ABSTRACT

Title of Document:	HIERARCHICAL MODELS FOR ANALYSIS OF SPECIES DISTRIBUTIONS AND ABUNDANCES: DEVELOPMENT AND APPLICATIONS
	Elise Faye Zipkin, PhD, 2012
Directed By:	Professor William F. Fagan Department of Biology

There is a strong need for statistical methods that can maximize the utility of ecological data while providing accurate estimates of species abundances and distributions. This dissertation aims to build on current statistical models using Bayesian hierarchical approaches to advance these methods.

Chapters one, two, and three utilize a multi-species modeling framework to estimate species occurrence probabilities. *Chapter one* presents a model to assess the community response of breeding birds to habitat fragmentation. The results demonstrate the importance of understanding the responses of both individual, and groups of species, to environmental heterogeneity while illustrating the utility of hierarchical models for inference about species richness. *Chapter two* demonstrates how the multi-species modeling framework can be used to evaluate conservation actions through a component that incorporates species-specific responses to

management treatments. In *Chapter three*, I develop a method for validating predictions generated by the multi-species model that accounts for detection biases in evaluation data. I build competing models using wetland breeding amphibian data and test their abilities to predict occupancy at unsampled locations.

Chapters four and five develop count models that are used to estimate population abundances in relation to environmental and climate variables. In *Chapter four,* I employ a Poisson regression designed to determine how climate affects the annual abundances of migrating monarch butterflies. I incorporate the climate conditions experienced both during a spring migration phase, as well as during summer recruitment. In *Chapter five*, I analyze sea duck data to characterize the spatial and temporal distributions along the U.S. and Canadian Atlantic coast. I model count data for five species using a zero-inflated negative binomial model that includes latitude, habitat covariates, and the North Atlantic Oscillation. The results from these two chapters demonstrate how Bayesian models can be used to elucidate complicated species-climate relationships.

The chapters of this dissertation illustrate creative development and application of advanced statistical methods to complex biological systems. These applications provide a practical framework for dealing with highly aggregated species and uneven species distributions in community analyses, as well as a method for evaluating occurrence estimates that accounts for detection biases. My results highlight the dynamic relationships between population and community structure, habitat, and climate.

HIERARCHICAL MODELS FOR ANALYSIS OF SPECIES DISTRIBUTIONS AND ABUNDANCES: DEVELOPMENT AND APPLICATIONS

By

Elise Faye Zipkin

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2012

Advisory Committee:
Professor William F. Fagan, Chair
Professor Ralph Dubayah
Associate Professor Karen R. Lips
Dr. J. Andrew Royle
Dr. Emily D. Silverman
Associate Professor Jonathan Z. Simon

Acknowledgements

I would like to thank my advisors, Bill Fagan and Andy Royle, whose wisdom, guidance, and help over the last several years has been invaluable. I also thank Emily Silverman, who has been a wonderful mentor to me for more than ten years, as well as the other members of my committee, Karen Lips, Jonathan Simon, and Ralph Dubayah. I fully appreciate that there would be no dissertation without the support and commitment of everyone on my committee.

I have had several brilliant and productive collaborators over the past several years who have taught me a tremendous amount including Beth Gardner, Evan Grant, Amielle DeWan, Viviana Ruiz-Gutierréz, Leslie Ries, Sarah Converse, Cliff Kraft, Marc Kéry, Angela White, John Sauer, and Jim Nichols. The G2 basement office at Patuxent has provided an immensely fun and collaborative work environment over the last four years and I thank everyone who has had a desk in that room, especially Florent Bled, Mitch Eaton, Sophie Veran, Sabrina Servanty, Richard Chandler, Dave Miller, Pete Blank, Brady Mattsson and Charles Yackulic. Additionally, the Fagan lab group has been a remarkable source of support especially Thomas Mueller, Elise Larsen, Paula Casanovas, and Chris Che-Castaldo.

I also thank everyone who participated in the data collection efforts. Without their work, my work would not be possible.

Finally I thank my family: my parents who have opened every possible door for me; my siblings Mollie, Ariel, and Derek, who teach me how life should be lived; and my fiancé Brian, who makes the idea of graduating and moving forward all the more exciting!

Table of Contents

List of Tables

List of Figures

Introduction

The discipline of ecology is fundamentally the study of species abundance and distribution (Ricklefs 1996). Much research in ecology is devoted to testing hypotheses about the biotic and abiotic processes that affect patterns of species occurrences. Understanding the biological mechanisms that create these patterns requires accurate information on the spatial locations of organisms. Thus, inherent in the study of ecology is the need for reliable counts of individuals, species in an area, communities within a region, and so on. Yet, it is nearly impossible to obtain such information for most all species, because data collection efforts that are designed to census an area are inevitably limited by budget and personnel constraints, and organisms move, hide, or are simply difficult to detect. Because of these limitations, statistical methods that accurately summarize data to estimate abundance and explain distributional patterns are essential to ecological inference and conservation decision-making (Brown and Gibson 1983; Hanski 1999; MacArthur and Wilson 1967; Kerr 1997; Ricklefs 2004).

Heterogeneity in abundance and distribution, which is a key manifestation of the processes that ecologists strive to understand, also creates difficulties during the estimation process. Estimation of population size is frequently frustrated by the spatial and temporal aggregation of individuals, which lead to highly-skewed distributions and many zero counts. The same problem confronts researchers seeking simple numerical descriptions of ecological communities (e.g., richness and composition) because, during sampling, common species are overrepresented while rare species are missed.

The challenges to understanding species distribution and abundances are compounded when observers fail to detect rare or solitary organisms. Detection probabilities that vary based on behavioral or habitat characteristics can result in misleading inferences on the abundance and occurrences of species as well as their relationships to habitat (Boulinier et al. 2008; MacKenzie et al. 2002; Tyre et al. 2003). In the context of community analyses (e.g., inferences on groups of taxonomically similar species), failure to account for heterogeneity in detection can lead to an underestimation of the number and distribution of rare species (Queheillalt et al. 2002) and can alter conservation decision-making (Meir et al. 2004).

As the bias introduced by detection heterogeneity exemplifies, the estimation of population abundance and the quantification of community structure (e.g., species richness) is complicated by variability in landscape structure (Gaston 2003), which can as easily confound as elucidate the processes being investigated. Thus, it is necessary to explicitly determine the relationship between species occurrence probabilities and/or expected abundance with various habitat and climate features in order to correctly estimate population abundance and community richness. Understanding the species-habitat relationship allows researchers to determine how landscape heterogeneity affects patterns of species occurrence and is essential for making predictions about species' responses to future environmental and climate changes.

My research is focused on the development and application of methods to more accurately and effectively describe populations and communities, using sound metrics to quantify species abundances and distribution, as well as richness and composition. In this dissertation, I advance current methodologies by building five unique Bayesian hierarchical models. I utilize a generalized linear modeling framework for each of these studies, tailoring my approach to address a specific question or hypothesis. The dissertation is broadly divided into two sections. The first section (chapters one, two and three) focuses on the analysis of species occurrences and distributions, while also emphasizing community-level assessments based on species-level models. The chapters in the first section use a modeling framework to fit individual species occurrence models and link them at the community level (Dorazio and Royle 2005; Dorazio et al. 2006), while accounting for the detection probabilities of each species. I refer to this type of model as either a “multi-species” or “community” model throughout the dissertation.

Chapter one presents a case study of the basic version of the multi-species occurrence model to a community of breeding birds in a fragmented landscape in upstate New York. This chapter reveals the utility of the community modeling approach by demonstrating 1) the importance of accounting for individual species responses to habitat features (rather than combining rare or functionally similar species) and 2) how the hierarchical structure of the modeling framework leads to improved inferences at the species and community levels.

Chapter two builds on the work of the first chapter by using the multi-species modeling framework to compare estimates of bird assemblage and richness in different regions within the Catoctin Mountains in Maryland. While the first chapter presents an occurrence analysis based on habitat features, the second chapter takes this one step further by including covariates that account for differences in habitat structure that might be influenced by management strategies within regions. Furthermore, the model in this chapter includes data augmentation, a technique that allows for species richness estimation by using the multi-species model to analyze an augmented dataset that includes all-zero encounter histories for every potential, unobserved, species in the community in addition to the original data. My use of data augmentation provides a framework for considering how conservation and management actions may affect all species in a region and not just those that are common or were observed during data collection.

Chapter three presents an approach for validating occurrence estimates generated by the multi-species model using amphibian data from wetlands in the Chesapeake and Ohio Canal National Historical Park in Maryland. In this chapter, I use the area under the receiver operator curve (AUC) to determine which of several competing models is best able to predict the occurrences of multiple species at unsampled wetlands and in future years. In modifying the use of receiver operator curves, I account for potential detection biases in the data that are used during model evaluation, providing an improved method for assessing the predictive abilities of multi-species occurrence models.

The second section of the dissertation (chapters four and five) shifts from modeling occurrence data to modeling population abundances in relation to environmental and climate characteristics. The chapters in this section use count models (Poisson and negative binomial) to describe on how spatially heterogeneous landscapes can result in patchy or aggregated distributions of individuals within a population.

In Chapter four, I use a Poisson regression model to assess how weather variables affect the spatial and temporal abundances of monarch butterflies in Ohio, using data collected across the state and over 13 years. The model in this chapter contains a number of parameters that account for both local climate conditions (e.g., drought indices and growing degree day) as well as the environment experienced by individuals along their migratory route (e.g., precipitation and temperature). The results indicate that there are a number of important, interacting, climate factors affecting the final abundances of monarchs at their breeding grounds. I show that simpler analyses that do not include interactions among variables would have been unable to capture the complex ways in which climate can impact a migrating species.

Chapter five presents a more complicated version of a count model using ten years of data from five sea duck species along the eastern Atlantic coast. Unlike monarch butterflies, sea ducks tend to aggregate spatially, requiring a count model with a higher variance to mean ratio. As such, I developed a negative binomial model to estimate how environmental and climate variables affect local abundances of sea ducks. Because the sea duck survey was not designed to collect data according to each species' latitudinal range, I included a zero-inflation component (similar to the occurrence models in the first section) to account for the spatial distribution of each species. The results show that while local habitat characteristics can affect sea duck abundances, the North Atlantic Oscillation was the only factor to have a significant, yet variable, affect on all five species.

The complex and uncontrollable aspects inherent in living and dynamic ecosystems present significant challenges not only to field researchers, but also to statisticians. To improve statistical methods for ecology, it is necessary to understand more than sophisticated quantitative methodologies; it is also critical to understand the details of the biological and environmental system under study and the techniques used to measure the system. Thus, the goal of my dissertation is to advance the development of statistical methodologies through specific examples. Each case study presents an instance in which traditional analyses were less informative in answering the research question as compared to the Bayesian hierarchical approach.

Chapter 1: Impacts of forest fragmentation on species richness: a hierarchical approach to community modeling

Published in: Journal of Applied Ecology, 46, 815-822, 2009.

Coauthors: Amielle DeWan, J. Andrew Royle

Abstract

Species richness is often used as a tool for prioritizing conservation action. One method for predicting richness and other summaries of community structure is to develop species-specific models of occurrence probability based on habitat or landscape characteristics. However, this approach can be challenging for rare or elusive species for which survey data are often sparse. Recent developments have allowed for improved inference about community structure based on species-specific models of occurrence probability, integrated within a hierarchical modeling framework. This framework offers advantages to inference about species richness over typical approaches by accounting for both species-level effects and the aggregated effects of landscape composition on a community as a whole; thus leading to increased precision in estimates of species richness by improving occupancy estimates for all species, including those that were observed infrequently. We developed a hierarchical model to assess the community response of breeding birds in the Hudson River Valley, New York to habitat fragmentation and analyzed the model using a Bayesian approach. The model was designed to estimate species-specific occupancy and the effects of fragment area and edge (as measured through the perimeter and the perimeter/area ratio), while accounting for imperfect detection of species. We used the fitted model to make predictions of species richness within forest fragments of variable morphology. The model revealed that species richness of the observed bird community was maximized in small forest fragments with a high perimeter/area ratio. However, the number of forest interior species, a subset of the community with high conservation value, was maximized in large fragments with low perimeter/area ratio. Our results demonstrate the importance of understanding the responses of both individual, and groups of species, to environmental heterogeneity while illustrating the utility of hierarchical models for inference about species richness for conservation. This framework can be used to investigate the impacts of land-use change and fragmentation on species or assemblage richness, and to further understand trade-offs in species-specific occupancy probabilities associated with landscape variability.

Introduction

With increasing development pressure on natural landscapes, managers and conservation scientists must determine the most effective ways to preserve the integrity of ecosystems and maintain biodiversity. Inherent in the goals of any conservation effort is the desire to protect as many ecosystem components and processes as possible (Margules and Pressey 2000; Williams et al. 1996). Many conservation and monitoring programs focus on species or population-level approaches because this can be a concrete and clear way to aid in the preservation of biodiversity (e.g. Myers et al. 2000; Pearce et al. 2008; Wilhere et al. 2008). Species richness (the total number of species in a region) is another more comprehensive, and frequently used, state variable on which to base conservation and management decisions (Yoccoz et al. 2001). However, it can be difficult to gauge richness in variable environments (O’Dea et al. 2006; Vellend et al. 2008). Thus, to prioritize conservation action it is critical to have reliable estimates of species richness and to understand how environmental factors affect species-specific patterns of occurrence across a landscape (Boulinier et al. 2001; Cabeza et al. 2004; Fischer et al. 2004; Lepczyk et al. 2008; Soares and Brito 2007)

There are two challenges in using community level summaries such as species richness in conservation and management applications. First, species identity is not preserved in many standard analyses used for inference about richness, which are based on simple aggregate species numbers (species-accumulation curves, Gotelli and Colwell 2001) or encounter frequencies (capture-recapture methods, Boulinier et al. 1998). However, species-specific patterns of occurrence should be accounted for in modeling approaches (Fischer et al. 2004) because the response of species richness to features that can be manipulated (landscape, habitat) is necessarily species-specific. A second issue is that in most practical situations species are detected imperfectly. The importance of addressing the biasing effects of imperfect detection on community assessments is widely acknowledged (Boulinier et al. 1998; Kéry et al. 2008; Nichols et al. 1998; O’Dea et al. 2006). Moreover, because detectability naturally varies by species (Boulinier et al. 1998), we expect that observed summaries of community structure (e.g. based on species lists) are biased towards abundant and widespread species, which are likely to show diminished response to ecological gradients.

One method for examining species richness in heterogeneous landscapes is to estimate species occurrence probabilities, or occupancy, based on localized habitat characteristics (MacKenzie et al. 2006). Occupancy can be an effective assessment method (Manley et al. 2005), generally requires less effort and expense than estimating total abundance of all species (MacKenzie et al. 2006), and readily allows for imperfect detection of species (MacKenzie et al. 2002). Multi-species occupancy models have been used for inference in community studies in a number of situations, including estimation of richness and community overlap (Dorazio and Royle 2005), construction of individual species-based accumulation curves (Dorazio et al. 2006), and in determining the influence of habitat and landscape variation on richness (Kéry and Royle 2008; Kéry and Royle 2009; Russell et al. 2009).

In addition to understanding total species richness, inferences on the number of rare, endangered, or functionally important species are frequently a variable of interest in conservation planning and monitoring programs (Samu et al. 2008). Occupancy estimates for rare species and guild or assemblage richness (number of species in a subset of the population) can be more informative about areas of high conservation priority than assessments on only species that are common. Unfortunately, it can be difficult to get reliable estimates of occupancy for rare and/or elusive species because traditional sampling efforts often do not generate enough data for standard analyses (Queheillalt et al. 2002; Stockwell and Peterson 2002). Some approaches to mitigating this problem combine data on rare, but functionally similar, species (e.g. by genus) or use indicator species to deduce occupancy of those species with limited data (Fleishman et al. 2001; O'Connell et al. 2000; Sergio et al. 2006). Such approaches discard valuable information about species-specific responses, and could be misleading or erroneous if rarely observed species respond differently than indicator species (Andelman and Fagan 2000; Kéry et al. 2008; Lawler and White 2008). The question remains regarding the most efficient and cost effective method for estimating the occurrence and distribution of uncommon and elusive species (MacKenzie et al. 2005; Thompson 2004).

Our research is motivated by a desire to develop a community-level quantitative framework for predicting areas of conservation value, and to provide high quality baseline data for vertebrate monitoring programs in urbanizing landscapes. To this end, we present a recently developed approach for assessing community composition based on species-specific occupancy and detection (Dorazio and Royle 2005) in which individual species occurrence models are linked together within a hierarchical (or multi-level) model (Gelman and Hill 2007; Royle and Dorazio 2008). Many multi-species field studies and monitoring programs have limited data on a large portion of observed species; as such, typical species-by-species analyses are simply unable to provide occurrence estimates or information about the effects of environmental factors on occurrence probabilities. An advantage of the hierarchical modeling framework over typical species richness analyses is that it accounts for both species-level effects as well as aggregated effects of landscape/habitat on the community as a whole (Kéry and Royle 2008; Kéry and Royle 2009), leading to a more efficient use of available data and increased precision in occupancy estimates, especially for infrequently observed species. We demonstrate the strengths of this approach by applying the hierarchical modeling framework to a bird community in forest fragments across the Hudson River Valley (HRV), New York (DeWan et al. 2009), a biologically diverse and ecologically significant region that is under intense development pressure, in the northeastern United States (Finton et al. 2000; Smith et al. 2001). Efforts are underway to prioritize the landscape for conservation actions, yet little is known about many of the species in the region (DeWan et al. 2009). We focused our analyses on the community response to habitat fragmentation by modeling species-level changes in occupancy to two factors with well-established effects on the success of breeding birds: forest fragment area and edge-effects as measured by responses to perimeter, and perimeter/area ratio (P/A) (Helzer and Jelinski 1999; Rafe et al. 1985).

Methods

Background

We used a hierarchical model that links species-specific detection and occupancy, which are then related (across species, at the community level) through an additional component of the hierarchical model (Dorazio and Royle 2005; Dorazio et al. 2006). A hierarchical (sometimes referred to as multi-level or state-space) model is one in which various biological and sampling components are formally specified and related to one another in a pyramid-like structure (Gelman and Hill 2007; Royle and Dorozio 2008). For example in the context of estimating occupancy, hierarchical models can help distinguish absence from non-detection by explicitly incorporating models that specify presence vs. absence as one process and then detection vs. non-detection as another process that is dependent upon whether or not the species is in fact present. Hierarchical models posit weak, stochastic relations rather than deterministic relations among parameters and processes (Link 1999; Link et al. 2002), resulting in improved estimation of individual parameters by considering them in context of a group of related variables (Bayesian shrinkage: "borrowing strength from the ensemble") (Link and Sauer 1996). In the context of our community model, this allows for increased precision of occurrence estimates for rare or elusive species through utilization of collective community data (Russell et al. 2009) and improved “composite” analyses of species groups (Sauer and Link 2002). With limited resources and budgets, many multi-species data collection efforts have very small sample sizes – to such an extent that it is not possible to carry out formal inference on a species-by-species basis. The hierarchical modeling approach allows for the most effective use of available data while not requiring *a priori* assumptions on group structure or relatedness among species.

Study site

The data come from a breeding bird survey collected over a two-year period (15 May - July 1, 2006, and 15 May - July 1, 2007) at 72 randomly selected independent points in deciduous and mixed-deciduous forest fragments across the Hudson River Valley, New York. The sampling locations ranged over the entire 9546 km^2 region which includes all or part of nine counties that border the Hudson River, north of New York City. Points were located at least 500 m apart using Hawth’s stratified random sampling tool (Beyer 2004), and then mapped and field-checked, eliminating those that: 1) had recent disturbance that altered the cover classification (n=1), 2) were too dangerous to access (e.g. steep ravine) (n=4), or 3) did not receive private landowner permission to access the site (n=21). Forest fragments ranged in size from 0.14 – 8677.4 hectares (μ = 533.7 ha), while perimeter/area ratio ranged from 0.08 – 1.5 km/ha (μ = 0.2). Two trained observers recorded the presence of all species seen or heard during the 10-minute, 250 m fixed-radius point counts at each sampling station (Hutto et al. 1986). Sites were visited on three separate occasions during the breeding season (once each per 2-week period) although not all sites were surveyed both years. The perimeter and area of the fragment in which the point occurred was recorded. A total of 78 species were observed in this study. Of these, the data for 32 species were particularly sparse with less than 20 detections each over the entirety of the sampling season. Because of the small size of the dataset, typical single species approaches for estimating occupancy were inadequate for the majority of observed species. For more details on the sampling design and region see DeWan et al. (2009).

The model

The repeated sampling protocol allows for non-detection to be discerned from point-level absence at each location (MacKenzie et al. 2002). We developed a hierarchical model which assumes that site-specific occupancy (i.e., “true” presence/absence) for species $i=1,2,\ldots,N$ at site $j=1,2,\ldots,J$, denoted $z(i,j)$, where $z(i,j)$ = 1 if species i occurs in site j and is zero otherwise. The model for occurrence is specified as $z(i,j) : Bern\left(\psi_{i,j}\right)$ where $\psi_{i,j}$ is the probability that species i occurs at site j. The state variable z(i,j) is usually not known with certainty. Instead, we observe data $x(i,j,k)$ for species i at site j during sampling period k, which are also assumed to be Bernoulli random variables if species *i* is present (i.e., if $z(i,j) = 1$); otherwise, if $z(i,j) = 0$, then $x(i,j,k) = 0$ with probability 1. The observation model is represented by $x(i, j,k) \sim Bern\left(p_{i,j,k} \cdot z(i, j)\right)$ where $p_{i,j,k}$ is the detection probability of species *i* for the k^{th} sampling period at site *j*, if species *i* is present at site *j*. Note that the model satisfies the condition that detection is a fixed zero when a species does not occur (because $z(i,j) = 0$).

In the simplest specification of the model, the occurrence and detection probabilities, ψ and p, are determined by unspecified species and site level effects (Dorazio et al. 2006). These effects are incorporated into the model linearly on the logit-probability scale: $\text{logit}\left(\psi_{i,j}\right) = u_i + \alpha_j$ and $\text{logit}\left(p_{i,j}\right) = v_i + \beta_j$ where u_i and v_i are species level effects and α_j and β_j are site level effects on occurrence and detection, respectively. Because high abundance species are likely to be both easier to detect and more prevalent across the landscape, we modeled a correlation (ρ) between occurrence and detection in the model by allowing u_i and v_i to be jointly distributed such that $\left[u_i, v_i \middle| \Sigma\right] \sim N\left(0, \Sigma\right)$ where $\left(\sigma_u^2, \sigma_v^2\right)$ are the variance components among species for occurrence and detection, respectively, and σ_{uv} is the covariance of the 2 x 2 matrix Σ (Dorazio and Royle 2005; Kéry and Royle 2008).

Extensions of this basic model have explicitly incorporated landscape and survey characteristics into the probabilities of occupancy and detection (Kéry and Royle 2009; Russell et al. 2009). We followed this approach, and modeled the occurrence probability for species *i* at *j* by incorporating site-specific habitat characteristics. In this case we used the size and relative shape of the forest fragment in which the point count occurred. Since counts were conducted in a 250 m radius, occupancy and detection estimates for individual species are provided at the point (not fragment) level. Thus we are considering how occupancy at a random point is affected by the area and shape of the forest fragment in which it occurs. We incorporated fragment area, perimeter, and P/A in the occupancy estimates by assuming that the logit transform of the occurrence probability was a linear combination of a species effect and the site specific habitat characteristics as follows:

$$\text{logit}\left(\psi_{i,j}\right) = u_i + \alpha 1_i \text{perimeter}_j + \alpha 2_i \text{area}_j + \alpha 3_i \text{P/A}_j .$$

We standardized the covariates so that the means of the perimeter, area and P/A data were zero. Thus, the inverse-logit of u_i is the occurrence probability for species *i* in sites with "average" habitat characteristics. The coefficients $\alpha 1_i$, $\alpha 2_i$ and $\alpha 3_i$ are the effects of perimeter, area and P/A, for species *i*, respectively. The detection probability for species *i* was assumed to vary based on the date of the survey (linear and squared effects) and the year of the survey. We assumed that the community was closed (i.e. the species pool remained constant) over the two years during which the survey was conducted, but added in a year effect (constant across species) to account for shifting detection between the two years as a result of annual fluctuations in seasonality:

$$\text{logit}\left(p_{i,j,k}\right) = v_i + \beta 1_i \text{date}_{j,k} + \beta 2_i \text{date}^2{}_{j,k} + \beta 3\ \text{year}_{j,k} .$$

Our model contains seven parameters for each species in the community, and one (year effect) that is estimated across species. Since observations were sparse for many species in the sample, estimating all of these parameters would not be possible if the data were analyzed on a species-by-species basis. As such, we added an additional hierarchical component of the model by assuming that the species-level parameters were random effects, each governed by community-level "hyper-parameters". For example, we assumed that $\alpha 1_i \sim N(\mu_{\alpha 1}, \sigma_{\alpha 1})$ where $\mu_{\alpha 1}$ is the community response (mean across species) to perimeter and $\sigma_{\alpha 1}$ is the standard deviation (among species), thus the hyper-parameters are simply the mean and variance for each habitat and sampling covariate as measured across species (Kéry and Royle 2009).

We estimated model parameters and community summaries using a Bayesian analysis of the model with vague priors for the hyper-parameters (e.g. uniform distribution from 0 to 1 for community level occupancy and detection covariates; normal distributions with mean zero and variance 1000 for community level habitat and sampling covariates). Hierarchical models are naturally analyzed by Bayesian methods (Gelman and Hill 2007). We carried out our analysis with WinBUGS (Spiegelhalter et al. 2003), general purpose software for Bayesian analysis that uses Markov chain Monte Carlo (MCMC). The advantage of WinBUGS is that it only requires specification of the model, and not a technical development of the MCMC algorithm (see Appendix 1.1 for model code and additional details).

Results

Species richness and community level responses

The mean estimates for the community response to fragment perimeter and area were negative, while the response to P/A was positive (see Table 1.1 for summaries of the hyper-parameters). This suggests that, in general, the mean probability of occupancy across species in this community was higher at points in smaller, more irregularly shaped fragments than in larger fragments with less edge. The posterior intervals for each of the community hyper-parameters contain both positive and negative values (Table 1.1), which is a manifestation of the variability in the community. In our study, which encompasses a diverse bird community, we would naturally expect the response of individual species to vary with landscape fragmentation. Thus, diffuse posterior distributions for the community level habitat covariates are as expected and simply reflect the diversity within the community.

We used the model to make predictions of species richness at localized points across a landscape with heterogeneous forest fragments that varied by area and P/A (Figure 1.1). Species richness was maximized in small areas with high perimeter to area ratios (large amounts of edge habitat) (Figure 1.1 – left panel). However, assemblage richness of forest interior breeding birds (17 species), a subset of the population with high conservation value, was maximized in large fragments with less edge (Figure 1.1 – right panel).

Species-specific responses

Mean probabilities of occurrence varied widely among species, ranging from 6.5% to 98.5%. Detection was low for many species and also varied widely (7.1%-75.9%). There was a strong correlation between occupancy and detection (posterior mean for ρ was 0.73, 95% posterior interval: 0.52-0.88; Figure 1.2), a phenomenon that is likely due to heterogeneity in abundance among species (Dorazio and Royle 2005). Fragment area, as compared to perimeter or P/A, had a large impact on mean estimates of occupancy for many species within the community. Over the range of surveyed fragments, 24 species showed (on average) an increase in occurrence probability as area increased (greater than 10% change in mean estimates of occupancy from minimum to maximum fragment size in the survey), 31 species showed a decrease in occurrence probability (greater than 10%) with increasing area and 23 species showed no change in occurrence probability with area (less than 10% change).

Many species whose mean occurrence probabilities increased in response to increased area were forest dependent species of high conservation concern. On average, nine forest-interior breeders (Acadian flycatcher *Empidonax virescens*, black-and-white warbler *Mniotilta varia*, blackburnian warbler *Dendroica fusca*, black-throated blue warbler *Dendroica caerulescens*, black-throated green warbler *Dendroica virens*, cerulean warbler *Dendroica cerulea*, hooded warbler *Wilsonia citrina*, worm-eating warbler *Helmitheros vermivorum*, and winter wren *Troglodytes troglodytes*) showed substantial increases in occupancy probabilities as fragment area increased, but less response to changes in perimeter or P/A ratio (Figure 1.3). Although the number of observations for these species was fairly low (6-36 for each), the community approach allowed us to obtain estimates of the response of each species to fragment area and regularity of shape. The precision on species-level estimates of occupancy and effects of fragmentation increased for most species in the community model compared to standard species-specific models (see Appendix 1.2 and Figure A1.1 for selected results comparing the community model to a single species modeling approach). When modeling each species separately, occupancy estimates for species with sparse data could not be obtained without exhibiting extreme sensitivity to the prior. For the above nine forest-interior species, the standard deviations on the estimated species specific effects of area were generally lower using the hierarchical community model (range 1.24-1.83) than a standard species level model (range 1.40-2.03; Appendix 1.2). Three species (ovenbird *Seiurus aurocapilla*, scarlet tanager *Piranga olivacea*, and veery *Catharus fuscescens*) also had a positive response to area, but the effects were less discernable on estimates of occupancy because they were widely observed (e.g. occupancy was universally high). A few forest dependent species (brown creeper *Certhia americana*, Canada warbler *Wilsonia canadensis*, northern parula *Parula americana*, red-breasted nuthatch *Sitta canadensis*, and wood thrush *Hylocichla mustelina*) responded more closely to the community-level response by decreasing in occupancy probabilities as fragment area increased (Figure 1.4).

Discussion

Although reliable summaries of species occurrences and distributions are required for effective conservation, analysis of multi-species data can be challenging because sampling techniques often identify numerous species with few detections. One way to address this issue is to utilize models that integrate data across species, allowing for composite analyses of communities or groups of species. Hierarchical models are particularly valuable in this context, in part because they do not require *a priori* assumptions about community structure; any composite analysis will improve estimates on metrics of interest, regardless of relationships among species (Sauer and Link 2002). For conservation purposes, it is generally useful to consider species from one community or related communities; otherwise community-level summaries may not be meaningful. In some situations it may be possible to incorporate additional group structure into the model when relationships among species have been well established. Estimates for rarely observed species will naturally be drawn to community averages ("Bayesian shrinkage" toward the mean; Link 1999), but precision of estimates can be improved with even a minimal number of observations (Appendix 1.2 and Figure A1.1). Accuracy of species-specific estimates will always be limited by the amount of available data, which is reflected in the diffuse posterior distributions for many habitat covariates. Such estimates can only be objectively improved through additional data collection efforts. However, as with meta-analysis in classical statistics (Osenberg et al. 1999), many "weak" inferences can be combined to make a stronger collective response. Thus, by accounting for both species-level effects as well as the aggregated effects of landscape covariates on the community as a whole, hierarchical models provide a valuable alternative to single species analyses of community data.

Our model produced a number of key findings relevant to prioritizing conservation actions and was capable of making predictions of bird species richness based on fragment area and edge effects (Figure 1.1), which should be verified through additional sampling. Understanding the relationship between environmental factors and species richness will improve the efficacy of conservation efforts in the protection of biodiversity in urbanizing landscapes. For example, our estimates of the community and species-level relationships between occupancy probabilities and habitat characteristics allows a direct valuation of forest fragments in terms of either total species richness (Figure 1.1 – left panel) or assemblage richness (Figure 1.1 –

right panel), and illustrates an explicit trade-off between these two competing objectives. Overall, the community level response to area and P/A suggests that many species increased in occupancy in response to fragmentation inducing a concomitant increase in species richness. These results are consistent with the intermediate disturbance hypothesis (Connell 1978; Grime 1973; Horn 1975) which suggests that diversity is maximized in areas of moderate disturbance. Similar to Lepczyk et al. (2008), we found that extremely large fragments with extensive forest-interior may be less common (DeWan et al. 2009) and estimates of species richness would be expected to decline if sites were dominated by edge-tolerant or generalist species. In a conservation context, our overall estimates of species richness may not be particularly valuable; however the hierarchical framework offered a means to acquire improved precision in estimates of occupancy for rarer species, which we used to determine assemblage richness for a subset of the community with high conservation value.

Many of the forest-breeding species responded to increased fragmentation with decreased probabilities of occupancy (Figure 1.3). However, occupancy for some forest-breeding species responded negatively to fragment area (Figure 1.4). Although this may not be surprising for more urban-tolerant species (e.g. red-breasted nuthatch), these results were not typical for others that are sometimes considered sensitive to fragmentation (e.g. Canada warbler, wood thrush). In addition, some area-sensitive species were so common that their relationship to area would not have been discernible through typical occupancy approaches. Scarlet tanager, ovenbird and veery were observed frequently during sampling and had high occupancy estimates. If we had *a priori* grouped these species together as an indicator of sensitivity to fragmentation, without testing the assumptions, we would have been unable to discern differences among species in their response to fragment area and P/A.

