are often used to investigate questions regarding the processes that influence patch occupancy dynamics and are prominent in the fields of population and community ecology and conservation biology (Simberloff 1969, Hanski 1999, Moilanen 1999, Amarasekare and Possingham 2001, Hill et al. 2004). The development of statistical inference methods that permit estimation of parameters for these models while accounting for imperfect detectability (MacKenzie et al. 2002, MacKenzie et al. 2003, MacKenzie et al. 2006) has led to increased use of patch occupancy models in metapopulation studies (Martin et al. 2009a, Martin et al. 2010, MacKenzie et al. 2012) and large-scale monitoring programs (e.g. Muths et al. 2005, O'Connell et al. 2006, Collier et al. 2010).

Most applications of occupancy models focus on presence/absence of a species and the dynamic processes influencing the occupancy status of patches over time. Occupancy dynamics are described through a first-order Markov process, in which the probability a patch is occupied

by a target species at time t is dependent on the state of the patch in time t-1 (MacKenzie et al. 2006, Martin et al. 2009b):

$$\psi_t = \psi_{t-1} \times 1 - \epsilon_{t-1} + 1 - \psi_{t-1} \times \gamma_{t-1},$$
 eqn 1

where ψ_t represents the probability a patch is occupied at time *t* and ϵ_{t-1} and γ_{t-1} are conditional, time-specific probabilities of local extinction and colonization, respectively. This model can also be written in matrix form (MacKenzie et al. 2006; Martin et al. 2009b):

$$\Pi_t = \Phi_{t-1} \Pi_{t-1}, \qquad \text{eqn } 2$$

where

$$\Pi_{t-1} = \begin{array}{c} \psi_{t-1} \\ 1 - \psi_{t-1} \end{array}$$

and

$$\Phi_{t-1} = \begin{array}{cc} 1 - \epsilon_{t-1} & \gamma_{t-1} \\ \epsilon_{t-1} & 1 - \gamma_{t-1} \end{array}$$

The matrix Φ_{t-1} is a transition probability matrix, with elements representing the probabilities of patches remaining within a state from *t*-1 to *t* or transitioning to the other state. The transition probability of row *m* and column *n* corresponds to the probability that a patch will be in state *m* in *t* given it was in state *n* at *t*-1; states correspond to rows in the state vector, Π_{t-1} . For example, a patch that is unoccupied at *t*-1 (i.e. row 2 in Π_{t-1}), will become occupied in *t* with the probability γ_{t-1} (i.e. row 1, column 2 in Φ_{t-1}). Written in matrix form, Martin et al. (2009b) noted the clear parallels with population projection matrices for which sensitivity or elasticity is commonly evaluated (e.g. Crouse et al. 1987, Brault and Caswell 1993, Doak et al. 1994, Heppell et al. 1994).

More recently, dynamic occupancy models have been developed to allow for multiple occupancy states and account for imperfect detection and state misclassification (Nichols et al. 2007, MacKenzie et al. 2009). Multistate occupancy models are versatile and have been applied to dynamic systems involving reproductive states, relative abundance states and joint habitatoccupancy states (MacKenzie et al. 2009, Martin et al. 2010). Changes in occupancy states are modelled using first-order Markov transition rates. If these transition rates are constant over time, the system will reach a stable-state equilibrium distribution (Caswell 2001, Martin et al. 2009b). The equilibrium state distribution (Π^*) can be calculated as the eigenvector associated with the dominant eigenvalue of Φ , with the eigenvector elements scaled to sum to 1.0 (Caswell 2001). It is natural to profess interest in the sensitivity of elements of this stable state distribution to changes in system transition rates (Martin et al. 2009b), just as many investigators have noted the utility of sensitivity analyses for the study of population and community dynamics (de Kroon et al. 1986, Heppell et al. 2000, Caswell 2001, Hill et al. 2004), yet the sensitivities of multistate occupancy models have not been examined.

In this paper, I give two general examples of dynamic multistate occupancy models. The first example represents a common case where occupied sites are separated into those with and without successful reproduction. I use published estimates of transition rates associated with occupancy and reproduction for California spotted owl *Strix occidentalis occidentalis* surveys to examine the sensitivity of the probability of successful reproduction to each of the transition probabilities. The second example describes a novel approach for systems that are best described as second-order Markov processes, which may be especially useful for species with unobservable life history stages. Here, I develop a model describing the dynamics of wood frog *Lithobates sylvatica* aquatic life history stages at Patuxent National Research Refuge, Maryland, USA. In both examples, I clearly define an expression for equilibrium occupancy and explore the

sensitivities of equilibrium occupancy to each parameter in the transition probability matrix, Φ , and discuss implications for management decisions.

METHODS

Generally, state parameter distributions are functions of the transition probabilities represented as elements of the transition matrix, Φ (see eqn 2 and examples below). In each of my multistate examples, my first step in examining sensitivities for the state parameters was to derive expressions for each in terms of the transition probabilities. For a given transition probability matrix Φ , the eigenvector (*w*, elements scaled to sum to 1) associated with the dominant eigenvalue (λ) represents the stable state distribution and is defined by the following equation,

$$\Phi w = \lambda w \qquad \qquad \text{eqn } 3$$

(Caswell 2001, Hill et al. 2004). For stochastic matrices in which elements (transition probabilities) in each column (or row) sum to 1, the dominant eigenvalue (λ) will be 1 (Caswell 2001) and $\Phi w = \lambda w$. By multiplying Φ by *w* and setting the product equal to *w*, the elements of the stable state distribution vector can be written in terms of the lower level parameters that define the transition matrix elements. Sensitivity expressions are then derived for each lower level parameter (see specific expressions in examples below) by first identifying the equilibrium state of interest and then taking the partial derivative of this quantity with respect to the focal lower level transition parameter.

EXAMPLE 1: CALIFORNIA SPOTTED OWLS

The California spotted owl, one of three subspecies of spotted owl, occurs entirely within California and northern Baja California, Mexico (Franklin et al. 2004). Concern over the limited range of the species has led to several studies investigating factors influencing demographics and dynamics (Seamans et al. 2001, Franklin et al. 2004, Seamans 2005). Multistate occupancy models have been applied to assess occurrence and reproductive success at established owl territories in the Sierra Nevada, California (Nichols et al. 2007, MacKenzie et al. 2009, MacKenzie et al. 2012). Here I use estimates based on the fieldwork of R.J. Gutiérrez and M.E. Seamans and published by MacKenzie et al. (2009) to parameterize the transition matrix in the model presented below.

Model development

The California spotted owl system includes three occupancy states including territory sites that are: unoccupied (state=0), occupied without reproduction (state=1) and occupied with reproduction (state=2). MacKenzie et al. (2009) expanded the standard dynamic occupancy model (equation 2) to include these three states. The probability a territory is in state *m* at time *t* is given by $\pi_t^{[m]}$ and $\pi_t^{[0]} = 1 - \pi_t^{-1} - \pi_t^{[2]}$. The probability of a territory (site) being occupied at time *t*, given that it was in state *m* at time *t*-1, is given by $\phi_t^{[m]}$. Conditional on occupancy at time *t*, $R_t^{[m]}$, is the probability of successful reproduction at the territory (state 2), given it was in state *m* at time *t*-1. The probability of a territory supporting successful reproduction in year *t*, given that it was in state *m* in year *t*-1, is the product, $\phi_t^{[m]} \times R_t^{[m]}$, given the territory was in state *m* at time *t*-1 (MacKenzie et al. 2009). It is important to note that these $\phi_t^{[m]}$ parameters are equivalent to $\psi_t^{[m]}$ described by MacKenzie et al. (2009).

The model can be written in the same matrix form as equation 2, where

$$\Pi_t = 1 - \pi_t^{1} - \pi_t^{2} \pi_t^{1} \pi_t^{2},$$

where T denotes the transpose of a vector, and

$$\Phi = \begin{array}{ccc} 1 - \phi^{0} & 1 - \phi^{1} & 1 - \phi^{2} \\ \phi^{0} (1 - R^{0}) & \phi^{1} (1 - R^{1}) & \phi^{2} (1 - R^{2}) \\ \phi^{0} R^{0} & \phi^{1} R^{1} & \phi^{2} R^{2} \end{array}$$

Assuming constant transition rates, the system will eventually reach equilibrium where $\Pi_t = \Pi_{t-1}$.

Sensitivity expressions

Using the general approach described in the first paragraph of the Methods section, I defined expressions for equilibrium state parameters (π^{m}) as functions of the lower level transition parameters:

$$\pi^{0} = 1 - \pi^{1} - \pi^{2} = \frac{1 - \phi^{1} + R^{1} \phi^{1} - \phi^{1} \phi^{2} + \phi^{2} R^{2} (\phi^{1} - 1)}{D}$$
 eqn 4

$$\pi^{1} = \frac{\phi^{0} - \phi^{0} \phi^{2} R^{2} - R^{0} (\phi^{0} - \phi^{0} \phi^{2})}{D}$$
 eqn 5

$$\pi^{2} = \frac{\phi^{0} \phi^{1} R^{1} + R^{0} (\phi^{0} - \phi^{0} \phi^{1})}{D}, \qquad \text{eqn 6}$$

where $D = 1 + \phi^{0} - \phi^{1} + R^{0} \phi^{0} \phi^{2} - \phi^{0} \phi^{1} + R^{1} \phi^{1} 1 + \phi^{0} - \phi^{1} \phi^{2} + R^{2} \phi^{2} (\phi^{1} - \phi^{0} - 1).$

In the California spotted owl multistate system, the probability a territory is occupied and supports reproduction (i.e., π^2) may be of most interest to managers. Sensitivities of π^2 * (i.e. defined as equilibrium probability of occupancy with reproduction) to small changes in each parameter of interest, 6 (6 is simply a parameter used to define a lower level parameter), describe how π^2 * changes as θ changes, in cases where the perturbations preserve the column sums of Φ (true in my case because all matrix elements were written as functions of conditional binomial parameters). Sensitivities are computed as the partial derivative of π^{2*} with respect to θ ($s_{\theta} = \partial \pi^{2*} / \partial \theta$; Caswell 2001, Martin et al. 2009b). The sensitivities of π^{2*} given in equation 6 to each of the six parameters defining Φ are given by the equations:

$$s_{\phi^{0}} = \frac{\phi^{1} R^{[1]} + R^{0} 1 - \phi^{1}}{D}$$
 eqn 7

$$\frac{1+R^{0} \phi^{2} - \phi^{1} + \phi^{1} R^{1} - \phi^{2} R^{2} \times \phi^{0} R^{0} 1 - \phi^{1} + \phi^{0} \phi^{1} R^{1}}{D^{2}}$$

$$s_{R^{0}} = \frac{\phi^{0}(1-\phi^{0})}{D} - \frac{\phi^{0}\phi^{2}-\phi^{1}\times\phi^{0}\phi^{1}R^{1}+\phi^{0}R^{0}1-\phi^{1}}{D^{2}}$$
eqn 8

$$s_{\phi^{1}} = \frac{\phi^{0} R^{1} - R^{0}}{D}$$
 eqn 9

$$-\frac{\phi^{0} \phi^{1} R^{1} + R^{0} 1 - \phi^{1} \times \phi^{2} R^{2} + R^{1} 1 + \phi^{0} - \phi^{2} - \phi^{0} R^{0} - 1}{D^{2}}$$

$$s_{R^{1}} = \frac{\phi^{0} \phi^{1}}{D} - \frac{\phi^{0} \phi^{1} + \phi^{0} - \phi^{2} \times \phi^{1} R^{1} + R^{0} + 1 - \phi^{1}}{D^{2}}$$
eqn 10

$$s_{\phi^{2}} = \frac{-\phi^{0} \phi^{1} R^{1} + R^{0} 1 - \phi^{1} \times \phi^{0} R^{0} - \phi^{1} R^{1} + R^{2} \phi^{1} - \phi^{0} - 1}{D^{2}}$$
eqn 11

$$s_{R^{2}} = \frac{-\phi^{0} \phi^{2} \phi^{1} - \phi^{0} - 1 \times \phi^{1} R^{1} + R^{0} 1 - \phi^{1}}{D^{2}}$$
 eqn 12

Model parameterization

I used the parameter estimates of MacKenzie et al. (2009) for the above model and examined the sensitivity of π^{2*} to changes in each of the six lower level transition parameters. Sensitivity analysis and equilibrium occupancy distributions rely on the premise of time-constant transition probabilities but the best fitting model for the California spotted owl data suggested that conditional probabilities of reproduction varied among years, R_t^m (MacKenzie et al. 2009). Still, I believe the concepts of equilibrium states and associated sensitivities are relevant even when a stationary Markov process does not exist (see similar arguments in Caswell 2001, Martin et al. 2009b). Accordingly, I used the time-constant parameter estimates for occupancy, ϕ^m , and averaged the year-specific estimates of conditional reproduction parameters to obtain the following parameter estimates for my analysis (see Fig. 1 in MacKenzie et al. 2009): $\phi^{0} = 0.17$ (95% CI = 0.11, 0.26), $\phi^{1} = 0.87$ (0.79, 0.92), $\phi^{2} = 0.91$ (0.83, 0.95), $R^{0} = 0.13$ (range = 0.00, 0.93), $R^{1} = 0.51$ (range = 0.05, 0.85), $R^{2} = 0.50$ (range = 0.15, 0.78). Using these parameter estimates as starting values, I systematically varied each parameter individually between zero and one, while holding the other five parameters constant and calculated the sensitivities of π^{2*} using equations 7-12 for each combination of parameter values. *Results*

The equilibrium distribution of occupancy states using the transition rate estimates reported in MacKenzie et al. (2009) was $\pi^* = [0.396 \ 0.324 \ 0.280]$, suggesting that at equilibrium ~ 60% of owl territories were occupied ($\pi^{[1]*} + \pi^{[2]*}$) and 28% supported successful reproduction ($\pi^{[2]*}$). The equilibrium probability that a territory is occupied and supports reproduction, $\pi^{[2]*}$, was most sensitive to changes in the ϕ^m parameters, with $s_{\phi^{-1}} = 0.666$, $s_{\phi^{-0}} = 0.652$ and $s_{\phi^{-2}} = 0.572$, and was less sensitive to changes in the conditional reproduction rates (Figs. 1.1 and 1.2). Intuitively, at low colonization rates ($\phi^{-0} = 0.17$) I would expect $\pi^{[2]*}$ to be most sensitive to ϕ^{-0} because there are more unoccupied patches ($\pi^{[0]*} = 0.396$) for ϕ^{-0} to act upon. If colonization rates remain low, $\pi^{[2]*}$ is relatively insensitive to variation in R^{-0} because few unoccupied territories are colonized. Because the probability of local extinction is low (($1 - \phi^{-1}$) = 0.13, ($1 - \phi^{-2}$) = 0.09), $\pi^{[2]*}$ is more sensitive to R^{-1} and R^{-2} , than R^{-0} ($s_{R^{-1}} = 0.302$, $s_{R^{-2}} = 0.273$, $s_{R^{-0}} = 0.072$).

In general, sensitivities of $\pi^{[2]*}$ to the parameters are all positive and follow predictable patterns, assuming that only one parameter changes at a time, though the magnitudes are

dependent on the combinations of parameter values (Fig. 1.2). Increases in $\phi^{[0]}$ result in a decline in $s_{\phi^{0}}$ because, as more territories become occupied, there are fewer unoccupied territories that may become colonized. Similarly, as owl persistence, $\phi^{[1]}$ or $\phi^{[2]}$, increases, the sensitivity of π^{2} to each of these parameters increases because more territories become occupied and, therefore, more territories support reproduction.

EXAMPLE 2: WOOD FROG SECOND-ORDER MARKOV MODEL

The wood frog is one of the most widely distributed frog species in North America, ranging from the southern Appalachians to Alaska (Martof and Humphries 1959). Wood frogs rely on small, temporary, predator-free vernal pools for breeding (Berven 1982, Berven 1990, Hopey and Petranka 1994, Lichko and Calhoun 2003) but reside in adjacent upland habitats during the non-breeding season (Berven and Grudzien 1990, Regosin et al. 2003, Rittenhouse and Semlitsch 2007). With human development as an ever increasing threat to vernal pool habitat, federal lands may become isolated refugia for many amphibian species. However, even in protected areas, climate change may jeopardize the existence of amphibian species that rely on vernal pools and active management may be necessary to maintain viable populations of these species, yet little is known about which actions land managers could, or should, take to prevent, reverse or stop the loss of vernal pools and their associated fauna. Based on wood frog life history in the Mid-Atlantic region. I developed a multistate occupancy model to describe the dynamics of wood frog breeding and successful metamorphosis and determined what parameter(s) are most influential in increasing the probability of successful metamorphosis to guide management efforts.

Model development

The occurrence of breeding frogs at a pool at time (year) *t* is likely to be influenced by two processes: (1) the return of breeding adults from the previous year (*t*-1) and (2) first time (female) breeders that successfully metamorphosed two years prior (*t*-2) and returned to their natal pond. Because the occurrence of breeding wood frogs may depend on a pond's occupancy state in each of the previous two years and because the 1-year-old female class is not available for sampling, I developed a multistate occupancy model, where the occupancy states reflect this second-order Markov process. Specifically, 6 mutually exclusive occupancy states, $\pi_t^{s_{t-1},r_t,s_t}$, represent a combination of egg mass (denoted *r*) state in the current year and late-stage tadpole (denoted *s*) state in the current and previous years, *t* and *t*-1. Thus, the occupancy state vector $\mathbf{\Pi}_t$ in my model can be written as:

$$\Pi_t = \pi_t^{000} \quad \pi_t^{010} \quad \pi_t^{011} \quad \pi_t^{100} \quad \pi_t^{110} \quad \pi_t^{111} \quad .$$

For example, π_t^{010} represents the probability that a pool had egg masses but no metamorphs in year t ($r_t = 1$, $s_t = 0$) and that it failed to produce metamorphs in year t-1 ($s_{t-1} = 0$). I use the presence of late-stage tadpoles to signify successful metamorphosis and my model assumes that "occurrence" of eggs and metamorphs is assessed during both periods (breeding and metamorphosis) each year.