Our approach allows for estimation of occupancy and detection probabilities of all observed species, even if they are poorly represented in the sample data. Detection probabilities were very low for many species (Figure 1.2), further supporting a number of studies that have demonstrated the importance of accounting for detection in occupancy and abundance modeling (Bailey et al. 2004; Kéry et al. 2008; MacKenzie et al. 2006). Detection probability can also be significantly affected by abundance (Royle and Nichols 2003), which is evidenced in our analysis by the high correlation between detection and occupancy. Variance around species-specific estimates of occupancy, detection, and the covariates will inevitably be high for species with limited data. However, the community level approach typically provides more precise estimates for rare species than traditional species-level analyses (Appendix 1.2 and Figure A1.1) and was especially valuable for the nine forest interior species that were sensitive to habitat fragmentation, yet would not have yielded reliable estimates of occupancy due to low sample size. Our analysis framework should be particularly effective in reducing cost and increasing efficiency for organizations where funding for field-based data collection is limited.

Many conservation and management decisions rely on estimates of species richness to prioritize areas for protection and monitoring. For example, DeWan et al. (2009) developed a map of high priority conservation areas in the Hudson River Valley region based on indices of richness for a subset of forest interior bird species. Their analyses were limited to species that were neither too common nor too rare. The results from our community level approach can be used to improve such maps and more accurately determine areas of high conservation value to protect from urban development. We demonstrated, using a diverse bird community, the applicability and relevance of our hierarchical modeling approach to: 1) assess species richness while accounting for individual species; 2) improve the precision on estimates of occupancy and detection for many species, even species with relatively sparse data; and 3) investigate the impacts of fragmentation on breeding birds at the community and species levels. Our hierarchical framework offers an exciting tool for wildlife agencies and conservation organizations who struggle to effectively monitor and protect biological diversity. Monitoring the status and distribution of biodiversity and rare species is a priority at local, national, and international scales (Oberbillig 2008). Because of challenges in sampling and cost, lack of quality data has been identified as a serious challenge for biodiversity conservation, particularly for rarer species (The Heinz Center 2002). Many sampling designs already include data collection on multiple species (Heyer 1994; Wilson et al. 1996) and multi-species inventory techniques can reduce sampling costs and effort (Manley et al. 2005; Vesely et al. 2006). The community approach allows researchers to use data from all sampled species to improve estimates of species richness and generate previously unavailable estimates of occupancy for rare or elusive species. The flexibility of hierarchical modeling can provide greater insight on how a particular taxonomic community responds to environmental changes, while also accounting for species-specific differences. If incorporated into monitoring and assessment programs, this framework could improve estimation of species richness and inferences for rare species, and provide scientifically sound information to support conservation planning and action.

Table 1.1 Community level summaries of the hyper-parameters for the detection and occupancy covariates.

Community-level hyper-parameter		Mean	Standard deviation	95% Posterior intervals
$\mu_{\alpha 1}$	mean - perimeter	-0.06	0.75	(-1.65, 1.32)
$\sigma_{\alpha 1}$	standard deviation - perimeter	0.64	0.34	(0.20, 1.51)
$\mu_{\alpha 2}$	mean - area	-0.25	0.83	(-1.79, 1.48)
$\sigma_{\alpha 2}$	standard deviation - area	1.83	0.47	(0.82, 2.75)
$\mu_{\alpha 3}$	mean - P/A	0.07	0.12	(-0.15, 0.32)
$\sigma_{\alpha 3}$	standard deviation - P/A	0.54	0.18	(0.26, 0.96)
$\mu_{\beta 1}$	mean - date effect (linear term)	-0.04	0.04	(-0.12, 0.05)
$\sigma_{\beta 1}$	sd - date effect (linear term)	0.25	0.04	(0.17, 0.33)
$\mu_{\beta 2}$	mean - date effect (squared term)	-0.03	0.05	(-0.13, 0.08)
$\sigma_{\beta 2}$	sd - date effect (squared term)	0.25	0.05	(0.16, 0.36)
$\beta 3$	mean - year effect	0.11	0.05	(0.01, 0.21)

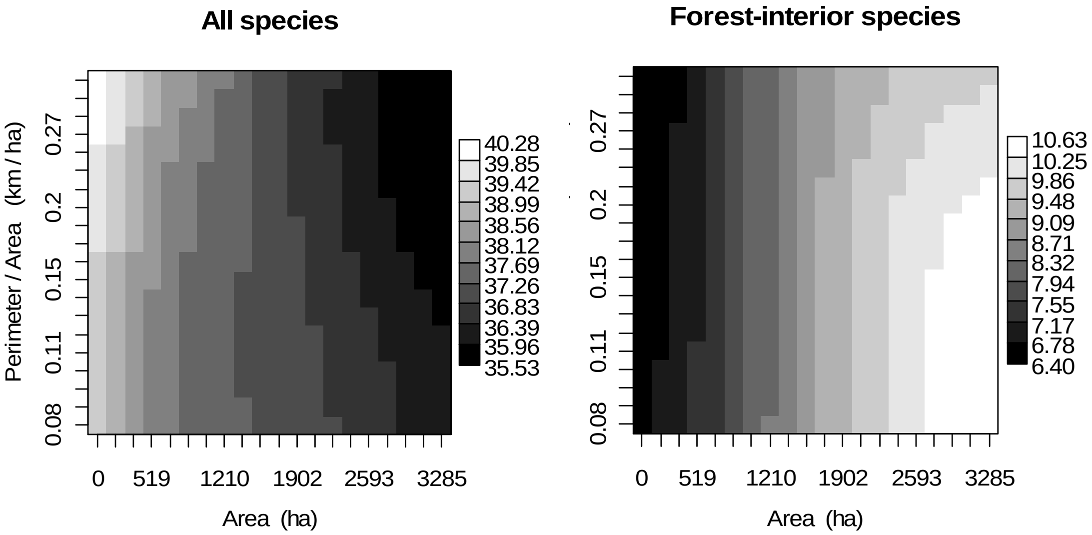


Figure 1.1 Total estimated species richness (left) based on area and P/A and estimated assemblage richness of forest interior species (right - 17 observed species: Acadian flycatcher, black-and-white warbler, blackburnian warbler, black-throated blue warbler, black-throated green warbler, brown creeper, Canada warbler, cerulean warbler, hooded warbler, northern parula, ovenbird, red-breasted nuthatch, scarlet tanager, veery, worm-eating warbler, winter wren, and wood thrush).

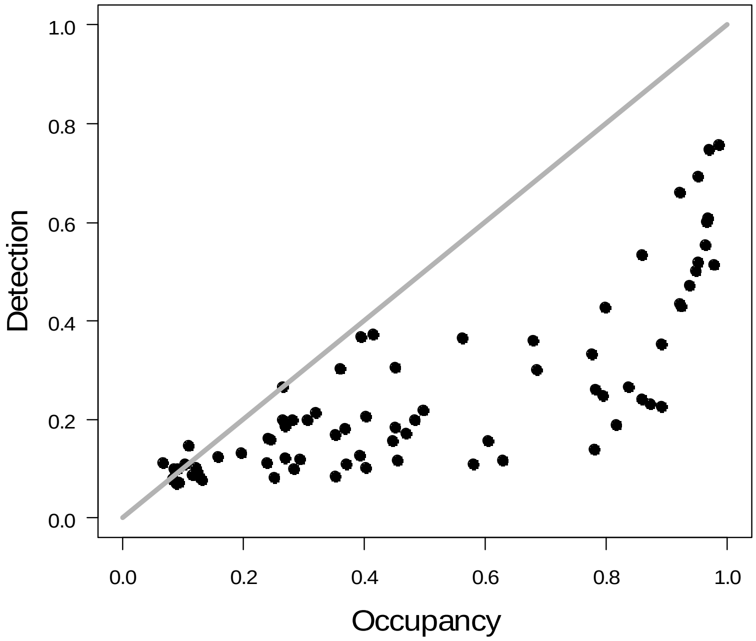


Figure 1.2 Mean estimated values of occupancy and detection for the 78 observed species. The shaded line shows the one to one relationship.

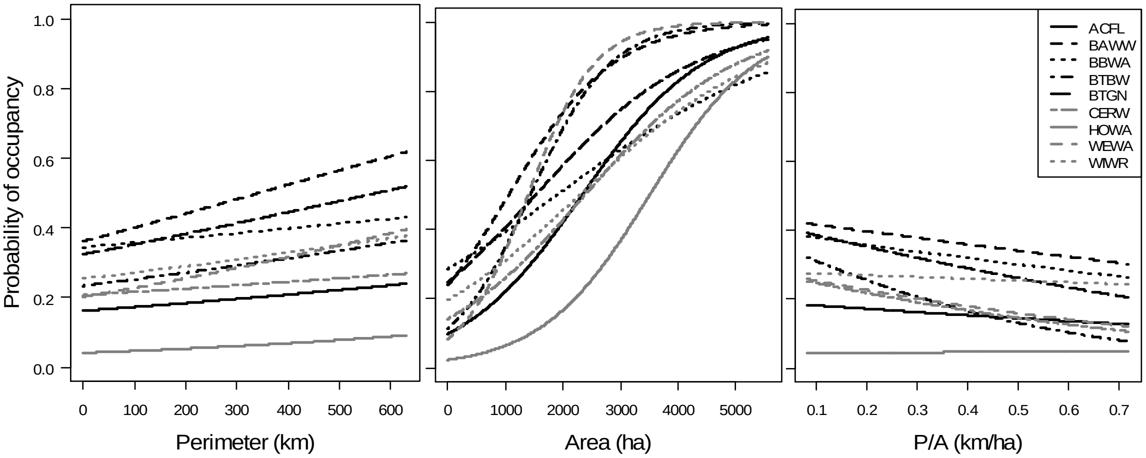


Figure 1.3 Mean marginal probabilities of occupancy for nine forest interior breeding bird species (Acadian flycatcher, black-and-white warbler, blackburnian warbler, black-throated blue warbler, black-throated green warbler, cerulean warbler, hooded warbler, worm-eating warbler, and winter wren) in relation to fragment perimeter, area, and perimeter/area ratio (P/A).

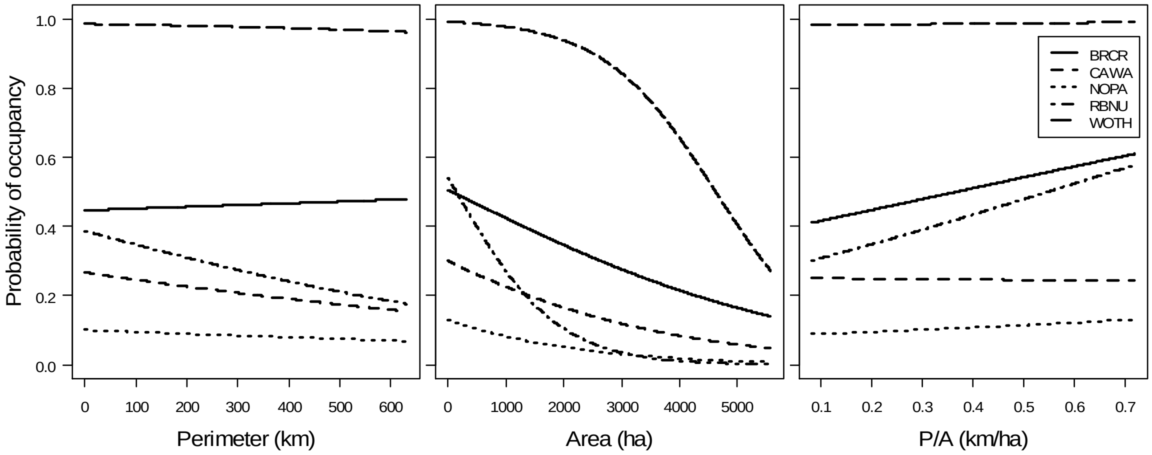


Figure 1.4 Mean marginal probabilities of occupancy for five forest interior breeding bird species (brown creeper, Canada warbler, northern parula, red-breasted nuthatch, and wood thrush) in relation to fragment perimeter, area, perimeter/area ratio (P/A).

Chapter 2: Multispecies occurrence models to evaluate the effects of management and conservation actions

Published in: Biological Conservation, 143, 479-484, 2010.

Coauthors: J. Andrew Royle, Deanna K. Dawson, Scott Bates

Abstract

Conservation and management actions often have direct and indirect effects on a wide range of species. As such, it is important to evaluate the impacts that such actions may have on both target and non-target species within a region. Understanding how species richness and composition differ as a result of management treatments can help determine potential ecological consequences. Yet it is difficult to estimate richness because traditional sampling approaches detect species at variable rates and some species are never observed. We present a framework for assessing management actions on biodiversity using a multi-species hierarchical model that estimates individual species occurrences, while accounting for imperfect detection of species. Our model incorporates species-specific responses to management treatments and local vegetation characteristics and a hierarchical component that links species at a community level. This allows for comprehensive inferences on the whole community or on assemblages of interest. Compared to traditional species models, occurrence estimates are improved for all species, even for those that are rarely observed, resulting in more precise estimates of species richness (including species that were unobserved during sampling). We demonstrate the utility of this approach for conservation through an analysis comparing bird communities in two geographically similar study areas: one in which white-tailed deer (*Odocoileus virginianus*) densities have been regulated through hunting and one in which deer densities have gone unregulated. Although our results indicate that species and assemblage richness were similar in the two study areas, point-level richness was significantly influenced by local vegetation characteristics, a result that would have been underestimated had we not accounted for variability in species detection.

Introduction

Conservation and management actions are generally designed to target a particular species of interest (e.g., Howe et al. 2007; Pauliny et al. 2008; Wang et al. 2009). However, actions focused on maintaining or improving habitat for a single species may also affect other species (e.g., Tikkanen et al. 2007)**.** For example, management designed to improve conditions for the endangered red-cockaded woodpecker (*Picoides borealis*), such as forest burning and thinning, may have adverse impacts on neotropical migrant birds that nest in midstory and understory vegetation (Powell et al. 2000; Moore et al. 2005). Initial studies on wood thrush (*Hylocichla mustelina*) found that treatments had no effect on short term density and survival (Powell et al. 2000). However, further analyses have suggested that burning and thinning may be “incompatible” with wood thrush persistence (Moore et al. 2005). Many conservation plans explicitly view management as influencing a variety of species, and balancing the losses and gains of species is an implicit part of managing biodiversity (e.g., Rich et al. 2004; Suarez-Rubio and Thomlinson 2009). It is therefore important to consider the effects of management actions on not only the target species, but also on other species within a region.

One method for assessment is to compare local species richness (i.e., total number of species) in areas that are affected and unaffected by a specific action. Yet, determining species richness is complicated by variability in detection rates, which can vary across species or by landscape characteristics (Boulinier et al. 1998; Kéry and Schmidt 2008) and may be affected by actions that create a change in habitat. As a result, estimates of species richness and composition would be biased if species-specific detection is not accounted for properly. This may feign a non-existing management effect or mask a genuine effect.

Rare species, many of which are of conservation concern, may show disproportionate responses to changes in habitat as compared to common species. Often there are inadequate data on rare species, which may be detected infrequently or not at all during sampling, resulting in limited inferences about occurrence (MacKenzie et al. 2005). However, management evaluations should include all species, not just those species that produce enough data. Recent advances in statistical methodology have improved the ability to account for imperfect detection and low occurrence of rare species through a community-level hierarchical modeling approach (Dorazio and Royle 2005; Dorazio et al. 2006), a multi-species extension of the occurrence model described in MacKenzie et al. (2002). The fundamental idea behind the multi-species modeling approach is that collective community data can inform the occurrence probabilities for all observed species, even those that are rare or elusive, and allow for occurrence estimation of species that were never observed in the sample plots. This results in an improved composite analysis of the community and increased precision in species-specific estimates of occurrence (Kéry and Royle 2009; Zipkin et al. 2009). Furthermore, the hierarchical model can be specified to incorporate habitat and sampling effects that influence occurrence and detection, respectively (Russell et al. 2009). Thus a multi-species approach can provide more precise estimates of species richness, while accounting for variation in occurrence and detection among species. Understanding how species richness and composition differ as a result of management treatments and habitat characteristics can aid in determining the ecological consequences of management.

In this paper, we explore the use of community hierarchical models in a conservation context by comparing bird species richness in two similar study areas in the Catoctin Mountains, Maryland (USA): one with an unharvested population of white-tailed deer (*Odocoileus virginianus*) and one in which deer densities have been regulated through hunting and are much lower as a result (Bates et al. 2005). White-tailed deer can severely alter vegetation structure and composition, reducing habitat availability and quality for some bird species (Cote et al. 2004; McShea and Rappole 2000). Efforts to control deer densities have been implemented for a variety of reasons including to reduce wildlife/human conflicts (e.g., vehicle collisions, minimize human exposure to ticks) and to protect vegetation growth. Our interest lies in understanding how management decisions to control deer densities (in this case, by allowing hunting) affect total bird species richness as well as the richness of functional species groups, specifically assemblages of species that nest and forage on the ground or in the understory relative to the midstory and canopy. To this end, we built our model to include both a treatment effect (hunting vs. no hunting) as well as local vegetation characteristics to estimate species and assemblage richness at point-level, study area, and regional spatial scales.

Methods

The hierarchical community model is a multi-species approach to obtain composite information by estimating individual species occurrence probabilities (Dorazio and Royle 2005; Dorazio et al. 2006). The basic idea is that (1) non-detection can be distinguished from absence through repeated sampling and (2) species-specific estimates of occurrence can be improved using collective data on all species observed during sampling. This approach is especially useful for communities that include rare (or unobserved) species, which often yield too few detections to estimate occurrence. Because species are detected imperfectly, it is likely that some species do not appear in the sample. Inference about species richness, including the number of unobserved species, is a central objective in studies of species distributions (e.g., Cam et al. 2002; Husté et al. 2006) and can be a useful metric in assessing the impacts of management actions. The hierarchical multi-species model can produce estimates of richness that account for species unobserved during sampling (Dorazio et al. 2006). Before outlining the specific details of the model, we describe the study area and data.

Study area and data collection

High densities of white-tailed deer have lead to increasing concern about the effects of intense browsing on biological resources and forest processes in the eastern

United States and elsewhere. The United States National Park Service (NPS) implemented an assessment to determine whether deer in the Catoctin Mountain Park (CATO) should be managed to address declining forest regeneration to ensure that natural processes support native vegetation and wildlife in the region (Bates et al. 2005). As part of the assessment, bird surveys were conducted in CATO, where white-tailed deer abundance is unregulated, and in the nearby Frederick City Watershed Cooperative Wildlife Management Area (FCW), where deer are hunted. Estimates of white-tailed deer densities were more than seven times higher in CATO than in FCW (Bates et al. 2005). Sampling occurred at 35 random points in each study area in late May through early July 2002. During 12-minute counts, all birds seen or heard were recorded. Bird species that were detected within 75 m of the point were considered present for the specified sampling occasion. All points were sampled on at least three separate days distributed throughout the breeding season and at different times in the morning. For each point, the percent cover by understory foliage (UFC) and the basal area of trees (BA) were also measured during a separate sampling effort carried out from mid-July to August. See Bates et al. (2005) and Royle et al. (2004) for further details on the data collection process.

Modeling framework

We define occurrence $z(i,j)$ as a binary variable in which $z(i,j)=1$ if species i occurred within 75 m of point j (and zero otherwise). The occurrence state is assumed to be the outcome of a Bernoulli random variable, denoted by $z(i,j) \sim Bern\left(\psi_{i,j}\right)$, where $\psi_{i,j}$ is the probability that species i occurs at site j. True occurrence is imperfectly observed, which confounds the estimation of $\psi_{i,j}$. However, sampling at a point *j* with *k*>1 temporal replicates over a short period (such that the community remains closed for the duration of the survey) allows for a formal distinction between species absence and non-detection, which is specified through a detection model for the observed data *x*(*i*,*j*,*k*) (MacKenzie et al. 2002). We define the detection model for species *i* at point *j* during replicate *k* as $x(i,j,k) \sim Bern\left(p_{i,j,k} \cdot z(i,j)\right)$ where $p_{i,j,k}$ is the detection probability of species *i* for the *k*th replicate at point *j*, given that species *i* is in fact present at point *j*. Thus the detection model satisfies the condition that detection is a fixed zero when a species is not present because *z*(*i*,*j*)=0.

We assumed that the occurrence ($\psi_{i,j}$) and detection ($p_{i,j,k}$) probabilities varied by species and were influenced by habitat and survey characteristics, respectively. These effects were incorporated into the model using the logit link function (Kéry and Royle 2008; Kéry et al. 2008; Russell et al. 2009). We estimated the occurrence probabilities for species *i* at point *j* dependent on whether point *j* was in CATO (*Ind*=1) or FCW (*Ind*=0), thus allowing for species-level effects to differ between the two study areas. We also incorporated the point-specific habitat characteristics: UFC and BA. We included both linear and quadratic terms for UFC and BA so that species associations with these habitat characteristics could be maximized at any intermediate level (e.g., some understory foliage vs. 0% or 100%) and standardized the data to have mean zero. The occurrence model for species *i* at point *j* is specified:

$$\text{logit}\left(\psi_{i,j}\right) = uCATO_i(Ind_j) + uFCW_i(1 - Ind_j) + \\ \alpha 1_i UFC_j + \alpha 2_i UFC_j^2 + \alpha 3_i BA_j + \alpha 4_i BA_j^2 .$$

In this case, $uCATO_i$ and $uFCW_i$ are the occurrence probabilities (on the logit scale) for species *i* at points in the CATO and FCW study area, respectively, for average values of UFC and BA. The coefficients for the four α_i terms are the linear and squared effects of understory foliage and tree basal area on species *i*. The detection model was similarly designed to estimate detection separately for each species in the two study areas. We included the survey date (linear and squared effects) and the time from sunrise (linear, since all surveys occurred in the morning) as possible species-specific detection covariates. The detection covariates were also standardized to have mean zero:

$$\begin{aligned}\text{logit}\left(p_{i,j,k}\right) = vCATO_i(Ind_j) + vFCW_i(1 - Ind_j) \\ + \beta 1_i \,\text{date}_j + \beta 2_i \,\text{date}_j^2 + \beta 3 \text{ sunrise}_j \ .\end{aligned}$$

The species-specific occurrence and detection processes were related to one another through an additional component where it was assumed that each of the species parameters was drawn from a common (community-level) distribution. A major benefit of the multi-species approach is that it does not require *a priori* community or group designation; combining data from similar species will be an improvement over individual species models, provided that species occurrence responses can conceivably come from a common distribution (Sauer and Link 2002). By linking the individual species occurrence probabilities through this community hierarchical component, precision of species-specific estimates is improved leading to enhanced composite analyses and a more efficient use of available data (Kéry and Royle 2008; Zipkin et al. 2009).

The community-level hierarchical component of the model assumes that each of the species-level occurrence $\left(uCATO_i, uFCW_i, \alpha_i\right)$ and detection $\left(vCATO_i, vFCW_i, \beta_i\right)$ parameters were random effects, governed by "hyper-parameters". For example, we assumed that $uCATO_i \sim N\left(\mu_{uCATO}, \sigma_{uCATO}\right)$ where μ_{uCATO} is mean occurrence across the community in CATO and σ_{uCATO} is the standard deviation among species. We similarly specified the mean and standard deviations for each of the twelve community-level habitat parameters (mean and standard deviation parameter μ, σ for each species-specific random effect $uCATO, uFCW, \alpha 1, \alpha 2, \alpha 3, \alpha 4$) and the ten detection parameters (mean and standard deviation for $vCATO, vFCW, \beta 1, \beta 2, \beta 3$).

Bayesian analysis of the model was carried out using the method of data augmentation described in Royle et al. (2007) and Kéry and Royle (2009), which allows for estimation of the number of species in the community that were unobserved (either locally or never detected) during the sampling process. Analysis by data augmentation assumes a uniform (0,*M*) prior for *N*, the "true" species richness, where *M* is a fixed constant chosen to be much greater than the number of observed species (*n*) and such that the resulting posterior distribution is not truncated. Implementation of the model with a uniform prior is done by augmenting the data set with *M-n* all-zero encounter histories. Then the model for the augmented data set is a zero-inflated version of a model where the actual number of species in the community (*N*) is known (Kéry and Royle 2009; Royle et al. 2007). The occurrence process is modified so that $z(i, j) \sim Bern\left(\psi_{i,j} \cdot w_i\right)$ where $w_i \sim Bern(\Omega)$ for species

$i = 1, 2, ..., n,\ n + 1,\ n + 2, ...,\ N,\ N + 1,\ N + 2, ...,\ M$. The interpretation of this modified occurrence process is that if $w_i = 1$ (corresponding to species that were observed or that were unobserved but available for sampling), the probability of occurrence is simply $\psi_{i,j}$. If $w_i = 0$ (indicating that a species was unavailable for sampling), then occurrence is zero by definition (i.e., a structural zero). The model is now modified to estimate the parameter Ω . The value of *M* need only be large enough to not truncate the posterior distribution of *N*, which can be assessed by running short initial trials. Interpretation of the posterior of *N* must be done cautiously. It is not necessarily the number of species that occur in a particular landscape; rather, it is equivalent to the asymptote of a species accumulation curve (Kéry and Royle 2009). In the context of deer browsing, *N* is the intrinsic capacity of bird species in the study areas, suggesting the possible number of species that could occur in regions with similar vegetation characteristics and management actions.

We calculated species richness including unobserved species in the two study areas as well as at each point location by summing the number of estimated species in the occurrence matrix. We also estimated the degree of similarity in community composition between study areas by calculating the "coincidence index" (Dice 1945; Dorazio and Royle 2005 pg. 387), a value between zero and one where zero indicates no overlap and one indicates complete overlap. Following McShea and Rappole (2000), we classified observed species into two assemblages that might respond differently to deer densities or vegetation characteristics: (1) low/ground nesting and foraging species and (2) midstory/canopy nesting species. We then estimated point-specific richness and the coincidence index between study areas for these assemblages, which we used for comparison. Recognizing the limitations of the design (confounding of study area and management regime), we compared the point-specific associations of richness with the habitat attributes that reflect understory openness (UFC) and forest maturity (BA). We note that the model does not build in explicit relationships between point-specific richness and covariates; instead we inferred these relationships from the point-specific richness results.

The model was analyzed using a Bayesian approach in the programs R and WinBUGS (Spiegelhalter et al. 2003). We used independent, diffuse proper prior distributions for the community-level hyper-parameters. We ran three chains of length 10,000 after a burn-in of 20,000 and thinned the posterior chains by 10. Convergence was assessed using the R-hat statistic, which examines the variance ratio of the MCMC algorithm within and between chains across iterations (Gelman and Hill 2007).

Results

A total of 58 bird species were observed during sampling: 52 species in CATO and 46 in FCW. The model estimated 60.3 species in the whole of the region (95% Posterior Interval, PI: 58-64) with 55.8 (52-60) and 51.2 (47-58) species in the CATO and FCW study areas, respectively. The species composition of the two study areas was similar with an estimated coincidence index of 0.89 (0.83-0.96). However, detection probabilities were low, with greater than 80% of observed species having mean detection probabilities of less than 0.5 per sampling occasion in both study areas (Figure 2.1). There was a positive, but weak, relationship ($P<0.02$,

R^2_{CATO}=0.12, R^2_{FCW}=0.10) between estimates of occurrence and detection across species in both CATO and FCW, but no difference between study areas.

There was no difference between point-specific estimates of species richness in CATO and FCW (Figure 2.2 – left panel) and most species had similar occurrence probabilities in the two study areas (Figure 2.2 – right panel). The mean estimated point-specific richness was 29.3 (19-43) species in CATO and 27.4 (19-38) species in FCW. In contrast, the mean observed number of species was 17.2 (range: 9-33) in CATO and 14.0 (range: 4-24) in FCW. Species-specific detection probabilities were also similar between the two study areas, with varying effects of survey date on detection probability and a generally negative effect as time from sunrise increased (Figure 2.3).

Estimated point richness for an assemblage of 14 observed understory species was 4.9 (1-10) in CATO and 7.2 (3-11) in FCW. The 29 observed midstory/canopy species had an estimated point richness of 16.3 (11-22) in CATO and 13.4 (9-18) in FCW. The coincidence index suggested that the composition was similar in the two study areas for both understory species (0.96; 95% PI: 0.92-1.0) and midstory/canopy species (0.87; 95% PI: 0.79-0.96). Although posterior distributions for occurrence estimates in CATO and FCW overlapped for all bird species, a few notable species had visibly higher mean occurrence probabilities in one of the two study areas. Several ground-nesting species had higher occurrence probabilities in FCW (and relatively little overlap in posterior distributions), including black-and-white warbler (*Mniotilta varia*, difference in mean occurrence between areas: 0.43), ovenbird (*Seiurus aurocapilla*, 0.20), and worm-eating warbler (*Helmitheros vermivorus*, 0.57), a species of continental and regional conservation concern (Rich et al. 2004; Rosenberg 2003). Species with higher occurrence probabilities in CATO included others of high conservation priority (Rich et al. 2004; Rosenberg, 2003), such as cerulean warbler (*Dendroica cerulea*, 0.70) and yellow-throated vireo (*Vireo flavifrons*, 0.26).

Point-specific richness and individual species occurrence probabilities were significantly influenced by local vegetation characteristics (Figure 2.4). The effect of vegetation characteristics on species richness was understated in an analysis that included only the locally observed number of species. There was a strong positive relationship between estimated point-specific species richness and understory foliage cover (UFC; $P<0.001$ for estimated richness compared to $P=0.017$ for observed richness) and a strong negative relationship between point-specific richness and tree basal area (BA; $P<0.001$ for estimated richness compared to $P=0.138$ for observed richness). As noted above, these relationships were deduced from species-specific responses to the covariates (i.e., Figure 2.4 depicts the posterior means of the estimated richness for each sampled point plotted against the covariates used in the analysis). Additionally, there was a significant negative relationship between UFC and BA but no difference in the overall vegetation characteristics between the two study areas.

Discussion

Management actions can have significant impacts on the broader plant, animal, and bird communities. Our results demonstrate how multi-species models can be used in a conservation context to assess differences in the richness and composition of multi-species data based on (1) whether an area is affected by a specific management action and (2) local habitat or landscape characteristics. The strength of the approach lies in the ability to estimate species-specific occurrence and detection separately, while linking members of the community. This leads to greater precision in species-specific parameter estimates, especially for rare or infrequently observed species (Zipkin et al. 2009) as well as an improved understanding of the overall community response to management actions.

Many species in our study had low detection probabilities. Inferences on occurrence distributions can be misleading without properly accounting for detectability (Gu and Swihart 2004; Kéry et al. 2008; Nichols et al. 1998). Had the model not accounted for variability in detection probabilities among species, we would have underestimated point-level richness and the effects of local vegetation characteristics (Figure 2.4). Additionally, several species had too few detections to yield occurrence estimates under individual species models. Yet for comprehensive assessments, it is important to examine the effects of management actions on all species, not just those species that produce enough data for standard analyses.

For conservation agencies interested in improving conditions for bird species, it may be more important to focus on the manipulation of local vegetation characteristics rather than on regional deer densities. In our study, we found no differences between the overall bird communities in CATO, where deer are unmanaged, and FCW, where deer density is regulated through hunting (Figure 2.2). We found that point-specific richness estimates were most strongly associated with the local habitat characteristics, UFC and BA (Figure 2.4), which is consistent with other studies that have examined the relationships between deer, vegetation, and birds (e.g., deCalesta 1994; DeGraaf et al. 1991; McShea and Rappole 1992; McShea and Rappole 2000). Since understory foliage and tree basal area are negatively correlated covariates, the response of species richness to these vegetation characteristics is necessarily opposing. To better understand the independent effects of UFC and BA on species richness, additional controlled studies should be conducted to sample a wider range of BA for prescribed levels of UFC (and vice versa). The vegetation in both study areas is heterogeneous, with species composition, stem density, and structure influenced not only by deer browsing, but by other factors, including soil type and depth, slope and aspect, and land use history. Despite the high deer densities in CATO, sections of the park still retain relatively high stem densities of woody understory plants such as spicebush (*Lindera benzoin*), which deer generally do not browse on, and points in these sections generally had higher richness than where understory was sparse (Bates et al. 2005). We did not detect a difference in the total percent of understory foliage between CATO and FCW. However, Bates et al. (2005) did find differences in understory foliage by height class, with significantly less foliage with heights between 0.1-1.5 meters in CATO, which may account for decreased occurrence estimates for some understory species in CATO as compared to FCW. Although the limited design of the study does not permit experimental evaluation of a wide array of habitat changes associated with deer browsing, the associations of point-specific vegetation characteristics and estimated bird community attributes can provide park managers with initial models for manipulating habitats to improve bird occurrence and abundance. In addition, the modeling framework allows for explicit calculations of assemblage richness and composition, which should be helpful in further understanding trade-offs in species occurrences associated with management actions.

Multi-species hierarchical models can be used to advance understanding of how conservation and management actions affect birds and other taxa at the species and community levels. The approach offers a unified framework for simultaneously estimating species and assemblage richness as well as occurrence and distribution of individual species at local and regional spatial scales. Covariates can be included in models to make spatial or temporal comparisons, or to assess the effects of factors that likely influence the occurrence or detection of species, thus refining parameter estimates. Recent advancements have extended the hierarchical multi-species model to account for colonization and extinction (Kéry et al. 2009), which should be useful for conservation agencies interested in studying the effects of management actions over time. Our approach can improve understanding of how species and communities respond to management actions, allows for explicit comparisons relevant to management (such as how deer influence understory vs. canopy birds), and provides enhanced information on manageable factors (i.e., density of understory shrubs) affecting species richness. Incorporating this approach into conservation should improve biodiversity assessments of species and community responses to management actions.

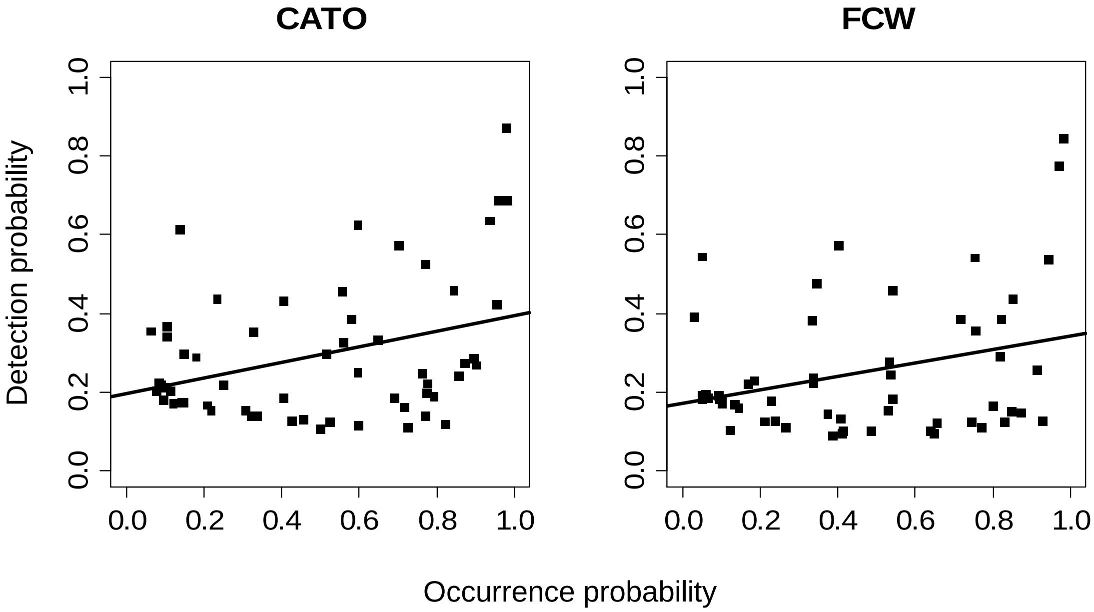


Figure 2.1 Comparison of mean occurrence and detection probabilities for all bird species observed on surveys conducted during the nesting season of 2002 in the Catoctin Mountain Park (CATO) and the Frederick City Watershed (FCW), Maryland.

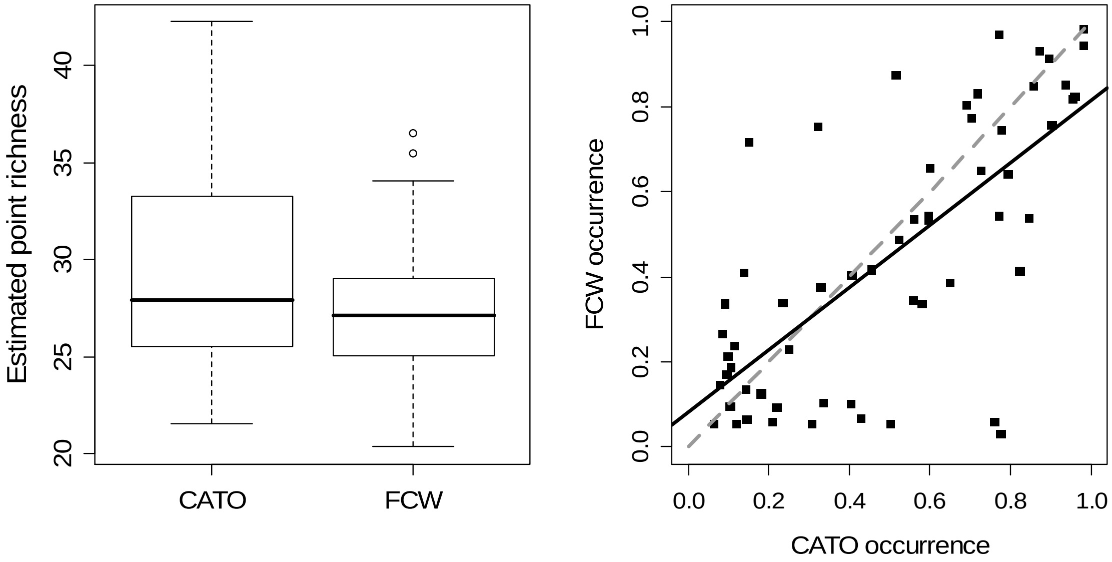


Figure 2.2 Estimated point-specific bird species richness (including unobserved species) in the Catoctin Mountain Park (CATO) and the Frederick City Watershed (FCW; left panel) and mean estimated species-specific probabilities of occurrence in CATO vs FCW (right panel; the solid black line shows the regression line and the dashed grey line is a 1-to-1 line).

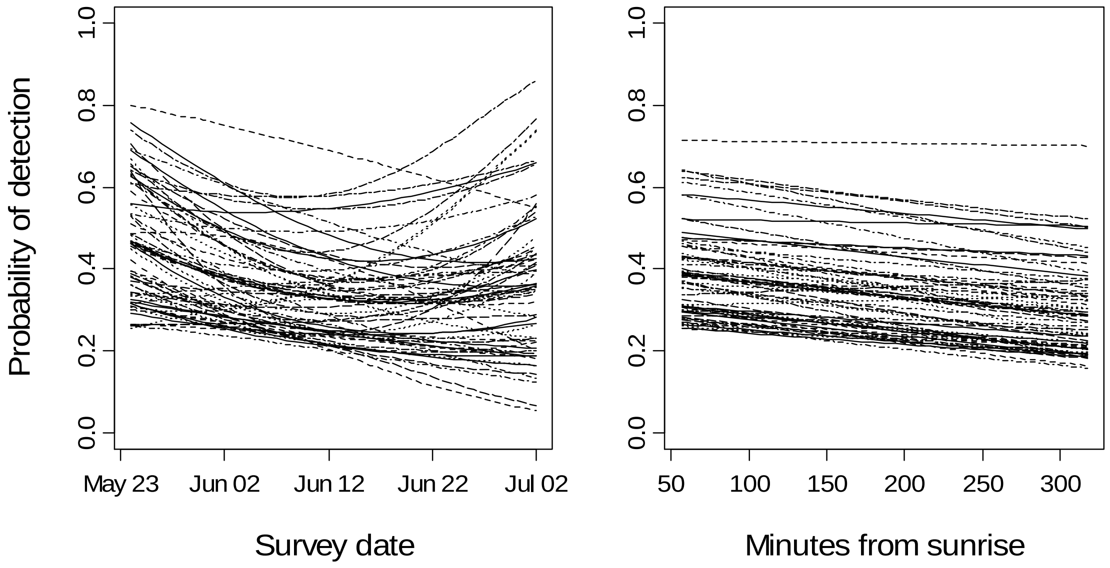


Figure 2.3 Species-specific sampling effects on detection probabilities: survey date (left panel) and survey time (right panel).

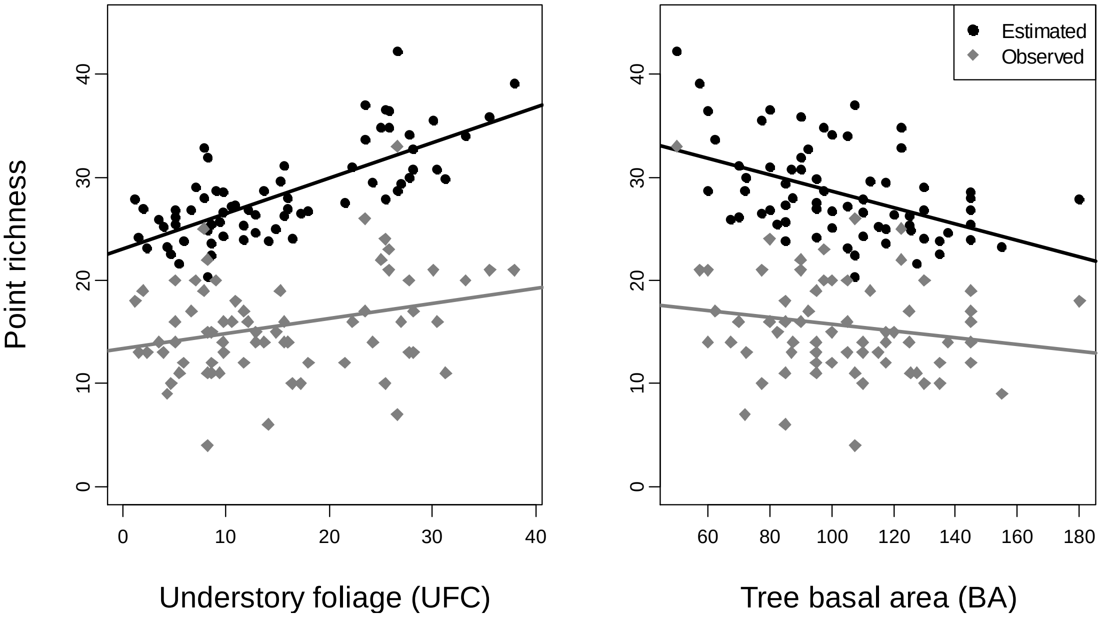


Figure 2.4 Estimated (black circle) and observed (grey diamond) point-specific bird species richness compared to understory foliage (UFC; left panel) and tree basal area (BA; right panel), from the combined bird and vegetation data collected in the two study areas in the Catoctin Mountains, Maryland.

Chapter 3: Evaluating the predictive abilities of community occupancy models using AUC

Accepted pending revisions: Ecological Applications.

Coauthors: Evan H. Campbell Grant, William F. Fagan

Abstract

The ability to accurately predict patterns of species' occurrences is fundamental to the successful management of animal communities. To determine optimal management strategies, it is essential to understand species-habitat relationships and how species habitat use is related to natural or human-induced environmental changes. Using five years of monitoring data in the Chesapeake and Ohio Canal National Historical Park, Maryland, USA, we developed four multi-species hierarchical models for estimating amphibian wetland use that account for imperfect detection during sampling. The models were designed to determine which factors (wetland habitat characteristics, annual trend effects, spring/summer precipitation, and previous wetland use) were most important for projecting future habitat use. We used the models to make predictions of species occurrences in sampled and unsampled wetlands and evaluated model projections using additional data. Using a Bayesian approach, we calculated a posterior distribution of receiver operating characteristic area under the curve (ROC AUC) values, which allowed us to quantify explicitly the uncertainty in the quality of our projections and to account for false negatives in the evaluation dataset. We found that wetland hydroperiod (the length of time that a wetland holds water) as well as the occurrence state in the prior year were generally the most important factors in determining occupancy. The model with only habitat covariates best predicted species occurrences; however, knowledge of wetland use in the previous year significantly improved predictive ability at the community level and for two of 12 species/species complexes. Our results demonstrate the utility of multi-species models for understanding which factors affect species habitat use and provide an improved methodology using AUC that is helpful for quantifying the uncertainty in model projections while explicitly accounting for detection biases.

Introduction

For many species, occurrence patterns (i.e., the number and geographic distribution of species occurrences) are targets of resource managers, especially when management objectives include multiple species (DeWan et al. 2009; Manley et al. 2004). An essential component of effective management includes understanding how habitat characteristics affect species distributions and how changes in habitat features can alter species occurrence patterns (Guisan and Thuiller 2005; Williams et al. 2002). Multi-species occupancy and fine-scale distribution models can improve conservation efforts by providing decision-makers with the information necessary to evaluate whether proposed actions are beneficial to species individually and to the community as a whole (Kéry and Royle 2008; Zipkin et al. 2010). Such models can help assess tradeoffs in the expected occurrences of species associated with different management actions (Suarez-Rubio et al. 2009). Moreover, models that are designed to assist with management must provide clear insight into the accuracy, reliability, and inherent uncertainty of their projections. Characterizing the uncertainty of model predictions is a vital, but often overlooked, component of conservation management. Yet, it is crucial for adequate assessments of competing actions and objectives.

Arguably, the most common method for evaluating the predictive abilities of occupancy and species distribution models is to estimate the area under the receiver operating characteristic (e.g., Anderson and Raza 2010; Elith et al. 2006; Kharouba and Kerr 2010; Phillips et al. 2006; Rebelo et al. 2010; although AIC is a popular model selection criterion for occupancy models, it not generally used for prediction). In its use for evaluating occupancy models, the receiver operating characteristic (ROC) is based on a confusion matrix that summarizes the prediction results in terms of true/false presences/absences. The confusion matrix is a two by two table of the true outcome versus the predicted outcome that sums the number of locations that both correctly and incorrectly identified presences and absences of the species. The predicted outcome for species occurrences is generally represented as a probability and not a binary response, leading to construction of the ROC. The ROC plots the ratio of true positives, called sensitivity (e.g., the species is present when the model predicts that it is present), to false positives, termed 1-specificity (e.g., the species is not present when the model predicts that it should be present), for all possible cutoff values of the estimated occupancy probability (ranging from 0-1). The area under the ROC (termed AUC and also ranging from 0-1) measures a model’s discrimination, or ability to correctly determine which locations are occupied (Hosmer and Lemeshow 2000). With the advent of software such as MAXENT, Garp, and Biomapper, which allow for easy implementation of species distribution models, the use of AUC for evaluating such models has become increasing popular. However, in using AUC to evaluate a model’s discrimination abilities, current methods fail to consider the influence of species’ detection probabilities (Elith et al. 2006; Phillips et al. 2006). While imperfect detection during sampling can lead to biases in estimates of occupancy, potential errors can be reduced by using statistical methods that account for the detection process (MacKenzie et al. 2002; Tyre et al. 2003). In the context of AUC, detection biases leading to false negatives (e.g., a species is not detected in a location even though it is present) in the data that are used for model evaluation, and not in model development, present an additional challenge in accurately determining a model’s performance. This is because nondetection of a species does not necessarily imply absence, which can alter both the sensitivity and specificity of the confusion matrix, biasing estimates of AUC. Despite the potential for misleading results, we have not seen attempts to address this issue in the literature. Yet, the implications of using models that have been evaluated with biased data could be serious for species management.

Models that predict the occurrences of species within a given region in future years and under a plausible range of environmental conditions are useful decision-making tools. Building such models can be a daunting task, considering that many research projects have short time series of data (relative to the longevity of a species or the temporal scale of environmental changes) and are conducted on relatively restricted spatial scales. Our objective is to present a framework for predicting the occurrence dynamics of a community of wetland breeding amphibian species that (1) explicitly characterizes the uncertainty in the predictive success of model projections and (2) incorporates detection uncertainty in both model development and evaluation.

The conservation of amphibian communities presents a formidable challenge to resource managers because populations respond to both local and broad-scale factors (which may differ among species that share the same habitat), potentially limiting the suite of possible management actions available within protected areas (Green 2003; Mattfeldt et al. 2008). As such, amphibians are ideal for exploring the utility of multi-species models for management designed to mitigate the declines of populations and communities. Amphibian populations are declining worldwide, although the ultimate causes of these declines are uncertain and likely differ among regions and populations (Cushman 2006; Wake and Vrendenburg 2008). Accordingly, resource managers in the Chesapeake and Ohio Canal National Historical Park (CHOH) in Maryland, USA, recognized that increasing urbanization in the surrounding region, combined with regional projections of future climate change, may decrease the suitability of wetland habitats within the park that are necessary for successful amphibian breeding.

Three pieces of information are needed to understand how management actions can improve local species richness in CHOH: 1) wetland-specific occurrence information for the complete amphibian community, 2) an understanding of how wetland characteristics affect species-specific patterns of occurrence and how management actions can affect wetland characteristics, and 3) reliable models for projecting probabilities of species occupancy in unsampled wetlands and in future years. Here, we evaluate the ability of multi-species occupancy models, to predict the occurrences of wetland breeding amphibians in CHOH. We apply competing hierarchical community occupancy models to five years of detection/nondetection amphibian data, and determine the predictive potential of our models using data collected in the sixth year at locations that had previously been sampled as well as from new locations. To achieve our objectives, we build models that account for imperfect detection in both the data that we use for estimating occupancy probabilities and the data used for evaluating the accuracy and precision of the occupancy estimates. We utilize a Bayesian approach to estimate the parameters in our model, essentially treating occupancy probabilities as random variables. In addition, we take advantage of this Bayesian framework to create a posterior distribution of AUC values and generate confidence intervals of our estimates, allowing us to quantify explicitly the uncertainty in the predictive success and the discriminatory ability of our models.

Methods

Study area

The data were collected over six field seasons (2005-2010) in CHOH at 33 randomly chosen wetlands (out of a possible 274) that were each sampled on four occasions during March-July in each year of 2005-2010. In 2010, an additional 30 wetlands were sampled on four occasions using the same protocols. All wetlands held water on at least one sampling occasion during every year of sampling. If a wetland was dry at a given sampling occasion, it was recorded as “not available” and that sampling occasion was not used in our analysis. During each sampling occasion, two independent observers (n = 32 total observers over the six sampling seasons, all trained in field methods and identification) walked the full perimeter of the wetland (starting from opposite ends) and recorded the life stage and species of each amphibian encountered. We treat each observer at a given wetland as one sampling replicate (rep). Thus, for the purposes of estimating annual occupancy (here defined as wetland use at any point during the breeding season), we assume that within a year, a given wetland could be sampled on up to eight (4 visits x 2 observers) separate occasions. In estimating annual occupancy, we are interested in whether a species uses the habitat during the course of the sampling period (March-July) and assume that each population is closed during that time frame.

Fourteen species were observed over the six years of sampling: *Lithobates clamitans* (total of 441 observations at 31 different wetlands), *Ambystoma maculatum* (347, 24), *Lithobates sylvaticus* (227, 23), *Lithobates catesbeianus* (149, 25), *Anaxyrus americanus/fowleri* (146, 24), *Lithobates palustris* (134, 15), *Pseudacris crucifer* (125, 21), *Notopthalmus viridescens* (111, 8), *Lithobates sphenocephala* (100, 17), *Hyla versicolor/chrysocelis* (53, 17), *Ambystoma opacum* (41, 8), and *Hemidactylium scutatum* (11, 3). Two species' complexes were analyzed: *Anaxyrus americanus/fowleri* and *Hyla versicolor/chrysocelis* because their tadpoles are difficult to distinguish in the field.

Three wetland characteristics that affect the occurrence probabilities of amphibian species were also recorded: hydroperiod, area, and connectivity. Hydroperiod is the characteristic amount of time that a wetland holds water, and each site was classified into one of three hydroperiod categories using the National Wetland Inventory (Cowardin et al. 1979): temporary (typically dry up annually), semi-permanent (typically dry up every few years) or permanent (always hold water). Area is a static covariate, defined as the wetland's minimum length times minimum width not including instances when the wetland was dry. Thus wetland area is defined as the smallest size of a given wetland during a survey event when it was not dry (Mattfeldt et al. 2009). Connectivity is a measure of a wetland's distance to other wetlands, and is calculated as $conn_i = \ln\left(\sum_{j \neq i} \exp(-\theta d_{ij}) area_j\right)$ where $\frac{1}{\theta}$ is the mean migration distance for a species, d_{ij} is the pairwise distance between wetlands i and j, and $area_j$ is the area of wetland j (Moilanen and Nieminen 2002; Werner et al. 2007). Area is included in the measure of connectivity because larger wetlands can generally support larger population sizes of amphibians, which increases the potential pool of dispersers originating from a given wetland. Because data on dispersal distances are lacking, we conservatively set θ to 750m for all species (Smith and Green 2005). For more details on the sampling protocols refer to Mattfeldt et al. (2009).

Model description

We used a multi-species hierarchical modeling framework (Dorazio and Royle 2005; Dorazio et al. 2006; Gelfand et al. 2005), which links individual single-species occupancy models (MacKenzie et al. 2002; Tyre et al. 2003) at the community level by assuming that each of the species-specific parameter values are drawn from a common distribution (for more details see Dorazio and Royle 2005; Dorazio et al. 2006; Kéry and Royle 2008; Royle and Dorazio 2008; Walls et al. 2011). This leads to an improved composite analysis at the species (Zipkin et al. 2009) and community levels (Russell et al. 2009). The model is based on the survey-specific detection/non-detection records of all 12 species/species complexes across all life stages. The observations, $x_{i,j,t,k}$, denote detection (*x*=1) or non-detection (*x*=0) of species *i* (1,2,…,12) at wetland *j* (1,2,...,63) in year *t* (2005, 2006,...,2010) during sampling occasion *k* (1,2,…,8). True occupancy is only partially observable and is modeled as a Bernoulli random variable, $z_{i,j,t} \sim Bern\left(\psi_{i,j,t}\right)$ with probability $\psi_{i,j,t}$, where $z_{i,j,t} = 1$ when species *i* is present at wetland *j*, during year *t*, and zero otherwise. Detection of a species is assumed to be Bernoulli random variable dependent on the occupancy state: $x_{i,j,t,k} \sim Bern\left(p_{i,j,t,k} \cdot z_{i,j,t}\right)$ where $p_{i,j,t,k}$ is the detection probability for species *i* at wetland *j* in year *t* during sampling rep *k*, given that the species is present. Thus, the repeated sampling protocol (*k* >1) over the breeding season allows us to differentiate non-detection from true absences in a given year by estimating the detection probability for each species during each sampling occasion.

We modeled the occupancy probability $\psi_{i,j,t}$ for species *i* in wetland *j* during year *t* using the three wetland-specific covariates: hydroperiod (a discrete variable), wetland area and connectivity (both continuous variables, each standardized to have mean of zero and standard deviation of one). We developed four versions of the model: 1) a model with the three wetland-specific habitat covariates only; 2) a model with the wetland covariates and an annual trend in occupancy; 3) a model with the wetland covariates and cumulative spring precipitation (March through June); and 4) a model with the wetland covariates and an autologistic term (an additional covariate to measure the effect of occurrence at wetland *j* in year *t*-1 on the occupancy probability in year *t*). We modeled $\psi_{i,j,t}$ for each species *i* using the logit link function:

$$\text{logit}\left(\psi_{i,j,t}\right) = \alpha 1_{i,hydro_j} + \alpha 2_i area_j + \alpha 3_i conn_j \\ + \alpha 4_i trend_t + \alpha 5_i precip_t + \alpha 6_i z_{i,j,t-1}$$

where the intercept term ($\alpha 1_i$) is dependent on the hydroperiod class (hydro = temporary, semi-permanent, or permanent) and $\alpha 2_i$ and $\alpha 3_i$ are the effects of the wetland area and wetland connectivity (included in all versions of the model). The parameters $\alpha 4_i$, $\alpha 5_i$, and $\alpha 6_i$ are, respectively, an annual trend (standardized so that year 2007 is zero), the effect of precipitation (standardized to have mean of zero and standard deviation of one), and an autologistic term (an effect on occupancy based on whether the species was present at the wetland in the previous year). In fitting the autologistic model with the latent species occurrences (the *z* matrix), our model accounts for imperfect detection rather than simply using observed species, which likely contain false negative errors. Each of the parameters $\alpha 4 - \alpha 6$ are included in only one of the four models (2nd, 3rd, and 4th, respectively). We note that in the autologistic model, species-specific occupancy can be specified by colonization ($\alpha 1_i$ on the logit scale) and persistence ($\alpha 1_i + \alpha 6_i$) probabilities. Our specification of the autologistic model is a restricted form of dynamic occupancy models such as those described in Dorazio et al. 2010 and Kéry et al. 2009 where we assume that the effects of the wetland covariates are equal on colonization and persistence.

Detection was similarly modeled for each species *i* at wetland *j* and sampling rep *k*, with covariates for annual (linear and squared) effects of the sampling date

(Julian day standardized to have a mean of zero and standard deviation of one) on the species-specific detection probability (Kéry and Royle 2008). We note that in specifying the model this way that detection probability represents a combination of both observer effects as well as temporal replication. However, we do not believe that this affects our estimates of occupancy because observers were well trained, there was reasonable congruence between observers (>60%) and species-specific detection (and covariate values) were allowed to vary annually.

We expected hydroperiod to influence species' abilities to both colonize and persist in a given wetland. Temporary wetlands do not provide suitable breeding habitat for some species (e.g., *Lithobates clamitans* whose tadpoles require two years to metamorphose), though they may be used for foraging or breeding by others. Though many amphibian species only use wetlands during the breeding season, persistence (e.g., wetland use from one spring/summer to the next) in temporary wetlands is likely to be lower compared to semi-permanent or permanent wetlands where water is retained longer during the season. Additionally, because permanent wetlands are available during the full annual cycle, they are comparatively easier for species to colonize. We expected hydroperiod to have a large effect on the occupancy probabilities for all species, with *Lithobates sylvaticus, Hemidactylium scutatam, Ambystoma opacum, Ambystoma maculatum,* and *Pseudacris crucifer* having higher occupancy in more temporary wetlands and *Lithobates clamitans*, *Lithobates catesbeianus, Lithobates palustris*, and *Notophthalmus viridescens* having higher occupancy in permanent wetlands. We believed that wetland area and connectivity would have positive effects on species occurrences. Larger wetlands tend to have higher colonization rates because they are larger targets for dispersing amphibians (Armstrong 2005; Haddad and Baum 1999; Whitehead and Jones 1969). Wetlands with high connectivity values are more likely to be colonized compared to wetlands that are less connected because travel distances are shorter. Due to concerns that the amphibian community is declining in CHOH, we included the trend model to determine if species-specific occupancy probabilities had in fact declined over the study. Because increased precipitation over the breeding period leads to wetlands holding water longer and provides more suitable conditions for breeding and foraging at a given wetland, we hypothesized that precipitation would have a positive effect on both persistence and colonization. Even though amphibian wetland use is ephemeral and can vary annually, the site fidelity exhibited by many species suggests that use of a wetland in time *t*-1 would have a positive effect on wetland use in year *t* (e.g., persistence; Smith and Green 2005).

Each of the species-specific parameter values were assumed to come from a normal, community-level, prior distribution (Dorazio et al. 2006; Kéry and Royle 2008). We estimated parameters using a Bayesian approach with Markov chain Monte Carlo (MCMC) implemented in the programs R (with the R2WinBUGS package; Sturtz et al. 2005) and WinBUGS (Lunn et al. 2000) using flat priors for each of the community-level parameters. In a Bayesian analysis, each parameter is treated as a random variable. The MCMC approach allows us to explicitly measure variation in parameter values by examining a posterior distribution for each parameter. We ran three chains of each model for 5000 iterations, thinned by 5, after a burn-in of 5000 iterations (resulting in 3000 posterior samples for each parameter) and assessed model convergence using the R-hat statistic (Gelman and Hill 2007).

Evaluating model projections using AUC

We fit each model separately using data from the 33 wetlands sampled in 2005-2009. We then used the posterior covariate values (and the precipitation conditions of 2010 and occurrence states of 2009, when applicable) to generate species-specific occupancy estimates for both (1) the 33 sites that had previously been sampled and (2) the 30 new sites that were sampled only in 2010. To determine whether or not a species was present at each of the wetlands in 2010, we fit an additional model with the three wetland-specific covariates, hydroperiod, area, and connectivity, using only the 2010 data (all 63 wetlands) to generate the latent *z* values for each species *i* at each wetland *j*, which we considered to be the true 2010 species occurrences. Thus, if species *i* was observed on at least one sampling occasion at wetland *j* in 2010, $z_{i,j,2010} = 1$ for every draw of the posterior distribution. However, if the species was not observed at a wetland *j*, then $z_{i,j,2010} = 0$ or $z_{i,j,2010} = 1$ depending on the species' detection probability and the wetland characteristics (i.e., the posterior distribution for $z_{i,j,2010}$ would likely contain both 0 and 1 values).

We estimated the AUC for each of the individual species models (Hosmer and Lemeshow 2000). We also calculated the AUC for all species at every location, and separately, for all species in the previously sampled wetlands and for all species in the new wetlands. As mentioned earlier, the AUC (ranging from 0-1) measures the discrimination of a model, which in this case corresponds to the ability to correctly project which wetlands are occupied. A value of 0.5 indicates that the model performs no better than random. Values greater than 0.5 indicate progressively better discriminatory capabilities (Hosmer and Lemeshow 2000). Rather than use average values to determine a single point estimate, we used the full posterior distribution (3000 draws) and the R package ROCR (Sing et al. 2005) to quantify the uncertainty in model estimates, essentially producing a posterior sample of ROC plots and AUC values. For the purposes of evaluating the efficacy and utility of our models, we consider the top model to be the one with the highest predictive capability (e.g., AUC value) for species' occurrences at each of the wetlands.

Results

Although the number of detections was small for some species, our hierarchical multi-species modeling approach allowed us to use all the available data and estimate the occurrence probabilities and covariate effects for each of the 12 species/species complexes. For all species, hydroperiod was the most significant wetland covariate affecting occurrence probabilities (Figure 3.1). This result was fairly consistent across all models. Occurrence probabilities for all species were generally lowest in temporary wetlands and highest in permanent wetlands. In the autologistic model, which allowed us to examine colonization and persistence probabilities, mean species-specific colonization ranged from 0.02-0.19 in temporary, 0.02-0.41 in semi-permanent, and 0.05-0.49 in permanent wetlands, while persistence ranged from 0.29-0.55 in temporary (with one species, *Ambystoma maculatum*, having a value of 0.75), 0.36-0.81 in semi-permanent, and 0.52-0.92 in permanent wetlands (when other covariates were at their average values). This suggests that persistence was generally higher in all wetland types compared to colonization and that colonization increased with hydroperiod. Area had a significant positive effect on the occupancy probabilities of almost all species in the habitat-only, precipitation, and trend models (except for *Hemidactylium scutatum*, possibly because of its small sample size). In the autologistic model, area had a significant positive effect on all but four species (*Ambystoma maculatum*, *Ambystoma opacum*, *Hemidactylium scutatum*, and *Notopthalmus viridescens*). Connectivity was not significant for any of the species except for *Lithobates sylvaticus*, which surprisingly showed a negative effect.

The observed number of species per wetland was lower in 2010 compared to the average number of observed species per wetland in 2005-2009 (Figure 3.2). Thus, predicted wetland richness was generally overestimated in 2010 using the habitat-only model (Figure 3.3). However, the trend and precipitation effects were not significant (i.e., 95% posterior intervals overlapped zero) for any of the 12 species/species complexes, in their respective models. The mean trend estimate was negative for nine species and the probability that the trend was negative was greater than 70% for seven species (i.e., >70% of samples from the posterior distribution were negative). Together with the overestimates of wetland richness, these results suggest that some species may be declining (e.g., occupancy probabilities may have decreased over the time period from 2005 to 2010), but more data are needed for definitive conclusions.

The autologistic model confirmed our expectation that occurrence at a wetland in one year had a strong impact on species occupancy probabilities in the following year, indicating a difference in the colonization and persistence rates at wetlands. The autologistic term was significant and positive for all species and was generally more important than even hydroperiod in estimating occupancy. For many species, there were smaller differences in occupancy estimates among hydroperiod class as compared to whether or not the species had been present the previous year.

Evaluating model projections using AUC

The AUC was virtually identical in the trend and precipitation models as compared to the habitat-only model. This is because the mean values of the trend and precipitation effects were centered on zero, and other covariate values were consistent among these models. Because these covariates were not informative in predicting occupancy of any species, we focus on comparing the predictive abilities of the habitat-only and autologistic models.

At the community level, the habitat-only (AUC for all species at all wetlands: mean 0.71; 95% PI: 0.66-0.75; Figure 3.4) and autologistic (AUC: mean 0.74; 95% PI 0.68-0.78) models performed well, and their AUC values had overlapping posterior intervals. However, the autologistic model performed significantly better for the 2010 data in the 33 wetlands that had been previously sampled from 2005-2009 (AUC: mean 0.80; 95% PI: 0.76-0.83; Figure 3.4) compared to the habitat-only model (AUC: mean 0.71; 95% PI: 0.67-0.74). The habitat-only model predicted species occupancy in 2010 equally well for the wetlands that had been sampled from 2005-2009 as well as the unsampled wetlands (AUC: mean 0.71; 95% PI: 0.65-0.76). The autologistic model had a poorer performance in predicting occupancy in unsampled wetlands (AUC: mean 0.69; 95% PI: 0.62-0.74) compared to wetlands that had been sampled, but was not significantly worse than the habitat-only model in the newly sampled wetlands.