Next, I define lower level transition probability parameters:

- $\phi_{t-1}^{s_{t-2},r_{t-1}}$ = probability that a pool is occupied with egg masses (state r = 1) in year t given that it was in metamorph state s in year t-2 and egg state r in year t-1
- δ_t = probability that a pool is in state s = 1 in year t, given that it is in state r = 1 in year t (i.e., probability that pool produces metamorphs, given it had eggs).

Under this model, a pool with no metamorphs in year *t*-2 and both egg masses and metamorphs in year *t*-1 (probability associated with such a pool denoted π_t^{011}) could transition to one of three mutually exclusive states in year *t*, with corresponding transition probabilities:

(1) Support wood frog breeding (egg masses) but not have successful metamorphosis:

Pr
$$(r_t = 1 \text{ and } s_t = 0 | s_{t-2} = 0 \text{ and } r_{t-1} = 1) = \phi_{t-1}^{01}(1 - \delta_t)$$

(2) Support wood frog breeding (egg masses) and have successful metamorphosis:

Pr (
$$r_t = 1$$
 and $s_t = 1 | s_{t-2} = 0$ and $r_{t-1} = 1$) = $\phi_{t-1}^{01} \delta_t$

(3) Support no wood frog breeding and, thus, no metamorphs:

Pr
$$(r_t = 0 \text{ and } s_t = 0 | s_{t-2} = 0 \text{ and } r_{t-1} = 1) = 1 - \phi_{t-1}^{01}$$

By defining similar transition probabilities for all six occupancy states, I used combinations of the parameters above to construct my time-constant transition probability matrix,

By expanding the number of states and associated transition probabilities I have accommodated the second-order Markov dynamic process into a multistate occupancy model with the familiar form, $\Pi_t = \Phi_{t-1}\Pi_{t-1}$, as Brownie et al. (1993) and Pradel (2005) did with second-order Markov processes in capture-recapture situations.

Sensitivity expressions

Since I am interested in the equilibrium probability that a pool produces metamorphs, I defined a relevant equilibrium occupancy, π^* , as:

$$\pi^* = \pi^{011*} + \pi^{111*}, \qquad \text{eqn 13}$$

where π^{011*} and π^{111*} are the equilibrium occupancy probabilities for pools with successful breeding and metamorphosis (i.e. where $r_t = s_t = 1$). Expanding the expression to include system dynamics and writing the state parameters in terms of the underlying lower level transition parameters yields:

$$\pi^* = \frac{\phi^{00}\delta \ 1 + \delta \ \phi^{01} - \phi^{11}}{A}, \qquad \text{eqn 14}$$

where $A = 1 + \phi^{00} + \delta + \phi^{01} + \delta^2 \phi^{00} + \delta - 1 + \phi^{10} + \phi^{01} + \delta - \delta^2 + \phi^{11} + \delta^{10} + \delta^{00} + \delta - \delta^2 + \delta^$

$$s_{\phi^{00}} = \frac{\delta \ 1+\delta \ \phi^{01}-\phi^{11}}{A} - \frac{1+\delta \ 1+\phi^{01}\delta-\phi^{11}-\phi^{11}\delta \ \times \ \phi^{00}\delta \ 1+\phi^{01}\delta-\phi^{11}\delta}{A^2} \qquad \text{eqn 15}$$

$$s_{\phi^{01}} = \frac{\delta^2 \phi^{00}}{A} - \frac{\delta \phi^{10} \ 1 - \delta + \phi^{00} \delta + 1 \ -1 \ \times \ \phi^{00} \delta \ 1 + \phi^{01} \delta - \phi^{11} \delta}{A^2}$$
eqn 16

$$s_{\phi^{10}} = \frac{-\delta \ \phi^{01} - 1 - \phi^{01} \delta + \phi^{11} \delta \times \phi^{00} \delta \ 1 + \phi^{01} \delta - \phi^{11} \delta}{A^2}$$
eqn 17

$$s_{\phi^{11}} = \frac{-\delta^2 \phi^{00}}{A} - \frac{\delta \phi^{10} \delta - \phi^{00} \delta - \phi^{00} - 1 \times \phi^{00} \delta + \phi^{01} \delta - \phi^{11} \delta}{A^2}$$
eqn 18

$$s_{\delta} = \frac{\phi^{00} \ 1+2\delta \ \phi^{01} - \phi^{11}}{A} - \frac{\phi^{00}\delta(1+\phi^{01}\delta - \phi^{11}\delta)}{A} \times$$
eqn 19

$$\frac{\phi^{00} + \phi^{01} \ 1 + 2\phi^{00}\delta \ + \phi^{10} \ \phi^{01} \ 1 - 2\delta \ -1 \ + \phi^{11} \ \phi^{00} \ -1 - 2\delta \ + 2\phi^{01}\delta - 1}{A}$$

Model parameterization

I obtained parameter estimates for the model described above and examined the sensitivity of π^* to each of the model parameters using wood frog occupancy data collected at Patuxent Research Refuge (PRR). PRR consists of mainly upland hardwood forest and is located approximately 30 km from Washington, DC. Vernal pools were located using a dual-frame sampling design (see Van Meter et al. 2008). Occupancy surveys for breeding wood frogs (i.e.

egg masses) and late-stage tadpoles have been conducted at 55 vernal pools at PRR since 2006. Visual encounter surveys, involving multiple independent observers, were used to detect egg masses in early spring (generally early-March) and dip-net surveys were conducted in late-May to early-June to target late-stage tadpoles (Mattfeldt et al. 2009).

I analyzed the data from PRR using the robust design occupancy model in Program MARK (White and Burnham 1999) to obtain estimates for the transition rate parameters, $\phi^{s,r}$ and δ . I estimated $\phi^{s,r}$ parameters using covariates, assuming known (i.e. $p^* = 1$) metamorph, s, and egg mass, r, states (1 = present/occupied, 0 = unoccupied) and modeled both $\phi^{s,r}$ and ϵ (i.e. extinction probability between egg and metamorph stages, $1 - \delta$) as time-varying or constant. Because pools were surveyed by multiple independent observers, I could estimate the overall probability of observing egg masses or metamorphs at least once at occupied pools and found it to be high ($p^* = 0.992$) providing justification for the use of observed states as covariates, though this approach may not be appropriate for cases in which p^* is not close to 1. Similar to the results for the California spotted owl, the top model for the PRR wood frog data suggested that $\phi^{s,r}$ estimates were time-constant but δ estimates varied among years (range: 0.35–0.79). Because of the time-constancy implied by sensitivity analyses and equilibrium occupancy rates. I used the model that included a time-constant estimate of δ . Estimates, with standard errors, are as follows: $\phi^{00} = 0.06 (0.03), \phi^{01} = 0.47 (0.13), \phi^{10} = 0.26 (0.21), \phi^{11} = 0.84 (0.11), \delta = 0.42$ (0.11).

I varied each parameter from zero to one while holding the other parameters constant using the estimates presented above and calculated the sensitivity of π^* to small changes in each individual parameter using equations 15-19. Because ϕ^{00} appeared to be the most influential parameter in my current system (see Fig 1.3a) and because I believed that it could be influenced via management, I repeated the exercise using medium (0.20) and high (0.50) levels of ϕ^{00} to investigate how sensitivities would change if this parameter was successfully increased via management. Hereafter, I refer to ϕ^{00} as colonization, as it represents the probability of breeding given the pool was unoccupied by eggs and metamorphs in the preceding 2 years. I also calculated equilibrium occupancy for all combinations of colonization, ϕ^{00} , and δ (hereafter, probability of metamorphosis), to examine the simultaneous influence of these two parameters on equilibrium occupancy. Most conceivable management actions would be likely to influence both colonization and metamorphosis probabilities (e.g. enhancing or enlarging pools, pool construction, translocation of eggs, addition of water to pools).

Results

Parameter estimates from PRR revealed that only 5.4% of pools produced metamorphs at equilibrium ($\pi^* = 0.054$, $\Pi^* = [0.847 \ 0.057 \ 0.041 \ 0.024 \ 0.017 \ 0.013]$). Most pools do not support wood frog breeding, (e.g., $\pi^{000*} = 0.85$). Thus, even though colonization probabilities are low ($\phi^{00} = 0.06$), this transition rate is over four times more influential than metamorphosis probabilities, the parameter to which π^* is next most sensitive ($s_{\phi^{00}} = 0.76$, $s_{\delta} = 0.16$, Fig. 1.3a). Of the remaining transition rates, only ϕ^{01} significantly influenced equilibrium occupancy and only when values greatly exceeded current estimates at PRR (Fig. 1.3a).

If colonization probabilities were increased (e.g. via management) to $\phi^{00} = 0.20$, equilibrium occupancy would be $\pi^* = 0.133$ and most sensitive to colonization rate ($s_{\phi^{00}} = 0.41$) followed closely by probability of metamorphosis ($s_{\delta} = 0.37$; Fig. 1.3b). In systems with high colonization probabilities ($\phi^{00} = 0.50$), equilibrium occupancy increased to 21.3% and was most sensitive to probability of metamorphosis ($s_{\delta} = 0.54$) and only somewhat sensitive to ϕ^{01} ($s_{\phi^{01}} = 0.21$) and colonization ($s_{\phi^{00}} = 0.17$; Fig. 1.3c). Interestingly, the transition rates, ϕ^{10} and ϕ^{11} , roughly corresponding to persistence of breeding adults, had very little influence on equilibrium occupancy for any of the scenarios I considered (Fig. 1.3).

To summarize, when colonization rates are less than 0.20, equilibrium occupancy is most influenced by colonization probabilities, unless the probability of metamorphosis is also low (i.e. $\delta < 0.34$), (Figs. 1.4 and 1.5). At current transition probabilities, once colonization probabilities exceed 0.217, equilibrium occupancy (with metamorphs) responds more to the conditional probability of metamorphosis and the effects of increasing the colonization rate quickly become negligible (Fig. 1.4).

DISCUSSION

My perturbation analysis of multistate occupancy models provided various insights about associated dynamics that can be generalized to other multistate systems. I have described two common scenarios for the use of multistate occupancy models. The California spotted owl example represents a typical multistate system involving two occupied states, whereas the wood frog example illustrates how a second-order Markov process may be modified to fit a multistate framework. Few studies have examined second-order Markov processes (but see Hestbeck et al. 1991, Brownie et al. 1993, Ehrlen 2000, Picard et al. 2003, Pradel 2005) and none has involved occupancy as a state variable. However, I believe many species have breeding populations composed of returning adults and maturing juveniles (e.g. neotropical migrant birds). If juveniles (e.g. the stage between metamorphs and breeding adult wood frogs) can be observed, then modeling such a system as a first-order process with age/stage structure is a reasonable approach; however, when intermediate stages or year classes are unobservable, then models such as those presented above may be useful. More generally, such models could be used in systems where a

time-lag is expected or where the effects of management actions or stochastic events may not be immediate.

In standard occupancy scenarios, the probabilities of a patch being occupied or unoccupied are complementary and, therefore, the resulting equilibrium occupancy equation (equation 1) and sensitivity metrics are simple expressions (Martin et al. 2009b). However, in the case of multistate occupancy dynamics, the stable state distribution is not always so simply expressed. Additionally, the state of interest (e.g. equilibrium occupancy, π^*) in dynamic multistate occupancy models depends on the interests of the investigator. For standard dynamic occupancy models, the definition of equilibrium occupancy is straightforward (i.e., ψ^*); however, with dynamic multistate models, equilibrium occupancy rate can be defined by one state or a sum of multiple states. In my California spotted owl example, I chose to focus on the sensitivity of equilibrium patches at which breeding occurs (π^2) but if the probability of a territory being occupied (regardless of breeding status) was of interest, equilibrium occupancy could be redefined as $\pi^{1*} + \pi^{2*}$. In the case of successful wood frog metamorphosis at PRR, I defined equilibrium occupancy state as $\pi^* = \pi^{011*} + \pi^{111*}$, representing the equilibrium probability a pool produces metamorphs. For systems in which the goal is to reduce occupancy rates (e.g. systems involving disease or invasive species), sensitivities to the unoccupied state may be most relevant to questions associated with treatment. It is important that equilibrium occupancy be defined on a case-by-case basis, to reflect focal occupancy state(s) and appropriate sensitivities. As usual, relevance of any inference about sensitivity is determined by the larger program of science or management within which the inference is embedded.

Despite subtle differences in calculating sensitivities and stable state distributions between standard and multistate models, there are several analogous relationships between

sensitivities and equilibrium occupancy. As in Martin et al. (2009b), I found that when colonization probabilities (i.e. ϕ^{0} and ϕ^{00} for my two examples, respectively) are small and the majority of patches (or sites) are unoccupied, the system is strongly influenced by small changes in the colonization probability. This is due to the larger number of unoccupied patches for colonization to act upon. Martin et al. (2009b) found that when $\psi^* < 0.50$, ψ^* was more sensitive to γ (local colonization); likewise, ψ^* was more sensitive to ϵ (local extinction) when $\psi^* > 0.50$. In my wood frog example, if colonization levels were increased above approximately 0.22, sensitivity of π^* to the parameter that influences successful metamorphosis increased (i.e. δ).

Despite potential uncertainty about estimates of transition probabilities, my findings, as well as those by Martin et al. (2009b), suggest that knowledge of the state distribution itself can inform management decisions. Assuming the system is near equilibrium, if few patches are occupied, then focusing management activities on improving colonization, or transitions from unproductive to productive states, is likely to increase the overall equilibrium occupancy as defined in my examples. I acknowledge that many populations may not be near equilibrium, but I believe equilibrium concepts and associated sensitivities based on stationary dynamic processes are relevant and useful for examining the relative effects of different management alternatives or assessing uncertainties related to sampling error (see Martin et al. 2009b and Caswell 2007 for similar arguments for simple occupancy matrices and population projection matrices). It would be much wiser to base management decisions on estimates of both dynamic parameters and current state distributions. As seen in the wood frog example (Fig. 1.3), the ability to change transition rates via management may influence future management decisions because sensitivities of the equilibrium state distribution to each of the transition rates may change. In other words, if management is successful at influencing dynamic parameters and, thus,

occupancy states, then optimal management actions in future time steps may change. In my examples, if management successfully increased colonization to a consistent level above 0.2, then the future management actions should shift to efforts to improve the probability of successful reproduction/metamorphosis conditional on occupancy (i.e. $R^{[m]}$ and δ). Management actions that target both colonization and reproduction, given occupancy, simultaneously should be favored. These recommendations assume that the costs associated with changing the different parameters are roughly equal. If this is not the case, results may be misleading (Link and Doherty 2002, Nichols and Hines 2002, Baxter et al. 2006) and alternative sensitivity expressions incorporating relative costs of changing parameters could be developed and used to explore the sensitivities of the stable equilibrium to changes in dynamic parameters that are scaled to management actions per unit cost (see Martin et al. 2009b).

In closing, I make two points about the computation of the sensitivity values. First, my approach was to first express the stable state distribution in terms of transition parameters, and to then compute the partial derivatives of the focal state equilibrium value(s) with respect to the various transition parameters. Caswell (2001) provided a general expression for the computation of sensitivities for scaled eigenvectors (such as my equilibrium state distribution) that may be more easily implemented than my approach. Indeed, I checked the results of my computations with this alternative approach. Second, the rows or columns (in my case) of my stochastic transition matrices must sum to 1; thus, any perturbation of one matrix element (e.g., a transition parameter) must be compensated by corresponding changes to other matrix elements. This issue requires computation of a total, rather than a partial derivative, and specification of an approach to compensation (Caswell 2001, Hill et al. 2004). In both of my examples, transition matrix elements were written in terms of conditional binomial parameters. For example, with the

spotted owls a site was either occupied (ϕ_t^m) or not $(1 - \phi_t^m)$ and, conditional on occupancy, reproduction either was (R_t^m) or was not $(1 - R_t^m)$ successful. Compensation occurs naturally under this parameterization; e.g., a small increase in R_t^m is naturally compensated by an equivalent decrease in $1 - R_t^m$. When more general multinomial parameterizations are used, I recommend that the reader consult Caswell (2001) for various approaches to maintaining the stochastic matrix constraint.



Figure 1.1. Equilibrium occupancy probabilities for California spotted owls in the Sierra Nevada, California, USA. Multistate occupancy probabilities include: unoccupied, occupied without reproduction and occupied with reproduction. Panels **a-f** show the results of varying a single parameter (x-axis) from 0-1, while maintaining the other parameters at constant baseline rates estimated by MacKenzie et al. (2009): $\phi^0 = 0.17$, $\phi^1 = 0.87$, $\phi^2 = 0.91$, $R^0 = 0.13$, $R^1 = 0.51$, $R^2 = 0.50$. Filled circles represent the occupancy rates at these baseline values.



Figure 1.2. Sensitivity of equilibrium probability of occupancy with reproduction (π^{2*}) to changes in the values of parameters, ϕ^{m} and R^{m} , for California spotted owls in the Sierra Nevada, California, USA. Sensitivities are calculated for each parameter identified on the x-axis using equations 7-12, varying the focal parameter (x-axis) from 0-1 and holding all other parameters fixed at values as estimated by MacKenzie et al. (2009): $\phi^{0} = 0.17$, $\phi^{1} = 0.87$, $\phi^{2} = 0.91$, $R^{0} = 0.13$, $R^{1} = 0.51$, $R^{2} = 0.50$. Filled circles represent the sensitivities at these baseline values.


Figure 1.3. Sensitivity of equilibrium occupancy (π^*) to changes in the parameter values of ϕ^{s_{t-1},r_t} and δ based on estimated values for wood frogs at Patuxent Research Refuge, Maryland, USA. Sensitivities are calculated using equations 15-19; each line represents the sensitivity of π ' to the designated transition parameter (x-axis), being varied from 0-1, while all other parameters are fixed at estimated values: $\phi^{01} = 0.47$, $\phi^{10} = 0.26$, $\phi^{11} = 0.84$, $\delta = 0.42$ and ϕ^{00} , where ϕ^{00} is low representing current conditions ($\mathbf{a}, \phi^{00} = 0.06$). I also present sensitivities where the baseline colonization rate, ϕ^{00} , is raised via management to $\phi^{00} = 0.20$ (\mathbf{b}) or $\phi^{00} = 0.50$ (\mathbf{c}). Filled circles represent the sensitivities at these baseline values.



Figure 1.4. The relationship between equilibrium occupancy (π^* ; probability a pool produces post-metamorphic wood frogs) and both colonization rate (ϕ^{00}) and the conditional probability of metamorphosis (δ). Increasing colonization rates when they are < 0.20 results in a larger influence on equilibrium occupancy, while equilibrium occupancy is most influenced by probability of metamorphosis at colonization rates > 0.15. Other parameters are fixed at estimated values: $\phi^{01} = 0.47$, $\phi^{10} = 0.26$ and $\phi^{11} = 0.84$.



Figure 1.5. The line denotes the parameter levels at which the most sensitive transition parameter shifts from colonization (ϕ^{00}) to the conditional probability of successful metamorphosis (δ) for wood frog equilibrium occupancy (i.e. π^* ; the proportion of pools producing metamorphs). For combinations of values of δ and ϕ^{00} above the line, π^* is most sensitive to δ , while for combinations below the line, π^* is most sensitive to ϕ^{00} . The other parameter values are fixed at values estimated from occupancy data collected at Patuxent Research Refuge: $\phi^{01} = 0.47$, $\phi^{10} = 0.26$, and $\phi^{11} = 0.84$.

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CHAPTER 2: EVALUATING BREEDING AND METAMORPH OCCUPANCY AND VERNAL POOL MANAGEMENT EFFECTS FOR WOOD FROGS USING A HIERARCHICAL MODEL

Worldwide 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. I 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. My objectives were to obtain estimates of breeding occurrence and metamorph occupancy and evaluate the success of current management actions. 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 my predictions, previous occupancy states had little effect on breeding and metamorph occupancy probabilities, which is likely due to high correlation of occupancy with hydroperiod length. Additionally, I did not observe a relationship between breeding occupancy probabilities and the spatial arrangement of pools. Though sample sizes were small, management actions resulted in an increase in both breeding and metamorph occupancy probabilities. I demonstrate that management actions targeting short-hydroperiod pools favorably influence both components of breeding success. Still, 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 into the future.

INTRODUCTION

Declines in amphibian populations have been observed around the world in recent decades (Wake 1991, Stuart et al. 2004, Wake and 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 northeastern region of the U.S., climate change and continued urbanization are considered the primary threats to amphibian populations, especially those associated with seasonal or vernal pools (Calhoun and 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. 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 northeastern U.S. 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 et al. 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 Northeast and Mid-Atlantic regions of the United States to begin programs to locate and monitor vernal pools on protected lands (Van Meter et al. 2008). This research agrees with current literature suggesting that the distributions of many pond-breeding amphibian populations are dynamic and strongly dependent on the hydroperiod length of individual pools (Semlitsch et al. 1988, Semlitsch and Wilbur 1988, Chelgren et al. 2006, Rothermel and Semlitsch 2006, Mattfeldt et al. 2009, Matthews et al. 2012, Zipkin et al. 2012). These habitats and the associated local amphibian population dynamics are related to environmental conditions (Berven 1990, Berven and 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 and Hunter 2002, Petranka et al. 2003, Petranka et al. 2004, Vasconcelos and 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 et al. 2009, Zipkin et al. 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 and Hunter 2002, Calhoun et al. 2003, Baldwin et al. 2006, Petranka et al. 2007), yet none has 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 and Calhoun 2003, Vasconcelos and Calhoun 2006, Shoo et al. 2011). I chose to focus my study on the wood frog (*Lithobates sylvatica*) because it relies on small, temporary, predator-free vernal pools for breeding (Berven 1982, Berven 1990, Hopey and Petranka 1994, Lichko and Calhoun 2003) and is widely spread across North America (Martof and Humphries 1959, Lannoo 2005). Because of its short life span and propensity for annual breeding, 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, MacKenzie et al. 2003, MacKenzie et al. 2006) are often used in metapopulation studies (Martin et al. 2009, Martin et al. 2010, MacKenzie et al. 2012) and large-scale monitoring programs (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 and Kéry 2007, Royle and Dorazio 2008). In addition, many studies using occupancy models are interested in both 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 straight forward way of estimating finite sample occupancy and its associated precision (Royle and Kéry 2007). I 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. My objectives were to obtain estimates of breeding and metamorph 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 et al. 2008), that 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 et al. (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 et al. 2009). Surveys were conducted at 53 vernal pools at PRR from 2006-2010.

Based on life history knowledge for this species, I modeled 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, I am 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. I also included precipitation data from the weather station in Laurel, Maryland, as covariates explaining variation in occupancy estimates. I modeled the probabilities of breeding occurrence and successful metamorphosis as a function of the average precipitation (cm) per month for the five months prior to egg laying (Oct – Feb; range: 6.41-11.54 cm/month) and the average precipitation per month for the 3 months during larval development (Mar – May; range: 10.71-14.91 cm/month), respectively.

Few short-hydroperiod pools supported breeding or retained water long enough for metamorphosis; therefore, I focused my 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. I 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 et al. 2003, Babbitt 2005, Baldwin et al. 2006). Therefore, I expected wood frog breeding occupancy rates to increase with hydroperiod length. Additionally, I 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, though isolated pools tend to have larger breeding populations (Baldwin et al. 2006). Likewise, I 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_i^j , where y_i^j 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). I assumed that y_i^j was distributed binomially when pool *i* was truly occupied by wood frogs in state *j* (i.e., $z_i^j = 1$)

$$y_i^j \sim \frac{Bin \ T_i^j, p^j}{0, \ z_i^j = 0},$$
 eqn 1

where T_i^j is the number of sampling occasions 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_i^1 , is described by

$$z_i^1 \sim Bern \ \psi_i^1$$
, eqn 2

where ψ_i^1 is the probability of wood frog breeding (i.e., egg masses). Because a pool can only be occupied by tadpoles if eggs are present, I modeled metamorph occupancy, ψ_i^2 , conditional on the site supporting breeding, as

$$z_i^2 \sim \frac{Bern \ \psi_i^2}{0}, \quad z_i^1 = 1$$
. 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_i^1 only. Therefore, I deterministically modeled ψ_{ij} as a function of these covariates, such that

$$logit \ \psi_i^1 = \mathbf{x}_i^{1'} \boldsymbol{\beta} \qquad \text{eqn 4}$$

and

$$logit \ \psi_i^2 = \mathbf{x}_i^{2\prime} \boldsymbol{\alpha}, \qquad \text{eqn 5}$$

where $x_i^{1\prime}$ and $x_i^{2\prime}$ are covariate vectors and β and α are regression coefficient vectors.

I 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). I obtained 50,000 MCMC samples and used a burn-in period of 25,000 iterations. I used vague prior distributions for all estimated parameters:

$$p^j \sim Beta(1,1)$$
 eqn 6

and

$$\boldsymbol{\alpha}, \boldsymbol{\beta} \sim Norm \ 0,100 \ .$$
 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 and Hill 2007). Where conjugate full-conditional distributions were analytically tractable, they were calculated for p^{j} and z_{i}^{j} , and Gibbs sampling was used. In this case, detection probabilities were sampled from a beta full-conditional distribution

$$p^{j} \sim Beta \qquad y_{i}^{j} + \eta_{p^{j}}, \qquad (T_{i}^{j} - y_{i}^{j}) + \omega_{p^{j}}, \qquad \text{eqn 8}$$

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_{i}^{j} , for all sites where $y_{i}^{1} = 0$ (with an ambiguous occupancy status) were sampled from a Bernoulli full-conditional distribution with probability ψ_{i}^{j} , where

$$\psi_{i}^{1} = \frac{1 - p^{1} {}^{T_{i}^{1}} \psi_{i}^{1} \psi_{i}^{2} {}^{z_{i}^{2}} (1 - \psi_{i}^{2})^{1 - z_{i2}}}{1 - p^{1} {}^{T_{i}^{1}} \psi_{i}^{1} \psi_{i}^{2} {}^{z_{i}^{2}} (1 - \psi_{i}^{2})^{1 - z_{i2}} + 1 - \psi_{i}^{1}}, \qquad \text{eqn 9}$$

and, for all sites where $z_i^1 = 1$ and $y_i^2 = 0$,

$$\psi_i^2 = \frac{\left(1 - p^2\right)^{T_i^2} \psi_i^2}{\left(1 - p^2\right)^{T_i^2} \psi_i^2 + 1 - \psi_i^2}$$
eqn 10

In order to determine when the algorithm had converged, I used two chains and computed the Gelman-Rubin convergence statistic, which was < 1.1 for all model parameters in my case (Gelman and Rubin 1992, Brooks and 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 proportion of pools supporting wood frog breeding and metamorphosis (finite occupancy rates, $\psi^{(fs)}$; Royle and Kéry 2007) varied from year to year (Table 2.1), though there was little uncertainty pertaining to the annual estimates due to high detection probabilities (Tables 2.1 and 2.2). Breeding occupancy probability was highest in 2010 and lower in 2008 and 2009, showing a positive relationship with precipitation amounts (Fig. 2.1, Table 2.3), and the same pattern occurred with successful metamorphosis. Conditional metamorph occupancy rates were higher in 2008 and 2009, corresponding to higher amounts of spring precipitation (Fig. 2.2).

The probability a pool supported wood frog breeding increased with hydroperiod length (Table 2.3 and Fig. 2.1), and all long-hydroperiod pools supported breeding in every year. Contrary to my expectations, clustered pools had a lower breeding occupancy rate than isolated pools, though not significantly, and all managed pools 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 ψ_i^2 values intermediate to those of natural short- and medium-hydroperiod pools. Previous occupancy states had little influence on either occupancy probability (Table 2.3). I expected both covariates representing past occupancy states

to have a positive influence on breeding probability, and while the estimates of the coefficients were both positive, the 95% credible intervals included zero.

DISCUSSION

While several studies provide a temporal snap-shot of differences in counts of amphibians between natural and man-made or manipulated pools (Pechmann et al. 2001, DiMauro and Hunter 2002, Vasconcelos and Calhoun 2006), few studies have explicitly estimated occupancy rates for both breeding and successful metamorphosis in response to anthropogenic change over time (Petranka et al. 2003, Petranka et al. 2007) and none has accounted for imperfect detection. I present estimates of the effect of precipitation on wood frog occupancy rates, and I provide some evidence of a positive effect of vernal pool management on breeding and late-stage tadpole occupancy probabilities, though my 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 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 supported breeding, allow for successful metamorphosis, and likely protect both the local population and metapopulation from extinction (Berven 1990, Berven and Grudzien 1990, Berven 1995). My results, and those from other studies (Berven 1990, Berven 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 ψ_i^1 and ψ_i^2 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 (ψ_t^1), contrary to my prediction of positive influences. I 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, I thought that pools that supported metamorphosis in *t*-2 would have higher breeding occupancy probabilities in *t* due to first time breeding females (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 et al. (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, I believe that much of the variation in occupancy probabilities was accounted for by including hydroperiod covariates in the model. I 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 (ψ_i^1) in isolated pools were consistent with other studies that found larger populations at isolated pools (Calhoun et al. 2003, Petranka et al. 2004, Baldwin et al. 2006), though the effect of the spatial arrangement in my study was not significant (Table 2.3). 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 2.2). However, detection probabilities may not be as high in other systems (Church 2008, Mattfeldt et al. 2009), and an optimal survey design should be determined on a case-by-case basis. Censuses or methods which result in a very high detection probability result in little to no variance in finite occupancy estimates ($\psi^{(fs)}$) 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 2.1 provide inference for the entire population of pools at PRR (estimated to be 2,272 pools (SE=663); Van Meter et al. 2008) and have appropriately larger variances than the finite occupancy rates of sampled pools (Table 2.1). 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 (ψ and ψ^{fs}) is dependent on the state variable of interest and associated management decisions.

The positive relationships between winter precipitation and breeding occupancy (Fig. 2.3a) and spring precipitation and metamorph occupancy (Fig. 2.3b) 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 et al. 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.

My results provide some insight into potential increases in metamorph occupancy from the management of vernal pools; however, I only have one year of post-management data to include in my analysis and cannot determine whether any negative effects may occur in subsequent years (see Pechmann et al. 2001, Petranka et al. 2003, Vasconcelos and Calhoun 2006). The goal of the management experiment was to increase the hydroperiod length of pools and, therefore, increase the probability of metamorphosis (ψ_i^2) and the long-term probability of breeding (ψ_i^1) . Wood frogs utilized managed pools for breeding in the first year after management occurred, and the conditional probability of metamorphosis was comparable to unmanaged pools with longer hydroperiods, suggesting that deepening and installing liners in poorly-performing pools may benefit overall occupancy rates. However, I observed the colonization and successful breeding by predators (i.e., green frogs) in managed pools at the beginning of the second year after installing liners (i.e., 2011). My 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, I still believe that my 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 further experimentation 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). My model can easily be adopted

by programs 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. My 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 et al. 2007). **Table 2.1.** Posterior means for the number of sampled vernal pools supporting wood frog breeding and successful metamorphosis (53 total sampled pools) and the finite sampling occupancy rates (ψ^{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 value as the mean. Therefore, I omitted the credible intervals 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.

	Breeding		Metamorphosis	
Year	Number	$\psi^{1\ fs}$	Number	$\psi^{2\ fs}$
 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 2.2. 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 (<i>j</i> =1)	0.945	(0.896, 0.980)
Late-stage tadpole (<i>j</i> =2)	0.962	(0.897, 0.995)

Table 2.3. 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 (<i>j</i> =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 ¹	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 (<i>t</i> -2)	0.11	(-1.81, 2.11)
Late-stage tadpole (<i>j</i> =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 ²	0.51	(0.15, 0.91)
	management	2.40	(-1.58, 6.13)

¹Winter precipitation was measured as the mean amount (cm) of precipitation/month from the five months prior to breeding (i.e., Oct-Feb)

² Spring precipitation was measured as the mean amount (cm) of precipitation/month from the three months between breeding and metamorphosis (i.e., Mar-May)



Figure 2.1. Probability of occupancy for breeding wood frogs (ψ_i^1) in vernal pools at Patuxent Research Refuge, Maryland, USA. Because metamorph occupancy status in *t*-2 had little effect on breeding occupancy probability, I report only the estimates of ψ_i^1 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.



Figure 2.2. Probability of occupancy for metamorphic (given breeding occurred) wood frogs (ψ_{i2}) 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.



Figure 2.3. The relationship between wood frog (a) breeding occupancy probability, ψ_i^1 , and average monthly winter precipitation (Oct-Feb) and (b) metamorph occupancy probability, ψ_i^2 , and average monthly spring precipitation (Mar-May) for vernal pools at Patuxent Research Refuge, Maryland, USA. I 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.