To determine how well we would expect the models to perform (i.e., the maximum AUC values possible for a given model), we calculated AUC values for simulated datasets generated using the model results. We used the habitat-only model to simulate ten datasets using the estimated mean species- and wetland-specific occupancy values (to obtain the latent *z* state) as well as the detection covariates (to simulate the observed “data”, *x*) for the 2005-2010 data. We then fit the habitat-only model to these simulated data (using the same specifications as the real data in WinBUGS and R) and estimated occupancy probabilities for each species at each wetland for each simulated dataset (ten replicate trials). We calculated the AUC values using these new covariate estimates and a similar dataset simulated for 2010. Our results indicate that the mean of the upper bound of the AUC for the habitat-only model is 0.78 (95% PI: 0.74-0.81; with standard error on these estimates <0.01 among the ten simulations), with upper bounds of 0.76 (95% PI: 0.71-0.81; standard error <0.01) and 0.79 (95% PI: 0.73-0.84; standard error <0.01) in previously sampled and unsampled wetlands, respectively.

Species-specific AUC values were generally acceptable (i.e., mean values greater than 0.6 for all species except *Hemidactylium scutatum*, *Lithobates sylvaticus* in the previously sampled locations, and *Ambystoma opacum* in the wetlands that had not been previously sampled; Table 3.1) with nine species having overall mean AUC values greater than 0.7 in one or both of the habitat-only and autologistic models. While the mean species-specific AUC values were generally higher in the autologistic model (using previously sampled locations only), the difference was only significant for two species: *Ambystoma maculatum* and *Notopthalmus viridescens*.

Discussion

The value of AUC in evaluating model projections and quantifying uncertainty

The use of the receiver operating characteristic and the AUC has been debated in ecology and species distribution modeling and has been cautioned in its use when species absences are unknown (Lobo et al. 2007). While it is increasingly common to use detection/nondetection data for estimating AUC (e.g., Manel et al. 2001) and to evaluate presence only models (e.g., Rebelo et al. 2010), such methods fail to consider that nondetection may occur either because a species was absent or because the species was overlooked during the sampling process (MacKenzie et al. 2002; Tyre et al. 2003). In our approach to using AUC, we explicitly account for detection biases by using the estimated “true” occurrence (*z* matrix) of each species. Thus if a species was not detected, we account for the possibility that the species was truly present, but overlooked during sampling, leading to a more inclusive picture of the variability and transient use of habitat inherent in many systems.

In using the full posterior distribution of species-specific wetland occupancy and “true” occurrence, we were able to calculate a posterior distribution of ROC and AUC values. This allowed us to quantify the uncertainty associated with our model’s discrimination abilities (e.g., by providing a confidence interval of our estimate). In many applications of AUC in species distribution modeling, there is no mention of uncertainty in model discrimination (e.g., Anderson and Raza 2010; Kharouba and Kerr 2010). Liu et al. (2011) highlight the need for determining the accuracy of AUC and suggest bootstrapping and randomization methods for estimating confidence intervals. Our approach, using a Bayesian analysis, presents an alternative method by assuming that uncertain quantities such as AUC are best described by examining their full posterior distributions. This allows for a more complete characterization of model discrimination, including measures for determining the accuracy and precision of estimates.

We note that in our analysis we discovered that the AUC ceiling for our models was less than one. By this we mean that if the actual data-generating model is known and the AUC is computed, then you would still expect to achieve some AUC value < 1.0. In considering which model best predicts occupancy status of wetland breeding amphibians, it may thus be important to consider a model's maximum AUC value. It is not clear whether it is always best to choose a model with the highest AUC value or if it is better to choose a model with an AUC value that is close to its ceiling (for predictive purposes). There is no clear model selection criterion for hierarchical models; although other approaches such as BIC (Bayesian Information Criterion) and loss functions (Gelfand and Ghosh 1998) may prove useful.

AUC is quickly becoming a standard method for evaluating species distribution models, in part because it is readily calculated in software packages such as MAXENT (Elith et al. 2006; Philips et al. 2006). However, in our Bayesian approach, it is also possible to directly calculate the confusion matrix by simulating the binary data using the species- and site- specific occupancy probabilities. In this way, we calculated the true positive and true negative rates (e.g., the fraction of times with correct predictions) for the habitat-only and autologisitic models (Table 3.2).

Comparison of these results shows that the two models perform equally well, except for in previously sampled wetlands where the autologisitic model has a significantly higher true positive rate. In all cases the true positive rates were significantly lower than the true negative rates. Although examining the confusion matrix does not change our inference, calculation of these rates highlights the difficulty in predicting presences compared to absences for ephemeral species with low prevalence, such as the wetland breeding amphibians in CHOH. For example, we would expect the true positive rate to increase with increasing prevalence (assuming reasonably high detection probabilities). AUC provides an understanding of a model’s predictability by determining whether a randomly selected wetland where a species occurred had a higher occupancy probability than a randomly selected wetland where the species did not occur. Thus AUC provides a measure different than an examination of the confusion matrix (Hosmer and Lemeshow 2000). However, we believe that direct calculations of the true positive and negative rates using a Bayesian approach can provide more intuitive comparisons among models and facilitate understanding of a model’s predictive abilities; we suggest calculating these quantities when possible.

Management implication for CHOH

In establishing the utility of our multi-species occupancy models for informing management decisions, we are specifically interested in evaluating how well our models can predict species occurrences in two situations: 1) in future years for sites where sampling has previously occurred and 2) in unsampled wetlands. Determining the predictive capability of our models is important for both identifying wetlands that may benefit most from management actions (e.g., increasing hydroperiod or area) and for evaluating the success of management (critical steps in an adaptive management program as well as other management scenarios, Williams et al. 2002). At the community level, the habitat-only model (wetland hydroperiod, area, connectivity) was the top model because of its overall performance (mean AUC of 0.71 from an average possible ceiling of 0.78) and parsimony (the other models had similar AUC values but each had one extra parameter). For specific wetlands where data are available, knowledge of species use during the previous year improved predictive ability for the amphibian community, as was demonstrated by the autologistic model. Though knowledge of the prior year's wetland use led to a significant gain in AUC at the community level, individual species' AUC values were only significantly improved for two out of 12 species/species complexes.

The habitat and autologistic models had fairly high predictive abilities for most species (Table 3.1). In some instances (e.g., *Lithobates sylvaticus* in the previously sampled locations and *Ambystoma opacum* in the wetlands that had not been previously sampled; Table 3.1), the model performed worse than would be expected by chance. It is possible that the hierarchical structure of our model, in which information is shared across species, may be inappropriate for some species (e.g., pulling estimates of covariate effects of extreme species, for which few data exist, towards the community mean). Also possible is that wetland use in 2010 was inconsistent with wetland use in previous years for some species. In fitting occupancy models separately for each species (e.g., no community level structure), we determined that there were not enough data to estimate occupancy — with the relevant covariates — individually for most species (results not shown, but see

Mattfeldt et al. 2009 for more on individual species occupancy models at CHOH). Thus, we believe that the utility of the model is greatest when focusing on management of the community rather than on individual species. Indeed, at CHOH as well as many other monitoring programs (DeWan and Zipkin 2010; Manley et al. 2004; Weir et al. 2005), the objective — in this case, to maintain species richness — is targeted at the community level.

Neither spring precipitation nor trend had significant effects on occupancy for any species, yet the habitat-only model overestimated richness in 2010 at nearly all wetlands (Figure 3.3). Likewise, the breeding season in 2010 had lower cumulative precipitation (9.32 inches) in CHOH compared to any of the others years of the survey (mean: 17.89 inches; range: 10.49-23.18), which could help explain why the observed number of species was lower in 2010 compared to previous years (Figure 3.2), and thus why the models overestimated wetland richness. Wetland use by amphibians has high temporal variability (Green 2003). Weather variables, including precipitation, can influence the occurrence of species at wetlands. Finer resolution precipitation (e.g., wetland specific) data, including timing of rainfall, may better predict wetland use by amphibians. It is also possible that other environmental variables in the region (e.g., wetland use by other taxa, including humans; urbanization outside the park) are influencing amphibian use of wetlands in CHOH and cannot be captured by a simple trend effect.

Conclusions

The use of predictive models can aid decision makers in determining the optimal course of action for a given set of objectives (Williams et al. 2002). However, it is important to first assess whether model projections are reliable. Our approach for evaluating the predictive power of multi-species occupancy models accounts for potential detection biases and incorporates the inherent variability found in species-habitat relationships. In accounting for false negative errors and estimating a full posterior distribution of covariate as well as AUC values, we were able to understand better the accuracy and precision of our model results. The conservation and management of species and their habitats require a clear understanding of species-habitat relationships and the potential tradeoffs associated with alternative management actions.

Table 3.1 Species-specific AUC values for the habitat-only and autologistic models for the 33 wetlands that had been sampled continuously from 2005-2009 and for the 30 wetlands that were unsampled in 2005-2009. The table shows the mean of the posterior distributions as well as the 95% posterior intervals.

Habitat model

	AUC (sampled wetlands)			**AUC (unsampled wetlands)**		
	Mean	*95-Low*	*95-High*	*Mean*	*95-Low*	*95-High*
Ambystoma maculatum	0.60	0.54	0.65	0.64	0.48	0.78
Ambystoma opacum	0.75	0.43	0.91	0.41	0.31	0.56
Anaryxus americanus/fowleri	0.82	0.66	0.92	0.77	0.54	0.91
Hemidactylium scutatum	NA	NA	NA	0.51	0.10	0.88
Hyla versicolor/chrysocelis	0.64	0.46	0.80	0.77	0.54	0.91
Notopthalmus viridescens	0.74	0.64	0.79	0.80	0.73	0.88
Pseudacris crucifer	0.68	0.57	0.78	0.82	0.68	0.92
Lithobates catesbeiana	0.78	0.59	0.92	0.82	0.63	0.93
Lithobates clamitans	0.71	0.61	0.79	0.86	0.77	0.92
Lithobates palustris	0.84	0.72	0.90	0.64	0.56	0.74
Lithobates sphenocephala	0.79	0.64	0.90	0.79	0.54	0.94
Lithobates sylvatica	0.41	0.32	0.52	0.63	0.57	0.70

Autologistic model

	AUC (sampled wetlands)			**AUC (unsampled wetlands)**		
	Mean	*95-Low*	*95-High*	*Mean*	*95-Low*	*95-High*
Ambystoma maculatum	0.89	0.86	0.93	0.66	0.47	0.82
Ambystoma opacum	0.70	0.37	0.88	0.45	0.32	0.62
Anaryxus americanus/fowleri	0.80	0.63	0.93	0.75	0.49	0.94
Hemidactylium scutatum	NA	NA	NA	0.59	0.10	0.93
Hyla versicolor/chrysocelis	0.64	0.45	0.83	0.75	0.49	0.94
Notopthalmus viridescens	0.97	0.85	0.99	0.78	0.61	0.95
Pseudacris crucifer	0.79	0.66	0.88	0.80	0.64	0.92
Lithobates catesbeiana	0.78	0.59	0.94	0.77	0.56	0.93
Lithobates clamitans	0.80	0.71	0.88	0.82	0.67	0.93
Lithobates palustris	0.85	0.71	0.92	0.62	0.47	0.78
Lithobates sphenocephala	0.83	0.69	0.91	0.77	0.52	0.96
Lithobates sylvatica	0.50	0.43	0.59	0.61	0.49	0.73

Table 3.2 The posterior means of true positive rate (TPR) and true negative rate (TNR) for the habitat only and autologistic models using data from all wetlands, from the 33 wetlands that had been sampled continuously from 2005-2010, and from the 30 wetlands that were only sampled in 2010. The values in the parentheses are the 95% posterior intervals.

	TPR	TNR
Habitat model		
All wetlands	0.40 (0.32-0.48)	0.77 (0.74-0.81)
Sampled wetlands	0.41 (0.31-0.52)	0.76 (0.71-0.80)
Unsampled wetlands	0.39 (0.29-0.50)	0.79 (0.74-0.85)
Autologistic model		
All wetlands	0.52 (0.43-0.60)	0.76 (0.73-0.80)
Sampled wetlands	0.59 (0.47-0.69)	0.77 (0.72-0.81)
Unsampled wetlands	0.44 (0.33-0.55)	0.76 (0.71-0.81)

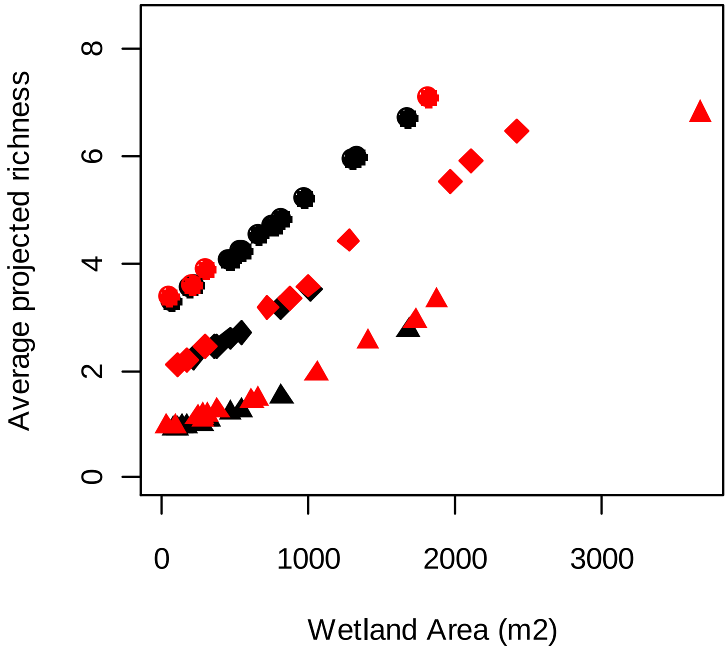


Figure 3.1 Average projected wetland richness (as estimated using the habitat only model with data from 2005-2009) for each of the 63 wetlands (circles - permanent, diamonds – semi-permanent, triangles – temporary) plotted against the area of the wetland. The red points are wetlands with below average connectivity.

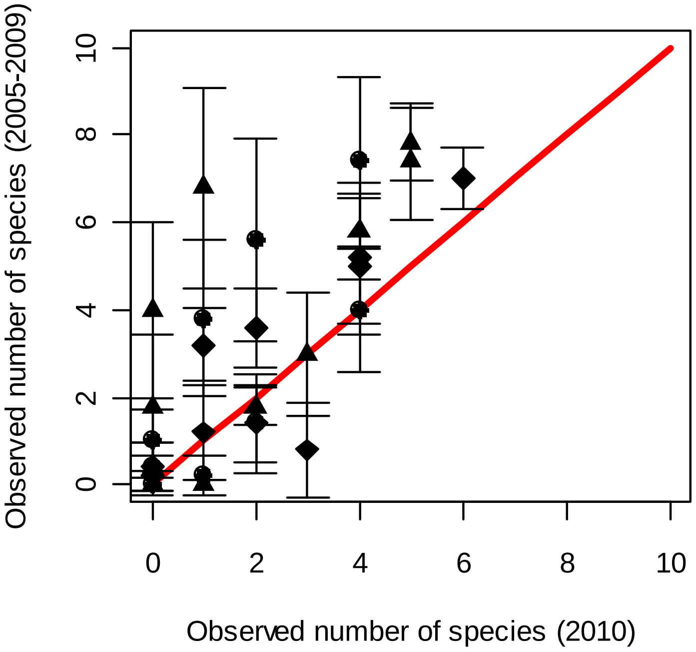


Figure 3.2 Observed number of species in 2010 plotted against the average number of observed species in 2005-2009 for the 33 wetlands that have been sampled continuously over the duration of the study.

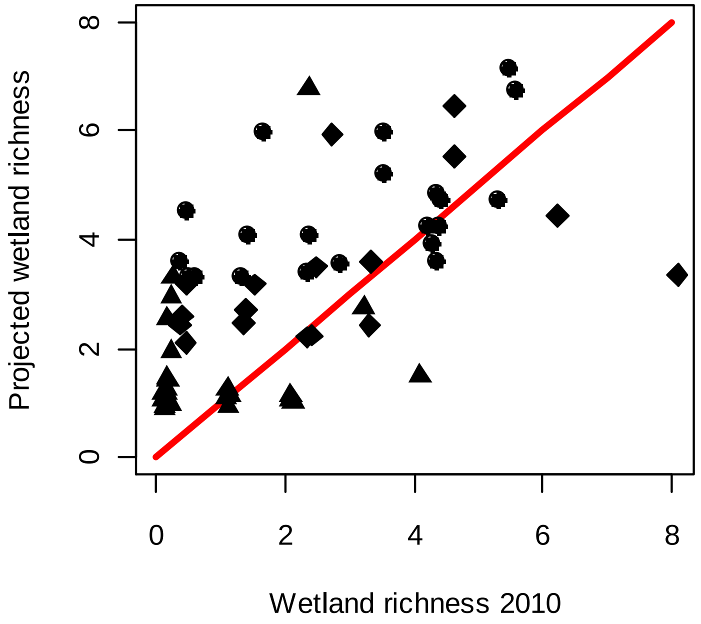


Figure 3.3 Species richness (accounting for detection errors) at the 63 wetlands in 2010 as estimated using the habitat-only model (on only the 2010 data) plotted against the projected wetland richness as calculated by summing the individual occurrence probabilities for each species at each wetland as estimated using the habitat model for the 2005-2009 data.

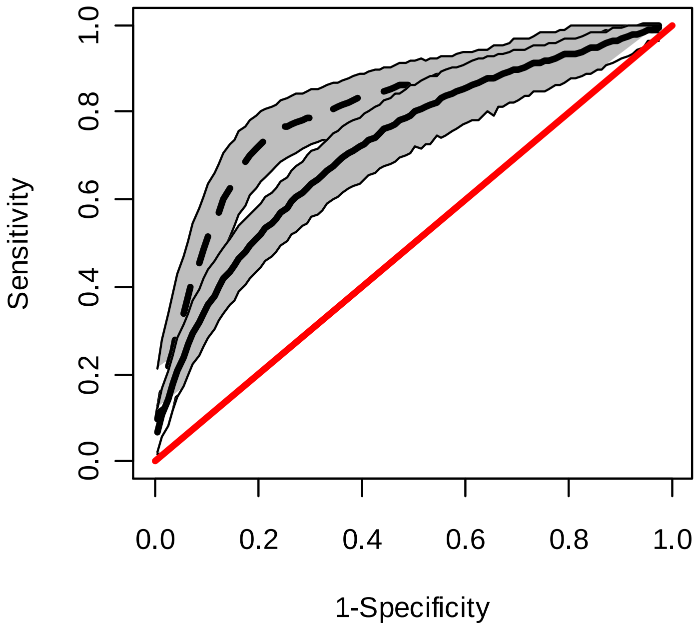


Figure 3.4 Receiver operator curves for the habitat model (solid line with 95% PI in grey; calculated using all species at each of the 63 wetlands) and autologistic model (dashed line with 95% PI in grey; calculated using all species in the 33 wetlands that had been sampled all years of the survey. *Hemidactylium scutatum* is excluded since it was not observed in 2010 in any of these 33 wetlands.)

Chapter 4: Tracking climate impacts on the migratory monarch butterfly

In review: Global Change Biology.

Coauthors: Leslie Ries, Rick Reeves, James Regetz

Abstract

Understanding the impacts of climate on migratory species is complicated by the fact that these species travel through several climates that may be changing in diverse ways throughout their complete migratory cycle. Yet, most studies are not designed to tease out the direct and indirect effects of climate at various stages along the migration route. We assess the impacts of spring and summer climate conditions on breeding monarch butterflies, a species that completes its annual migration cycle over several generations. No single, broad-scale climate metric can explain summer breeding phenology or the substantial year-to-year fluctuations observed in population abundances. As such, we built a Poisson regression model to help explain annual arrival times and abundances in the Midwestern United States. We incorporated the climate conditions experienced both during a spring migration/breeding phase in Texas as well as during subsequent arrival and breeding during the main recruitment period in Ohio. Using data from a state-wide butterfly monitoring network in Ohio, our results suggest that climate acts in conflicting ways during the spring and summer seasons. High or low spring precipitation is associated with the largest annual population growth in Ohio and the earliest arrival to the summer breeding ground, as is intermediate spring temperatures. On the other hand, arrival to the summer breeding grounds in Ohio is not affected by climate conditions within Ohio. Precipitation has minimal impacts on summer grounds, whereas warmer temperatures are generally associated with the highest expected abundances, yet this effect is mitigated by the average seasonal temperature of each location in that the warmest sites receive no benefit of above average summer temperatures. Our results highlight the complex relationship between climate and performance for a migrating species and suggest that attempts to understand how monarchs will be affected by future climate conditions will be challenging.

Introduction

A primary goal of global climate change research is to understand the connections between climate and biological phenomena so that specific predictions can be made about how species will be affected by future climate regimes (Parmesan 2006). While this is a difficult task for any organism, characterizing the responses of migratory species is particularly challenging. During the course of their life cycles, migratory species experience multiple climates that may be changing in different ways (Bowlin et al. 2010; Norris and Marra 2007). Perhaps not surprisingly, it has been suggested that climate change, along with other anthropogenic pressures, may be contributing to the overall decline of migration as a biological phenomenon (Brower and Malcolm 1991; Wilcove and Wikelski 2008). Here, we use the term “migratory” to refer to species that have a regular, long-distance pattern of “return” migration related to predictable, disjunct seasonal ranges, and not species that track resources within their own home ranges or that are nomadic and track unpredictable resources over large areas (sensu Mueller and Fagan 2008).

Establishing cause and effect relationships between climate and migratory dynamics is complicated. In addition to direct impacts on physiology at each location along the migration cycle, which may be carried over into subsequent migratory phases (Harrison et al. 2011), climate can also have indirect effects on the abundance or timing of food resources (Visser and Both 2005; Zalucki and Rochester 2004). Disentangling these multiple, interacting climate drivers is complex and studies are rarely designed to isolate causes to a particular migratory phase or effect (Gordo 2007; Norris and Marra 2007). Indeed, many studies have focused on large scale climate dynamics like the North Atlantic Oscillation (NAO), which are often associated with broad-scale weather patterns and have thus been found to be good predictors of both phenology (e.g., Adamik and Pietruszkova 2008; Palm et al. 2009) and abundance (e.g., Zipkin et al. 2010). Yet the use of large-scale climate metrics like the NAO makes it difficult to isolate how specific climate factors may be impacting particular phases of migration or the performance of species (Gordo 2007; Norris and Marra 2007).

The vast majority of studies on the impacts of climate on terrestrial, migratory species have focused on bird phenology, with the bulk of that research studying spring arrival times at breeding grounds in North America and Europe (Gordo 2007). In general, dates of spring arrival have been advancing for many species and those advancements are consistent with regional warming (Gordo 2007). While there is a great deal of interspecific variability in this phenomenon, there is also general within-species consistency (Rubolini et al. 2010). However, most studies have not specifically examined the climate conditions during the winter or migratory (stopover) phases, and instead have focused only on the environment at the point of arrival (Gordo 2007), despite the fact that it is very unlikely that birds are able to assess conditions at summer breeding grounds prior to their arrival. While some climate variables may operate on a large enough scale so that metrics from the arrival point are correlated to stopover or wintering climates (e.g., the NAO), this approach does not allow specific climate mechanisms to be identified (Norris and Marra 2007). Earlier arrivals to breeding locations can lead to either better access to resources (Kokko 1999) or, conversely, a phenological mismatch where access to optimal resources is diminished, possibly leading to decreased fitness or even population declines (Both et al. 2006; Saino et al. 2011). Studies of how climate impacts population size have been less common and more inconsistent, possibly because breeding performance responds to more complex interactions of factors both on and off the breeding grounds (Norris and Marra 2007).

Although butterflies have received intensive focus on the climate impacts related to phenology (Parmesan 2007), phenological mismatches (Doi et al. 2008; Singer and Parmesan 2010), local abundances (Hodgson et al. 2011; Warren et al. 2001) and range and elevational dynamics (Crozier and Dwyer 2006; Forister et al. 2010; Parmesan et al. 1999), none of the species in those studies exhibit return migration as defined here. Insects are not generally associated with return migration; instead, many species display spectacular mass movements out of natal areas, often called migration, but from which there is generally no subsequent return (Holland et al. 2006). One of the few known exceptions is the monarch butterfly (Danaus plexippus) which completes a regular migratory route each year, but over multiple generations (Brower 1986). Because of its spectacular migration, it has become a “flagship” species for both migration and the conservation of migratory phenomenon (Brower and Malcolm 1991; Wilcove and Wikelski 2008). Understanding how climate impacts monarchs will be a key factor in its conservation (Batalden et al. 2007; Oberhauser and Peterson 2003) and will expand our understanding of the impacts of climate on migratory species in general (Bowlin et al. 2010).

Study system

The monarch butterfly (*Danaus plexippus*) in North America has a regular seasonal migratory pattern that is completed over multiple generations rather than by single individuals (Brower 1986). There are three fairly distinct monarch populations in North America: the western migratory population (west of the Rocky Mountains that overwinters along the California coast), the eastern migratory population (east of the Rocky Mountains that overwinters in Mexico) and a small non-migratory population in southern Florida (Altizer et al. 2000). The eastern migratory population is the largest, and the focus of this study. During migration, monarchs use host plants in the subfamily *Asclepiadoideae* (milkweeds), which are common throughout North America.

The migration patterns of the eastern population are illustrated in Figure 4.1. Individuals from this population overwinter in a small forested area at the boundary of the Mexican states Michoacán and México (Brower 1986). During the winter, they remain clustered in dense colonies, which start breaking up in late February or early

March as individuals begin moving northward. The spring migrants move into Texas and its surrounding areas by mid-March (Brower et al. 2004) and begin laying eggs in mid- to late-March. These eggs become the year's first generation, which fans out over the rest of eastern North America. Throughout the summer breeding season, the population grows as an additional 2-3 generations are produced, with the bulk of recruitment occurring in the Midwest (Wassenaar and Hobson 1998). The size of the final generation, which migrates to Mexico, fluctuates substantially from year to year (Prysby and Oberhauser 2004; Swengel 1995). The causes of those fluctuations are currently unknown, although climate is assumed to be one contributing factor (Zalucki and Rochester 2004). Around the first of September, monarchs enter reproductive diapause, begin to move southward, and ultimately return to the Mexican overwintering sites (Brower 1986).

Climate effects on monarchs can be direct, impacting adult activity and juvenile development, or indirect, by impacting growth and vitality of their host plants. Niche models have suggested that monarchs during the breeding season have an optimal temperature and precipitation "envelope" that tracks northward as the season progresses, starting in Texas during March and April. Although that climate envelope continually shifts position throughout the summer growing season, much of the optimal range persists in the Midwest (Batalden et al. 2007). These modeling results are largely consistent with laboratory studies that bracket the minimum and maximum temperatures that promote monarch juvenile development (York and Oberhauser 2002; Zalucki 1982) and suggest climate should underlie some of the year-to-year variability in population dynamics (Zalucki and Rochester 2004). Studies in western populations suggest drought is a limiting factor (Stevens and Frey 2010) and that higher winter temperatures and increases in the previous season's rainfall can advance the onset of spring migration (Forister and Shapiro 2003). Our goal is to examine how climate experienced during the spring and summer impacts phenology as well as inter-annual fluctuations in abundance of the monarch butterfly on its summer breeding grounds. We focus our analysis on Ohio because there is a well-established series of butterfly survey sites throughout the state which falls within the major zone of monarch recruitment.

Methods

Our analysis focuses on the impacts of climate experienced by the first generation in the southern U.S. (developed from eggs laid by incoming spring migrants from Mexico) and during the main population growth phase in Ohio (from incoming first generation adults that emerged in Texas and the surrounding areas). We concentrated on temperature and precipitation, two main facets of weather known to affect monarchs (Batalden et al. 2007; Zalucki and Clarke 2004). Because initial explorations of the data suggested that coarse weather metrics could not explain inter-annual variations in abundance and phenology (Fig. 2), we developed a model that captured weekly dynamics at each Ohio survey site based on several climate metrics.

To account for timing in our model, we sequentially numbered each week in the season and we refer to those week designations throughout the rest of this paper. The onset of migration is approximately the beginning of March (week 1 always begins on March 1) and spring breeding in Texas occurs primarily between the last week in March through the end of April (weeks 4-9). The adults that emerge during spring breeding usually arrive in Ohio by the first week in May (week 10), but are relatively uncommon until mid-June to mid-July (weeks 15-20). Population growth continues through approximately the beginning of September (week 28).

Temperature impacts were captured by converting temperature into growing degree days (GDD). GDD accumulate the number of degrees that can contribute to development, assuming a minimum temperature below which a species cannot develop and a maximum temperature beyond which growth is no longer benefited (McMaster and Wilhelm 1997). GDD calculations are species-specific and were developed for the monarch by Zalucki (1982). The minimum temperature required for monarch growth is 11.5C while the maximum is 33C. GDD are accumulated over the season by summing the total GDD accumulated each day. Daily GDD are calculated using the mean of each day’s high and low (up to a maximum of 33C) and subtracting the minimum temperature required for growth, meaning that a maximum of 21.5 GDD can be accumulated each day for monarchs and 352 GDD are required for an egg to develop into an adult. Like temperature, the impacts of drought can accumulate over a season and the timing of rainfall is also critical. The Palmer Drought Index (PDI) integrates rainfall events, temperature, and other hydrological dynamics over the season to estimate water availability (Heim Jr. 2002). This metric can give more biologically relevant information than rainfall alone (Heim Jr. 2002), but PDI can also be confounded with temperature (Hu and Wilson 2000), a factor that we considered when constructing our model.

Monarch data collection

The Ohio data were collected at 90 locations that comprise a state-wide network of butterfly monitoring surveys (Fig. 1b). This monitoring program was launched in 1995 by the Ohio Lepidopterist Society (www.ohiolepidopterists.org) and we include data from 1996 (the first year with multiple locations) through 2008 (the last year for which we have acquired and processed data). The annual number of survey locations increased from 13 in 1996 to 56 in 2008. Each location was surveyed by a volunteer who visited their assigned location approximately once weekly during the study period, although not all locations were visited every week or during every year. Survey protocols were based on those developed by Pollard (1977) and follow similar protocols to other butterfly monitoring programs in North America and Europe. At each survey point, the observer walked a fixed transect of variable length and recorded all butterflies seen within approximately five meters. Transect lengths vary between sites, but remained fixed at sites from year to year. To account for variable transect lengths and effort, observers recorded the time spent on each survey.

Climate data

To calculate GDD, we first acquired daily minimum and maximum temperatures throughout Texas (weeks 4-9) and Ohio (weeks 10-28) for 1996-2008 from NOAA’s Global Summary of the Day network, a global network of weather stations that provides daily weather metrics (www.ncdc.noaa.gov/oa/gsod.html). For Texas, we used the daily minimum and maximum temperature values over the period of interest at each weather station in the state and averaged values across the entire state to arrive at a single GDD spring value for each year. In Ohio, we needed spatially-specific temperature values at each butterfly survey location based on the network of weather stations. To obtain these data, we performed spatial interpolation in R (R Development Core Team 2011) using an automatic kriging procedure implemented internally in the automap package (Hiemstra et al. 2008) and carried out via the intamap package (Pebesma et al. 2011). Using these time-series of interpolated minimum and maximum daily temperatures, we calculated GDD values for each survey location in Ohio on each day in each year, and accumulated them over phenologically relevant time periods as described below.

We obtained weekly PDI values from NOAA's Climate Data Center for each of the ten NOAA-defined climate divisions within Ohio (http://www.esrl.noaa.scr/psd/usclimate/map.html). In Texas, there was a strong correlation between GDD and PDI, averaged across the state's ten climate divisions. We therefore used mean rainfall to account for yearly precipitation patterns. We used totals from February, March and April to align with the growing season of both milkweed and monarchs. We downloaded state-wide summaries of February, March and April monthly rainfall totals for Texas from NOAA's Climate at a Glance for each year (http://www.ncdc.noaa.gov/oa/climate/research/cag3/cag3.html).

Unlike the Texas data, which we used to capture large-scale conditions averaged across the state, the GDD data from Ohio were summarized at the temporal and spatial scale of the individual monarch surveys. Although monarchs are able to move long distances, we assumed that once their migratory expansion was complete, populations responded to local climate conditions. For each survey location, we accumulated GDD from week 10 up to the week of each survey. To account for rainfall effects at survey locations in Ohio, we used the PDI calculated for week 28. Although it is possible that weekly changes in the drought index could affect monarch counts, PDI tended to be negatively correlated with week (i.e., the spring tends to be wetter than the summer in Ohio), so we opted to characterize the overall precipitation conditions at sites for each year. We believe that this adequately captures the necessary variation in PDI because the index is designed to remain fairly stable over the season and does not experience high variation based on a weekly weather patterns (Heim 2002).