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APPENDIX 2.A

I present one approach to estimation of the joint posterior distributions that requires iterative sampling from the full-conditional distributions. I sample p^j , z_i^j , α , and β for i = 1, ..., m, where *m* is the total number of sampled units, and j = 1 and 2, sequentially, from their respective conditional distributions given all other parameters. In my case, the conjugate full-conditional distributions for p^j and z_i^j are easily calculated, so I used Gibbs sampling for these parameters. The full-conditional distributions for α and β are non-conjugate and are sampled using Metropolis-Hastings updates, where parameter values are proposed and then accepted with a probability based on a conditional density ratio. Normalizing constants cancel out in this ratio and can be omitted without effect. The proportional full-conditional distributions for the model parameters are:

$$p^{j}| \cdot \propto \qquad Bin \ T_{i}^{j}, p^{j} \quad Beta \ \eta_{p^{j}}, \omega_{p^{j}},$$

$$z_{i}^{1}| \cdot \propto \qquad Bin \ T_{i}^{1}, p^{1} \ Bern \ \psi_{i}^{1} \quad N \ \boldsymbol{\beta} \ \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta},$$

$$z_{i}^{2}| \cdot \propto \qquad Bin \ T_{i}^{2}, p^{2} \ Bern \ \psi_{i}^{1} \ Bern \ \psi_{i}^{2}|z_{i}^{1} = 1 \qquad N \ \boldsymbol{\alpha} \ \boldsymbol{\mu}_{\alpha}, \boldsymbol{\Sigma}_{\alpha},$$

$$\boldsymbol{\beta}| \cdot \propto \qquad Bin \ T_{i}^{j}, p^{j} \ Bern(\psi_{i}^{1})Bern \ \psi_{i}^{2}|z_{i}^{1} = 1 \qquad N \ \boldsymbol{\beta} \ \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta},$$

$$\boldsymbol{\alpha}| \cdot \propto \qquad Bin \ T_{i}^{2}, p^{2} \ Bern \ \psi_{i}^{2}|z_{i}^{1} = 1 \qquad N \ \boldsymbol{\alpha} \ \boldsymbol{\mu}_{\alpha}, \boldsymbol{\Sigma}_{\alpha}.$$

The full-conditional distribution for p^{j} can be simplified to the form of a beta distribution:

$$p^{j} \sim Beta \qquad y_{i}^{j} + \eta_{p^{j}}, \qquad (T_{i}^{j} - y_{i}^{j}) + \omega_{p^{j}},$$
 all $z_{i}^{j=1}$

The true occupancy status of z_i^j only needs to be sampled when $y_i^j = 0$ (ambiguous occupancy status; $z_i^j = 1$ if $y_i^j > 0$). This allows the full-conditional distributions of z_i^1 and z_i^2 to be simplified to a Bernoulli distribution with probability ψ_i^1 and ψ_i^2 , respectively, where

$$\psi_{i}^{1} = \frac{1 - p^{1 T_{i}^{1}} \psi_{i}^{1} \psi_{i}^{2 Z_{i}^{2}} (1 - \psi_{i}^{2})^{1 - Z_{i}^{2}}}{1 - p^{1 T_{i}^{1}} \psi_{i}^{1} \psi_{i}^{2 Z_{i}^{2}} (1 - \psi_{i}^{2})^{1 - Z_{i}^{2}} + 1 - \psi_{i}^{1}}$$

and

$$\psi_i^2 = \frac{(1-p^2)^{T_i^2}\psi_i^2}{(1-p^2)^{T_i^2}\psi_i^2 + 1 - \psi_i^2}$$

At each sampling of p^j , z_i^j , α , and β , ψ_i^1 and ψ_i^2 are updated using equations 4 and 5, respectively. The Markov Chain Monte Carlo algorithm for this model can be implemented using the following steps:

- 1) Define initial starting values for each parameter where the full-conditional is nonconjugate: $\beta^{(0)}$ and $\alpha^{(0)}$. For all iterations, set all $z_i^j = 1$ when $y_i^j > 0$. Calculate initial values $\psi_i^{1(0)}$ and $\psi_i^{2(0)}$ using $\beta^{(0)}$ and $\alpha^{(0)}$ in equations 4 and 5, respectively. Sample $p^{1 \ 0}$ and $p^{2 \ 0}$ from their respective beta distributions and $z_i^{j \ 0}$ from a Bernoulli distribution with probability ψ_i^j to obtain initial values for these parameters.
- Set k = k + 1 and sample α^(*) from a proposal distribution, α^(*)|α⁽⁰⁾. Use equation 5 to calculate the proposal value ψ_i^{2 (*)} given α^(*). If the proposal distribution is symmetrical with respect to α^(*) and α^(k-1) (e.g., N(α * |α^{k-1}, a_αI), with tuning parameter a_α), let α^(k) = α^(*) if τ_α^{*} > u, where u~Uniform 0,1 and

$$\tau_{\alpha}^{*} = \frac{all \, z_{i}^{1} = 1}{all \, z_{i}^{1} = 1} \, Bern(\psi_{i}^{2 \, (k)}) \qquad all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \quad N(\alpha^{(*)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{1} = 1}{all \, z_{i}^{1} = 1} \, Bern(\psi_{i}^{2 \, (k-1)}) \qquad all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \quad N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{1} = 1} \, Bern(\psi_{i}^{2 \, (k-1)}) \qquad all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \quad N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{1} = 1} \, Bern(\psi_{i}^{2 \, (k-1)}) \qquad all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, N(\alpha^{(k-1)} | \mu_{\alpha}, \Sigma_{\alpha}) = \frac{all \, z_{i}^{2} = 1}{all \, z_{i}^{2} = 1} \, Bin(T_{i}^{2}, p^{2 \, k-1}) \, Bin(T_{i}^$$

where μ_{α} and Σ_{α} are the mean vector and covariance matrix of the prior distribution on α ; otherwise, $\alpha^{(k)} = \alpha^{(k-1)}$.

3) Sample β^(*) from a proposal distribution, β^(*)|β⁽⁰⁾. Use equation 4 to calculate the proposal value ψ_i^{1 (*)} given β^(*). If the proposal distribution is symmetrical with respect to β^(*) and β^(k-1) (e.g., N(β * |β^{k-1}, a_βI), with tuning parameter a_β), let β^(k) = β^(*) if τ_β^{*} > u, where u~Uniform 0,1 and

$$\tau_{\beta}^{*} = \frac{all \, z_{i}^{1} = 1}{all \, z_{i}^{1} = 1} \frac{Bin \, T_{i}^{1} p^{1 \ k-1} \quad Bern(\psi_{i}^{2 \ *})}{all \, z_{i}^{1} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(*)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{1} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1}) \quad N(\boldsymbol{\beta}^{(k-1)} | \boldsymbol{\mu}_{\beta}, \boldsymbol{\Sigma}_{\beta})}{all \, z_{i}^{2} = 1} \frac{Bin(T_{i}^{2} p^{2 \ k-1$$

where μ_{β} and Σ_{β} are the mean vector and covariance matrix of the prior distribution on β ; otherwise, $\beta^{(k)} = \beta^{(k-1)}$.

- 4) Sample $p^{1 k}$ and $p^{2 k}$ from their respective full-conditional distributions.
- 5) For all $y_i^2 = 0$, sample $z_i^{2(k)}$ from its full-conditional distribution $z_i^{2(k)} \sim Bern(\psi_i^{2(k)})$, where $\psi_i^{2(k)}$ is calculated using the current parameter values (i.e., $p^{2(k)}$ and $\psi_i^{2(k)}$) using equation 5. Set all $z_i^{1(k)} = 1$ where $z_i^{2(k)} = 1$ and/or $y_i^1 > 0$. Similarly, for all $z_i^{2(k)} = 0$ and $y_i^1 = 0$, sample $z_i^{1(k)}$ from its full-conditional distribution $z_i^{1(k)} \sim Bern(\psi_i^{1(k)})$.
- 6) Finite occupancy rates of breeding $(\psi^{1 \ fs})$ and late-stage tadpoles $(\psi^{2 \ fs})$ are calculated:

$$\psi^{j fs} = \frac{\prod_{i=1}^{n} z_i^j}{n},$$

where n is the total number of sampled pools. If predictions are desired for other combinations of covariates not observed in the data, the parameter values for iteration kcan be used to make posterior predictions:

$$logit(\psi_{pred}^1) = \mathbf{x}_i^{1'} \boldsymbol{\beta}^{(k)}$$

and

$$logit(\psi_{pred}^2) = \mathbf{w}_i^{2\prime} \mathbf{\alpha}^{(k)},$$

where $x_i^{1'}$ and $w_i^{2'}$ are vectors of covariates associated with the desired predictions. After convergence is obtained (i.e., k > b, where b is the burn-in period), sampled values and derived parameters can be saved and used to calculate posterior summary statistics. The algorithm can be iterated by repeating steps 2-6 until a sufficiently large sample has been obtained to approximate posterior distributions.

CHAPTER 3: USING DATA-BASED ECOLOGICAL THRESHOLDS TO DEFINE RELEVANT MANAGEMENT OBJECTIVES

Thresholds have been used for decades to inform management decisions, yet they are often unclear or not incorporated into an objective decision making framework. Thresholds used to make management decisions are often based on historic or arbitrary levels, which may or may not be relevant to management objectives. I performed a population viability analysis (PVA) using a dynamic occupancy model to evaluate potential ecological thresholds within two wood frog populations and then discuss how these ecological thresholds could be incorporated into an adaptive resource management framework. I projected wood frog populations for scenarios involving different numbers of pools using occupancy estimates of breeding and successful metamorphosis from two different study areas to evaluate the probability of quasi-extinction and the proportion of vernal pools producing metamorphs. Results from PVAs were similar for both study areas, suggesting that >50 pools are required to ensure long-term persistence with approximately 16% of pools producing metamorphs in stable populations. I demonstrate one way to incorporate the results of the PVA into a utility function that balances the trade-offs between ecological and financial objectives, which can be used within an adaptive resource management framework for making optimal, transparent decisions. My approach provides a framework for using a standard method (i.e., PVA) and available information to inform a formal decision process in order to determine optimal and timely management policies.

INTRODUCTION

Ecological thresholds describe the points or zones where the changes in values of system state variables result in changes in system dynamics or states (Bestelmeyer 2006, Martin et al. 2009), and they have been used for decades to guide natural resource management (e.g., Lande 1987, Lindenmayer et al. 1993, Shaffer et al. 2002). Ecological thresholds can be defined in many ways based on the habitat, species, context, and scale of interest (Huggett 2005). For example, arctic ponds have recently crossed the ecological threshold of desiccation due to changes in air temperatures and precipitation (Smol and Douglas 2007); extinction thresholds occur when a parameter or variable changes such that the probability of species persistence drops to zero (Lande 1987, Fahrig 2001). Despite their widespread use in management and conservation, ecological thresholds are not often clearly defined or incorporated into an objective decision making framework.

Martin et al. (2009) identify three types of thresholds used in conservation and management decisions and emphasize the importance of discerning among them. Ecological thresholds describe substantial changes in ecosystem characteristics due to changes in the ecosystem components or environmental drivers (Bestelmeyer 2006). These thresholds are a characteristic of the ecology of the system and are not a values-based objective defined by managers. A utility threshold describes the system states resulting in substantial changes in the value of the management outcome. Utility thresholds are subjective and determined by stakeholders' values, but ecological thresholds can be used to represent biological management objectives within a utility function that represents all management objectives, biological or otherwise. Finally, a decision threshold is based on values of system state variables that should prompt specific management actions, and they are determined by a utility function that may

incorporate a utility threshold. It seems logical that utility thresholds should often be based on ecological thresholds determined using available biological information, but often they are not. Thresholds used to guide management decisions are often based on historical levels (e.g., abundance) or arbitrarily chosen values with little or no justification (e.g., USDA Forest Service 1986, Francis 1992, Quinn et al. 1992, Lande et al. 1997, Cooke 1999, Moore and Conroy 2006). Historical or long-term data sets may be a useful source of information to set management objectives, but it is important to consider potential changes in dynamics or system drivers over time and to reevaluate the metrics relevant to management decisions using newer information, if possible (Bakker and Doak 2008).

In the absence of well-defined, quantifiable management objectives, ecological thresholds based on knowledge of the system may inform stakeholders of population levels above which species' persistence is likely. Population viability analysis (PVA) is a tool that has typically been used to evaluate population persistence in response to changes in demographic parameters or to determine the minimum viable population (MVP) size necessary for population persistence. The development of PVA corresponded with legislative mandates to sustain viable populations of terrestrial vertebrates (Beissinger 2002), and the metrics provided by PVA are often used to evaluate the impacts of potential conservation or management actions (e.g., Shaffer et al. 1983, Suchy et al. 1985, Lande 1988, Boyce et al. 1990, Boyce 1992, Ruggiero et al. 1994, Reed et al. 1998). These metrics can also provide a basis for an adaptive management framework (Holling 1978, Walters 1986, Boyce 1992). Here, I use a PVA to determine the number of occupied patches (breeding pools) needed to ensure long-term metapopulation persistence for two wood frog populations. I then use this ecological threshold as a management objective within a decision framework.

PVA has been criticized for its poor predictive abilities and inability to be tested. These criticisms are often attributed to poor data, difficulties in parameter estimation, the weak ability to validate models, and the potential effects of alternative model structures (Boyce 1992, Ralls and Taylor 1997, Beissinger and Westphal 1998, Groom and Pascual 1998, Reed et al. 1998, Beissinger 2002, Ellner et al. 2002). My approach addresses these shortcomings by using a large sample or complete census of breeding habitat, multiple years of data, and a model that includes what I believe are the major drivers of the system. Bakker and Doak (2008) developed an approach, Population Viability Management, to address some of these criticisms by accounting for environmental and demographic stochasticity, as well as the influence of expected monitoring data, to distinguish between the benefits of competing management strategies. However, this approach only considers one management action at a time and does not explicitly incorporate trade-offs between biological and non-biological (e.g., cost) objectives. By incorporating PVA within an adaptive resource management (ARM) framework, the criticisms of validating models and reducing uncertainty around the effects of alternative model structures are naturally and necessarily addressed through regular monitoring of the system and assessment of competing models, and competing objectives can be weighted to reflect interests of the stakeholders involved.

In this paper, I use a multistate dynamic occupancy model to evaluate potential ecological thresholds for two wood frog (*Lithobates sylvatica*) populations. I describe how these ecological thresholds could be incorporated into a utility threshold to determine optimal management decisions within an ARM framework. Incorporating ecological thresholds directly into the decision context addresses many of the criticisms of the use of projection matrix models in conservation management.

METHODS

Species' Biology and Data Collection

Wood frogs are widely distributed and range from the southern Appalachians to Alaska (Martof and Humphries 1959). They rely on small, seasonal wetlands (vernal pools) for breeding (Berven 1982, Berven 1990, Hopey and Petranka 1994, Lichko & Calhoun 2003), and reside in upland woodlands surrounding these wetlands during the non-breeding season (Berven and Grudzien 1990, Regosin et al. 2003, Rittenhouse and Semlitsch 2007). In my study areas, adult wood frogs migrate to breeding ponds in late-February or early-March, and juveniles emerge from the ponds in late-May or early-June. Adult females usually breed for the first time as two-year-olds, and the average life span for this species is thought to be three to five years (Berven 1990, Chapter 4).

My study areas consisted of two federal land holdings in or near Washington, D.C., USA. Patuxent Research Refuge (PRR) covers 5,280 ha and is located in central Maryland, USA; approximately 75% of the refuge is deciduous forest. Rock Creek Park (ROCR) is a 710-ha National Park within Washington, D.C., USA, consisting of approximately 85% mixed mesophytic forest. Fifty-three of an estimated 2,200 vernal pools (see Van Meter et al. 2008) at PRR have been monitored for the presence of amphibian breeding and successful metamorphosis since 2006. All nine of the known vernal pools at ROCR have been monitored for signs of amphibian breeding since 2006 and successful metamorphosis since 2009. I considered the aggregations of vernal pools at each study area as isolated populations due to the expansive urban areas outside of the parks.

Occupancy surveys were conducted at vernal pools shortly after wood frog egg masses were laid (i.e., late-February – early-March) to assess the breeding occupancy status each year.

Pools were then revisited in late-May or early-June to detect late-stage tadpoles, which I assume represented successful metamorphosis. Sampling occurred from 2006-2010 at PRR and 2008-2011 at ROCR. Details of the occupancy surveys can be found in Mattfeldt et al. (2010).

Model Structure and Parameterization

In previous work, I developed a hierarchical model to estimate breeding and successful metamorphosis occupancy rates of wood frogs (see Green et al. in press, Chapter 2) and fit it to the data from PRR and ROCR to obtain unique parameter estimates for each study area. Key parameters in this model include: ψ_{it}^1 , the probability that pool *i* supports wood frog breeding in year t, and conditional on breeding, ψ_{it}^2 is the probability that the pool supports successful metamorphosis in the same year (conditional probability of metamorphosis). Both occupancy parameters were modeled as functions of pool-specific characteristics, such as hydroperiod length (i.e., short, medium, long) and spatial arrangement (i.e., clustered, isolated for PRR data only). Pool hydroperiods were classified as: short-hydroperiod pools that rarely retained water through early-June (i.e., metamorphosis), medium-hydroperiod pools that retained water through early-June in wet years, and long-hydroperiod pools that retained water through early-June in most years. Spatial arrangement refers to the distance between vernal pools, with clustered pools typically being within 20 m of another pool and isolated pools >300 m from the nearest known pool. Previous occupancy states, namely breeding state (eggs/no eggs) in year t - 1, and metamorph state in year t-2, were also included as pool specific covariates when estimating breeding occupancy probability, ψ_{it}^1 . I modeled breeding occupancy probability as a function of past occupancy states because I thought the female breeding population of a pool (represented by the presence of egg masses) would primarily consist of returning breeding females (represented by breeding occupancy status in the previous year) and first-time breeding females (represented

by metamorph occupancy status two years prior). I modeled annual variation in occupancy probabilities using precipitation values obtained from local weather stations for months most likely to influence breeding habitat (October-February) and successful metamorphosis (March-May; see Chapter 2 for more details). No spatial arrangement effects were included in the model used to estimate occupancy at ROCR. I obtained annual posterior predictive distributions of breeding and metamorph occupancy for each study area (i.e., three years each) to provide estimates of annual variability due to environmental conditions (Table 3.1). I used these posterior predictive distributions and the same multistate occupancy model to stochastically project wood frog occupancy dynamics for scenarios described in the next section.

Simulations

Metapopulations are subject to a higher probability of extinction as the number of habitat patches (pools) decreases due to demographic and environmental stochasticity (Lande 1987, Lande 1998). Therefore, I performed simulations using different numbers of pools to investigate the relationships between the number of pools in the system (pool population size), probability of extinction, and time to extinction. As the pool population size increased, I expected the probability of extinction to approach zero (e.g., Shaffer and Samson 1985, White 2000) and the number of pools producing metamorphs to stabilize. I used estimated parameter distributions from each of my two study areas (PRR, ROCR) in combination with five levels of pool population sizes (5, 10, 25, 50, 75, and 100 pools) to create 12 different simulation scenarios.

For a given simulation scenario, I projected the occupancy dynamics over 100 years and repeated the projection for 1,000 iterations. For each iteration, the number of pools in each spatial/hydroperiod category was determined by randomly assigning the categories based on their frequencies in the corresponding study area. For example, to simulate dynamics for the

scenario involving 10 pools using the ROCR parameter distributions, the number of short, medium, and long pools were chosen with probabilities 0.556 (5/9), 0.333 (3/9), and 0.111 (1/9), respectively. For simulation scenarios involving PRR parameter distributions, pools were randomly assigned to categories that represented a combination of hydroperiod length and spatial arrangement with associated probabilities in parentheses: short, clustered (0.444); short, isolated (0.185); medium, clustered (0.222); medium, isolated (0.037); long, clustered (0.074); and long, isolated (0.037).

I included environmental variation in each simulation scenario by randomly assigning one of the years for which I obtained estimates (i.e., 2008, 2009, 2010 for PRR and 2009, 2010, 2011 for ROCR) to each year within an iteration. To simulate demographic stochasticity, one value for each of the occupancy probabilities associated with pool *i* was chosen from the posterior predictive distribution associated with the randomly selected year. For example, if the first year within an iteration was randomly assigned a value of "2009", all parameter values would be randomly selected from their respective posterior distributions associated with 2009 and used to project occupancy states to year 2 within the iteration. Breeding and metamorph occupancy states for year *t* were chosen from the following distributions

$$r_{i,t} \sim Bern(\psi_{i,t}^1)$$

and

$$s_{i,t} \sim \begin{array}{c} Bern \ \psi_{i,t}^2 \ , \ r_{i,t} = 1 \\ 0, \ r_{i,t} = 0 \end{array}$$

where $r_{i,t}$ is the breeding occupancy state for pool *i* in year *t*, $\psi_{i,t}^1$ is the breeding occupancy probability for pool *i* in year *t*, $s_{i,t}$ is the metamorph occupancy status for pool *i* in year *t*, and $\psi_{i,t}^2$ is the metamorph occupancy probability for pool *i* in year *t*. The metamorph occupancy state is conditional on a pool supporting breeding because the presence of egg masses is necessary for metamorphosis.

If all pools failed to produce metamorphs for two consecutive years within a given iteration, I deemed the wood frog metapopulation quasi-extinct, and the simulation was aborted. I believe that this accounts for the storage-effect of surviving adult frogs returning to breed after a year of complete reproductive failure. Female wood frogs are thought to usually breed for the first time in their second year and live three to five years; two years of reproductive failure would likely cause substantial declines in the adult population, rendering the population effectively extinct.

At the end of each iteration, I determined whether the metapopulation went quasi-extinct during the 100 year time horizon, and if so, the year of extinction was recorded. In all cases, I recorded the number of pools producing metamorphs in each year. To summarize all 1,000 iterations for each simulation scenario, I calculated the probability of extinction as the proportion of iterations where the population went quasi-extinct, the mean year of extinction for iterations where the metapopulations went extinct, and the average proportion of pools producing metamorphs (hereafter, metamorph occupancy rate) from all iterations in each year of the simulation. Using the results from simulation scenarios with a probability of extinction ≤ 0.05 , I calculated the mean proportion of pools producing metamorphs. I used only the results from years 30-100 to allow the occupancy rate to stabilize and eliminate any variation due to transitions from the starting state to the stable state.

RESULTS

Simulations resulted in similar outcomes using estimates from both PRR and ROCR because, on average, the estimates were similar between the two study areas. The probability of quasi-extinction decreased rapidly as the number of pools in the system increased, while the mean time to extinction (TTE) increased with the number of pools in the system (Fig. 3.1). The probability of quasi-extinction fell below 0.05 when there were at least 50 pools in the system using estimates from either PRR or ROCR. The mean TTE for iterations in which the population went quasi-extinct increased with the number of pools in the system: for PRR scenarios, TTE increased from 14 years for 5 pools to 46 years for 25 pools (i.e., the smallest number of pools resulting in the probability of quasi-extinction >0.00) and from 11 years with only 5 pools to 73 years with 50 pools for ROCR scenarios.

The metamorph occupancy rate declined rapidly for scenarios involving a small number of pools, and the magnitude of the decline was slightly different among study areas (Fig. 3.2). The metamorph occupancy rate declined more rapidly for PRR scenarios with 5 and 10 pools compared to ROCR scenarios with the same number of pools. However, for systems containing enough pools to ensure long-term persistence (i.e., \geq 50 pools, where probability of quasiextinction \leq 0.05), the metamorph occupancy rate stabilized at almost the same value. Using estimates from PRR, the mean metamorph occupancy rate for years 30-100 was 0.156 (SD: 0.002), and similarly, the mean metamorph occupancy rate using estimates from ROCR was 0.158 (SD: 0.002).

DISCUSSION

Using available information to determine ecological thresholds seems logical, yet few studies have taken this approach. Recovery goals and management objectives are often based on historical or arbitrarily chosen population levels that may or may not reflect important ecological features of the system. Often, managers are interested in the persistence of a species (e.g., probability of extinction) or a stable population (e.g., population growth rate, $\lambda \ge 1$), and population simulations can provide managers with a useful target. By using available information and well-established techniques (i.e., PVA), I provide a method for defining and quantifying relevant ecological thresholds that can be used within an adaptive management framework. The use of existing data to determine ecological thresholds provides an objective and transparent approach for setting appropriate objectives that are the basis for management decisions.

An ecological threshold is a characteristic inherent to an ecosystem and is based only on system dynamics. However, ecological thresholds can be used to represent biological management objectives, and PVA is a useful tool to quantify these thresholds to inform utility thresholds, which are inherently value-based. This is especially true when decision makers have little information on historical levels or are uncertain which biological objectives to use as a measure of ecosystem health. PVA is most criticized for its inability to predict extinction probabilities and MVP (Beissinger 2002) due to poor information on important parameters and the inability to evaluate competing models (Boyce 1992, Ralls and Taylor 1997, Beissinger and Westphal 1998, Groom and Pascual 1998, Reed et al. 1998). I addressed these elements by developing a projection model specific to my biological systems capturing what I believe are the major drivers of the system, parameterizing the model with estimates based on several years of

data, and accounting for both sampling and process variance. However, I acknowledge that there may be other factors that influence wood frog occupancy dynamics that are not currently included in my simulations. For example, *Ranavirus* (Family: Iridovirus) has been known to cause localized reproductive failure in many amphibian species (Green et al. 2002), and occasional die-offs have been observed at select ponds PRR (Evan Grant, U.S. Geological Survey, personal communication). The inclusion of additional years of occupancy data would likely better capture the inherent variability in vernal pool systems and its impact on wood frog populations. Despite only including three years of estimates in the PVA, I believe that it is still justified to use available data to help make more informed management decisions, updating the estimates over time with monitoring data.

Incorporating ecological thresholds into an ARM framework allows for structural, environmental, parameter, and management uncertainties to be explicitly accounted for in determining an optimal management strategy and many of the criticisms of PVAs can be addressed. Criticisms of the weak ability to validate models and the effects of alternative model structures, as well as the issues of poor data and parameter estimates, can also be addressed by structuring management decisions in an adaptive management framework (Williams et al. 2002, Williams et al. 2009). By periodically updating models and parameter estimates using data from monitoring efforts, one can differentiate amongst competing models over time and reduce uncertainties around parameter estimates, resulting in more precise and accurate ecological thresholds (Nichols and Williams 2006).

Incorporating stochasticity into PVAs is important for making appropriate predictions and management decisions (Coulson et al. 2002, White 2002), especially as environmental conditions may change in the future. The iterative nature of ARM provides a useful framework

for addressing potential future changes in ecological processes or parameter values because the components of the decision analysis are revisited on a regular basis. New models can be added to the model set to reflect new factors influencing the system, and parameter estimates can be updated as more information is gathered through a monitoring program.

In my wood frog systems, I determined a minimum of 50 pools is necessary to ensure a 0.95 probability of population persistence over 100 years. If a population has \geq 50 pools, approximately 16% of the pools should support wood frog metamorphosis, given the occupancy estimates from either PRR or ROCR. These values can be incorporated into a utility function to evaluate the state of the metapopulation system and determine the best management approach to meet the biological objectives while considering the cost of management. For example, managers at PRR or ROCR may consider constructing new pools or modifying existing, but unproductive, pools in order to mitigate the effects of increasing temperatures and more variable rainfall, which may result in shorter hydroperiods and increased reproductive failure. These actions incur cost but have the potential to increase the number of pools producing metamorphs and, therefore, the metamorph occupancy rate. In my case, I incorporated the results of the PVAs into example utility functions for PRR,

$$U_t = \begin{array}{cc} 0.2870 \ln N & -0.1792 & \times (1 - 0.05x), if \ \psi_t^2 \ge 0.156 \\ 0, & if \ \psi_t^2 < 0.156 \end{array}$$

and ROCR,

$$U_t = \begin{array}{cc} 0.2372 \ln N + 0.0052 \times (1 - 0.05x), & if \ \psi_t^2 \ge 0.158 \\ 0, & if \ \psi_t^2 < 0.158 \end{array}$$

where U_t is the utility value at time *t* for a system with *N* pools, ψ_t^2 is the metamorph occupancy rate for the system at time *t*, and *x* is the number of managed pools. The logarithmic term represents the interpolated probability of persistence based on the PVA for a given number of pools in the system. The term containing the number of pools managed represents a discount for the cost associated with managing vernal pools. I truncated the utility function at zero and one. In my case, management actions that result in expected ψ_t^2 greater than the ecological threshold (i.e., 0.156 and 0.158 at PRR and ROCR, respectively) receive a utility value equal to the probability of persistence minus the cost of management. As *N* decreases while the threshold for ψ_t^2 is met, the utility decreases logarithmically. For actions resulting in expected ψ_t^2 dropping below the threshold level, there is no value associated with that management action (i.e., $U_t = 0$). Using these utility functions, management decisions can balance the competing objectives of maintaining the wood frog population and minimizing cost.

My utility functions represent my values for each of the biological and financial objectives; hence, these are simply examples. These utility functions should be modified to represent appropriate stakeholders' values for each objective in a particular scenario. For example, the penalty associated with the cost of management may be larger or smaller than the one I chose. Additionally, the decrease in utility as expected ψ_t^2 falls below the threshold could be gradual as opposed to the step-function I propose. These changes may ultimately change management decisions based on the inherent values of the stakeholders, but the framework used in the decision process is the same.

In the past, PVAs were often used to evaluate and compare the effects of different management actions on a population (Burgman et al. 1988, Shaffer 1990, Boyce 1992, Lindenmayer et al. 1993, Ruggiero et al. 1994, Mills et al. 1996). More recently, Bakker and

Doak (2008) developed an approach to explicitly incorporate the effects of management actions, while accounting for environmental and demographic stochasticity and structural uncertainty. However, these approaches rely on a predefined management strategy independent of the state of the system, making it difficult to evaluate the benefits of using multiple management actions within a given time period or account for the effects of current decisions on future decisions. Using PVA alone to establish management strategies may result in suboptimal decisions, but a model that forms the basis of a PVA can be used within a more formal decision process to guide decisions. Formal optimization routines, such as stochastic dynamic programming, identify management policies for a particular combination of values of management objectives that are state-dependent (Bellman 1957, Lubow 1995) and can be implemented within an ARM framework (Williams et al. 2002).

Using existing data and its associated uncertainties, to determine ecological thresholds and incorporate them into utility functions is consistent with the aims of ARM, in that current information current information to make the most informed decisions and update objectives and models as more information is gathered. Future decisions made through ARM are based on current information, but are updated on a regular basis to reduce uncertainty and incorporate changing stakeholder objectives.

Table 3.1. Means (SD) of posterior predictive distributions of the probability of vernal pools supporting wood frog breeding (ψ^1) at Patuxent National Research Refuge, Maryland, USA. Values were sampled from the entire posterior distribution and used to project the occupancy dynamics of wood frogs in a population viability analysis. The breeding occupancy status in year *t*-1 is represented by r_{t-1} and the metamorph occupancy status in year *t*-2 by s_{t-2} (0 = absent, 1 = present).

Hydroperiod	Spatial	r_{t-1}	S_{t-2}	2008	2009	2010
Short	Clustered	0	0	0.058 (0.023)	0.033 (0.017)	0.140 (0.053)
		0	1	0.094 (0.095)	0.059 (0.069)	0.192 (0.152)
		1	0	0.125 (0.065)	0.074 (0.044)	0.270 (0.125)
		1	1	0.168 (0.141)	0.108 (0.111)	0.314 (0.194)
	Isolated	0	0	0.148 (0.064)	0.089 (0.049)	0.307 (0.112)
		0	1	0.200 (0.159)	0.132 (0.127)	0.356 (0.206)
		1	0	0.274 (0.121)	0.176 (0.096)	0.482 (0.161)
		1	1	0.319 (0.194)	0.221 (0.170)	0.511 (0.211)
Medium	Clustered	0	0	0.385 (0.107)	0.258 (0.100)	0.611 (0.122)
		0	1	0.426 (0.207)	0.310 (0.200)	0.627 (0.190)
		1	0	0.569 (0.116)	0.422 (0.122)	0.763 (0.108)
		1	1	0.592 (0.177)	0.457 (0.195)	0.774 (0.136)
	Isolated	0	0	0.615 (0.156)	0.477 (0.172)	0.792 (0.123)
		0	1	0.630 (0.206)	0.505 (0.230)	0.795 (0.150)
		1	0	0.766 (0.118)	0.648 (0.150)	0.886 (0.082)
		1	1	0.776 (0.139)	0.664 (0.182)	0.893 (0.083)
Long	Clustered	0	0	0.976 (0.053)	0.960 (0.082)	0.989 (0.028)
		0	1	0.978 (0.055)	0.963 (0.086)	0.990 (0.028)
		1	0	0.989 (0.023)	0.981 (0.039)	0.995 (0.011)
		1	1	0.991 (0.022)	0.984 (0.038)	0.996 (0.010)
	Isolated	0	0	0.989 (0.028)	0.981 (0.045)	0.995 (0.016)
		0	1	0.990 (0.028)	0.982 (0.046)	0.995 (0.013)
		1	0	0.995 (0.011)	0.992 (0.018)	0.997 (0.006)
		1	1	0.996 (0.009)	0.993 (0.015)	0.998 (0.004)

Table 3.2. Means (SD) of posterior predictive distributions of the probability of vernal pools supporting wood frog breeding (ψ^1) at Rock Creek National Park, Washington, DC, USA. Values were sampled from the entire posterior distribution and used to project the occupancy dynamics of wood frogs in a population viability analysis. The breeding occupancy status in year *t*-1 is represented by r_{t-1} (0 = absent, 1 = present).

Hydroperiod	r_{t-1}	2009	2010	2011
Short	0	0.061 (0.118)	0.253 (0.246)	0.079 (0.141)
	1	0.098 (0.164)	0.365 (0.336)	0.127 (0.191)
Medium	0	0.478 (0.280)	0.830 (0.191)	0.571 (0.266)
	1	0.555 (0.246)	0.860 (0.182)	0.640 (0.234)
Long	0	0.929 (0.183)	0.991 (0.033)	0.944 (0.166)
	1	0.960 (0.115)	0.993 (0.026)	0.971 (0.090)

Table 3.3. Means (SD) of posterior predictive distributions of the probability of vernal pools supporting wood frog breeding (ψ^2) at Patuxent National Research Refuge, Maryland, USA and Rock Creek National Park, Washington, DC, USA. Values were sampled from the entire posterior distribution and used to project the occupancy dynamics of wood frogs within a population viability analysis.

Study area	Hydroperiod	2008	2009	2010	2011
Patuxent	Short	0.119 (0.104)	0.188 (0.145)	0.036 (0.045)	-
	Medium	0.677 (0.112)	0.781 (0.110)	0.335 (0.115)	-
	Long	0.743 (0.106)	0.831 (0.091)	0.415 (0.147)	-
Rock Creek	Short	-	0.109 (0.236)	0.306 (0.352)	0.186 (0.277)
	Medium	-	0.152 (0.278)	0.312 (0.242)	0.173 (0.196)
	Long	-	0.936 (0.142)	0.979 (0.086)	0.981 (0.066)



Figure 3.1. The probability of quasi-extinction and the mean time to extinction (TTE) for wood frog populations. Simulation scenarios consisted of combining estimated parameters distributions from (a) Patuxent National Research Refuge, Maryland, USA and (b) Rock Creek Park, Washington, DC, USA with different numbers of vernal pools: 5, 10, 25, 50, 75, and 100 pools. One thousand iterations were run for each scenario. Quasi-extinction occurred when no pools produced metamorphic wood frogs for two consecutive years. Quasi-extinction was not observed in simulations involving >50 pools.



Figure 3.2. The mean proportion of vernal pools (from 1,000 iterations) supporting wood frog metamorphosis in simulations using occupancy estimates from (a) Patuxent National Research Refuge, Maryland, USA, (b) and Rock Creek Park, Washington, DC, USA, over a 100-year time horizon for scenarios including 5, 10, 25, 50, 75, and 100 pools. Labels represent the number of pools in the scenario, and overlapping lines represent scenarios for 50, 75, and 100 pools.

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CHAPTER 4: ESTIMATING SURVIVAL, DISPERSAL, AND BREEDING PROBABILITIES OF WOOD FROGS USING MULTISTATE MARK-RECAPTURE MODELS

Many studies have investigated the factors influencing growth and survival of amphibian larval stages and assume that certain characteristics result in long-term advantages in survival and breeding. Unfortunately, few studies have investigated whether these characteristics actually influence the post-metamorphic vital rates that most influence population growth rates. I used multistate mark-recapture models to investigate the influences of natal-pond and metamorph characteristics on wood frog population dynamics at Patuxent National Research Refuge, Maryland, USA. Estimates of annual juvenile survival were negatively influenced by conductivity within natal pools (range: 0.01–0.48) but showed little relationship to metamorph characteristics. Estimates of recruitment and dispersal probabilities indicated that males mature earlier than females, and a small percentage of each sex disperses to breed at ponds other than their natal pool. Survival probabilities for adults during the non-breeding season (mid-Marchmid-February) were similar but less variable (range: 0.20 - 0.45); survival probabilities were lower for females and negatively related to mean monthly precipitation during the same period. Survival of adults during the breeding season was generally very high, and most estimates were near 1.0. Using modern analytical methods, I provide the first robust estimates of postmetamorphic vital rates of wood frogs that allow for variation in capture probabilities across time and space. I found little evidence for an effect of recent metamorph traits on juvenile survival, suggesting that wood frogs may be able to overcome initial disadvantages to have similar postmetamorphic performance. My results, combined with the large collection of knowledge on premetamorphic vital rates, provide a more complete picture of factors influencing wood frog population dynamics.