Analysis

We modeled monarch abundance at each survey site within Ohio throughout the summer breeding season based on spring and summer climate metrics. We used Poisson regression to model expected counts at each location j that varied annually (by year t) and by week within season (denoted as k). The objective of our model is to characterize local monarch dynamics based on relevant climate variables during the spring and summer. We opted not to include spatial location (e.g., latitude and longitude) as a factor in the model but instead used a proxy for location in the form of mean GDD accumulated by the end of the season (averaged over the 13 year study period). This allowed us to capture the average overall condition of a site (i.e., whether it tended to be relatively warmer or cooler) while still allowing the model to remain general, increasing the potential to transfer it to other locations.

Although we incorporated variables from the spring, our model predicts expected counts during the summer breeding season (weeks 10-28). That week range roughly corresponds to the time period from before the first arrival of most monarchs into Ohio (from Texas and the surrounding areas) to just prior to the southerly migration back to Mexico. We modeled expected monarch counts at each location *j* (1-90) in week *k* (10-28) within year *t* (1996-2008) on the log scale using the following model:

$$
\begin{aligned}
&\log\left(\lambda_{j,t,k}\right) = \alpha 1 + \alpha 2 \cdot week_k + \alpha 3 \cdot spPREC_t + \alpha 4 \cdot spPREC_t^2 \\
&+\alpha 5 \cdot spGDD_t + \alpha 6 \cdot spGDD_t^2 + \alpha 7 \cdot spPREC_t \cdot week_k + \alpha 8 \cdot spGDD_t \cdot week_k \\
&+\alpha 9 \cdot GDDdiff_{j,t,k} + \alpha 10 \cdot avgGDD_j + \alpha 11 \cdot avgGDD_j^2 \\
&+\alpha 12 \cdot GDDdiff_{j,t,k} \cdot week_k + \alpha 13 \cdot GDDdiff_{j,k,t} \cdot avgGDD_j \cdot week_k \\
&+ \alpha 14 \cdot PDI_{j,t} + \alpha 15 \cdot PDI_{j,t}^2 + \alpha 16 \cdot PDI_{j,t} \cdot week_k + \alpha 17 \cdot open_j + \log\left(effort_{j,k,t}\right)
\end{aligned}
$$

with $\alpha 1$ as the intercept term and $\alpha 2 - \alpha 17$ as parameters that affect the count annually, weekly, and by location. We standardized each covariate so that it had a mean of 0 and a standard deviation of 1. The annual migration northward retains a fairly consistent within-season temporal schedule. Because of this consistency and because we hypothesized that the effects of several of the weather covariates may vary over the course of the season, we included a covariate on week ($\alpha 2$, linear term because monarch abundance in Ohio will generally be increasing during this time frame). The parameters $\alpha 3 - \alpha 8$ deal with the effects of the spring conditions in Texas on monarch counts, where $\alpha 3$ and $\alpha 4$ are the linear and squared effects of cumulative precipitation in Texas, $spPREC_t$, and $\alpha 5$ and $\alpha 6$ are the linear and squared effects of GDD in Texas, $spGDD_t$. We also included parameters $\alpha 7$ and $\alpha 8$ as interaction terms with spring precipitation/GDD and week, respectively, because we hypothesized that spring conditions in Texas may affect monarch counts in Ohio differently over the course of the breeding season.

Parameters $\alpha 9 - \alpha 13$ are effects related to the accumulating GDD at the survey point *j*. Because GDD increases throughout the spring and summer, we used the difference from the mean GDD, $GDDdiff_{j,k,t}$, at a given point *j* across all 13 years of the survey (Hodgson *et al.* 2011). Thus we were able to capture whether the GDD accumulated by the end of each week of the survey were above or below the average for that site at that time. We included only a linear effect ($\alpha 9$) on $GDDdiff_{j,k,t}$ because a squared term did not come out as significant in earlier versions of the model. The average GDD, $avgGDD_j$, accumulated at the end of the summer season (week 28 in our model) across all 13 years of sampling, accounted for location effects. We included linear ($\alpha 10$) and squared ($\alpha 11$) effects for $avgGDD_j$. We hypothesized that the importance of $GDDdiff_{j,k,t}$ might vary by week over the course of the sampling period and may have an increasing influence on monarch abundance as the season progresses (because abundance is always very low during the early part of the season). We similarly suspected that a site's $avgGDD_j$ may be important in understanding how variation in $GDDdiff_{j,k,t}$ affects abundance over the spring and summer seasons (i.e., the effect of above average GDD may depend on whether or not that site is typically a warmer or cooler location). Covariates $\alpha 12$ and $\alpha 13$ account for these possible interactions. Parameters $\alpha 14 - \alpha 16$ are effects related to site-specific PDI values. The covariate $PDI_{j,t}$ is the annual metric of the drought index at each survey location and we included linear ($\alpha 14$) and squared ($\alpha 15$) effects as well as an interaction with survey week ($\alpha 16$).

We included two nuisance terms in our model: the covariate $open_j$ is the proportion of area along the *j*th transect that is unforested. Although we are not specifically interested in how differences in habitat affect monarch abundance, we included $\alpha 17$ because milkweed tends to grow in open areas. Similarly, survey durations and transect lengths vary and we included an offset term, $\log\left(effort_{j,k,t}\right)$, measured in survey minutes to account for variable effort.

We analyzed the model using a Bayesian approach with the programs R and WinBUGS (Lunn et al. 2000). We ran three chains for 3000 iterations after a burn-in of 3000 iterations and thinned the chains by 3. Model convergence was assessed using the R-hat statistic (Gelman and Hill 2007).

Results

In contrast to coarse-scale comparisons which showed no relationship between any single climate metric and yearly monarch abundance (Figure 4.2), our model results suggest that climate in both Texas and Ohio does impact expected counts in Ohio. All parameters that were included in the model had significant effects and standard errors for each parameter were generally small (Table 4.1). The interactions between week and the spring climate variables (Texas GDD and precipitation) as well as the GDD differentials at locations in Ohio were all positive, suggesting that the importance of these climate variables increases over the course of the summer. This is an expected result because counts remain near zero for the first few weeks of the modeling period then increase rapidly through the remainder of the study period. Results for both spring and summer climate impacts are displayed in Figures 4.3 and 4.4; in all cases the displayed results assume that all other covariates in the model are held at their mean values.

Spring weather conditions in Texas had significant effects on the magnitude of monarch counts later in the season in Ohio, with wetter springs ($spPREC_t$) and average spring temperatures ($spGDD_t$) leading to the highest predicted abundances at the end of the season (Figure 4.3). Spring weather conditions in Texas also affected emergence phenology of monarchs in Ohio, with earlier observations and faster increases in expected abundance during the wettest and, to a lesser degree, driest springs (Fig. 4.3a), when other parameters are held constant. Our results further indicate that intermediate values of spring GDD were associated with earlier observations and greater increases of monarchs in Ohio (Figure 4.3 – bottom panel), although the magnitude of the effect was not as great as for spring precipitation (Figure 4.3 – top panel).

Monarchs' response to climate experienced on their summer breeding grounds in Ohio showed some key differences compared to spring effects. First, GDD was much more important than precipitation during summer (Table 4.1). The impacts of precipitation (as measured with annual PDI) were minor and did not have a consistent effect on timing or abundance (results not illustrated). On the other hand, expected monarch abundance was greatest when GDD was above average for each site. However, that effect was strongest for the coolest sites (Figure 4.4 – top panel) and diminished as sites became warmer (Figure 4.4 – middle panel), with the pattern beginning to reverse at the warmest sites (Figure 4.4 – bottom panel). The effect was increasingly pronounced as the season progressed. The highest observed counts were found late in the season in the coolest locations (min $avgGDD_j$ values) that had accumulated above average GDD ($GDDdiff_{j,k,t}$) values (Figure 4.4 – top panel). Conditions in Ohio had no obvious impact on monarch arrival phenology (Figure 4.4).

Discussion

Our results show that climate is a major driver of monarch population dynamics, but that the relationships are complex. We showed that no simple climate metric (seasonal summaries of temperature and precipitation) on either the spring or summer breeding grounds could explain annual abundances in Ohio (Figure 4.2). Instead, a combination of interacting climate factors on both the spring and summer breeding grounds seems to set the stage for migration phenology and differences in annual population growth (Figures 4.3 and 4.4). These results emphasize the difficulties in trying to understand how climatic conditions impact migrating species and highlight the challenges associated with making predictions on how monarchs and other migrating species will do under future climate regimes.

According to our model, spring precipitation was the factor associated with the greatest potential for population growth, with the wettest springs leading to the highest population numbers (Figure 4.3). This relationship was curvilinear, with low precipitation also leading to slightly higher predicted values compared to average precipitation. Yet, this relationship is obviously complex. We first note that the year with the lowest population (2004) occurred during the second wettest spring (Figure 4.2). More in line with these results, the year with the highest population (1997) also occurred in the wettest spring, but this year was an unusually abundant one (highlighted as an outlier in all four panels of Figure 4.2). This raises the question of whether the result could have been driven by that one potentially aberrant year. To explore this, we reran the model excluding the data from 1997. The results were strikingly similar to those illustrated in Figures 4.3 and 4.4 with two notable differences. First, the strength of the effect for spring precipitation was weaker, with both wet and dry springs still leading to higher numbers, but in a weaker and more symmetrical fashion. Results were unchanged for spring GDD. Second, the strength of the effect of summer GDD was stronger, but the interaction effect with average site GDD, while still present, was weaker with no reversal of effect occurring at the warmest sites.

Based on the results from the model runs with the full and reduced data sets, we conclude that the climate factors leading to optimal population growth include wetter or drier springs and intermediate temperature zones in Texas and Ohio. In Texas, average temperatures are optimal while in Ohio, warmer summers (within the range experienced during this 13-year study) generally lead to higher monarch numbers, except at the very warmest sites. Areas south of Ohio are too warm to support optimal growth during summer months (Batalden et al. 2007; Malcolm et al. 1987) and these results are in line with laboratory studies that highlight both lethal and sub-lethal effects of hot temperatures (York and Oberhauser 2002). Our results suggest that any future temperature regimes across monarchs’ growing range are likely to have divergent effects depending on latitude and also the time of the season. In both runs of the model, only spring climate metrics impacted the expected timing of arrival in a substantive way, with wetter or drier springs and average temperatures in Texas associated with earlier sightings in Ohio (Figures 4.3 and 4.4). This is consistent with our hypothesis that climate in Texas should have a bigger impact on arrival than conditions in Ohio.

Despite these general trends, these climate factors cannot in and of themselves explain all the observed year-to-year variability in monarch abundances (Figure 4.2). The purpose of our model was to determine how spring and summer climate conditions affect inter-annual monarch abundances and the phenology of arrival to breeding locations in Ohio. However, additional factors may affect monarch population dynamics, including size of the wintering population and winter mortality, annual milkweed growth, and parasitism. The area occupied by the wintering population is often used to indicate overall monarch population size (Brower et al. 2011), but the values used in previous studies are measured near the start of the overwinter period and do not account for wintering mortality (Rendon-Salinas et al. 2011), which can be highly variable. Despite this, it is worth noting that 1997, which experienced an exceptionally cool spring and summer (factors associated with smaller population sizes) nevertheless produced an extremely large population that year (Figure 4.2). This may or may not be related to the 1996-1997 overwinter colony sizes, which were the largest ever recorded (Rendon-Salinas et al. 2011). Similarly, overwinter mortality during 2003-2004 was high, possibly contributing to the small population size observed in 2004. Yearly milkweed growth is also likely to be an important factor in monarch population sizes, both in Texas and Ohio, and the timing of growth may be particularly important. Anecdotal evidence suggests that monarch arrivals sometimes occur when milkweed has barely emerged, leading to food depletion, crowding, and potentially increased parasitism rates (Karen Oberhauser personal communication), which could have an effect on local population abundances. Parasitism and disease are other well studied and important factors in monarch biology (Prysby 2004) and it is currently unknown how they may interact with arrival phenology, crowding, and/or climate.

Climate predictions across North America (implemented by www.climatewizard.org, based on data from Maurer et al. 2007) suggest that springs in Texas may become hotter and drier while the summers throughout eastern North America may also be hotter and slightly wetter (based on a high emission, 50 year scenario). If spring precipitation in Texas remains within the range captured by our 1996-2008 study period, then our model results suggest that this could potentially have a slight benefit for monarchs since low precipitation is associated with earlier arrivals and more growth. Anecdotal observations from 2011, the driest spring in Texas on record since 1895 (based on summaries from NOAA’s Climate at a Glance), offers some support for this result. Arrivals into Ohio in 2011 were early (based on Journey North sightings http://www.learner.org/jnorth/) and reports on breeding abundances for the year seem to be above normal, at least in some areas (Oberhauser 2011). Although it is possible for drier spring conditions to help monarch populations, if springs in Texas become too hot the result could be decreased abundances as the optimal spring temperature for monarchs is in the intermediate range of current conditions. The impacts of increased summer temperatures and precipitation are harder to gauge. Our model suggests that monarchs in Ohio are likely to experience increased growth with warmer summers, but at some point this relationship may slow or reverse (Figure 4.4 – bottom panel). At a large scale, warming is expected to be more intense further north and west, which could be helpful to monarch growth, but again at some point, the heat may slow growth or even cause mortality. These crude projections are in line with niche modeling that shows the optimal climate window tracking north based on a 50 year climate projection (Batalden et al. 2007). No modeling approach has yet captured the full complexity of how climate interacts with all the potential factors that influence monarch population growth, including incoming Mexican migrants, milkweed growth and congruence with monarch arrivals, natural enemies, and appropriate climatic environments for activity and growth throughout each phase of their migratory pathway. Further consideration of the effects of climate on monarchs will ultimately need to include changing climate during their overwinter and fall migration phases as well. Research has already shown that changes in climate in Mexico could have devastating consequences for this population (Oberhauser and Peterson 2003). Piecing together the mechanisms that drive these dynamics will be crucial to understand monarch biology in general and how this unique species may respond under future climate scenarios.

Migrating species have an intricate and complicated relationship with climate variables, one that cannot easily be described by simple weather variables. Our results shed light on how monarchs respond to both local and regional climate factors. They also demonstrate how optimal climate conditions can change for a species over the migration route and how phenology may be impacted more severely by climate conditions along the migratory route than at the destination, something that is rarely considered in studies of migratory species (Gordo 2007). These findings highlight the importance of ongoing research into understanding the effects of climate on migrating species dynamics and particularly emphasize the need to determine which variables are most important along specific points of the migratory path.

Table 4.1 Parameter descriptions, point estimate (posterior mean), posterior standard deviation and 95% posterior interval. The subscripts represent transect location (*j*), week within season (*k*), and year of survey (*t*).

Parameter	**Covariate Description**	**Estimate**	**SD**	**95% PI**
$\alpha 1$	Intercept	-0.578	0.025	(-0.63,-0.53)
$\alpha 2$	Week in season	1.376	0.014	(1.35,1.40)
$\alpha 3$	Spring precipition in Texas (linear)	-0.070	0.015	(-0.10,-0.04)
$\alpha 4$	Spring precipition in Texas (squared)	0.364	0.011	(0.34,0.39)
$\alpha 5$	Spring GDD in Texas (linear)	-0.198	0.022	(-0.24,-0.15)
$\alpha 6$	Spring GDD in Texas (squared)	-0.229	0.014	(-0.26,-0.20)
$\alpha 7$	Spring precipitation and week interaction	0.100	0.017	(0.07,0.13)
$\alpha 8$	Spring GDD and week interaction	0.109	0.013	(0.08,0.13)
$\alpha 9$	Weekly GDD differential at transects in Ohio	-0.049	0.020	(-0.09,-0.01)
$\alpha 10$	Average GDD at transects in Ohio (linear)	-0.091	0.011	(-0.11,-0.07)
$\alpha 11$	Average GDD at transects in Ohio (squared)	0.055	0.011	(0.03,0.08)
$\alpha 12$	GDD differential and week interaction	0.080	0.015	(0.05,0.11)
$\alpha 13$	GDD differential, average GDD, week interaction	-0.031	0.006	(-0.04,-0.02)
$\alpha 14$	PDI at transects in Ohio (linear)	-0.104	0.016	(-0.14,-0.07)
$\alpha 15$	PDI at transects in Ohio (squared)	-0.059	0.009	(-0.08,-0.04)
$\alpha 16$	Palmer drought index and week interaction	-0.108	0.014	(-0.14,-0.08)
$\alpha 17$	Proportion unforested at transects in Ohio	0.303	0.010	(0.28,0.32)

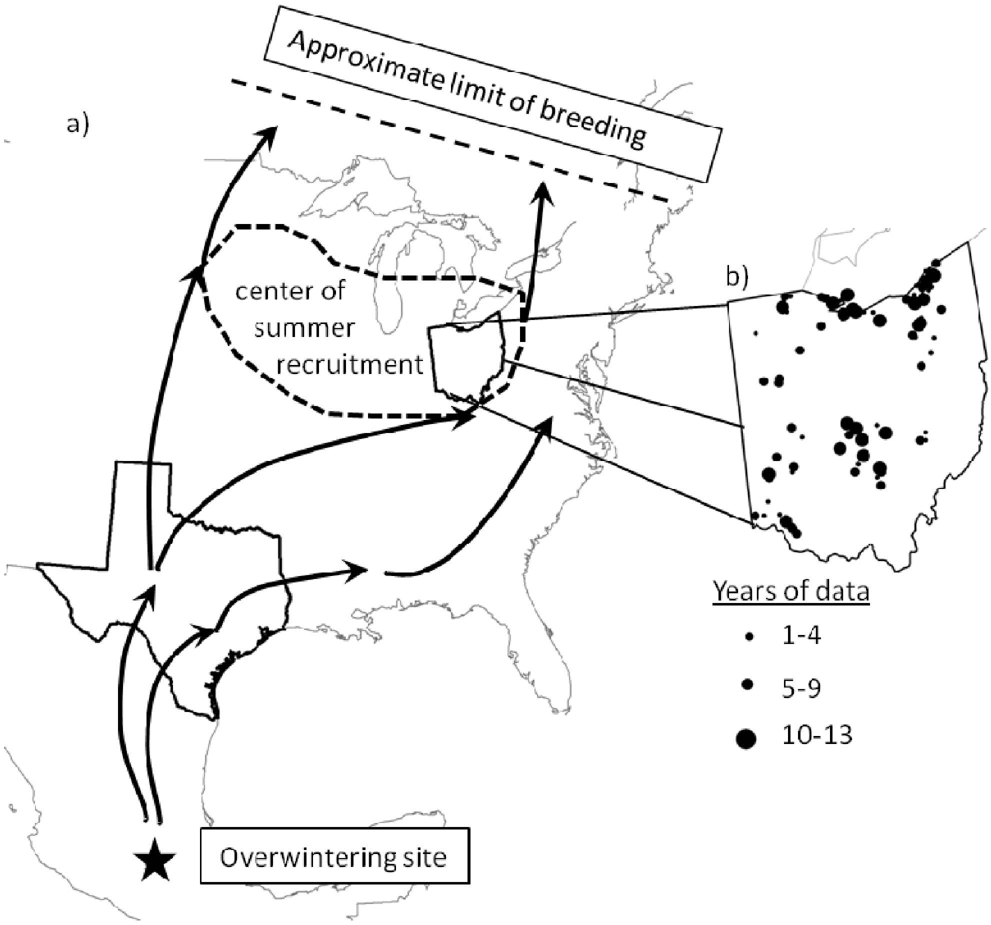


Figure 4.1 Breeding dynamics of the eastern migratory monarch population (a). Adults overwinter in a small area in Mexico (star), then fly north in spring and lay eggs in the southern US with most known breeding in Texas. Adults emerge and fan out to occupy the rest of the breeding range over the summer. Two or three more generations are produced during this time with most recruitment occurring in the Midwest, including Ohio where there is a network of butterfly monitoring stations that was established in 1995 (b). In September, most adults enter reproductive diapause and return to the overwintering sites in Mexico.

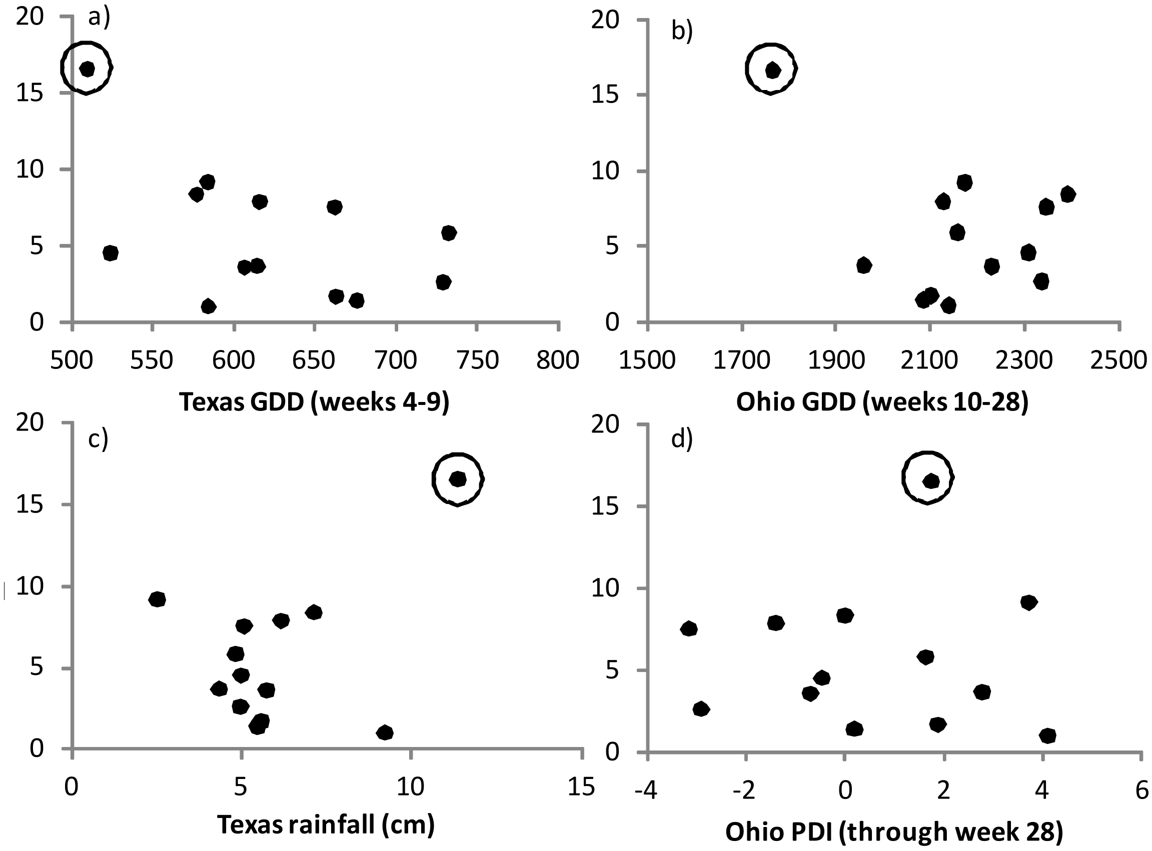


Figure 4.2 The relationship between an index of monarch yearly abundance (averaged over all sites during weeks 26-28) and a) spring GDD in Texas (accumulated from weeks 4-9), b) summer GDD in Ohio (accumulated from weeks 10-28), c) Feb-Apr rainfall in Texas, and d) mean Palmer Drought Index in Ohio. An outlier (1997) is circled in each panel.

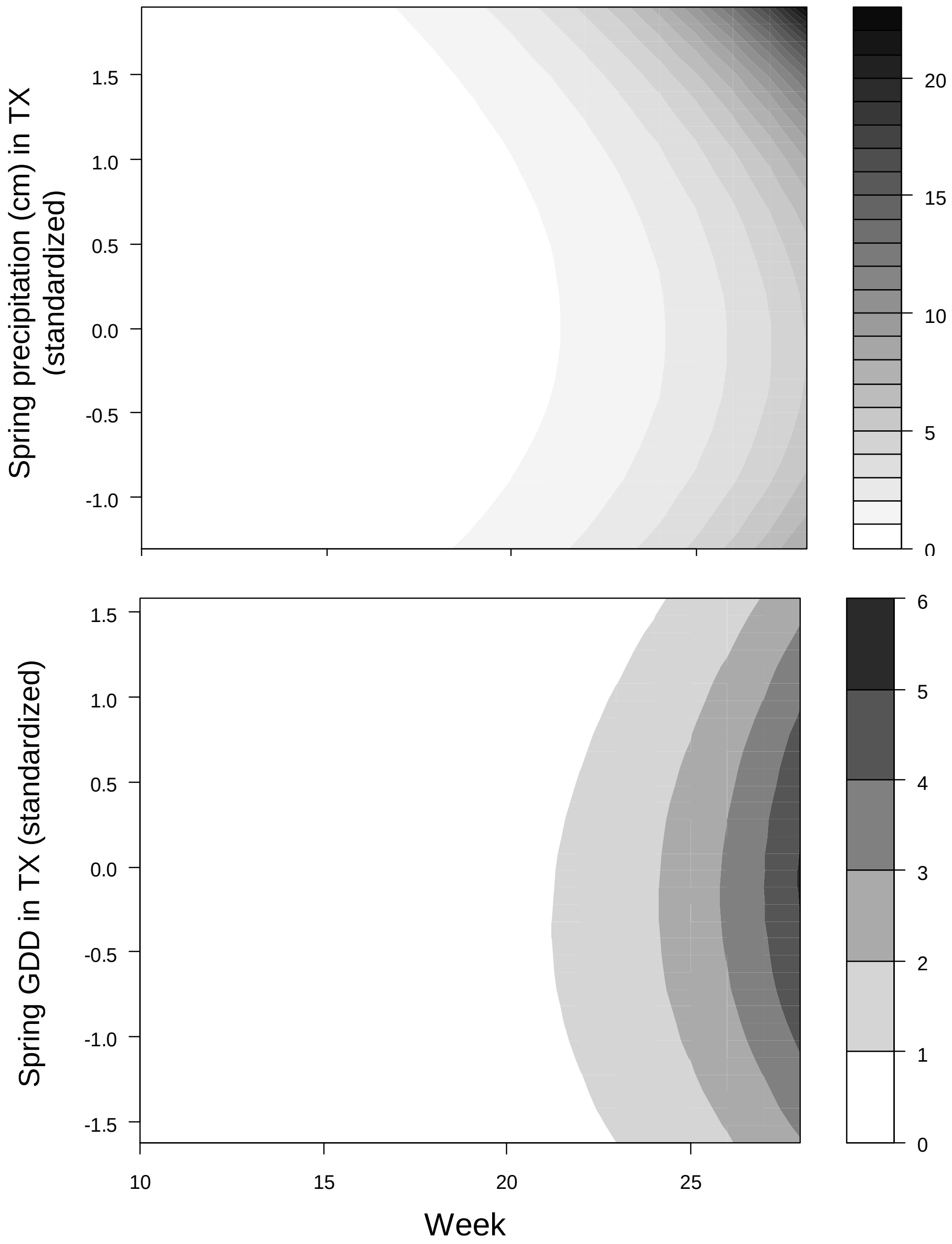


Figure 4.3 Expected monarch count by week for the range of observed spring precipitation in Texas (top panel) and spring GDD in Texas (bottom panel) where all other parameter values were held at their average values. The precipitation and GDD covariates are shown on a standardized scale such that the mean and standard deviation for each are 0 and 1, respectively.

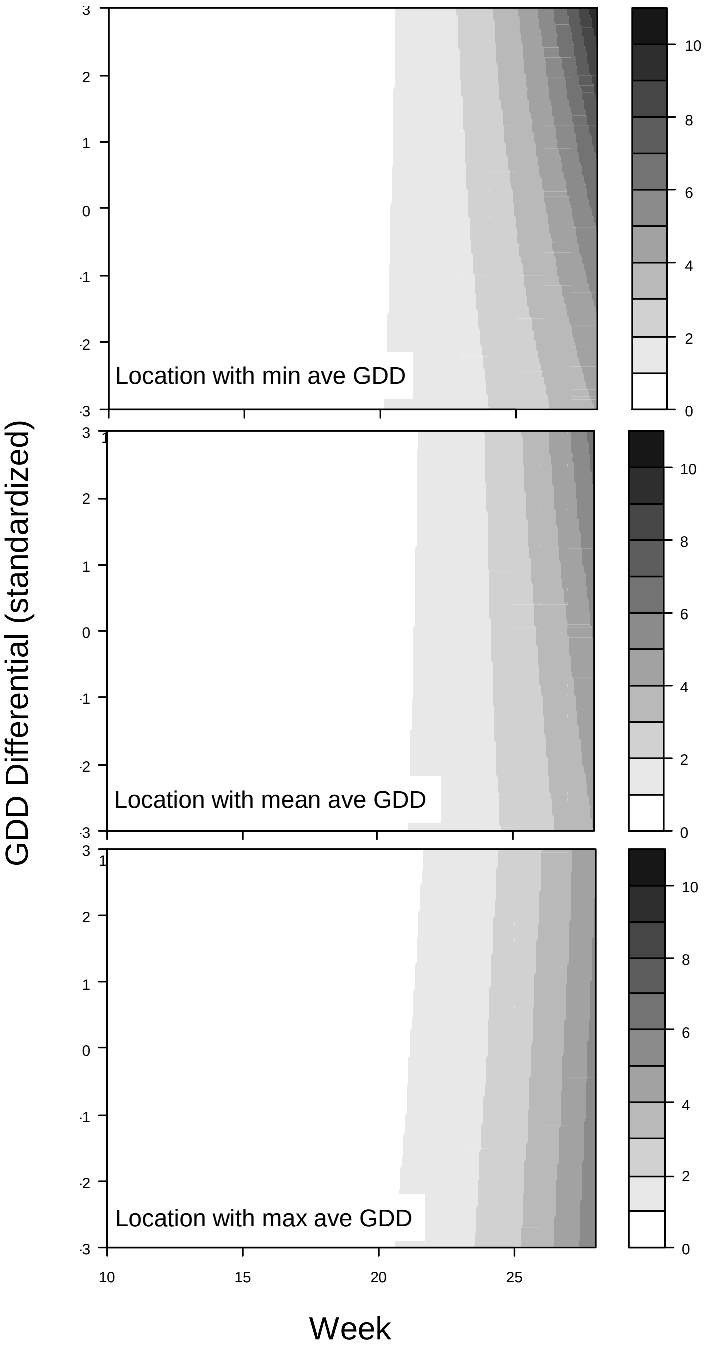


Figure 4.4 Expected monarch count by week as plotted against the GDD differential (standardized to have a mean of 0 and a SD of 1) for the coolest survey location in Ohio (minimum avgGDD – top panel), a location with average temperatures (mean avgGDD – middle panel), and the warmest survey location (maximum avgGDD – bottom panel).

Chapter 5: Distribution patterns of wintering sea ducks in relation to the North Atlantic Oscillation and local environmental characteristics

Published in: Oecologia, 163, 893-902, 2010.

Coauthors: Beth Gardner, Andrew T. Gilbert, Allan F. O’Connell, J. Andrew Royle, Emily D. Silverman

Abstract

Twelve species of North American sea ducks (Tribe Mergini) winter off the eastern coast of the United States and Canada. Yet, despite their seasonal proximity to urbanized areas in this region, there is limited information on patterns of wintering sea duck habitat use. It is difficult to gather information on sea ducks because of the relative inaccessibility of their offshore locations, their high degree of mobility, and their aggregated distributions. To characterize environmental conditions that affect wintering distributions, as well as their geographic ranges, we analyzed count data on five species of sea ducks (black scoters *Melanitta nigra americana,* surf scoters *M. perspicillata,* white-winged scoters *M. fusca,* common eiders *Somateria mollissima,* and long-tailed ducks *Clangula hyemalis*) that were collected during the Atlantic Flyway Sea Duck Survey for ten years starting in the early 1990s. We modeled count data for each species within 10 nautical mile segments using a zero-inflated negative binomial model that included four local-scale habitat covariates, (sea surface temperature, mean bottom depth, maximum bottom slope, and a variable to indicate if the segment was in a bay or not), one broad-scale covariate (the North Atlantic Oscillation), and a temporal correlation component. Our results indicate that species distributions have strong latitudinal gradients and consistency in local habitat use. The North Atlantic Oscillation was the only environmental covariate that had a significant (but variable) effect on the expected count for all five species, suggesting that broad-scale climatic conditions may be directly or indirectly important to the distributions of wintering sea ducks. Our results provide critical information on species-habitat associations, elucidate the complicated relationship between the North Atlantic Oscillation, sea surface temperature, and local sea duck abundances, and should be useful in assessing the impacts of climate change on seabirds.