INTRODUCTION

The conditions experienced by an animal during one stage or time period in its life have been shown to affect its performance and fitness later in life (see Harrison et al. 2010). Many studies have shown influences of habitat selection and body condition in one season or life history stage on growth, fecundity, and survival at a future time, and these carry-over effects have been seen in a wide variety of taxa, including invertebrates (Phillips 2002, Hettinger et al. 2012), fish (Hamilton et al. 2008, Auer et al. 2012), birds (Norris et al. 2004, Norris and Taylor 2006, Sorenson et al. 2009), mammals (Festa-Bianchet et al. 1998, Cook et al. 2004), and reptiles (Madsen and Shine 2000). In species with complex life cycles, such as amphibians, the effects of conditions on larval stages may carry over to influence survival or fecundity within adult stages and, subsequently, population dynamics (Wilbur 1980). However, few empirical studies have tested the influence of the larval conditions on post-metamorphic demographic parameters in amphibians using robust estimation methods (but see Schmidt et al. 2012).

Many studies have investigated the factors influencing growth and survival of amphibian larval stages (e.g., Wilbur 1977, Berven 1990, Chelgren et al. 2006). Higher densities have been shown to prolong the larval period and have a negative effect on larval survival and growth rates (Wilbur 1977, Berven 1990, Berven 1995, Werner and Glennemeier 1999, Skelly et al. 2002). Additionally, size at metamorphosis has been shown to have a positive relationship with return rates and survivorship in some amphibian species (Smith 1987, Berven 1990), but other studies have found little to no effect on these same metrics (Semlitsch et al. 1988, Boone 2005).

Additionally, return rates are a product of multiple processes, namely probabilities of survival, recruitment into the breeding population, and detection; few studies have investigated how larval rearing conditions or metamorphic characteristics influence these processes (but see Schmidt et al. 2012). The studies that have followed individuals after metamorphosis often followed them for short periods (Goater 1994, Chelgren et al. 2006) or *ex situ* (Scott 1994, Morey and Reznick 2001, Altwegg and Reyer 2003).

A large number of studies have examined early life history stages of amphibians because it has been suggested that the juvenile stage is very important in regulating populations (Lampo and De Leo 1998, Hels and Nachman 2002, Conroy and Brook 2003). This implies that adult survival is relatively high and consistent; however, few studies have estimated adult survival or investigated the factors influencing it (but see Smith 1987, Berven 1990, Schmidt et al. 2012). Studies by Berven and colleagues (Berven 1990, 1995), based on life tables constructed via return rates, suggested that local wood frog (Lithobates sylvatica) population regulation should occur during the pre-metamorphic stage due to relatively high and stable adult survival. In one of the few studies to incorporate detection probabilities, Chelgren et al. (2006) found that body size and timing of metamorphosis strongly influenced the survival and initial movement probabilities for newly metamorphosed northern red-legged frogs (*Rana aurora aurora*); however, due to the nature of the study, mortality and settling probabilities were confounded. The authors acknowledge that additional studies are needed to uniquely evaluate the influence of the aquatic environment on survival, movement and breeding probabilities for post-metamorphic life history phases. I am only aware of one study that has investigated the influence of metamorphic traits on survival to first breeding occasion and breeding probabilities of amphibians using modern markrecapture methods (Schmidt et al. 2012), and these authors suggested that, despite initial

differences, smaller or later metamorphosing individuals could overcome any potential disadvantages, resulting in similar post-metamorphic performance.

I examine the widely held beliefs that conditions experienced during the larval stage influence post-metamorphic performance and address some of the shortcomings of previous studies. I conducted a mark-recapture study to investigate the influences of natal-pool and metamorph characteristics on wood frog population dynamics, specifically juvenile survival, age-specific breeding probabilities, and dispersal between breeding pools. My approach allows me to account for imperfect detection of frogs and provides robust estimates of vital rates, and evaluates the influence of covariates on these parameters. Specifically, I expected juvenile survival to be negatively related to tadpole densities, as several studies have shown that high larval densities result in delayed metamorphosis, which may have negative effects on survival to first breeding (Scott 1994, Morey and Reznick 2001, Rothermel and Semlitsch 2002). Likewise, I thought post-metamorphic survival would be positively related to the mean size at metamorphosis of each cohort (Smith 1987, Berven 1990, Morey and Reznick 2001, Altwegg and Reyer 2003). Several studies have documented the negative effect of road salt on wood frog tadpoles (Sanzo and Hecnar 2006, Karraker et al. 2008), reporting decreased survival, increased abnormalities, and reduced weight and activity with increasing levels of road salt. I expect survival probabilities of post-metamorphic individuals reared in similar habitats (as measured via conductivity, μS) would also suffer (i.e., I expected a negative relationship between juvenile survival and mean conductivity in the larval environment).

Several studies have shown that larger individuals have a decreased probability of desiccation (Thorson 1955, Ray 1958, Rittenhouse et al. 2008, Rittenhouse et al. 2009) and increased locomotor abilities (John-Alder and Morin 1990). Therefore, I expected natal dispersal

probabilities to be positively related to size at metamorphosis and increased precipitation. Transition probabilities from juvenile to adult states represent recruitment into the breeding population. I expected cohorts of larger metamorphs may recruit at an earlier age (Smith 1987, Berven 1990), and males may recruit before females. Berven (1990) found that most male wood frogs first returned to the natal pond as 1 year olds and females at 2 years old; therefore, I expected probabilities of transitions from juvenile to adult classes to be age and gender specific.

METHODS

Study Species

The wood frog is one of the most widely distributed frog species in North America and ranges from the southern Appalachians to Alaska (Martof and Humphries 1959). Wood frogs live approximately 3-5 years (Berven 1982, Bastien and Leclair 1992). They rely on small, temporary, predator-free pools for breeding (Berven 1982, Berven 1990, Hopey and Petranka 1994, Lichko and Calhoun 2003) and use upland habitats surrounding breeding pools during the non-breeding season (Berven and Grudzien 1990, Regosin et al. 2003, Rittenhouse and Semlitsch 2007). Wood frogs are explosive breeders, with all breeding within a pool occurring within approximately one week (Berven 1990). At my study site, breeding occurred from late-February to early-March, and metamorphs emerged from the pools approximately three months later in late-May or early-June.

Study Area and Field Methods

My research was conducted at Patuxent Research Refuge (PRR), Laurel, Maryland, USA. PRR covers 5,280 ha, and approximately 75% of the refuge is deciduous forest consisting mainly of oak (*Quercus*) and hickory (*Carya*). Van Meter et al. (2008) estimated that approximately
2,200 vernal pools are located on PRR, and 53 of those pools have been monitored for the presence of amphibian breeding and successful metamorphosis since 2006. Vernal pools at PRR are typically $< 4,000 \text{ m}^2$ and characterized by nearly complete canopy cover and little aquatic vegetation. The terrestrial habitat surrounding most pools consists of open understory.

Using the subset of monitored pools at PRR, I selected four pairs of pools (Table 4.1) to use in an experiment to examine the effects of a chosen management action (i.e. liner installation) on wood frog population parameters. Each pair included one pool that supported successful metamorphosis during most years, while the other pool rarely supported metamorphosis due, in part, to short hydroperiods. I attempted to extend the hydroperiod of the poorly producing pool in each pair by deepening the pool basin and installing an ethylene propylene diene monomer (EPDM) liner. Liners were installed during the summer of 2009 following amphibian metamorphosis. Lastly, two pairs of pools were isolated from other pools and each other by \geq 300 m (isolated), while the other two pairs of pools were part of a cluster of three or four pools separated by < 30 m (clustered). This allowed me to test the effect of distance between pools on dispersal probabilities.

Mark-recapture sampling began during the breeding season before pools were manipulated (in 2009) by capturing adults by hand and dip net (Fig. 4.1). After the breeding period, but prior to tadpole metamorphosis, drift fences and pitfall traps were installed surrounding all eight pools to capture newly metamorphosed wood frogs. Fences consisted of aluminum flashing buried to a depth of 15 cm approximately 5 m from the edge of the high water level of each pool. Pitfall traps consisted of 36-L buckets placed every 5 m on either side of the fence. Fences were removed after tadpoles metamorphosed but were replaced each of the

subsequent 3 years prior to the breeding season to capture breeding individuals entering and exiting the pool and each year's metamorph cohort.

I captured and marked adult wood frogs during the breeding seasons 2009-2012. Adults captured in pitfalls were sexed based on external features (size, color, nuptial pads), and unmarked individuals were given a unique visual implant elastomer (VIE) mark. After handling, frogs were released on the opposite side of the fence on which they are captured. Breeding adults were captured both entering and exiting the breeding pools. A major assumption of markrecapture studies is that marks are not lost or misidentified, and there are concerns that these assumptions may be violated with VIE marks (Grant 2008). Marked animals were examined by >2 observers during initial marking and every recapture occasion to verify color combinations and reduce the chance of misidentification, and a batch toe clip, specific to the pool and year of initial capture, was used to evaluate mark loss. Post-metamorphic juvenile frogs were intercepted at the fences from 2009-2011, and all, or a subset, were batch marked with a toe clip unique to their natal pool and year of metamorphosis. The snout-vent length (SVL) of all marked juvenile frogs was measured at the time of capture, and I included the average size at metamorphosis (mm) for each cohort in models to explain variation in juvenile cohort survival and dispersal probabilities.

Pool-specific characteristics thought to influence survival, dispersal, or breeding probability were measured several times throughout each breeding season and averaged for use in analysis. These included conductivity (μ S) and egg mass density (egg masses/m³; as a surrogate for tadpole density). I obtained estimates of the number of egg masses in each pool using a dependent double observer sampling technique (Nichols et al. 2000); the estimated number of egg masses was then divided by the volume of the pool (mean volume as measured

throughout the breeding season) to obtain egg mass density (masses/m³). I also obtained precipitation totals from the weather station at Baltimore-Washington International Airport, Baltimore, Maryland, USA, and used monthly precipitation during the nonbreeding season (Jun-Feb) as a covariate on adult survival during the non-breeding season.

Model Structure and Parameterization

General Model.-I used a multistate mark-recapture model (MSMR; Arnason 1973, Lebreton et al. 2009) to obtain estimates of survival and transition probabilities for individuals in states representing location (pools), age, and sex. I estimate apparent survival for two periods during each year: (1) the breeding season, which typically occurs in late-February and lasts approximately 1 week, and (2) the non-breeding season, which corresponds to the approximately 51 week period between breeding seasons. I define my four general parameters as: (1) recapture probability, p_{ij}^k , is the probability that a marked individual of state k is captured, given it is alive, in year i (i = 2009, 2010, 2011, 2012) on survey j (entering pool, j = 1; exiting pool, j = 2), (2) breeding survival probability, ϕ_{i1}^k , is the probability that a marked individual in state k in year i survives the breeding period, (3) apparent non-breeding survival probability, ϕ_{i2}^k , is the probability that a marked individual in state k in year i survives the non-breeding period and remains within the study area (cohort-specific for juvenile states), and (4) transition probability, ψ_c^{rs} , is the probability that an individual from metamorph cohort c in state r in year i transitions to state s in year i+1, given it survived. Transitions were not possible during the breeding season, so all transitions occurred during the non-breeding season (i.e., between *i* and i+1; Fig. 4.1).

State definitions and model constraints.—To address my hypotheses regarding the influence of covariates on post-metamorphic survival and breeding probabilities, I considered five states that an individual could be in at each pool, where each state represented the

individual's age, and when possible, sex (Fig. 4.2). These states include: recent metamorph (J_0), 1-year-old juvenile (J_1), 2-year-old juvenile (J_2), adult male, or adult female. Recent metamorphs were initially captured as they left their natal pool, and given they survived the nonbreeding season, they must transition to an 1-year-old juvenile or recruit to become a breeding adult at either their natal pool (male: Ad_M^A , female: Ad_F^A) or disperse to breed at the paired pool (male: Ad_M^B , female: Ad_F^B). Likewise, surviving 1-year-old juveniles must transition to 2-year-old juveniles or become a breeding adult at either their natal or paired pool. Based on previous studies, I assumed that all surviving juveniles bred by their third year (Berven 1990), so 2-yearold juveniles must transition to one of the four possible adult states. Finally, adult wood frogs are thought to have 100% fidelity to the pool in which they first breed (Berven 1990), and I did not observe any movements of adults between pools. Accordingly, I assumed adults did not transition between states ($\psi_i^{ss} = 1$, where *s* is the same adult state in year *i* and *i*+1, Fig 4.2).

Juveniles did not breed, and therefore, were not available to be detected. I fixed the detection probability for these states at 0. Survival probabilities for unobservable states are not uniquely estimable in MSMR models (Kendall et al. 1997, Kendall 1999, Kendall and Nichols 2002), so I chose to set survival of all juvenile states (J_0 , J_1 , J_2) equal. I fixed the survival probabilities for juvenile states during the breeding season to 1 and interpreted the nonbreeding survival estimates as annual survival probability.

Model Set.—In addition to the previously discussed variables I thought may influence juvenile survival, I also investigated the effects of an experimental management action intended to increase the hydroperiod of certain pools; I expected a positive response in juvenile survival following liner installation in the managed pools. I also included other covariates explaining variation in adult survival probabilities, to avoid bias in my estimates of juvenile survival,

dispersal, and breeding probabilities. I expected survival of adults during the breeding period to vary by sex, but it was not obvious which sex may have higher survival probability. Females may have larger energy demands from egg development, but they typically spend little time in the breeding pool. Conversely, males spend more time in the pool and may suffer negative effects from calling and competing for females. The effects of these energy requirements may also carry over into the non-breeding season, resulting in differences in survival during this period. I expected adult survival during the non-breeding period to be positively related to mean monthly precipitation because of the reduced likelihood of desiccation within the terrestrial habitat (Berven 1990, Rittenhouse et al. 2008, Rittenhouse et al. 2009). For similar reasons, I expected females to have higher non-breeding survival probabilities than males because of their larger size on average.

Because the model set was very large when considering all possible combinations of covariates, I used a sequential approach to model selection. Using a general model structure for my parameters of biological interest, I fit models that included all possible combinations of factors thought to influence detection probability (Table 4.3). Then, using the most parsimonious detection structure(s), I tested my hypotheses related to transition probabilities (recruitment and dispersal). Retaining the best transition probability model structures, I fit models that included all possible combinations of factors thought to influence survival probabilities. I acknowledge that this approach may not be optimal, but it provides a practical approach for dealing with many potential variables.

I used Program MARK (White and Burnham 1999) to obtain parameter estimates, and I used an information-theoretic approach for model selection (Burnham and Anderson 2002). The best model had the lowest Akaike's Information Criteria adjusted for small sample size and

overdispersion (QAIC_c). Additionally, I used Akaike weights, w_i , as a measure of the relative amount of evidence for each model in the model set. To determine the relative importance of my various factors on survival, I used cumulative QAIC_c weights ($w_+(j)$; Burnham and Anderson 2002), which are calculated by summing the Akaike weights of each model in which a covariate is included. Because cumulative QAIC_c weights rely on a balanced model set, I only calculated them for covariates influencing survival probabilities. A goodness-of-fit test is not currently available for MSMR models with individual covariates, so I used my global model and the median *c* approach to adjust my model selection criteria for overdispersion (White and Burnham 1999).

RESULTS

I captured 6,488 individual frogs with 7,549 total captures (Table 4.2). The pools in my first pair of clustered pools were <5m apart, making it difficult to determine the target pool for breeding adults. Individuals entered and exited the manipulated pool in successive days, usually exiting on the side adjacent to the control pool, and there was little evidence of breeding in the manipulated pool (only 8 egg masses). Because I could not definitively establish intended breeding location, I treated captures at these locations as a single pool (Table 4.2). This pool contained the second largest breeding population with 18% of all captured individuals. The largest breeding population accounted for ~70% of all captured individuals (Iso1C). Despite large adult breeding populations and abundant egg masses, all but one pool experienced complete reproductive failure in 2011 (Table 4.2). There appeared to be two potential causes of reproductive failure: 1) predation by green frog (*Lithobates clamitans*) tadpoles in some managed pools and 2) die-offs due to *Ranavirus* (Family: Iridovirus).

There was some evidence of overdispersion within my data (c = 1.60, SE = 0.04), so I used QAIC_c values when comparing models and associated weights. My most general model included egg mass density, conductivity, and size at metamorphosis effects on juvenile survival, $\phi^{J}(\text{egg_dens+cond+meta_size})$; pool, year, and sex effects on adult survival within the pool (i.e., breeding season, ϕ_{i1}^{Ad} (pool+yr+sex)); precipitation and sex effects on adult survival within terrestrial habitat surrounding the pools (i.e., nonbreeding season, ϕ_{i2}^{Ad} (precip+sex)); and pool, year, sex, and directional (i.e., entry or exit) effects on detection probability, p(pool+yr+sex+dir). I only observed four individuals move between pools; therefore, I was only able to fit models with constant dispersal probabilities, $\psi^{disp}(.)$, and modeled transition probabilities from juvenile to adult states dependent on age, sex, and size at metamorphosis, $\psi^{J,Ad}$ (age*sex*meta_size). I estimated a different intercept for each juvenile to adult transition, effectively resulting in an age, sex, and size at metamorphosis interaction. The mean values for each potential covariate included in models are shown in Table 4.1. The mean monthly precipitation was 12.05, 8.81, 12.76 cm/month during the 2009, 2010, and 2011 non-breeding seasons, respectively.