Introduction

Current evidence suggests that 10 of the 15 North American sea duck species may be in decline, including eight out of 12 species that winter off the Atlantic coast (Sea Duck Joint Venture 2003). Yet there is much uncertainty on the status of sea ducks because population data are limited. The causes of sea duck declines are not well understood, as relatively little is known about the distributions and habitat preferences of each species. The Atlantic coast of the United States (U.S.) and Canada is a major wintering area for a number of migratory species, including sea ducks, which face a variety of pressures associated with human populations and potential climate changes. For example, increased harvest pressure on sea ducks in the 1980s, resulting from more restrictive hunting regulations on other waterfowl (e.g., Canada goose *Branta canadensis*), led to concern about the condition of sea duck populations along the Atlantic flyway (Caithamer et al. 2000; Perry and Deller 1995). More recently, wind turbines, proposed in locations along the Atlantic coast (e.g., Kempton et al. 2007), are raising questions about potential adverse impacts on survival and habitat use (e.g., Larsen and Guillemette 2007). Before we can assess the influence of factors such as harvest, offshore energy development, contaminants, and climate change on sea duck populations, it is necessary to accurately characterize the spatial distribution, annual variability, and habitat associations of these species.

North American sea ducks breed at high northern latitudes throughout the U.S. and Canada; these ducks migrate south to winter in coastal waters, reaching as far as Florida on the Atlantic coast. Yet, despite the potential impacts resulting from their seasonal proximity to large, urbanized areas, we have comparatively limited information on winter habitat preference and use. It is difficult to gather information on sea ducks during the winter, not only because of the inaccessibility of their offshore locations, but also due to the tendency of some species to aggregate in large, mobile flocks. Outside of a few areas (e.g., Chesapeake Bay – Perry et al. 2007), the status and trends of sea ducks along the eastern U.S. and Canadian coasts have not been well established (Caithamer et al. 2000; Sea Duck Joint Venture 2003).

The spatial distribution of wintering sea ducks along the Atlantic coast is determined by both large-scale as well as local processes. General winter conditions and habitat gradients are likely to influence the northern and southern boundaries of their wintering ranges, while distributions within those ranges may be based on a variety of site-specific factors, including food availability, local environmental conditions, and habitat suitability (Lewis et al. 2008). Thus, it is necessary to examine how both large-scale processes, such as annual climatic conditions, as well as local factors, such as ocean depth, ocean floor topography, and sea surface temperature, affect the distributions and abundance of sea ducks.

The North Atlantic Oscillation (NAO) is a driver of climate variability, which has been shown to affect the marine environment (Hurrell et al. 2003) and ecosystems (Otterson et al. 2001; Stenseth et al. 2002) along the eastern coast of the U.S. and Canada. The NAO is the fluctuation in sea surface pressure across the northern Atlantic Ocean between areas of high (Azores High) and low (Icelandic Low) pressure; it exerts strong control over the climate in the Atlantic Ocean region, particularly in the winter (Hurrell 1995; Hurrell et al. 2003). A positive NAO index indicates an increase in winter storms with greater intensity in the northern Atlantic Ocean, leading to cold, dry winters in northern Canada and mild, wet winters in the eastern U.S. A negative NAO index indicates fewer and weaker winter storms in the Atlantic Ocean leading to cold and snowy conditions along the east coast of the U.S. and Canada (Bell and Visbeck 2009). The NAO is a composite measure of winter conditions and has been linked to ecological processes in plants (Post and Stenseth 1999), terrestrial invertebrates (Halkka et al. 2006), ungulates (Post and Forchhammer 2002; Post and Stenseth 1999), fish (Suski and Ridgway 2007), and amphibians (Forchhammer et al. 1998). In birds, the NAO has been linked to breeding phenology (Forchhammer et al. 1998; Moller 2002; Weatherhead 2005) and migration patterns (Hüppop and Hüppop 2003) and has been correlated specifically with adult survival (Sandvik et al. 2005; Sandvik and Erikstad 2008), breeding success (Lehikoinen et al. 2006; Sandvik and Erikstad 2008) and general population dynamics (Thompson and Grosbois 2002) in seabirds. Given these correlations, it is possible that climatic conditions, including the NAO, may also be influencing distributions of wintering sea ducks.

Studies from other regions provide evidence that distributions of sea ducks may be linked to local environmental characteristics, such as ocean depth and water temperatures. Common eiders (*Somateria mollissima*) in Greenland (Merkel et al. 2006) and surf scoters (*Melanitta perspicillata*) in British Columbia (Kirk et al. 2008) were found to have strong site fidelity within the wintering season, but Kirk et al. (2008) noted that prey availability influenced small scale movement. Wintering common eiders foraged most frequently in depths between 0-6 m, although they are capable of diving much deeper (Guillemette et al. 1993). Surf scoters, white-winged scoters (*Melanitta fusca*), and common eiders also appear to prefer coastal areas with relatively shallow depths (Guillemette et al. 1993; Lewis et al. 2008).

In the early 1990s, the U.S. Fish and Wildlife Service (FWS) initiated the Atlantic Flyway Sea Duck Survey (AFSDS) to assess distributions of sea ducks along the nearshore of the eastern U.S. and Canada (Migratory Bird Data Center 2009). Because the timing and scale of movements by wintering sea ducks are not well characterized, the survey offers limited information about the overall abundance of each species. This ten-year dataset can, however, provide critical information on how distributions of sea duck populations vary both spatially and temporally along the nearshore Atlantic coast. Using survey data from the AFSDS, we characterize the winter distributions of five sea duck species along the eastern U.S. and Canada and relate observed counts to pertinent broad and local scale environmental characteristics. Defining the relationships among sea duck distributions, latitude, and habitat will provide a quantitative basis for understanding wintering ecology and movements, help with the design of future monitoring programs, and inform targeted conservation and management actions.

Methods

Sea duck aerial surveys

The AFSDS was flown between mid-January and mid-February along the east coast of the U.S. and Canada in 1991, 1992, 1994, 1995, and 1997-2002 from southern Georgia (30.8°N, 81.4° W) to Nova Scotia (48.1°N, 64.8°W) (Figure 5.1). A single aerial transect was flown parallel to the coast, a quarter mile from the shore and data were reported within approximately 10 nautical mile segments. The segments were defined by drawing the survey transect on an aeronautical chart and marking increments of 10 nautical miles. Since the survey was initiated and conducted primarily in years when geographic positioning technology was unavailable to the crew (i.e., pre-GPS), 10 nautical miles, represented the smallest practical spatial unit for collecting and recording data. All sea ducks identified to species were counted within 500 m (250 m on each side of the route) of the transect line, which defined the boundaries for each segment (10 nautical miles by 500 m). Roughly 451 segments were flown once yearly, 335 of which were in the U.S. with the remaining segments in Canada. Two person crews conducted the surveys, flying at an altitude of 250 feet. The pilot and an observer recorded the species and number in each segment (Caithamer et al. 2000).

Eleven sea duck species were observed at least once during the ten years of the AFSDS survey. We focused our analyses on five species for which there were adequate data and whose wintering ranges sufficiently overlap with the study area: black scoters (*Melanitta nigra americana*; 85,000 observed over all years of the survey), surf scoters (100,000 observed), white-winged scoters (25,000 observed), common eiders (414,000 observed), and long-tailed ducks (*Clangula hyemalis*; 95,000 observed). We did not include counts in which sea ducks were not indentified to species (e.g., bird identified only as scoter).

Habitat and climate data

We used hand drawn maps of the survey route (the only maps available) to digitally recreate the survey path and identify start and stop points for each segment in ArcGIS 9.3 (Environmental Systems Research Institute Inc., Redlands, CA). The digital survey path was buffered by 250 m on each side in GIS to recreate the segments, which averaged 11.4 (SD 2.6) nautical miles long and 500 m wide. We validated the recreated digital route using GPS track data from flights in 2001 and 2002, the only years with a GPS record of the route, to ensure that our recreated transect segments included the areas in which sea ducks had been observed during the two years with known flight paths.

To characterize the yearly winter climatic conditions along the Atlantic coast, we obtained monthly values for NAO, based on the difference between the normalized sea level pressure over Gibraltar and the normalized sea level pressure over Southwest Iceland (Jones et al. 1997) from the Climatic Research Unit, University of East Anglia, Norwich, U.K.

(http://www.cru.uea.ac.uk/cru/data/nao.htm). We hypothesized that overall conditions (i.e., NAO) during migration would have a large effect on sea duck winter distributions, since previous research suggests that sea ducks may exhibit within season site fidelity, at least on local scales (Kirk et al. 2008). Thus we averaged the NAO values for the three months prior to the survey (October, November, December) to characterize the climatic conditions around migration. Average NAO values may differ from winter averages calculated using other measures of NAO (e.g., Cook et al. 2002), but data from the Climatic Research Unit provided a sufficiently long period of record for our study.

To assess local factors affecting sea duck distributions, we summarized relevant environmental data to characterize the habitat of individual segments. We included three static, segment-level variables: 1) whether or not the segment occurred in a bay (binary variable with 1 indicating that the segment was in a bay and 0 otherwise; Figure 5.1), 2) bottom depth, and 3) ocean floor topography. Coarse resolution bathymetry data is available for the global oceans, but no fine-scale data is available for both U.S. and Canadian Atlantic waters, so we acquired data separately from each country. We downloaded the coastal relief model for the U.S. Atlantic, available from the National Geophysical Data Center (Divins and Metzger 2008). U.S. bathymetry data were available in a 3 arc-second (approximately 90 m) grid, with depths resolved to 0.1 m. We obtained a similar bathymetry dataset from the Canadian Hydrographic Service (CHS), Fisheries and Oceans Canada, a new product produced for the Canadian Atlantic that is not yet available to the public. Bathymetry data were received from the CHS as point data with 500 m or closer spacing, from which a 500 m raster was created using routines developed in ArcGIS 9.3. Depths were again resolved to 0.1 m. For bottom depth, we averaged depth values for all pixels within a segment to achieve a single estimate for each segment. The segment-level depth values were measured in negative values (i.e., the surface is zero) and ranged from -80.16 m to 0 m (95% range: -31.29, -0.35; $\bar{x}_{bays} = -9.1$, $\bar{x}_{non-bays} = -6.2$). To characterize the ocean floor topography, we used the slope routine in ArcGIS 9.3 to calculate the bottom slope or the maximum rate of change for each depth cell (i.e., pixel) from its adjacent eight cells. We used the maximum slope for all depth cells within each segment, rather than the average, which provided a realistic measure of the topography range for each segment. The segment-level slope values ranged from 0 to 21.39 (95% range: 0.20, 10.55; $\bar{x}_{bays} = 3.0$, $\bar{x}_{non-bays} = 2.3$).

We also gathered monthly averages for sea surface temperature (SST) as measured through satellite data from the NOAA/NASA AVHRR Pathfinder Program (http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/). Data were downloaded from the NASA Physical Oceanography Distributed Active Archive Center (ftp://podaac.jpl.nasa.gov/pub/sea_surface_temperature/avhrr/pathfinder/data_v5/monthly/). We used the best estimate (BSST) from the 4.1 km resolution version 5, SST data. These data were derived using the Reynolds Optimally Interpolated SST, Version 2, methodology (Reynolds et al. 2002), which provides complete areal coverage even where clouds are masking the ocean by filling in missing data with optimally interpolated SST data. We hypothesized that segment level SST would likely affect movement within the winter season and calculated winter averages from monthly BSST data that coincided with the end of migration and the dates of the survey (December-February). Since the resolution of each SST pixel was larger (4100 m) than the buffered segment (500 m), we reduced the cell size of each seasonal SST pixel to 1/20th the original resolution and calculated the weighted average SST for each segment for every year of the survey. The segment-level SST values across all years ranged from 0.65°C to 22.65°C (95% range: 1.32, 21.45).

Model

The sea duck survey produced spatially- and temporally-indexed counts for which a modeling framework based on generalized linear models (GLMs) is appropriate (Clarke et al. 2003). Poisson GLMs are frequently used in analyses of count data for other avian monitoring programs, including trend analysis, models of abundance and distribution, and modeling landscape and habitat effects (e.g., the North American Breeding Bird Survey, Link and Sauer 2007). In most avian surveys and in the case of the AFSDS, the assumption of equality of mean and variance for Poisson models is not realistic, as there is high variation in the observed number of individuals. For the AFSDS, a high variance to mean ratio likely results because some sea duck species tend to be highly aggregated in the winter. Because of the extreme over-dispersion of the data in our survey, we modeled the counts using a zero-inflated negative binomial distribution (Hall 2000; Martin et al. 2005), which allows for a higher variance compared to the mean and has provided a better fit to data in previous analyses of other duck species (Wenger and Freeman 2008). To do so, we define $y_{i,j,t}$ as the count of species *i* at survey segment *j* in year *t*. The mean of the model is

$\mu_{i,j,t} = \lambda_{i,j,t} \cdot z_{i,j}$, where $z_{i,j} \sim Bernoulli\left(\psi_{i,j}\right)$ is random variable that indicates whether or not a segment should be included in the model (variable for each species but constant over the ten years of the survey). When $z_{i,j} = 1$, the count for species *i* in segment *j* at time *t* has a negative binomial distribution, $\left(y_{i,j,t} \mid z_{i,j} = 1\right) \sim NegBinom\left(r_i, p_{i,j,t}\right)$, with mean $\lambda_{i,j,t} = \frac{r_i\left(1 - p_{i,j,t}\right)}{p_{i,j,t}}$ and variance $\sigma^2{}_{i,j,t} = \frac{\lambda_{i,j,t}}{p_{i,j,t}}$. Thus, the parameter λ is the estimated mean count when $z_{i,j} = 1$, otherwise the expected count is zero. Since the AFSDS was not designed to accommodate the specific geographic range of each species, we hypothesized that *z* would vary by latitude and modeled the inclusion probability $\left(\psi_{i,j}\right)$ for each segment as a function of latitude such that $logit\left(\psi_{i,j}\right) = \beta 0_i + \beta 1_i \cdot lat_j$, where $\beta 0$ is the intercept and $\beta 1$ is the coefficient on latitude. Although a segment's inclusion probability could depend on a number of factors, we chose to include only latitude in order to (1) investigate the north-south range distributions for each species and (2) explore the effects of habitat covariates on the abundance of birds within the north-south boundaries of their range, because the available data limit further complexity (i.e., inclusion of habitat covariates in both the Bernoulli and negative binomial components of the model).

We modeled sources of variation in λ using a log-linear function:

$$\log\left(\lambda_{i,j,t}\right) = \alpha 0_i + \alpha 1_i \cdot NAO_t + \alpha 2_i \cdot SST_{j,t} + \alpha 3_i \cdot depth_j + \\ \alpha 4_i \cdot slope_j + \alpha 5_i \cdot bays_j + \alpha 6_i \cdot NAO_t \cdot SST_{j,t} \\ + a7_i \cdot \log\left(y_{i,j,t-1} + 1\right) + \log\left(offset_j\right)$$

where $\alpha 0$ is the intercept and $\alpha 1$ through $\alpha 6$ are the effects of each of the covariates for species *i* on the estimated count: NAO for each year $\left(NAO_t\right)$; sea surface temperature at each segment in each year $\left(SST_{j,t}\right)$; mean bottom depth at each segment $\left(depth_j\right)$; maximum slope at each segment $\left(slope_j\right)$; a binary vector indicating whether a segment was in a bay $\left(bays_j\right)$; and an interaction effect between segment-level sea surface temperature and NAO $\left(NAO_t \cdot SST_{j,t}\right)$. The latitude, SST, depth, and slope data were each standardized to have a mean of zero and a standard deviation of one. We incorporated temporal correlation into the model at the segment-level by estimating an effect $\left(\alpha 7\right)$ of the observed count in the previous year. The temporal effect was only estimated when data were available in the previous year (e.g., years 1991, 1994, and 1997 were excluded). An offset term was included to account for differences in counts due to variation in segment length. During development of the model, we included an explicit spatial correlation using a conditional autoregressive (CAR) model. The results from the CAR model were uninformative when habitat covariates were not incorporated (likely due to the high variation in the data) and parameter estimates would not converge with inclusion of both explicit spatial correlation and covariates. The purpose of including spatial correlation in a model is based on the notion that counts are likely to be similar within some neighborhood (a predefined region). Often, the reason for such correlations is because of similarities in landscape features within a neighborhood. If sea ducks are responding to habitat factors, inclusion of relevant landscape covariates should account for variation in observed counts and render the inclusion of an explicit spatial correlation unnecessary. We determined that habitat covariates explained more of the variation in the data and we thus removed the CAR component.

We analyzed the model separately for each species and estimated the parameter values using a Bayesian framework with the programs R and WinBUGS. Since our model includes a temporal correlation $(\alpha 7)$, analysis using standard canned statistical software was not possible. As such, we specified code in R to estimate the parameter values using a Markov Chain Monte Carlo (MCMC) approach in the software program WinBUGS. The idea behind MCMC is that parameter estimates, which are assumed to be random variables, can be obtained by creating a posterior distribution of the variable (Gelman and Hill 2007). This can be preferable to finding a parameter's maximum likelihood when integrating the likelihood is difficult, as is the case with our model. An additional benefit of the Bayesian approach is that interpretation of parameter values is straightforward and intuitive. For example, if 95% of a parameter's posterior distribution does not overlap with zero, we can directly interpret that as a 95% probability that the parameter is nonzero. To run our model, we used uninformative priors for all of the covariates. We ran three chains for 10,000 iterations after a burn in period of 10,000 iterations and estimated the posterior distributions after thinning the chains by 10. We checked that the model and all parameters had converged by examining the R-hat scores (Gelman and Hill 2007).

Results

The model estimated significant temporal correlation in the mean count and a latitude effect in the inclusion parameter for all five species of sea ducks (see Table 5.1 for parameter estimates). There was a positive relationship at the segment-level between expected count in year *t* and observed count in the previous year $(\alpha 7)$ for all species, with white-winged scoters having the highest consistency in local habitat use. As expected, there was also a consistent and positive relationship to latitude $(\beta 1)$ in the inclusion parameter, indicating that the probability of observing each species increased from south to north, with common eiders followed by long-tailed ducks showing the strongest relationship (Figure 5.2).

The NAO $(\alpha 1)$ was the only environmental covariate that had a significant effect on all five sea duck species: negative for the three scoter species and positive for the common eiders and long-tailed ducks. This suggests that climatic conditions along the Atlantic coast during migration and settlement may have strong influences, either directly or indirectly (e.g., by affecting distributions of prey), on sea duck distributions, with the scoter species observed in higher abundances in the nearshore during cold, snowy winters and common eiders and long-tailed ducks observed in higher abundance in the nearshore during wet, mild winters. SST $(\alpha 2)$ had a significant negative effect on long-tailed duck and white-winged scoter counts and a positive effect on common eiders (but see below for details on the interaction between NAO and SST). A negative relationship with temperature suggests that the expected count increases with colder SST values for long-tailed ducks and white-winged scoters. Because the model incorporates a latitude-dependent inclusion parameter (Figure 5.2), the positive relationship between SST and the expected count for common eiders can be interpreted to mean that, within the northern latitudes where common eiders are present (greater than 40°N latitude), the ducks are found in higher abundance in segments with moderate temperatures (note x-axis temperature range in Figure 5.3 for eiders is smaller than the other four species).

The relationship among NAO, SST, and the expected count was highly variable by species (Figure 5.3). The expected count in the nearshore for all three scoter species was generally higher in years with a negative NAO index compared to years with a positive index for nearly all ranges of SST. Yet the difference in expected count was consistent across SST for black scoters, highest at warmer SST values for surf scoters, and highest at colder SST values for white-winged scoters (even reversing the relationship at very warm values of SST). In contrast, the expected count for common eiders and long-tailed ducks in the nearshore, although very different from each other, were generally higher in positive years, compared to negative NAO years, in warmer SST ranges (Figure 5.3). The expected count of common eiders, within the temperature range where they were observed, was fairly constant across SST in negative years, but had a strong positive relationship with SST in positive NAO years. Conversely, the expected count of long-tailed ducks tended to decrease with SST in both NAO scenarios.

All species, except for white-winged scoters (which had a similar, although not significant response), had positive relationships with ocean bottom depth $(\alpha 3)$, measured in negative values where zero is sea level, indicating that sea duck abundance is greater in shallower sections of the shoreline. Maximum slope $(\alpha 4)$ had a negative effect on all three scoter species (but was significant only for surf scoters) and positive effects on the other two species (but again, significant only for common eiders), suggesting that the scoters may occur in areas with flat topography, while eiders and long-tailed ducks may prefer areas with steeper, more rugged bottoms. Black scoters were significantly less abundant in bays $(\alpha 5)$, while white-winged scoters were significantly more abundant.

Discussion

Our results provide critical information on the spatial and temporal distributions of wintering sea ducks in the nearshore habitat of the U.S. and southern Canadian Atlantic coast. Sea duck distributions appear to be responding to a combination of local habitat conditions and broad-scale weather patterns. All species had strong consistency in local habitat use among years and exhibited significant responses to latitude. Yet, the effects of environmental conditions were largely species-specific with similarities among the scoter species and different responses by common eiders and long-tailed ducks. Common eiders and long-tailed ducks had sharp southern range boundaries compared to the scoters (Figure 5.2), which had more gradual range boundaries and were sometimes found in southern waters. Research within the last decade has demonstrated northerly extensions in some bird species ranges (Thomas and Lennon 1999) and, if climate induced winter range shifts do occur in sea ducks, they may be comparatively easier to detect in common eiders and long-tailed ducks.

The North Atlantic Oscillation was the only environmental covariate that had a significant effect on all five sea duck species (Table 5.1), suggesting that site-specific abundance may be influenced by large scale weather conditions. This result is consistent with recent studies on the NAO, which suggest that broad scale climatic indices, rather than measurements of local weather, can have stronger correlations with ecological processes (Hallett et al. 2004; Stenseth and Mysterud 2005). However, our results show that the response to NAO varied by species and was dependent on segment-level SST values (Figure 5.3). SST has been correlated with the NAO at interannual timescales and evidence suggests that the NAO itself may be altered by SST in the Atlantic Ocean on the order of six decades (Higuchi et al. 1999). Although we did not find a significant correlation between the NAO and mean annual SST values in our data, the relationship between the NAO and SST may be influencing sea duck distributions at differing scales (hence the inclusion of the interaction term of NAO and SST in our model) and may possibly have greater effects at longer time scales. Seabirds, in general, have shown variable and complex responses to the NAO (e.g., Lehikoinen et al. 2006; Sandvik and Erikstad 2008; Thompson and Grosbois 2002; Thompson and Ollason 2001) and climate change may affect the NAO in unpredictable ways (e.g., Hoerling et al. 2001). The response of sea duck distributions in the nearshore to fluctuations in the NAO and climate change is likely to be species-specific, due to differences in the influence of weather conditions, physiological constraints, and other habitat factors such as food availability. Lehikoinen et al. (2006), for example, found that in the Baltic Sea, the body condition of female common eiders during egg hatching was positively correlated with the

NAO. Together with our results, their work suggests that sea ducks may demonstrate complex and indirect responses to fluctuations in the NAO during the wintering and subsequent breeding seasons. To protect sea ducks from decline, it may be useful to make annual predictions about abundance in relation to NAO in areas along the Atlantic coast and mitigate or limit human interference where abundance of several species is predicted to be high.

We found ecologically relevant relationships between sea duck abundances and climatic conditions. However, survey data from the AFSDS was limited to one north-south transect, a quarter mile off the Atlantic coast; future research should investigate whether our results are relevant over the entire winter range. Because the available data represent nearshore observations, we cannot make inferences on overall sea duck abundances or determine whether the differences in mean counts reflect changes in wintering locations or more general shifts further offshore (Braeger et al. 1995). The results from our model can help determine optimal sampling strategies based on the estimated relationships among abundance, latitude, and the environmental covariates. For example, our results on the effect of latitude (Figure 5.2) suggest that it may be possible to exclude or limit effort in southerly portions of the coast in future surveys. Recent offshore survey efforts, conducted by the FWS and including transects extending offshore, as well as parallel to the coast, should help to further characterize sea duck distributions, their range limits, and the potential tradeoffs between nearshore and offshore abundance.

The relationships between the local habitat covariates and sea duck abundance were similarly variable across species. While all species were associated with shallow depths, there was greater variation in responses to bottom slope. As a group, the scoters were more abundant in flatter areas along the coast (Table 5.1), which is consistent with previous research that showed that black, surf, and white-winged scoters prefer sandy sections along the Atlantic shoreline (Stott and Olson 1973). Observational data from other studies have demonstrated that common eiders may prefer rugged substrate but long-tailed ducks have not been clearly linked to bottom substrate (Perry et al. 2007). These results, as well as bay associations, may be related to the resolution of the count and covariate data. The sea duck data in the AFSDS were recorded at a 10 nautical miles by 500 m resolution. Because we did not know the location of each observation more precisely (pre-GPS era), we used environmental covariate data at similar spatial and temporal resolutions. However, it is possible that sea ducks are responding to habitat factors that occur on much finer scales, such as upwellings or high local productivity. Future surveys with GPS coordinates of duck locations should be analyzed with finer scale covariate data to assess the strength of our results. Additionally, because the U.S. and Canada provide bathymetry data at different resolutions, slope values were smaller than expected for the Canadian segments, which might indicate that the 500 m resolution of this dataset was effectively “smoothing” the bottom surface, limiting our ability to detect the true ruggedness.

Knowledge of wintering sea ducks is limited and data from the AFSDS provide the only distributional information in the nearshore Atlantic across a large temporal and spatial scale. The results from our analyses clarify how both local and broad landscape factors can influence distributions of bird species. Specifically, we demonstrated the importance of climate and weather processes to distributions of sea ducks in North America. Given that NAO had a significant effect on all species in our study, it reasonable to believe that NAO, as well as other climatic factors, can exert powerful and complicated forces on distributions of bird species in North America, and worldwide. Our analysis improves understanding of inter-annual variation in sea duck distributions, interspecific differences in response to environmental conditions, and provides a basis for understanding how wintering sea ducks may respond to climate change, information that is critical for effective conservation planning and the design of future monitoring programs.

Table 5.1 Posterior summary of species-specific parameter estimates. The mean and standard error of the mean estimate (SD) are shown for each parameter. Environmentally relevant parameters that are statistically different from zero (95% posterior intervals that do not overlap zero) are highlighted in bold. Note that the intercepts for both count and inclusion terms were also statistically different from zero for all species.

Parameter		***Black Scoters***		***Surf Scoters***		***White-winged Scoters***		***Common Eiders***		***Long-tailed Ducks***	
Intercept - count	α0	3.10	(0.11)	3.31	(0.12)	1.38	(0.19)	5.96	(0.20)	2.20	(0.06)
NAO	α1	**0.42**	**(0.09)**	**0.36**	**(0.10)**	**0.71**	**(0.18)**	**0.70**	**(0.14)**	**0.38**	**(0.05)**
SST	α2	0.07	(0.10)	0.28	(0.15)	**0.55**	**(0.20)**	**1.27**	**(0.25)**	**1.04**	**(0.07)**
Depth	α3	**0.26**	**(0.08)**	**0.32**	**(0.07)**	0.21	(0.10)	**0.26**	**(0.06)**	**0.25**	**(0.03)**
Slope	α4	0.12	(0.09)	**0.41**	**(0.08)**	0.08	(0.11)	**0.16**	**(0.06)**	0.06	(0.04)
Bay	α5	**0.36**	**(0.16)**	0.27	(0.15)	**0.63**	**(0.20)**	-0.17	(0.13)	0.09	(0.07)
SST*NAO	α6	0.01	(0.11)	0.11	(0.17)	**0.52**	**(0.24)**	**1.18**	**(0.24)**	**0.39**	**(0.08)**
Year	α7	**0.22**	**(0.05)**	**0.17**	**(0.05)**	**0.38**	**(0.07)**	**0.18**	**(0.02)**	**0.18**	**(0.02)**
Intercept - inclusion	β0	2.35	(0.25)	2.19	(0.26)	0.53	(0.14)	-1.58	(0.42)	4.76	(0.54)
Latitude	β1	**0.88**	**(0.20)**	**1.23**	**(0.20)**	**1.19**	**(0.16)**	**13.99**	**(2.40)**	**3.30**	**(0.41)**

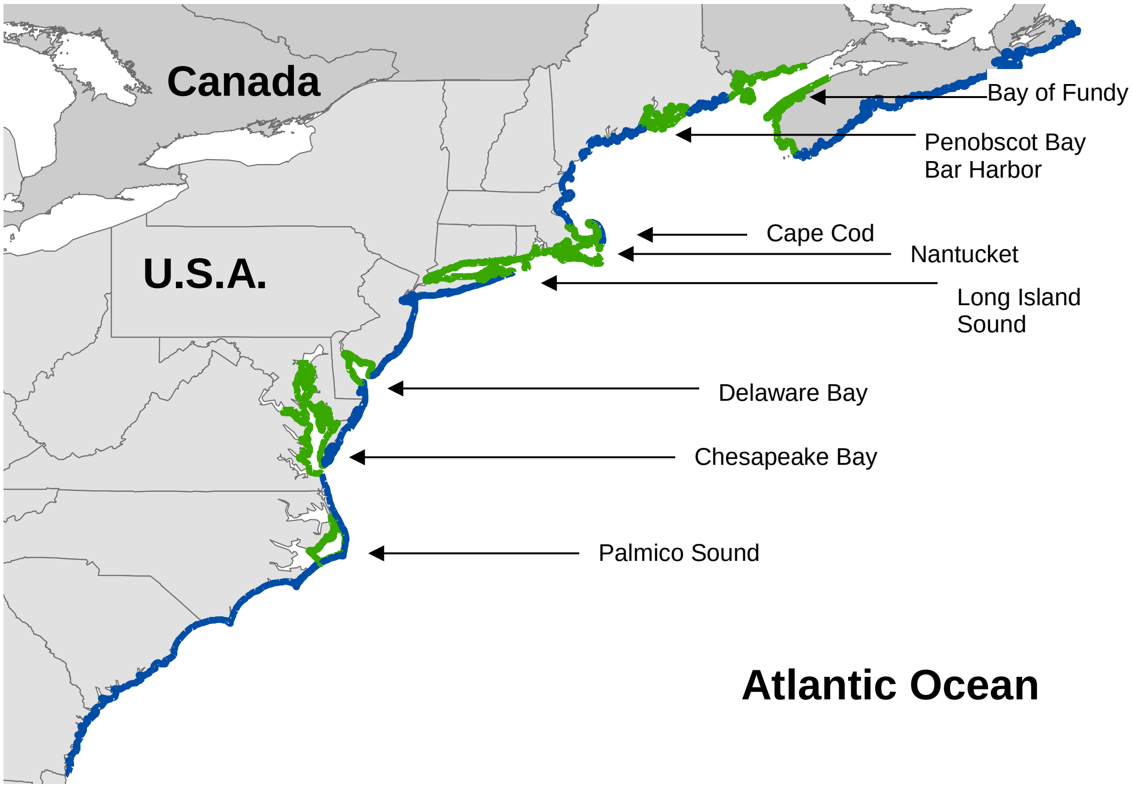


Figure 5.1 Map of the Atlantic Flyway Sea Duck Survey route flown ten years between 1991 and 2002. Segments shown in green were included as bays, all others are shown in blue.

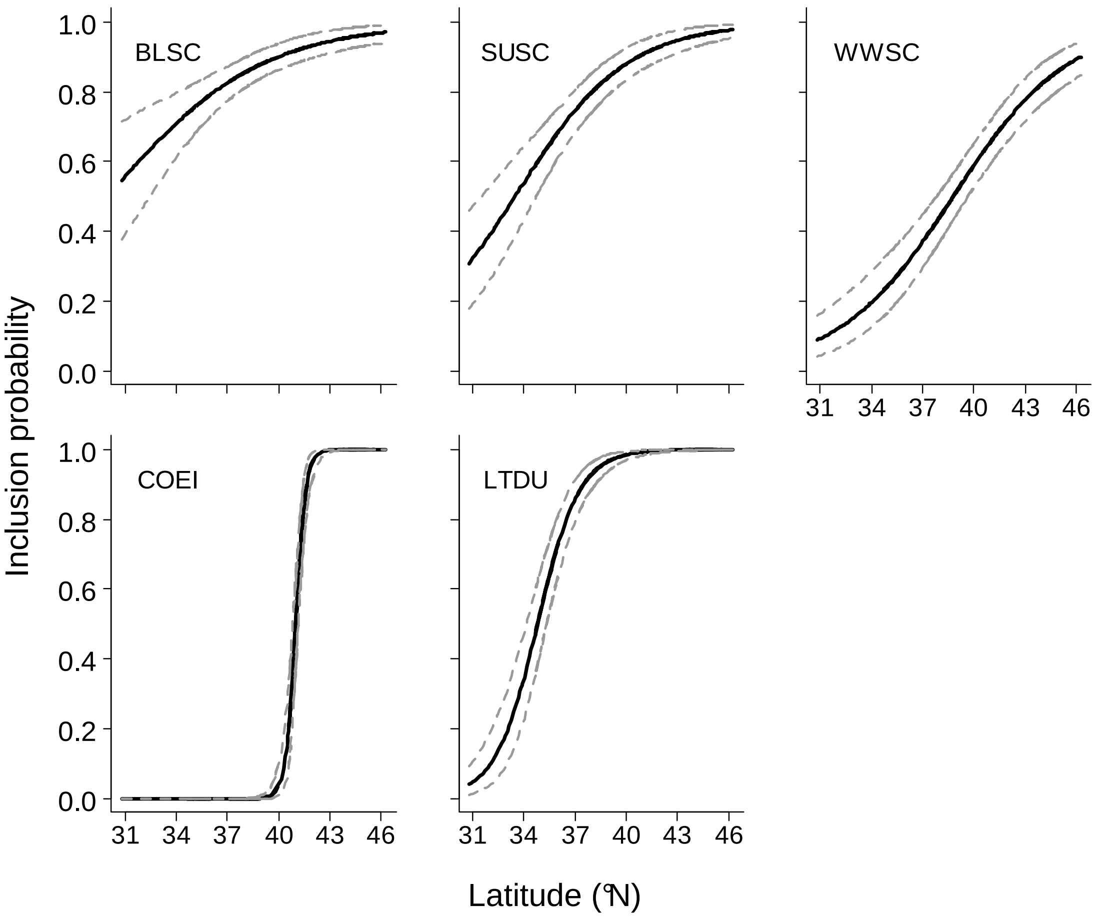


Figure 5.2 Probability of inclusion by latitude for each sea duck species. The mean estimate is shown in black and the 95% posterior interval is shown with gray dashed lines. BLSC = black scoters, SUSC = surf scoters, WWSC = white-winged scoters, COEI= common eiders, and LTDU = long-tailed ducks.

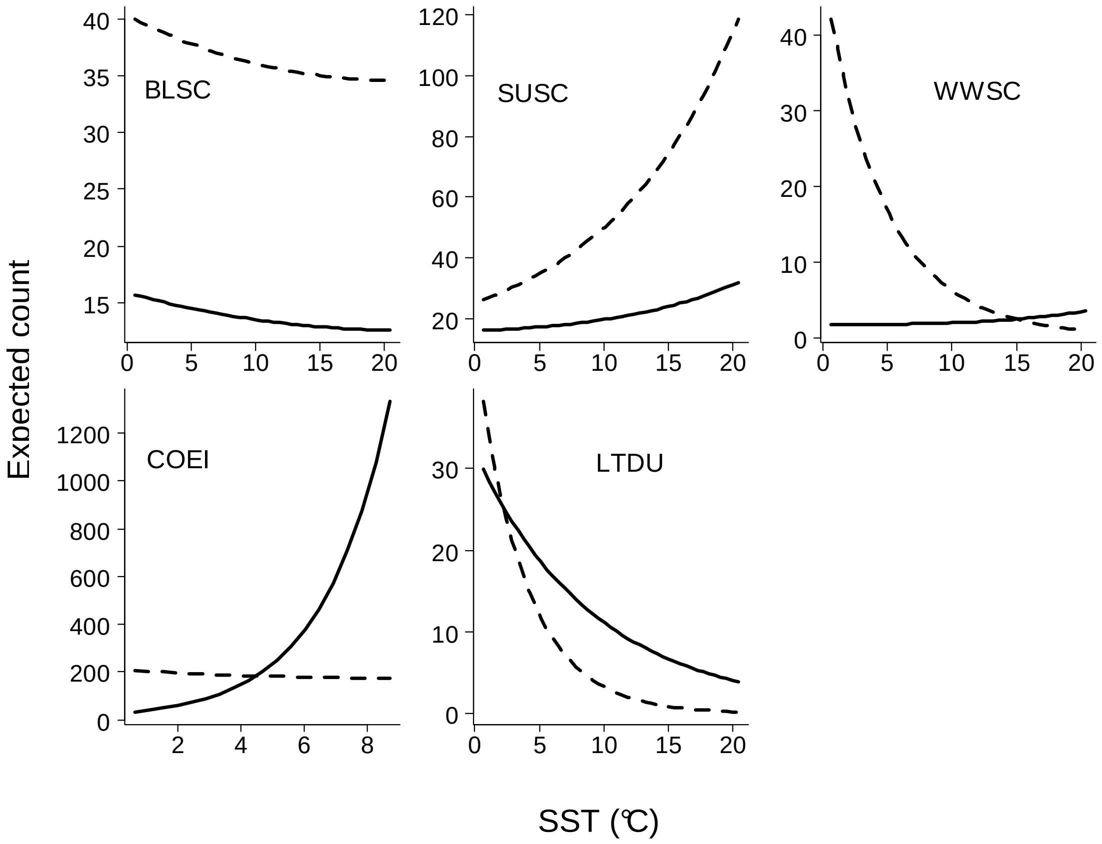


Figure 5.3 Expected count for each sea duck species (given inclusion, i.e., $z_{i,j} = 1$) by sea surface temperature (SST) in years with the highest positive (1994; solid line) and lowest negative (1998; dashed line) NAO values. BLSC = black scoters, SUSC = surf scoters, WWSC = white-winged scoters, COEI= common eiders, and LTDU = long-tailed ducks.

Conclusion

Statistical models will always be necessary in ecological research because of data limitations, the inherent complexities in ecological systems, and the desire to make predictions beyond the study system. My dissertation presents five case studies in which generalized linear models were developed to examine how habitat and climate variables affect the abundance and distributions of species including birds, amphibians, and butterflies. Through my dissertation work, I contributed to the development of modern estimation techniques on the occurrences and abundance of species using Bayesian inference. Specifically, I adapted and expanded on methods for dealing with highly aggregated species by incorporating covariates into a comprehensive model for simultaneously estimating distribution and abundance; I developed an approach for validating occurrence models that accounts for detection biases; and I advanced methods for dealing with uneven species abundances in community analyses of richness and composition.

My model developments can be used to help determine potential threats to populations and communities of species as well as to guide management planning. For example, the results from chapter three can be used to mitigate the declines in amphibian occurrences in the Chesapeake and Ohio National Historical Park. Managers could use the models to make predictions about the status of amphibian richness at all 274 wetlands in CHOH. This information could then be used to assess which wetlands might benefit most from management actions, such as translocating species or increasing wetland hydroperiod and/or area. All amphibian species had higher occurrence probabilities at semi-permanent or permanent as compared to temporary wetlands. Thus, one potential management strategy to reverse observed declines in amphibians would be to increase wetland hydroperiod (i.e., by increasing depth) of temporary wetlands during the breeding season. By using the estimated covariate effects, the models can be used to determine which temporary wetlands would produce the highest expected change in richness if they were altered to semi-permanent. This approach would allow managers to rank the potential efficacy of management alternatives and choose a strategy that meets their objectives.

The use of predictive models can aid decision makers in determining the optimal course of action for a given set of objectives (Williams et al. 2002). As such, the results from my models can also be used to make predictions about how species and communities may respond to environmental changes in habitat as well as climate. For example, the monarch butterfly model in chapter four can be used in conjunction with climate predictions on temperature and precipitation in Ohio and Texas to assess not only the potential sizes of local populations but also the uncertainty and variation in such predictions. This information can then be used to determine which locations are likely to be important for maintaining monarch populations and which therefore should be prioritized for conservation.

The work in my dissertation presents the first steps of my research objectives related to hierarchical model development. I have several projects planned or in the works that I aim to complete over the next few years, including:

- Comparison of traditional methods for estimating species richness to the multi-species modeling framework;

- Imposing additional structure in the community modeling framework, such as subdividing species according to functional groups and/or phylogenetic structure;
- Developing methodology within the multi-species modeling framework to explicitly model covariate effects (such as climate) on the timing of habitat use;
- Exploring other statistical distributions (such as power law) to more effectively model the extreme spatial aggregation in abundances that is observed in some species (e.g., seabirds).

My dissertation sets the stage for these additional methodological advances. The chapters from this dissertation along with code from my models (see the appendix and http://www.mbr-pwrc.usgs.gov/pubanalysis/communitymodeling/) will allow other researchers to build upon my work and adapt this modeling framework for their own study systems. It is my goal to illustrate the utility of hierarchical models while making the approach accessible to others wishing to employ these methods.

Appendices

Appendix 1.1 Hierarchical community model WinBUGS code

We ran the community model using MCMC with the programs R (using the R2Winbugs package) and WinBUGS for three chains of length 70,000 after a burnin of 7000 and thinned by 40. Convergence was assessed by examining the R-hat values for each parameter estimate (Gelman and Hill 2007). The model code, including the prior distributions, is presented below.

Winbugs model code:

```
model {

        #Prior distributions on the community level occupancy and detection covariates
          psi.mean ~ dunif(0,1)
          a <- log(psi.mean) - log(1-psi.mean)

          theta.mean ~ dunif(0,1)
          b <- log(theta.mean) - log(1-theta.mean)

          mu.alpha1 ~ dnorm(0, 0.001)
          mu.alpha2 ~ dnorm(0, 0.001)
          mu.alpha3 ~ dnorm(0, 0.001)

          mu.beta1 ~ dnorm(0, 0.001)
          mu.beta2 ~ dnorm(0, 0.001)
          beta3 ~ dnorm(0, 0.001)

          tau1 ~ dgamma(0.1,0.1)
          tau2 ~ dgamma(0.1,0.1)

          tau.alpha1 ~ dgamma(0.1,0.1)
          tau.alpha 2 ~ dgamma(0.1,0.1)
          tau.alpha 3 ~ dgamma(0.1,0.1)

          tau.beta1 ~ dgamma(0.1,0.1)
          tau.beta2 ~ dgamma(0.1,0.1)

          rho ~ dunif(-1,1)
```

```
           var.v <- tau2 /(1.-pow(rho,2))

           sigma1 <- 1/sqrt(tau1)
           sigma2 <- 1/sqrt(tau2)

for (i in 1:(N)) {

  #Prior distributions for the occupancy and detection covariates for each species
   u[i] ~ dnorm(a, tau1)

   mu.v[i] <- b + (rho*sigma2 /sigma1)*(u[i] – a)
   v[i] ~ dnorm(mu.v[i], var.v)

   alpha1[i] ~ dnorm(mu.alpha1, tau.alpha1)
   alpha2[i] ~ dnorm(mu.alpha2, tau.alpha2)
   alpha3[i] ~ dnorm(mu.alpha3, tau.alpha3)

   beta1[i] ~ dnorm(mu.beta1, tau.beta1)
   beta2[i] ~ dnorm(mu.beta2, tau.beta2)

  #Estimate the occupancy probability (latent Z matrix) for each species at each point
     for (j in 1:J) {
         logit(psi[j,i]) <- u[i] + alpha1[i]*perm[j] + alpha2[i]*area [j] + alpha3[i]*pa[j]
         Z[j,i] ~ dbin(psi[j,i], 1)

  #Estimate the species specific detection probability for every rep at each point
  # where the species occurs (Z=1)
    for (k in 1:K[j]) {
           logit(theta[j,k,i]) <- v[i] + beta1[i]*date1[j,k] + beta2[i]*date2[j,k] +
                                              beta3*year[j,k]
           mu.theta[j,k,i] <- theta[j,k,i]*Z[j,i]
           X[j,k,i] ~ dbin(mu.theta[j,k,i], 1)

    }
      }
         }

 }
```

Appendix 1.2. Comparison of the community model to species-level models

We developed and analyzed species-specific occurrence models (that accounted for detection) to compare the results with those obtained using the community model described in the main text of Chapter 1. For many species, including some of direct interest, we could not obtain MLEs of model parameters. This is manifested in the numerical optimization procedure (e.g., nlm() in the package R) as a singular Hessian matrix with typically one or more parameters that tend toward the boundary of the parameter space (+/- infinity for regression parameters). In the context of a Bayesian analysis, this appears as extreme sensitivity to the prior distribution or a posterior maximum at one of the boundaries for those priors having bounded support (e.g. a uniform prior on the interval [-B,B]),.

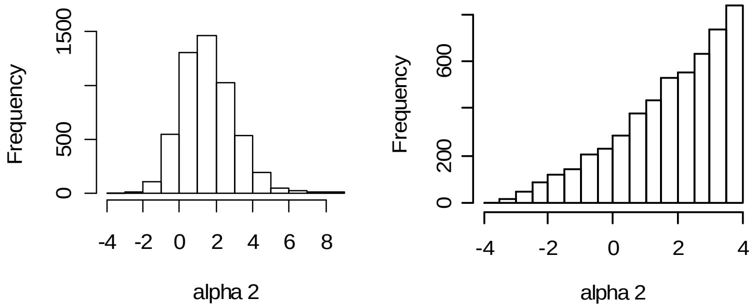
The WinBUGS model code for the single-species occupancy models is shown below. In this specification, we used uniform (-4,4) priors for the regression parameters. The results, summarized for area effect in Figure A1.1, compare the posterior distributions for the seventeen forest interior species as estimated in the community model to the individual species models. We again ran three chains of the species-by-species model for a length 70,000 after a burnin of 7000 and thinned the model by 40. Convergence was assessed by examining the R-hat values for each parameter estimate. The very diffuse posterior distributions (and in some cases, posterior modes on the boundary) is evidence that the parameters are non-identifiable under the single-species models. Therefore, in a classical analysis framework we would have to discard these data or possibly rely on pooling the species to increase sample size, inducing an assumption of homogeneity of effects across species.

Winbugs model code:

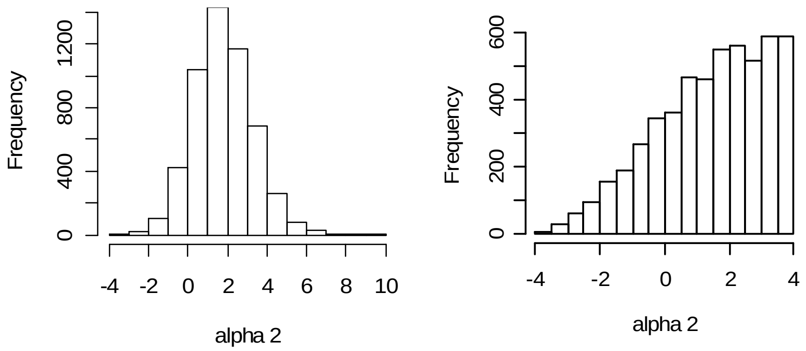
```
model {

for (i in 1:N) {

   #Prior distributions for the intercept terms: occupancy and detection
    expit.u[i]~dunif(0,1)
    u[i] <- log(expit.u[i]/(1-expit.u[i]))
    expit.v[i]~dunif(0,1)
    v[i] <- log(expit.v[i]/(1-expit.v[i]))

   #Prior distributions for the habitat and sampling covariates for each species
    alpha1[i] ~ dunif(-4,4)
    alpha2[i] ~  dunif(-4,4)
    alpha3[i] ~ dunif(-4,4)
    beta1[i] ~  dunif(-4,4)
    beta2[i]~  dunif(-4,4)
    beta3[i] ~  dunif(-4,4)

  #Estimate the occupancy probability (latent Z matrix) for each species at each point
   for (j in 1:J) {
       logit(psi[j,i]) <- u[i] + alpha1[i]*perm[j] + alpha2[i]*area1[j] + alpha3[i]*pa[j]
       mu.psi[j,i] <- psi[j,i]
       Z[j,i] ~ dbin(mu.psi[j,i], 1)

  #Estimate the species specific detection probability for every rep at each point where
the
  #species occurs (Z=1)
     for (k in 1:K[j]) {
            logit(theta[j,k,i]) <- v[i] + beta1[i]*date1[j,k] + beta2[i]*date2[j,k] +
beta3[i]*year[j,k]
            mu.theta[j,k,i] <- theta[j,k,i]*Z[j,i]
            X[j,k,i] ~ dbin(mu.theta[j,k,i], 1)

}
            }
                        }           }
```

Figure A1.1 Comparison of posterior distributions for α2 (effect of area) for seventeen forest interior species (Acadian flycatcher (ACFL), black-and-white warbler (BAWW), blackburnian warbler (BBWA), brown creeper (BRCR), black-throated blue warbler (BTBW), black-throated green warbler (BTGN), Canada warbler (CAWA), cerulean warbler (CERW), hooded warbler (HOWA), northern parula (NOPA), ovenbird (OVEN), red-breasted nuthatch (RBNU), scarlet tanager (SCTA), veery (VEER), worm-eating warbler (WEWA), winter wren (WIWR), and wood thrush (WOTH)) as estimated using the community hierarchical model (left column – Appendix A1.1 code) and with a Bayesian species-level model (right column – Appendix A1.2 code).

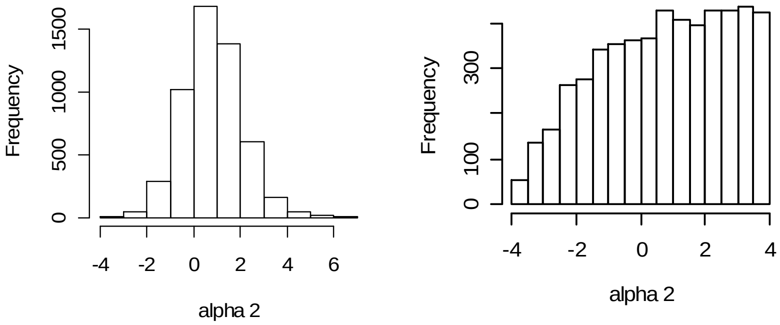
ACFL



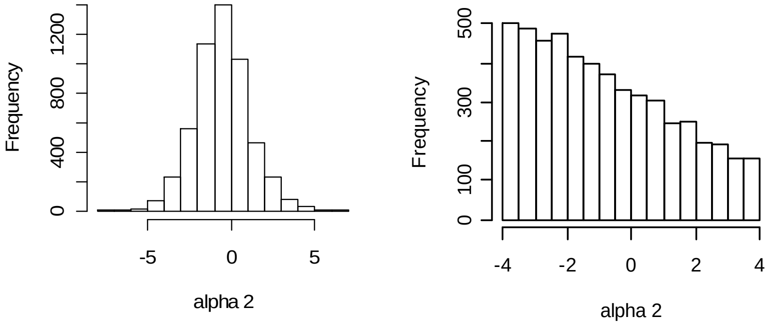
BAWW



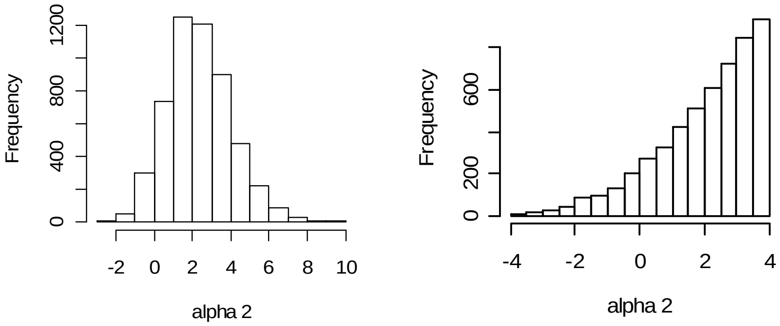
BBWA



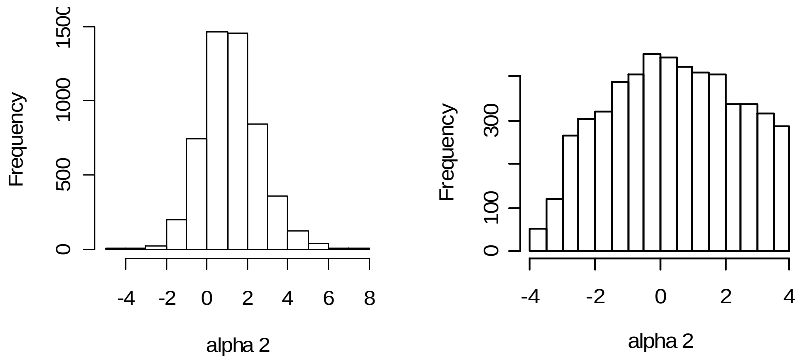
BRCR



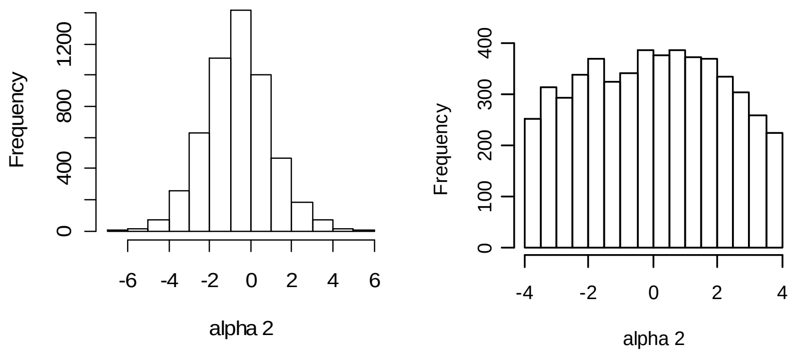
BTBW



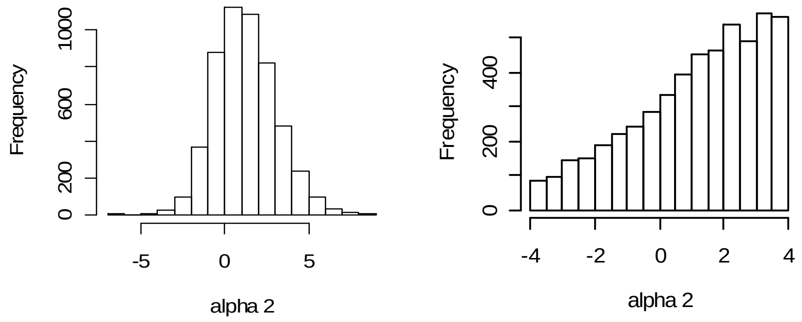
BTGN

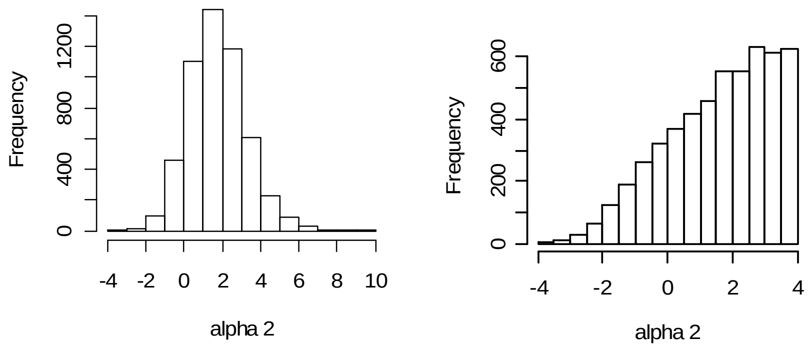


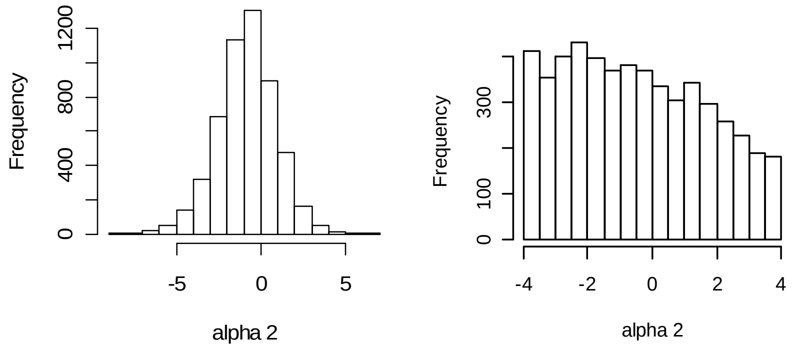
CAWA

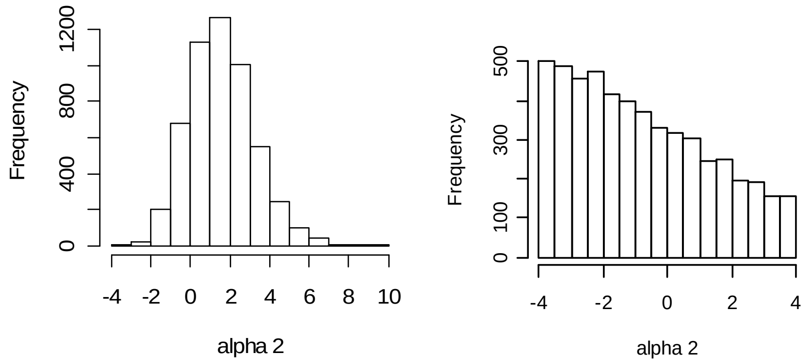


CERW

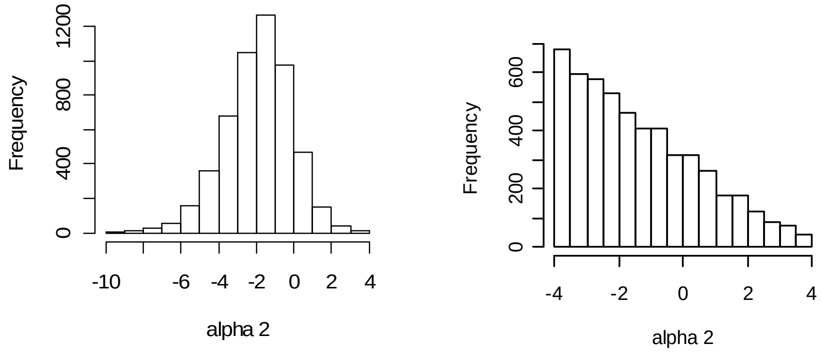



HOWA

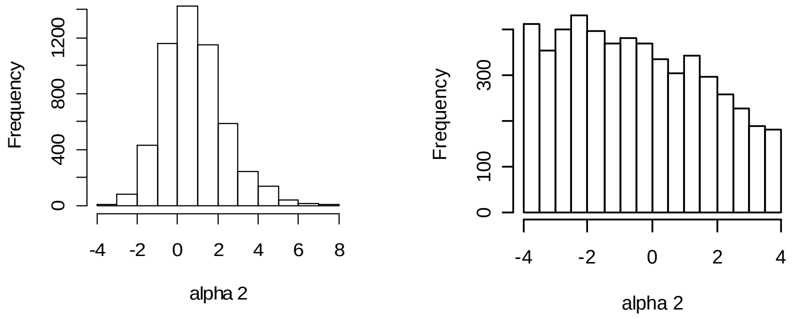

NOPA


OVEN

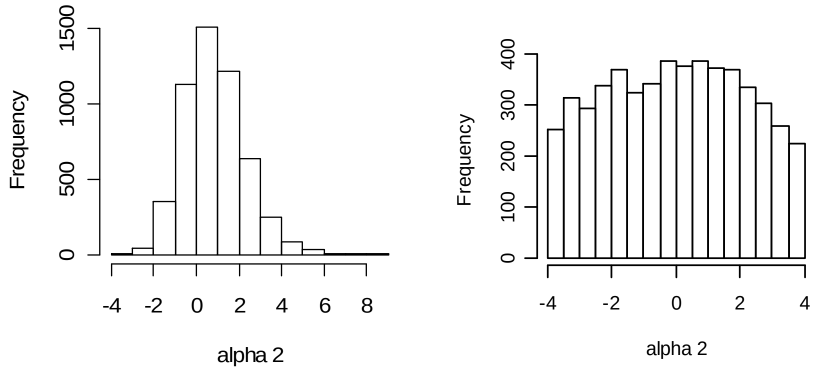
RBNU



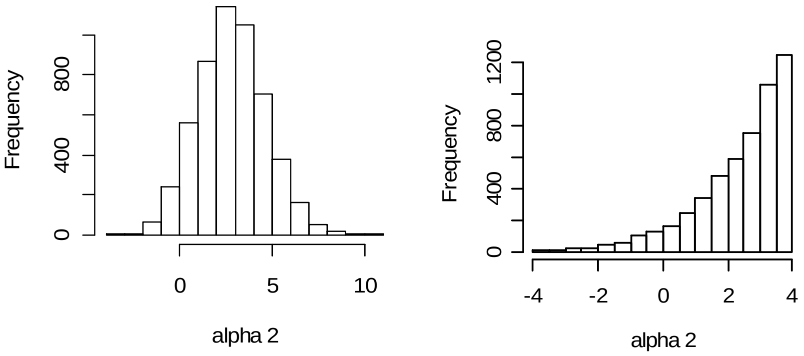
SCTA



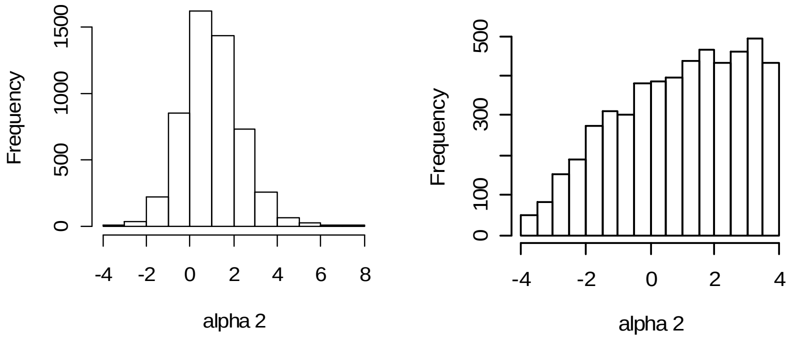
VEER



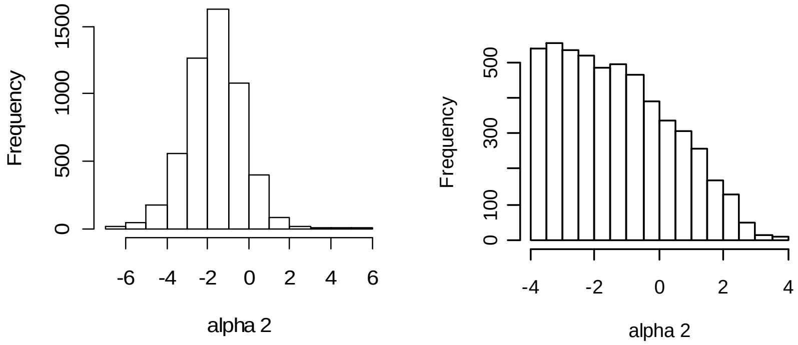
WEWA



WIWR



WOTH



Literature cited

Adamik, P. & Pietruszkova, J. (2008). Advances in spring but variable autumnal trends in timing of inland wader migration. *Acta Ornithologica*, 43, 119-128.

Andelman, S.J. & Fagan, W.F. (2000). Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences*, 97, 5954–5959.

Anderson, R.P. & Raza, A. (2010). The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents in Venezuela. *Journal of Biogeography*, 37, 1378-1393.

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

Bailey, L.L., Simons, T.R. & Pollock K.H. (2004). Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications*, 14, 692-702.

Batalden, R.V., Oberhauser, K. & Peterson, A.T. (2007). Ecological niches in sequential generations of eastern North American monarch butterflies (Lepidoptera: Danaidae): the ecology of migration and likely climate change implications. *Population Ecology*, 36, 1365-1373.

Bates, S., Dawson, D.K. & Royle, J.A. (2005). Vegetation characteristics and breeding bird densities in the Catoctin Mountain Park and the Frederick City

Watershed. *National Park Service Center for Urban Ecology*, Washington, DC.

Bell, I. & Visbeck, M. (2009). *The North Atlantic Oscillation*. Retrieved from Columbia University Lamont-Doherty Earth Observatory Web site: http://www.ldeo.columbia.edu/res/pi/NAO.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441, 81-83.

Boulinier, T., Nichols, J.D., Hines, J.E., Sauer, J.R., Flather, C.H. & Pollock, K.H. (2001). Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology*, 82, 1159-1169.

Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. & Pollock, K.H. (1998). Estimating species richness: the importance of heterogeneity in species detectability. *Ecology*, 79, 1018-1028.

Bowlin, M.S., Bisson, I.A. & Shamoun-Baranes, J. (2010). Grand challenges in migration biology. *Integrative and Comparative Biology*, 50, 261-279.

Braeger, I.S., Meissner, J. & Thiel, M. (1995). Temporal and spatial abundance of wintering Common Eider, Long-tailed Duck, and Common Scoter in shallow water areas of southwestern Baltic Sea. *Ornis Fennica*, 72, 19-28.

Brower, L.P. (1986). New perspectives on the migration biology of the monarch butterfly, Danaus plexippus L. Migration: mechanisms and adaptive significance. *University of Texas Contribution to Marine Science*, 748-785.

Brower, L.P., Kust, D.R. & Rendon-Salinas, E. (2004). Catastrophic winter storm mortality of monarch butterflies in Mexico during January 2002. In Oberhauser, K.S., & M.J. Solensky (Eds.) *The monarch butterfly: biology and conservation* (pp. 151-166). Ithaca: Cornell University Press.