Using this global model, I explore 14 other detection structures, representing simplifications of my general detection structure (Table 4.3). The most parsimonious model included pool and year effects (w = 0.45), as did all of the top four model structures, cumulatively accounting for 88.6% of the weight. Direction of movement (i.e., entry or exit) and sex had low cumulative model weights ($w_+(dir) = 0.309$, $w_+(sex) = 0.270$), and these covariates explained little of the variation in detection probabilities. These variables acted as "pretending variables" (Anderson 2008) because they did not improve the fit over the simpler model (i.e., nearly identical values of $-2\log(\mathcal{L})$), the regression coefficients were near zero, and the 95% confidence intervals widely overlapped zero. Therefore, I used the top detection model structure, p(pool+yr), in my subsequent models.

The most parsimonious model structure for age-specific recruitment probabilities included only age- and sex-specific transitions ($\psi^{J,Ad}$ (age*sex), QAIC_c = 4817.49). The model including an interaction between size at metamorphosis, age, and sex was within 3 QAIC_c units (QAIC_c = 4819.79), but the 95% confidence intervals for the coefficients overlapped zero indicating uncertainty about the effect of metamorph size on age-specific recruitment (ψ^{J_0,Ad_F^A} : β_{meta} = -0.03, SE = 0.08; ψ^{J_1,Ad_F^A} : β_{meta} = 0.17, SE = 0.27; ψ^{J_2,Ad_F^A} : β_{meta} = -0.56, SE = 4.42). I retained the best transition probability structures, $\psi^{disp}(.)$ and $\psi^{J,Ad}$ (age*sex), representing dispersal and natal pool recruitment, respectively, when exploring models explaining variation in survival probabilities.

The most parsimonious model suggested that juvenile wood frog survival was most influenced by conductivity in the natal pool, adult survival during the breeding season varied by pool and year, and adult nonbreeding survival varied by sex and mean monthly precipitation (w = 0.33; Table 4.4). However, there was considerable model uncertainty, as 14 models had QAIC_c weights >0.01 and accounted for 85.3% of the total weight. Conductivity (w_+ (cond) = 0.96) was the only covariate explaining variation in juvenile survival (i.e., $w_+(j) > 0.5$; Barbieri and Berger 2004). There was little evidence that larval density or size of metamorphosis influenced juvenile survival (w_+ (meta_size) = 0.37, w_+ (egg_dens) = 0.21). Variation in adult breeding survival was best explained by differences among pools (w_+ (pool) = 0.85) and years (w_+ (year) = 0.96). There was little evidence of differences in adult breeding survival between males and females (w_+ (sex) = 0.34). However, adult nonbreeding survival varied by mean monthly precipitation (w_+ (precip) = 0.92) and sex (w_+ (sex) = 0.97). The top model included only the variables with $w_+(j) > 0.5$, so

I made inferences about the effects of these variables on their respective parameters from the regression coefficient estimates from this top model.

Model-averaged estimates of annual juvenile survival (ϕ^{J}) varied widely among cohorts, ranging from 0.01 (SE = 0.05) to 0.48 (SE = 0.07) (Table 4.5), and increased conductivity in the natal pool resulted in decreases in juvenile survival (β_{cond} = -0.029, SE = 0.012). Adult breeding survival (ϕ_{i1}^{Ad}) was 1.0 in most pools in 2010 and 2011 (Table 4.6). However, survival during the 2012 breeding season was substantially lower, and 95% confidence intervals were wide. Adult survival during the non-breeding season (ϕ_{i2}^{Ad}) was fairly consistent but ranged from 0.20 (SE = 0.04) for females in 2011 to 0.45 (SE = 0.04) for males in 2010 (Table 4.7). Contrary to my prediction, ϕ_{i2}^{Ad} was negatively influenced by mean monthly precipitation (β_{precip} = -0.175, SE = 0.062; Fig. 4.3), but I did find some evidence for a difference among the sexes with females having lower survival probabilities than males (β_F = -0.587, SE = 0.198; Table 4.7 and Fig. 4.3).

Only 15% (SE = 3.3%) of surviving 1-year-old wood frogs attempted to breed, and most of these individuals returned to breed in their natal pool ($\psi^{J_0,Ad_M^A} = 0.13$, SE = 0.03; $\psi^{J_0,Ad_F^A} =$ 0.02, SE = 0.01; Table 4.8). A small portion of 1-year-olds were males that dispersed to the neighboring pool to breed ($\psi^{J_0,Ad_M^B} = 0.02$, SE = 0.02). Approximately half of surviving juvenile 2-year-old frogs attempted to breed, and similarly most returned to their natal pool ($\psi^{J_1,Ad_M^A} =$ 0.23, SE = 0.08; $\psi^{J_1,Ad_F^A} = 0.15$, SE = 0.05). A small percentage of 2-year-olds were females that dispersed to a neighboring pool and attempted to breed ($\psi^{J_1,Ad_F^B} = 0.05$, SE = 0.06). Approximately equal percentages of surviving 3-year-old frogs breeding for the first time were male ($\psi^{J_2,Ad_M^A} = 0.58$, SE = 0.23) and female ($\psi^{J_2,Ad_F^A} = 0.42$, SE = 0.23), and all attempted to breed in their natal pool. Model-averaged detection probabilities ranged from 0.03 (SE = 0.02) to 0.37 (SE = 0.06; Table 4.9). Most estimates of detection probabilities for pools with large breeding populations were generally between 0.25 and 0.40. Overall, detection was highest in 2011 and lowest in 2010.

DISCUSSION

Despite numerous studies investigating the influences of pool and larval characteristics on survival of amphibians (e.g., Wilbur 1977, Berven and Chadra 1988, Semlitsch et al. 1988, Semlitsch and Wilbur 1988, Berven 1990, Berven 1995, Werner and Glennemeier 1999, Skelly et al. 2002), there is little information on how these traits influence long-term survival, breeding, and dispersal probabilities to inform an understanding of pool-breeding amphibian population dynamics and few accounting for imperfect detection (but see Schmidt et al. 2012). Using a MSMR model, I was able to robustly test widely accepted hypotheses that conditions within natal pools affect survival and recruitment of individuals once they metamorphose. I also provide the first estimates of post-metamorphic and adult survival of wood frogs within terrestrial habitat surrounding breeding pools and age-specific recruitment and dispersal probabilities. My findings suggest that size at metamorphosis and larval densities in natal pools have little effect on annual juvenile survival of wood frogs at my study site and that juvenile and adult survival is similar. Unfortunately, due to a small number of dispersing metamorphs, I was unable to test my hypotheses regarding the influence of pool and larval characteristics on dispersal probabilities.

The lack of a relationship between either size at metamorphosis or egg mass density and juvenile survival in this study is consistent with other studies that suggest that survival to and age at first reproduction are not dependent on larval characteristics (Semlitsch et al. 1988, Beck and

Congdon 1999, Boone 2005, Schmidt et al. 2012). Despite initial size differences, smaller metamorphs may have higher growth rates post-metamorphosis (Beck and Congdon 1999, Boone 2005), effectively eliminating any potential size advantages relatively quickly. This may be especially true for species, such as the wood frog, that metamorphose early in the summer, such that there is a relatively long period in the terrestrial habitat prior to winter. Smaller metamorphic wood frogs may make up size differences within the terrestrial habitat prior to their first winter (Beck and Congdon 1999), resulting in similar survival probabilities. It is important to note that by using the mean size at metamorphosis of each cohort, I may have lost power to detect a relationship; however, there was little variation in size of metamorphs in each cohort (% coefficient of variation range: 0.03 - 0.06), suggesting that mean metamorph size may be a sufficient metric representing individual size at metamorphosis. The difficulty of individually marking metamorphs also precludes the use of individual covariates. The lack of carry-over effects from egg-mass density may suggest that densities were not high enough for competition to significantly affect development. In laboratory experiments, Wilbur (1977) and Berven and Chadra (1988) found that increased tadpole densities had negative effects on larval development, but Licht (1974) found that food was not a limiting resource in vernal pools. Though I observed extremely high densities at times (>2,400 tadpoles/ m^3 , assuming 642 eggs/egg mass; Berven 1988), these pools experienced complete reproductive failure prior to metamorphosis. Densities experienced by cohorts that did metamorphose were typically <500 tadpoles/m³, likely not high enough to be near carrying capacity. Future studies should investigate this further, as densitydependence may become more important if successful metamorphosis occurs when tadpole densities reach levels observed in this study.

Only one of my hypotheses regarding the effects of natal pool characteristics on juvenile survival was supported. As I hypothesized, there was a negative effect of increased conductivity levels on juvenile survival. This provides support to the growing body of literature indicating that natal pool conditions carry over to influence post-metamorphic survival of amphibians (e.g., Smith 1987, Semlitsch et al. 1988, Berven 1990, Scott 1994, Chelgren et al. 2006); however, this variable, in most cases, likely represents a measure of anthropogenic effects and not differences in life history strategies. Additionally, I observed low adult survival during the breeding season for frogs in Iso2C, which is near a road and had extremely high conductivity levels. Many of the adults exiting the pool were bloated, which may indicate some effect of the high conductivity levels. These relationships, both statistical and anecdotal, highlight the importance of reducing pollution run-off into vernal pools. Previous studies have shown that increased salt concentrations can limit populations through decreased larval survival (Sanzo and Hecnar 2006, Karraker et al. 2008), and I provide evidence that conductivity negatively affects juvenile, and perhaps adult, survival, further contributing to declines in populations (Biek et al. 2002, Vonesh and De la Cruz 2002).

My estimates of juvenile and adult non-breeding survival were similar to return rates of post-metamorphic wood frogs at vernal pools within 10 km of my study sites observed by Berven (1990). He observed 24-38% of wood frogs surviving their first year, while my estimates of annual juvenile survival were mostly between 27% and 49% (Table 4.5). However, he did not account for detection probabilities, which I found to be fairly low and variable. Survivorship in his studies may be biased low, and it is impossible to separate variation in survivorship from his study due to variation in detection or survival probabilities. Detection probabilities and/or survival may have been higher in his studies. I observed similar survival probabilities for post-

metamorphic juveniles, which are consistent with a 3-5 year life span (Berven 1982, Bastien and Leclair 1992), but adult survival was less variable. Berven and colleagues (Berven 1990, Berven and Grudzien 1990) suggested that adult survivorship was fairly consistent and that the large population fluctuations in this species were due to variability in pre-metamorphic survival. Increases in breeding adults occurred one and two years after reproductively successful years for males and females, respectively. Though I did not explicitly investigate tadpole survival, I observed similar responses in the breeding populations after successful years, as well as declines in captures after a year where only one pool produced metamorphs.

Survival of adult wood frogs during the breeding season was high, as would be expected for such a short time period (i.e., <2 weeks). With the exception of Iso2C, adult breeding survival was near 1.0 in 2010 and 2011 (Table 4.6). Iso2C was within 5 m of a heavily-used road, had high conductivity levels, and many adults captured exiting Iso2C were bloated, suggesting that the low estimates of breeding survival may be due to high amounts of runoff or some unknown disease. Adult survival during the 2012 breeding season was substantially lower, and estimates of variance were extremely large. This discrepancy may be due to the relatively small sample sizes for 2012 or it may be due to confounding between the last survival estimates and detection probabilities. The discrepancies in the last survival estimates may also be due to the assumption that all individuals breed by 3-years-old. If some individuals remain juveniles into their fourth year but are assumed to be available for capture, survival probabilities could be biased low. A longer term study is necessary to test this assumption.

My results provided evidence that both sex and precipitation were important in explaining variation in adult wood frog survival during the non-breeding season but not necessarily in the expected direction. I predicted that precipitation would have a positive

influence on adult non-breeding survival, but I observed the opposite (Fig. 4.3). Several studies have shown positive relationships between precipitation and wood frog survival (Berven 1990, Berven 1995, Rittenhouse et al. 2009), so it is not obvious why I might have observed this relationship. Increased precipitation has been shown to facilitate dispersal in amphibians (Thorson 1955, Ray 1958, John-Alder and Morin 1990, Rittenhouse et al. 2008, Rittenhouse et al. 2009), and the negative relationship may be due to permanent emigration out of the study area. Further investigation should be conducted to test this hypothesis by sampling all pools within an area to minimize the probability an individual will disperse outside of the study area or by combining mark-recapture and radio telemetry. I found that females had lower non-breeding survival probabilities than males (Fig. 4.3), which was also seen by Berven (1990). This may be due to larger energetic requirements of females during egg development prior to the breeding season (Church et al. 2008). Other longer-lived amphibian species skip breeding to offset the energetic requirements of breeding (Church et al. 2008), but wood frogs are thought to breed every year after reaching maturity, which I assumed in my models. Because >3 years of data are required to observe an individual transitioning from breeding to skipped breeding back to breeding, a longer data set is necessary to be able to robustly test this assumption and obtain precise estimates of the probability of skipping breeding.

Using the estimated juvenile survival from the largest cohort of marked juveniles (Iso1C in 2009; Table 4.5) and estimates of conditional transition probabilities (Table 4.8), I calculated the proportion of males and females recruiting at each age as:

$$\alpha_{y}^{sex,pool} = \frac{\delta_{y}^{sex,pool}}{\frac{B}{pool=A} \quad \overset{3}{y=1} \delta_{y}^{sex,pool}},$$

where $\alpha_y^{sex,pool}$ is the proportion of individuals of a particular sex surviving to breed for the first time at their natal (*A*) or neighboring pool (*B*) at age *y*. The probability an individual of a particular sex survives to and breeds for the first time at their natal (*A*) or neighboring pool (*B*) at age *y* is represented by $\delta_y^{sex,pool}$. For example, the probability that a male survives and returns to breed in its natal pool at age 2 is:

$$\delta_2^{M,A} = \phi^{J^2} \times \psi^{J0,J1} \times \psi^{J1,Ad_M^A}$$

The denominator represents the sum of all δ_y^{pool} , for a given sex, and rescales each δ_y^{pool} so that all α_y^{pool} for a given sex sum to 1. I also calculated the corresponding standard errors for each $\alpha_y^{sex,pool}$ using the delta method (Seber 1982, Powell 2007).

I observed similar patterns of recruitment as in other wood frog studies based on life tables (Berven 1982, 1990). Nearly half of all males bred for the first time in their natal pool as 1-year-olds ($\alpha_1^{M,A} = 0.48$, SE = 1.36), and all male dispersers bred as 1-year-olds ($\alpha_1^{M,B} = 0.08$, SE = 1.37). The proportion of males recruiting declined with age, with >80% recruiting by 2years-old ($\alpha_2^{M,A} = 0.28$, SE = 1.37; $\alpha_3^{M,A} = 0.16$, SE = 1.29). Most females did not begin breeding until 2-years-old ($\alpha_1^{F,A} = 0.19$, SE = 5.42; $\alpha_2^{F,A} = 0.41$, SE = 5.07; $\alpha_3^{F,A} = 0.26$, SE = 4.40), and all dispersing females bred at 2-years old ($\alpha_2^{F,B} = 0.15$, SE = 4.46). Based on life tables, Berven (1982, 1990) found a similar pattern at pools located within 10 km of my study area. However, Berven (1982) observed later maturity of individuals at study sites at higher elevations for both males and females. It appears that my estimates of age-specific recruitment are intermediate to those in Berven's two study areas, despite one of his sites being geographically close to my sites. One of my assumptions was that all individuals bred within one of the two paired pools, which may not be true. Wood frogs typically stay within 300 m of their breeding pool (Rittenhouse and Semlitsch 2007), but juveniles have been known to make long-distance movements up to 2.5 km (Berven and Grudzien 1990). I may have negatively biased estimates of dispersal and juvenile survival if individuals permanently emigrated from the sampled pools.

Wood frogs have been shown to have high phenotypic plasticity (Berven 1982, 1988, Berven and Gill 1983, Relya 2002), and many variables could influence age of maturity. The idea of "cohort iteroparity" (Wilbur and Rudolf 2006) may provide an evolutionary explanation for the large variation in age of recruitment in my study system (Schmidt et al. 2012). Short-lived species with highly variable reproductive success (e.g., wood frog) may benefit if individuals reach maturity at different ages, as an alternative to increasing adult survival. If the offspring of an individual recruit at different ages, it is likely that at least some of them will be able to reproduce successfully. This could potentially result in similar fitness for the parent without increasing life span.

My results suggest that dispersal between pools at my study area is less frequent than observed by Berven and Grudzien (1990). They observed 21% of males and 13% of females dispersing between two populations. I only observed 4 dispersal events and estimated 8.1% of males and 14.8% of females dispersed to the pool neighboring their natal pool. Additionally, all four individuals that dispersed were the only marked juveniles from their cohort (Iso1M in 2010), and they dispersed to a pool with a breeding population orders of magnitude larger (Iso1C). Despite marking thousands of juveniles at the larger pool (Table 4.2), I never observed any dispersal to the smaller population. This may suggest that some individuals are attracted to larger populations for any number of reasons, including greater numbers of calling males or better habitat (Marsh and Trenham 2001), but recolonization of small local populations that go extinct is unlikely (Green et al. 2011). It is more likely that surviving adults return to breed in

small populations despite occasional reproductive failure to keep the local population extant (Church et al. 2008). As long as reproductive failure does not occur several years in a row, adult survival is high enough to maintain at least a small population. This suggests that management actions attempting to influence dispersal probabilities may have less impact on population dynamics and persistence, for a given amount of effort, than those focusing on survival at all life history stages.