Brower, L.P. & Malcolm, S.B. (1991). Animal migrations: endangered phenomena. *American Zoologist*, 31, 265-276.

Brower, L.P., Taylor, O.R., Williams, E.H., Slayback, D.A., Zubieta, R.R. & Ramirez, M.I. (2011). Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? *Insect Conservation and Diversity*, Online early.

Brown, J.H. & Gibson, A.C. (1983). Biogeography. *Mosby Press*. MO, USA.

Cabeza, M., Araujo, M.B., Wilson, R.J., Thomas, C.D., Cowley, M.J.R. & Moilanen, A. (2004). Combining probabilities of occurrence with spatial reserve design. *Journal of Applied Ecology*, 41, 252-262.

Caithamer, D.F., Otto, M., Padding, P.I., Sauer, J.R. & Haas, G.H. (2000). Sea ducks in the Atlantic flyway: population status and a review of the special hunting seasons. *U.S. Fish and Wildlife Service,* Laurel, Maryland.

Cam, E., Nichols, J.D., Sauer, J.R. & Hines, J.E. (2002). On the estimation of species richness based on the accumulation of previously unrecorded species. *Ecography*, 25, 102–108.

Clarke, E.D., Spear, L.B., Mccracken, M.L., Marques, F.F.C., Borchers, D.L., Buckland, S.T. & Ainley, D.G. (2003). Validating the use of generalized additive models and at-sea surveys to estimate size and temporal trends of seabird populations. *Journal of Applied Ecology*, 40, 278-292.

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state. *Science*, 199, 1302-1310.

Cook, E., D'Arrigo, R. & Mann, M. (2002). A well-verified, multiproxy reconstruction of the winter North Atlantic Oscillation index since AD 1400. *Journal of Climate*, 15, 1754-1764.

Cote, S.D., Rooney, T.P., Tremblay, J-P., Dussault, C. & Waller, D.M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, 35, 113-147.

Cowardin, L., Carter, V., Golet, F. & LaRoe, E. (1979). Classification of wetlands and deepwater habitats of the United States. *U.S. Department of the Interior, Fish and Wildlife Service*, Washington, D.C.

Crozier, L. & Dwyer, G. (2006). Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *American Naturalist*, 167, 853-866.

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

Davis, A.K. (2012). Are migratory monarchs really declining in eastern North America? Examining evidence from two fall census programs. *Insect Conservation and Diversity*, Online early.

DeCalesta, D.S. (1994). Effects of white-tailed deer on song birds within managed forests in Pennsylvania. *Journal of Wildlife Management*, 58, 711–718.

DeGraaf, R.M., Healy, W.M. & Brooks, R.T. (1991). Effects of thinning and deer browsing on breeding birds in New England oak woodlands. *Forest Ecology and Management*, 41, 179-191.

DeWan, A.A., Sullivan, P.J., Lembo, A.J., Smith, C.R., Maerz, J.C., Lassoie, J.P. & Richmond, M.E. (2009). Using occupancy models of forest breeding birds to prioritize conservation planning. *Biological Conservation*, in press.

Dice, L.R., (1945). Measures of the amount of ecological association between species. *Ecology*, 26, 297-302.

Divins, D.L. & Metzger, D. (2008). NGDC Coastal Relief Model, NGDC Coastal Relief Model Vol. 01 and 02 Shaded Relief Images, Retrieved from http://www.ngdc.noaa.gov/mgg/coastal/coastal.html. Accessed: April 18, 2009.

Doi, H., Gordo, O. & Katano, I. (2008). Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. *Climate Research*, 36, 181-190.

Dorazio, R. M., Kéry, M., Royle, J. A. & Plattner, M. (2010). Models for inference in dynamic metacommunity systems. *Ecology*, 91, 2466–2475.

Dorazio, R.M. & Royle, J.A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of American Statistical Association*, 100, 389-398.

Dorazio, R.M., Royle, J.A., Söderström, B. & Glimskär, A. (2006). Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, 87, 842–854.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.McC., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S. & Zimmermann, N.E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129-151.

Finton, A.D., Novak, P.G., Schneider, K.J. & Weldy, T.W. (2000). Rare species and significant ecological communities of the counties bordering the Hudson River estuary north of New York City. *New York State Department of Environmental Conservation*, New York.

Fischer, J., Lindenmayer, D.B. & Cowling, A. (2004). The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. *Journal of Applied Ecology*, 41, 32-44.

Fleishman, E., Blair, R.B. & Murphy, D.D. (2001). Empirical validation of a method for umbrella species selection. *Ecological Applications*, 11, 1489-1501.

Forchhammer, M.C., Post, E. & Stenseth, N.C. (1998). Breeding phenology and climate. *Nature*, 391, 29-31.

Forister, M.L., McCall, A.C.,& Sanders, N.J. (2010). Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences*, 107, 2088-2092.

Forister, M.L. & Shapiro, A.M. (2003). Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biology*, 9, 1130-1135.

Gaston, K.J. (2003) The structure and dynamics of geographic ranges. *Oxford University Press*, Oxford, UK.

Gelfand, A.E. & Ghosh, S.K. (1998). Model choice: a minimum posterior predictive loss approach. *Biometrika*, 85, 1-11.

Gelfand, A.E., Schmidt, A.M., Wu, S., Silander, J.A., Latimer, A. & Rebelo, A.G. (2005). Explaining species diversity through species level hierarchical modeling. *Applied Statistics*, 65, 1-20.

Gelman, A. & Hill, J. (2007). *Data Analysis Using Regression and Multilevel/hierarchical Models*. New York: Cambridge University Press.

Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, 35, 37-58.

Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379-391.

Green, D.M. (2003). The ecology of extinction: population fluctuation and decline in amphibians. *Biological Conservation*, 111, 331-343.

Grime, J.P. (1973). Competition and diversity in herbaceous vegetation – reply. *Nature*, 244, 311-311.

Gu, W. & Swihart, R.K. (2004). Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. *Biological Conservation*, 116, 195-203.

Guillemette, M., Himmelman, J.H. & Barette, C. (1993). Habitat selection by common eiders in winter and its interaction with flock size. *Canadian Journal of Zoology*, 71, 1259-1266.

Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993–1009.

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

Halkka, A., Halkka, L., Halkka, O., Roukka, K. & Pokki, J. (2006). Lagged effects of North Atlantic Oscillation on spittlebug *Philaenus spumarius* (Homoptera) abundance and survival. *Global Change Biology*, 12, 2250–2262.

Hall, D. (2000). Zero-inflated Poisson and binomial regression with random effects: a case study. *Biometrics*, 56, 1030-1039.

Hallett, T.B., Coulson, T., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Grenfell, B.T. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, 430, 71-75.

Hanski, I. (1999). Metapopulation Ecology. *Oxford University Press*, Oxford, UK.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, 80, 4-18.

Heim Jr., R.R. (2002). A review of twentieth-century drought indices used in the United States. *Bulletin of the American Meteorological Society*, 83, 1149-1165.

Helzer, C.J. & Jelinski, D.E. (1999). The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications,* 9, 1448-1458.

Heyer, W.R. (1994). Measuring and monitoring biological diversity: standard methods for amphibians. *Smithsonian*, Washington DC.

Hiemstra, P.H., Pebesma, E.J., Twenhofel, C.J.W. & Heuvelink, G.B.M. (2008). Real-time automatic interpolation of ambient gamma dose rates from the Dutch Radioactivity Monitoring Network. *Computers & Geosciences*, Accepted for publication.

Higuchi, K., Huang, J. & Shabbar, A. **(**1999**).** A wavelet characterization of the North Atlantic oscillation variation and its relationship to the North Atlantic sea surface temperature. *International Journal of Climatology*, 19, 1119–1129.

Hodgson, J.A., Thomas, C.D., Oliver, T.H., Anderson, B.J., Brereton, T.M. & Crone, E.E. (2011). Predicting insect phenology across space and time. *Global Change Biology*, 17, 1289-1300.

Hoerling, M.P., Hurrell, J.W. & Xu, T. (2001). Tropical Origins for Recent North Atlantic Climate Change. *Science*, 292, 90-92.

Holland, R.A., Wikelski, D.S. & Wilcove, D.S. (2006). How and why do insects migrate? *Science*, 313, 794.

Horn, H.S. (1975). Markovian properties of forest succession. *Ecology and evolution* *of communities*, Cody, M.L., & J.M. Diamond (Eds.). Belknap Press.

Hosmer, D.W., & Lemeshow, S. (2000). *Applied logistic regression 2nd edition*. Wiley, New York, USA.

Howe, E.J., Obbard, M.E. & Schaefer, J.A. (2007). Extirpation risk of an isolated black bear population under different management scenarios. *Journal of Wildlife Management*, 71, 603-612.

Hu, Q. & Wilson, G.D. (2000). Effects of temperature anomalies on the Palmer Drought Severity Index in the central United States. *International Journal of Climatology*, 20, 1899-1911.

Hüppop, O. & Hüppop, K. (2003). North Atlantic Oscillations and the timing of spring migration in birds. *Proceeding of the Royal Society of London*, 270, 233-240.

Hurrell, J.W. (1995). Decadal trends in the North Atlantic Oscillation and relationships to regional temperature and precipitation. *Science*, 269, 676-679.

Hurrell, J.W., Kushnir, Y., Ottersen, G. & Visbeck, M. (2003). The North Atlantic Oscillation Climate Significance and Environmental Impacts. *Geophysical Monograph Series*, 134, 1-36.

Husté, A., Selmi, S. & Boulinier, T. (2006). Bird communities in suburban patches near Paris: determinants of local richness in a highly fragmented landscape. *Ecoscience*, 13, 249-257.

Hutto, R.L., Pletschet, S.M. & Hendricks, P. (1986). A fixed-radius point count method for nonbreeding and breeding season use. *Auk*, 103, 593-602.

Jones, P., Jonsson, T. & Wheeler, D. (1997). Extension to the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and South-West Iceland. *International Journal of Climatology*, 17, 1433-1450.

Kempton, W., Archer, C.L., Dhanju, A., Garvine, R.W. & Jacobson, M.Z. (2007). Large CO_2 reductions via offshore wind power matched to inherent storage in energy end-uses. *Geophysical Research Letter*, 34, L02817.

Kerr, J.T. (1997) Species richness, endemism, and the choice of areas for conservation. *Conservation Biology*, 11, 1094–1100.

Kéry, M., Royle, J.A. & Schmid, H., (2008). Importance of sampling design and analysis in animal population studies: A comment on Sergio et al. *Journal of Applied Ecology*, 45, 981-986.

Kéry, M. & Royle, J.A. (2008). Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology*, 45, 589-598.

Kéry, M. & Royle, J.A., (2009). Inference about species richness and community structure using species-specific occupancy models in the National Swiss Breeding Bird Survey MHB. Modeling demographic processes in marked populations (eds Thomson, D.L., Cooch E.G., and Conroy, M.J.), pp. 639-656. Springer.

Kéry, M., Royle, J. A., Plattner, M. & Dorazio, R. M. (2009). Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology*, 90, 1279–1290.

Kirk, M., Esler, D. & Iverson, S.A. (2008). Movements of wintering surf scoters: predator responses to different prey landscapes. *Oecologia*, 155, 859-867.

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, 68, 940-950.

Konvicka, M., Maradova, M., Benes, J., Fric, Z. & Kepka, P. (2003). Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Global Ecology and Biogeography*, 12, 403-410.

Larsen, J.K. & Guillemette, M. (2007). Effects of wind turbines on flight behaviour of wintering common eiders: implications for habitat use and collision risk. *Journal Applied Ecology*, 44, 516-522.

Lawler, J.J. & White, D. (2008). Assessing the mechanisms behind successful surrogates for biodiversity in conservation planning. *Animal Conservation*, 11, 270-280.

Lehikoinen, A., Kilpi, M. & Ost, M. (2006). Winter climate affects subsequent breeding success of common eiders. *Global Change Biology*. 12, 1355–1365.

Lepczyk, C.A., Flather, C.H., Radeloff, V.C., Pidgeon, A.M., Hammer, R.B. & Liu, J.G. (2008). Human impacts on regional avian diversity and abundance. *Conservation Biology*, 22, 405-416.

Lewis, T.L., Esler, D. & Boyd, W.S. (2008). Foraging behavior of surf scoters and white-winged scoters in relation to clam density: inferring food availability and habitat quality. *Auk*, 125, 149-157.

Link, W.A.,& Sauer, J.R. (2007). A hierarchical analysis of population change with application to cerulean warblers. *Ecology*, 83,2832-2840.

Link, W.A. (1999). Modeling pattern in collections of parameters. *Journal of Wildlife Management*, 63, 1017-1027.

Link, W.A. & Sauer, J.R. (1996). Extremes in ecology: avoiding the misleading effects of sampling variation in summary analyses. *Ecology*, 77, 1633-1640.

Link, W.A., Cam, E., Nichols, J.D. & Cooch, E.G. (2002). Of BUGS and Birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management*, 66, 277-291.

Liu, C., White, M. & Newell, G. (2011). Measuring and comparing the accuracy of species distribution models with presence–absence data. *Ecography*, 34, 232-243.

Lobo, J.M., Alberto Jiménez-Valverde, A. & Real, R. (2007). AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17, 145-151.

Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000). WinBUGS - A Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing*, 10, 325-337.

MacArthur, R.H. & Wilson, E.O. (1967) The Theory of Island Biogeography. *Princeton University Press*, NJ, USA.

MacKenzie, D.I. (2006). Modeling the probability of use: the effect of, and dealing with, detecting a species imperfectly. *Journal of Wildlife Management*, 70, 367-374.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology,* 83, 2248-2255.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006). Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. *Elsevier,* Oxford, UK.

MacKenzie, D.I., Nichols, J.D., Sutton, N., Kawanishi, K. & Bailey, L.L. (2005). Improving inferences in population studies of rare species that are detected imperfectly. *Ecology,* 86, 1101-1113.

Malcolm, S.B., Cockrell, B.J. & Brower, L.P. (1987). Monarch butterfly voltinism: effects of temperature constraints at different latitudes. *Oikos*, 49, 77-82.

Manel, S., Williams, H. C. & Ormerod, S.J. (2001). Evaluating presence–absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology,* 38, 921-931.

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

Manley, P.N., Schlesinger, M.D., Roth, J.K. & Van Horne, B. (2005). A field-based evaluation of a presence-absence protocol for monitoring ecoregional-scale biodiversity. *Journal of Wildlife Management,* 69, 950-966.

Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature*, 405, 243-253.

Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J., Tyre, A.J. & Possingham, H.P. (2005). Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters*. 8, 1235-1246.

Mattfeldt, S.D., Bailey, L.L. & Grant, E.H.C. (2009). Monitoring multiple species: estimating state variables and exploring the efficacy of a monitoring program. *Biological Conservation*, 142, 720-737.

McMaster, G.S. & Wilhelm, W.W. (1997). Growing degree-days: one equation, two interpretations. *Agricultural and Forest Meteorology*, 87, 291-300.

McShea, W.J. & Rappole, J.H., (1992). White-tailed deer as keystone species within forest habitats of Virginia. *Virginia Journal of Science*, 43, 177–186.

McShea, W.J. & Rappole, J.H., (2000). Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conservation Biology*, 14, 1161-1170.

Meir, E., Andelman, S. & Possingham, H.P. (2004). Does conservation planning matter in a dynamic and uncertain world? *Ecology Letters*, 7, 615-622.

Merkel, F.R., Mosbech, A., Sonne, C., Flagstad, A., Falk, K. & Jamieson, S.E. (2006). Local movements, home ranges and body condition of common eiders wintering in southwest Greenland. *Ardea*, 94, 639-650.

Migratory Bird Data Center. Retrieved from http://mbdcapps.fws.gov/mbdc/databases/afsos/aboutafsos.html. Accessed: January 10, 2009.

Moilanen, A. & Nieminen, M. (2002). Simple connectivity measures in spatial ecology. *Ecology*, 83, 1131-1145.

Moller, A. (2002). North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. *Journal of Animal Ecology*, 71, 201-210.

Moller, A.P., Rubolini, D. & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences*, 105, 16195-16200.

Moore, C.T., Plummer, W.T. & Conroy, M.J., (2005). Forest management under uncertainty for multiple bird population objectives, in: Ralph, C.J., Rich, T.D. (Eds.), Bird Conservation Implementation and Integration in the Americas: *Proceedings of the Third International Partners in Flight Conference*, USDA Forest Service General Technical Report PSW-GTR-191, pp. 373-380.

Mueller, T. & Fagan, W.F. (2008). Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos*, 117, 654-664.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.

Nichols, J.D., Boulinier, T., Hines, J.E., Pollock, K.H. & Sauer, J.R. (1998). Estimating rates of local species extinction, colonization, and turnover in animal communities. *Ecological Applications,* 8, 1213-1225.

Norris, D.R. & Marra, P.P. (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor*, 109, 535-547.

O'Connell, T.J., Jackson, L.E. & Brooks, R.P. (2000). Bird guilds as indicators of ecological condition in the central Appalachians. *Ecological Applications*, 10, 1706-1721.

O'Dea, N., Whittaker, R.J. & Ugland, K.I. (2006). Using spatial heterogeneity to extrapolate species richness: a new method tested on Ecuadorian cloud forest birds. *Journal of Applied Ecology*, 43, 189–198.

Oberbillig, D. (2008). State wildlife action plans: Working together to prevent wildlife from becoming endangered. Retrieved from http://www.wildlifeactionplans.org/pdfs/wildlife_action_plans_summary_report.pdf. Accessed October 2008.

Oberhauser, K. (2011). Get Ready for the Fall Migration! Newsletter.

Oberhauser, K. & Peterson, A.T. (2003). Modeling current and future potential wintering distributions of eastern North American monarch butterflies. *Proceedings of the National Academy of Sciences*, 100, 14063-14068.

Osenberg, C.W., Sarnelle, O., Cooper, S.D. & Holt, R.D. (1999). Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology*, 80, 1105-1117.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C. & Stenseth, N.C. (2001). Ecological effects of the North Atlantic Oscillation. *Oecologia* 128,1-14.

Palm, V., Leito, A., Truu, J. & Tomingas, O. (2009). The spring timing of arrival of migratory birds: dependence on climate variables and migration route. *Ornis Fennica*, 86, 97-108.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics*, 37, 637-669.

Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, 13, 1860-1872.

Parmesan, C., Ryrholm, N. & Stefanescu, C. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579-583.

Pauliny, A., Larsson, M. & Blomqvist, D., (2008). Nest predation management: effects on reproductive success in endangered shorebirds. *Journal of Wildlife Management*, 72, 1579-1583.

Pearce, J.L., Kirk, D.A., Lane, C.P., Mahr, M.H., Walmsley, J., Casey, D., Muir, J.E., Hannon, S., Hansen, A. & Jones, K. (2008). Prioritizing avian conservation areas for the Yellowstone to Yukon Region of North America. *Biological Conservation*, 141, 908-924.

Pebesma, E., Cornford, D. & Dubois, G. (2011). INTAMAP: The design and implementation of an interoperable automated interpolation web service. *Computers and Geosciences*, 37, 343-362.

Perry, M.C. & Deller, A.S. (1995). Waterfowl population trends in the Chesapeake Bay area. In: Hill, Nelson S (Eds.), Proceedings of the 1994 Chesapeake Research Conference; Toward a Sustainable Watershed: the Chesapeake Experiment. CRC Publication No. 149. Chesapeake Research Consortium, Edgewater, MD. pp 490-504.

Perry, M.C., Wells-Berlin, A.M., Kidwell, D.M. & Osenton, P.C. (2007). Temporal changes of populations and trophic relationships of wintering diving ducks in Chesapeake Bay. *Waterbirds 30*, (Special Publication 1), 4-16.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231-259.

Pollard, E. (1977). A method for assessing changes in the abundance of butterflies. *Biological Conservation*, 12, 115-134.

Post, E. & Forchhammer, M.C. (2002). Synchronization of animal population dynamics by large-scale climate. *Nature*, 420,168- 171.

Post, E. & Forchhammer, M.C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 363, 2369-2375.

Post, E. & Stenseth, N.C. (1999). Climatic variability, plant phenology, and northern ungulates. *Ecology*, 80, 1322-1339.

Powell, L.A., Lang, J.D., Conroy, M.J. & Krementz, D.G. (2000). Effects of forest management on density, survival, and population growth of wood thrushes. *Journal of Wildlife Management*, 64, 11-23.

Prysby, M. & Oberhauser, K.S. (2004). Temporal and geographic variation in monarch densities: Citizen scientists document monarch population patterns. In: The monarch butterfly: biology and conservation (eds. Oberhauser KS, Solensky MJ) pp. 9-20. Cornell University Press, Ithaca.

Prysby, M.D. (2004). Natural enemies and survival of monarch eggs and larvae. In: The monarch butterfly: biology and conservation (eds. Oberhauser KS, Solensky MJ) pp. 27-37. Cornell University Press, Ithaca.

Queheillalt, D.M., Cain, J.W., Taylor, D.E., Morrison, M.L., Hoover, S.L., Tuatoo-Bartley, N., Rugge, L., Christopherson, K., Hulst, M.D., Harris, M.R. & Keough, H.L. (2002). The exclusion of rare species from community-level analyses. *Wildlife Society Bulletin*, 30, 756-759.

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Rafe, R.W., Usher, M.B. & Jefferson, R.G. (1985). Birds on reserves- the influence of area and habitat on species richness. *Journal of Applied Ecology*, 22, 327-335.

Rebelo, H. & Jones, G. (2010). Ground validation of presence-only modelling with rare species: a case study on barbastelles Barbastella barbastellus (Chiroptera: Vespertilionidae). *Journal of Applied Ecology*, 47, 410-420.

Rendon-Salinas, E., Valera-Bermejo, C.A., Cruz-Pina, M. & Martinez-Meza, F. (2011). Monitoreo De Las Colonias De Hibernacion De Mariposa Monarca: Superficie Forestal De Ocupacion En Diciembre De 2010. World Wildlife Fund, Mexico, Mexico City.

Reynolds, R., Rayner, N., Smith, T., Stokes, D. & Wang, W. (2002). An improved in situ and satellite SST analysis for climate. *Journal of Climate*, 15, 1609-1625.

Rich, T.D., Beardmore, C.J., Berlanga, H., Blancher, P.J., Bradstreet, M.S.W., Butcher, G.S., Demarest, D.W., Dunn, E.H., Hunter, W.C., Iñigo-Elias, E.E., Kennedy, J.A., Martell, A.M., Panjabi, A.O., Pashley, D.N., Rosenberg, K.V., Rustay, C.M., Wendt, J.S. & Will, T.C. (2004). Partners in Flight North American landbird conservation plan. Cornell Lab of Ornithology, Ithaca, NY.

Ricklefs, R.E. (1996). The Economy of Nature. *Freeman and Company,* NY, USA.

Ricklefs, R.E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, 7, 1–15.

Rosenberg, K.V. (2003). Partners in Flight Bird conservation plan: The mid-Atlantic ridge and valley (physiographic area 12). American Bird Conservancy. <http://www.blm.gov/wildlife/pl_12sum.htm>. Accessed 10 Dec 2009.

Royle, J.A. & Dorazio, R.M. (2008). Hierarchical modeling and inference in Ecology. *Academic Press*, MA, USA.

Royle, J.A., Dawson, D. K. & Bates, S., (2004). Modeling abundance effects in distance sampling. *Ecology*, 85, 1591–1597.

Royle, J.A., Dorazio, R.M. & Link, W.A. (2007). Analysis of multinomial models with unknown index using data augmentation. *Journal of Computational and Graphical Statistics*, 16, 67–85.

Royle, JA. & Nichols, J.D. (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology*, 84, 777-790.

Rubolini, D., Saino, N. & Moller, A.P. (2010). Migratory behaviour constrains the phenological response of birds to climate change. *Climate Research*, 42, 45-55.

Russell, R.E., Royle, J.A., Saab, V.A., Lehmkuhl, J.F., Block, W.M. & Sauer, J.R. (2009). Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. *Ecological Applications*, 19, 1253-1263.

Saino, N., Ambrosini, R. & Rubolini, D. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B-Biological Sciences*, 278, 835-842.

Samu, F., Csontos, P. & Szinetar, C. (2008). From multi-criteria approach to simple protocol: Assessing habitat patches for conservation value using species rarity. *Biological Conservation*, 141, 1310-1320.

Sandvik, H. & Erikstad, K.E. (2008). Seabird life histories and climatic fluctuations: a phylogenetic-comparative time series analysis of North Atlantic seabirds. *Ecography*, 31, 73-83.

Sandvik, H., Erikstad, K.E., Barrett, R.T. & Yoccoz, N.G. (2005). The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology*, 74, 817–831.

Sauer, J.R. & Link, W.A. (2002). Hierarchical modeling of population stability and species group attributes from survey data. *Ecology*, 86, 1743-1751.

Sea Duck Joint Venture (2003). Species Status Report. http://www.seaduckjv.org/meetseaduck/species_status_summary.pdf.

Sergio, F., Newton, I., Marchesi, L. & Pedrini, P. (2006). Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology*, 43, 1049-1055.

Sing, T., Sander, O., Beerenwinkel, N. & Lengauer, T. (2005). ROCR: visualizing classifier performance in R. *Bioinformatics*, 21, 3940-3941.

Singer, M.C. & Parmesan, C. (2010). Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365, 3161-3176.

Smith, C.R. DeGloria, S.D., Richmond, M.E., Gregory, S.K., Laba, M.K., Smith, S.D., Braden, J.L., Fegraus, E.H., Fiore J.J., Hill E.A., Ogurcak D.E. & Weber J.T. (2001). The New York Gap Analysis Project. New York Cooperative Fish and Wildlife Research Unit, Cornell University, Ithaca, NY.

Smith, M.A. & Green, D.M. (2005). Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography*, 28, 110-128.

Soares, C. & Brito, J.C. (2007). Environmental correlates for species richness among amphibians and reptiles in a climate transition area. *Biodiversity Conservation*, 16, 1087-1102.

Spiegelhalter, D.J., Thomas, A., Best, N.G. & Lunn, D. (2003). WinBUGS Version 1.4 User Manual. MRC Biostatistics Unit, Cambridge, UK.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S. & Lima, M. (2002). Ecological effects of climate fluctuations. *Science*, 297, 1292-1296.

Stenseth, N.C., & Mysterud, A. (2005). Weather packages: finding the right scale and composition of climate in ecology. *Journal of Animal Ecology*, 74, 1195–1198.

Stevens, S.R. & Frey, D.F. (2010). Host plant pattern and variation in climate predict the location of natal grounds for migratory monarch butterflies in western North America. *Journal of Insect Conservation*, 14, 731-744.

Stockwell, D.R.B. & Peterson, A.T. (2002). Effects of sample size on accuracy of species distribution models. *Ecological Modeling*, 148, 1-13.

Stott, R.S. & Olson, D.P. (1973). Food-habitat relationship of sea ducks on the New Hampshire coastline. *Ecology*, 54, 996-1007.

Sturtz, S., Ligges, U. & Gelman, A. (2005). R2WinBUGS: A Package for Running WinBUGS from R. *Journal of Statistical Software*, 12,1-16.

Suarez-Rubio, M. & Thomlinson J.R., (2009). Landscape and patch-level factors influence bird communities in an urbanized tropical island. *Biological Conservation*, 142, 1311–1321.

Suski, C.D. & Ridgway, M.S. (2007). Climate and body size influence nest survival in a fish with parental care. *Journal of Animal Ecology* 76: 730–739.

Swengel, A.B. (1995). Population fluctuations of the monarch (*Danaus plexippus*) in the 4th of July butterfly count 1977-1994. *American Midland Naturalist*, 134, 205-214.

The Heinz Center. (2002) The state of our nation’s ecosystems. Island Press, Washington, DC, USA.

Thomas, C.D. & Lennon, J.J. (1999). Birds extend their ranges northwards. *Nature*, 399, 213.

Thompson, P. & Ollason, J. (2001). Lagged effects of ocean climate change on fulmar population dynamics. *Nature*, 413, 417-420.

Thompson, P.M. & Grosbois, V. (2002). Effects of Climate Variation on Seabird Population Dynamics. *Directions in Science*, 1, 50-52.

Thompson, W.L. (Ed). (2004). Sampling rare or elusive species: Concepts, Designs, and techniques for estimating population parameters. Island Press, Washington, DC, USA.

Tikkanen, O.P., Heinonen, T., Kouki, J. & Matero, J., (2007). Habitat suitability models of saproxylic red-listed boreal forest species in long-term matrix management: Cost-effective measures for multi-species conservation. *Biological Conservation*, 140, 359-372.

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K. & Possingham, H. P. (2003). Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications*, 13, 1790-1801.

Vellend, M., Lilley, P.L. & Starzomski, B.M. (2008). Using subsets of species in biodiversity surveys. *Journal of Applied Ecology*, 45, 161-169.

Vesely, D., McComb, B.C., Vojta, C.D., Suring, L.H., Halaj, J., Holthausen, R.S., Zuckerberg, B. & Manley, P.M. (2006). Development of protocols to inventory or monitor wildlife, fish, or rare plants. Gen. Tech. Rep. WO-72. U.S. Department of Agriculture, Forest Service, Washington, DC.

Visser, M.E. & Both, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B-Biological Sciences*, 272, 2561-2569.

Wake, D.B. & Vrendenburg, V.T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences*, 105, 11466-11473.

Walls, S.C., Waddle, J.H. & Dorazio, R.M. (2011). Estimating occupancy dynamics in an anuran assemblage from Louisiana, USA. *Journal of Wildlife Management*, 75, 751–761.

Wang, Y.P., Siefferman, L., Wang, Y.J., Ding, T.S., Chiou, C.R., Shieh, B.S., Hsu, F.S. & Yuan, H.W. (2009). Nest site restoration increases the breeding density of blue-tailed bee-eaters. *Biological Conservation*, 142, 1748–1753.

Warren, M.S., Hill, J.K. & Thomas, J.A. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414, 65-69.

Wassenaar, L.I. & Hobson, K.A. (1998). Natal origins of migratory monarch butterflies at wintering colonies in Mexico: New isotopic evidence. *Proceedings of the National Academy of Sciences*, 95, 15436-15439.

Weatherhead, P.J. (2005). Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds. *Oecologia*, 144, 168-175.

Weir, L.A., Royle, J.A., Nanjappa, P. & Jung, R.E. (2005). Modeling anuran site occupancy and detection probability on North American Amphibian Monitoring Program (NAAMP) routes in Maryland. *Journal of Herpetology*, 39, 627-639.

Wenger, S.J. & Freeman, M.C. (2008). Estimating species occurrence, abundance, and detection probability using zero-inflated distributions. *Ecology* 89, 2953-2959.

Werner, E.K., Yurewicz, D., Skelly, R. & Relyea, R. (2007). Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos*, 116, 1713-1725.

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

Wilcove, D.S. & Wikelski, M. (2008). Going, going, gone: is animal migration disappearing? *PLOS Biology*, 6, 1361-1364.

Wilhere, G.F., Goering, M. & Wang H. (2008). Average optimacity: An index to guide sate prioritization for biodiversity conservation. *Biological Conservation*, 141, 770-781.

Williams, B., Nichols, J. & Conroy, M. (2002). Analysis and Management of Animal Populations: Modeling, Estimation and Decision Making. Academic Press, San Diego, CA, USA.

Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humphries, C. & Pressey, R. (1996). A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology*, 10, 155-174.

Wilson, D.E., Cole, F.R., Nichols, J.D., Rudran, R. & Foster S. (1996). Measuring and monitoring biological diversity: standard methods for mammals. Smithsonian, Washington DC.

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

York, H.A. & Oberhauser, K.S. (2002). Effects of duration and timing of heat stress on monarch butterfly (*Danaus plexippus*) (Lepidoptera: Nymphalidae) development. *Journal of the Kansas Entomological Society*, 75, 290-298.

Zalucki, M.P. (1982). Temperature and rate of development in *Danaus plexippus* L. and D. chrysippus L. *Autralian Entomological Society*, 21, 241-246.

Zalucki, M.P. & Clarke, A. (2004). Monarchs across the Pacific: the Columbus hypothesis revisited. *Biological Jounral of the Linnean Society*, 82, 111-121.

Zalucki, M.P. & Rochester, W.A. (2004). Spatial and temporal populations dynamics of monarchs down-under: lessons for North America. In: The monarch butterfly: biology and conservation, Oberhauser KS, Solensky MJ (Eds.) pp. 219-228.

Zipkin, E.F., Gardner, B., Gilbert, A.T., O’Connell, A., Royle, J.A. & Silverman, E.D. (2010). Distribution patterns of wintering sea ducks in relation to the North Atlantic Oscillation and local environmental characteristics. *Oecologia*, 163, 893-902.

Zipkin, E.F., Royle, J.A., Dawson, D.K. & Bates, S. (2010). Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation*, 143, 479-484.

Zipkin, E.F., DeWan, A. & Royle, J.A. (2009). Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *Journal of Applied Ecology*, 46, 815-822.