Unfortunately, I was not able to test all of my *a priori* hypotheses due to low sample sizes and logistical constraints. Detection probabilities were fairly low and variable (Table 4.9), decreasing the precision of estimates of survival, recruitment, and dispersal probabilities. Pool conditions played a role in the integrity of the drift fences and the ability to open pit fall traps. Rainy periods resulted in flooded pit falls, making capture difficult, and gaps in drift fences, allowing frogs to trespass. Additionally, it is possible that some individuals wintered inside the drift fence, resulting in lower detection. Other studies of vernal-pool-breeding amphibians have exceptionally high detection probabilities (Church et al. 2008), likely due to relatively low vagility of the study species, highlighting the need to account for differences in detection on a case-by-case basis.

In summary, I provide some of the first estimates of survival, recruitment, and dispersal probabilities of a vernal-pool-breeding anuran using modern mark-recapture methods. I also identify important factors influencing these parameters and provide evidence to support more recent hypotheses that natal pool characteristics may not have as large an effect on post-metamorphic survival as previously thought. However, this hypothesis should be tested for other amphibian species with life histories that may not allow recent metamorphs to overcome differences experienced during the larval stage (e.g., metamorphosis in late summer). My results

suggest that post-metamorphic survival varies by year, cohort, and sex due to variation in abiotic factors, implying that post-metamorphic survival rates, juvenile survival in particular, may help regulate wood frog populations. I offer a more robust analysis of an important but little studied aspect of wood frog life history, which can be combined with the large collection of knowledge on pre-metamorphic vital rates to provide a complete picture of wood frog population dynamics.

Table 4.1. Mean values of covariates thought to influence annual juvenile apparent survival (ϕ^J) of wood frogs at 7 vernal pools at Patuxent National Research Refuge, Maryland, USA. Distance between pools is the distance between two paired pools, which share the same name prefix (e.g., Iso1 or Clust2). Pool names indicate spatial arrangement (Iso: isolated, Clust: clustered), pair (1 or 2), and whether a pool was managed (C: control, M: managed). I only report values for when cohorts of metamorphs were observed.

	Distance	Egg i (egg	mass de masses	ensity (m ³)		Con	ductivity	(µS)	Metam	orph size	e (mm)
Pool	between pools	2009	2010	2011	_	2009	2010	2011	2009	2010	2011
Iso1C	300 m	0.48	0.53			41.63	33.25		16.78	18.82	
Iso1M	500 III		0.08				64.86			20.10	
Iso2C	1 000 m			0.11				683.50			17.40
Iso2M	1,000 III		0.04				120.60			18.50	
Clust1C	NA	0.09	0.55			41.67	46.80		16.00	19.14	
Clust2C	20 m	0.05				31.14			17.40		
Clust2M	30 m										

Table 4.2. The number of newly marked individual wood frogs captured at seven vernal pools at Patuxent National Research Refuge, Maryland, USA, 2009-2012. Pool names describe the spatial arrangement (isolated: "Iso", clustered: "Clust"), pair (1 or 2), and whether a pool was managed or not (managed: "M", control: "C"). Juvenile frogs were captured after metamorphosis as they exited the natal pools, and it was not possible to determine sex of juveniles. Adult male and female frogs were captured as they entered and/or exited breeding pools. No juveniles were captured in 2012.

		2009			2010			2011		2	012	
Pool	Juvenile	Male	Female	Juvenile	Male	Female	Juvenile	Male	Female	Male	Female	Total
Iso1C	633	100	1	2,030	552	82	0	704	368	70	61	4,601
Iso1M	0	0	0	4	45	6	0	4	8	2	9	78
Iso2C	0	0	0	0	12	12	59	30	30	5	5	153
Iso2M	0	0	0	173	14	4	0	71	41	18	11	332
Clust1C	213	0	0	10	315	46	0	359	186	36	33	1,198
Clust2C	19	6	0	0	1	0	0	22	13	8	3	72
Clust2M	0	0	0	0	16	4	0	10	8	11	5	54
Total	865	106	1	2,217	955	154	59	1,200	654	150	127	6,488

Table 4.3. Model selection results for models explaining variation in detection probability of wood frogs at breeding pools at Patuxent National Research Refuge, Maryland, USA. Only models with QAIC_c weight (*w*) >0.01 are reported. Δ QAIC_c is the difference between QAIC_c values for a particular model and the top model, and *k* is the number of parameters. The QAIC_c value for the top model is 4017.49. Year and direction (i.e., entry or exit) are denoted yr and dir, respectively. The most general structure was used for all other parameters:

 $\phi^{J}(\text{egg_dens+cond+meta_size}), \phi^{Ad}_{i1}(\text{pool+yr+sex}), \phi^{Ad}_{i2}(\text{precip+sex}), \psi^{disp}(.), \psi^{J,Ad}(\text{age*sex+meta_size}).$

Model	ΔQAIC_{c}	Model Likelihood	W	k	$-2\log(\mathcal{L})$
pool + yr	0.00	1.00	0.45	40	7590.45
pool + yr + dir	1.57	0.46	0.20	41	7589.73
pool + yr + sex	2.01	0.37	0.16	41	7590.42
pool + yr + dir + sex	3.60	0.17	0.07	42	7589.73
pool	4.24	0.12	0.05	38	7603.72
pool + sex	5.50	0.06	0.03	39	7602.50
pool + dir	5.56	0.06	0.03	39	7602.60

Table 4.4. Model selection results for models explaining variation in juvenile (ϕ^J), adult breeding (ϕ^{Ad}_{i1}), and adult non-breeding (ϕ^{Ad}_{i2}) survival probabilities of wood frogs at breeding pools at Patuxent National Research Refuge, Maryland, USA, with QAIC_c weight (w) >0.01. Δ QAIC_c is the difference between QAIC_c values for a particular model and the top model, and k is the number of parameters. The QAIC_c value for the top model is 4812.30. Covariates include conductivity (cond), egg mass density (egg_dens), size at metamorphosis (meta_size), pool, year (yr), sex, and mean monthly precipitation (precip). I set the structure for dispersal (ψ^{disp}), recruitment ($\psi^{J,Ad}$), and detection (p) probabilities as: $\psi^{disp}(.)$, $\psi^{J,Ad}$ (age*sex), p(pool + yr).

Model	$\Delta QAIC_{c}$	Model Likelihood	W	k	$-2\log(\mathcal{L})$
$\phi^{J}(\text{cond}), \phi^{Ad}_{i1}(\text{pool} + \text{yr}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	0	1.00	0.33	34	7597.87
$\phi^{J}(\text{cond} + \text{meta_size}), \phi^{Ad}_{i1}(\text{pool} + \text{yr}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	1.09	0.58	0.19	35	7596.37
$\phi^{J}(\text{cond}), \phi^{Ad}_{i1}(\text{pool} + \text{yr} + \text{sex}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	2.59	0.27	0.09	35	7598.79
$\phi^{J}(\text{egg_dens} + \text{cond}), \phi^{Ad}_{i1}(\text{pool} + \text{yr} + \text{sex}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	3.44	0.18	0.06	36	7596.92
$\phi^{J}(\text{cond} + \text{meta_size}), \phi^{Ad}_{i1}(\text{pool} + \text{yr} + \text{sex}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	3.72	0.16	0.05	36	7597.35
$\phi^{J}(\text{egg_dens} + \text{cond} + \text{meta_size}), \phi^{Ad}_{i1}(\text{pool} + \text{yr} + \text{sex}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	5.19	0.07	0.02	37	7596.48
$\phi^{J}(\text{cond}), \phi^{Ad}_{i1}(\text{yr}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	5.42	0.07	0.02	28	7625.94
$\phi^{J}(\text{cond}), \phi^{Ad}_{i1}(\text{pool} + \text{yr} + \text{sex}), \phi^{Ad}_{i2}(\text{sex})$	6.23	0.04	0.01	34	7607.85
$\phi^{J}(\text{egg_dens} + \text{cond}), \phi^{Ad}_{i1}(\text{yr}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	6.27	0.04	0.01	29	7624.07
$\phi^{J}(\text{cond} + \text{meta_size}), \phi^{Ad}_{i1}(\text{yr}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	6.44	0.04	0.01	29	7624.34
$\phi^{J}(\text{egg_dens}), \phi^{Ad}_{i1}(\text{pool} + \text{yr} + \text{sex}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	6.59	0.04	0.01	35	7605.18
$\phi^{J}(\text{cond} + \text{meta_size}), \phi^{Ad}_{i1}(\text{pool} + \text{yr} + \text{sex}), \phi^{Ad}_{i2}(\text{sex})$	6.76	0.03	0.01	35	7605.46
$\phi^{J}(\text{egg_dens} + \text{meta_size}), \phi^{Ad}_{i1}(\text{pool} + \text{yr}), \phi^{Ad}_{i2}(\text{precip} + \text{sex})$	6.85	0.03	0.01	35	7605.61
$\phi^{J}(\text{egg_dens} + \text{cond}), \phi^{Ad}_{i1}(\text{pool} + \text{yr} + \text{sex}), \phi^{Ad}_{i2}(\text{sex})$	6.92	0.03	0.01	35	7605.72

Table 4.5. Model-averaged estimates of annual apparent survival probabilities (ϕ^J), standard errors (SE), and 95% confidence intervals (CI) for juvenile (i.e., pre-breeding) wood frogs and mean conductivity (μ/S) at Patuxent National Research Refuge, Maryland, USA. I only present survival estimates for cohorts for which I marked recently metamorphosed individuals.

Year	Pool	Mean conductivity (μ/S)	ϕ^J	SE	95% CI
2009	Iso1C	41.63	0.40	0.04	(0.32, 0.49)
	Clust1C	41.67	0.37	0.07	(0.26, 0.51)
	Clust2C	31.14	0.45	0.09	(0.28, 0.64)
2010	Iso1C	33.25	0.48	0.07	(0.35, 0.62)
	Iso1M	64.86	0.27	0.10	(0.12, 0.50)
	Iso2M	120.6	0.08	0.07	(0.01, 0.36)
	Clust1C	46.8	0.40	0.08	(0.26, 0.55)
2011	Iso2C	683.5	0.01	0.05	(0.00, 1.00)

Table 4.6. Model-averaged estimates of breeding survival probabilities (ϕ_{i1}^{Ad}) and 95% confidence intervals (CI) for adult male and female wood frogs at Patuxent National Research Refuge, Maryland, USA, 2010-2012. Pool names indicate each pool's spatial arrangement (Iso: isolated, Clust: clustered), pair (1 or 2), and treatment (C: control, M: managed). All individuals captured at Clust1C and Clust1M were combined for analysis.

			-	Female						Male		
		<u>2010</u>		<u>2011</u>		<u>2012</u>		<u>2010</u>		<u>2011</u>		<u>2012</u>
Pool	ϕ_{i1}^{Ad}	95% CI										
Iso1C	1.00		1.00		0.71	(0.34, 0.92)	1.00		1.00		0.73	(0.47, 0.89)
Iso1M	1.00		1.00		0.54	(0.01, 1.00)	1.00		1.00		0.39	(0.01, 0.99)
Iso2C	0.55	(0.04, 0.97)	0.72	(0.12, 0.98)	0.17	(0.00, 0.96)	0.34	(0.02, 0.92)	0.66	(0.10, 0.97)	0.12	(0.00, 0.97)
Iso2M	1.00		1.00		0.67	(0.19, 0.95)	1.00		1.00		0.53	(0.11, 0.91)
Clust1C	1.00		1.00		0.96	(0.09, 1.00)	1.00		1.00		0.97	(0.01, 1.00)
Clust2C	1.00		1.00		0.87	(0.00, 1.00)	1.00		1.00		0.69	(0.04, 0.99)
Clust2M	1.00		1.00		0.96	(0.09, 1.00)	1.00		1.00		0.97	(0.07, 1.00)

Table 4.7. Model-averaged estimates of non-breeding survival probabilities (ϕ_{i2}^{Ad}) and 95% confidence intervals (CI) for adult wood frogs at Patuxent National Research Refuge, Maryland, USA.

		Male		Female
Year	$\phi^{\it Ad}_{i2}$	95% CI	$\phi^{\it Ad}_{i2}$	95% CI
2009	0.34	(0.27, 0.41)	0.21	(0.15, 0.30)
2010	0.45	(0.37, 0.53)	0.31	(0.20, 0.44)
2011	0.31	(0.23, 0.41)	0.20	(0.13, 0.28)

Table 4.8. Model-averaged estimates of age-specific recruitment probabilities (ψ^{rs}) and standard errors (SE) of wood frogs at Patuxent National Research Refuge, Maryland, USA. The state in year *i* at sampling occasion *j* = 2 is represented by the superscript *r* and the state at *i* + 1, *j* = 1 by *s*. *J_y* represents a *y*-year-old juvenile, and Ad_{sex}^{site} represents an adult of sex *sex* (M: male, F: female) at natal pool *A* or neighboring pool *B*. For example, ψ^{J_0,J_1} is the probability that a recent metamorph (*J*₀) will remain a juvenile in its second year (*J*₁) and not attempt to breed, and ψ^{J_1,Ad_F^B} is the probability that a 1-year-old juvenile becomes a female breeding at the pool neighboring its natal pool as a 2-year-old. I assumed that all frogs recruited by 3 years old and that adults bred every year and at only one pool in their lifetime (i.e., $\psi^{Ad_M^A,Ad_M^A} = \psi^{Ad_F^A,Ad_F^A} = 1$).

Parameter	Estimate	SE
	0.02	0.04
$\psi^{j_{0},j_{1}}$	0.83	0.04
ψ^{J_0,Ad^A_M}	0.13	0.03
ψ^{J_0,Ad^B_M}	0.02	0.02
ψ^{J_0, Ad_F^A}	0.02	0.01
ψ^{J_0,Ad_F^B}	0.00	0.00
ψ^{J_1,J_2}	0.56	0.13
ψ^{J_1,Ad^A_M}	0.23	0.08
ψ^{J_1,Ad_M^B}	0.00	0.00
ψ^{J_1, Ad_F^A}	0.15	0.05
ψ^{J_1, Ad_F^B}	0.05	0.06
ψ^{J_2,Ad^A_M}	0.58	0.23
ψ^{J_2,Ad^B_M}	0.00	0.00
ψ^{J_2,Ad_F^A}	0.42	0.23
ψ^{J_2,Ad_F^B}	0.00	0.00

Table 4.9. Model-averaged estimates of detection probabilities (*p*) and 95% confidence intervals (CI) for adult wood frogs entering and exiting breeding pools at Patuxent National Research Refuge, Maryland, USA.

		• • • • •		• • • • •		0.010
		<u>2010</u>		2011		2012
Pool	p	95% CI	p	95% CI	р	95% CI
Iso1C	0.18	(0.14, 0.23)	0.27	(0.23, 0.31)	0.26	(0.19, 0.34)
Iso1M	0.03	(0.01, 0.10)	0.04	(0.01, 0.15)	0.04	(0.01, 0.15)
Iso2C	0.27	(0.07, 0.65)	0.37	(0.11, 0.73)	0.36	(0.10, 0.75)
Iso2M	0.27	(0.17, 0.39)	0.37	(0.27, 0.49)	0.36	(0.24, 0.51)
Clust1C	0.13	(0.10, 0.18)	0.20	(0.16, 0.25)	0.20	(0.14, 0.27)
Clust2C	0.03	(0.00, 0.21)	0.05	(0.01, 0.30)	0.05	(0.01, 0.29)
Clust2M	0.07	(0.03, 0.17)	0.11	(0.04, 0.25)	0.11	(0.04, 0.25)



Figure 4.1. A diagram of parameters estimated using multistate mark-recapture models across three sampling periods, denoted by the year *i* and entry (j = 1) or exit (j=2). This represents a subset of parameters estimated during my 3-year study from 2009 to 2012 (T = 7 total sampling periods). The parameters p_{ij} , ϕ_{i1}^k , ϕ_{i2}^k , and ψ_c^{rs} and states are defined in the *Methods: Model Structure and Parameterization* section. Breeding adults were captured as they entered and exited pools in late-February or early-March. I estimated survival, ϕ_{i1}^k , of adults in state *k* during the breeding season in year *i*. Drift fences were not installed until after breeding in 2009, so I was unable to estimate breeding survival probabilities for that year. I estimated recapture probabilities, p_{ij} , for each sampling occasion *j* (i.e., entry or exit) in each year *i* following the first sampling occasion (i.e., i = 2009, j = 2). Recently-metamorphosed wood frogs were captured and marked in early-June of each year and remained in an unobservable juvenile state until they became a breeding adult. Transition probabilities, ψ_c^{rs} , were estimated for the nonbreeding season for individuals from cohort *c* in state *s* at i = i, j = 2 and state *r* at i = i + 1, j = 1. I assumed that individuals remained within their state during the breeding season.



Figure 4.2. Possible transition probabilities between juvenile and adult life history stages of wood frogs. Transitions occur just prior to the breeding season each year. Conditional on survival, juveniles must remain a juvenile with probability, $\psi^{J_y, J_{y+1}}$, or transition to a breeding adult with probability, $\psi^{J_y, Ad_{sex}^{site}}$, where J_y is a *y*-year-old juvenile and Ad_{sex}^{site} is an adult of sex *sex* (M: male, F: female) at natal pool *A* or neighboring pool *B*. Solid lines represent age-class-only transitions (i.e., no dispersal), and dashed lines represent age and pool transitions. I assumed that all frogs recruited by 3 years old and that adults bred every year and at only one pool in their lifetime (i.e., $\psi^{Ad_M^A, Ad_M^A} = \psi^{Ad_F^A, Ad_F^A} = 1$).



Figure 4.3. The relationship between adult survival during the non-breeding season (ϕ_{i2}^k) and mean monthly precipitation (cm/month; Jun-Feb) for male and female wood frogs at Patuxent National Research Refuge, Maryland, USA. Light lines represent <u>+</u>1 SE.

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