

Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection

ELISE F. ZIPKIN,^{1,2,3} EVAN H. CAMPBELL GRANT,¹ AND WILLIAM F. FAGAN²

¹*USGS Patuxent Wildlife Research Center, 12100 Beech Forest Rd., Laurel, Maryland 20708 USA*

²*Department of Biology, University of Maryland, College Park, Maryland 20742 USA*

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 multispecies 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 occupancy) were most important for predicting future habitat use. We used the models to make predictions about 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 explicitly quantify the uncertainty in the quality of our predictions and to account for false negatives in the evaluation data set. 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 habitat-only covariates predicted species occurrences well; 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 multispecies models for understanding which factors affect species habitat use of an entire community (of species) and provide an improved methodology using AUC that is helpful for quantifying the uncertainty in model predictions while explicitly accounting for detection biases.

Key words: amphibians; area under the curve; Bayesian analysis; detection bias; hierarchical model; multispecies models; occupancy; receiver operating characteristic curve; uncertainty.

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 (Manley et al. 2004, DeWan et al. 2009). 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 (Williams et al. 2002, Guisan and Thuiller 2005). Multispecies 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 to assess trade-offs in the expected occurrences of species associated with different management actions

(Suarez-Rubio and Thomlinson 2009). Moreover, models that are designed to assist with management must provide clear insight into the accuracy, reliability, and inherent uncertainty of their predictions. 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 curve (e.g., Elith et al. 2006, Phillips et al. 2006, Anderson and Raza 2010, Kharouba and Kerr 2010, Rebelo and Jones 2010). Although Akaike information criterion (AIC) is a popular model selection procedure 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 vs. the predicted outcome,

Manuscript received 26 October 2011; revised 24 January 2012; accepted 3 May 2012. Corresponding Editor: S. P. Faulkner.

³ E-mail: ezipkin@usgs.gov

which sums the number of locations that both correctly and incorrectly identify 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. To construct the ROC curve, one 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 $1 - \text{specificity}$ (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 curve (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 increasingly popular (Hirzel et al. 2006, Phillips et al. 2006, Peterson et al. 2007). 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). Although 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 constructed or evaluated with biased estimators and erroneous 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 amphibians that (1) explicitly characterizes the uncertainty in the predictive success of model predictions 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 broadscale 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. 2009). As such, amphibians are ideal for exploring the utility of multispecies 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 probably differ among regions and populations (Cushman 2006, Wake and Vrendenburg 2008). Accordingly, resource managers at the Chesapeake and Ohio Canal National Historical Park (CHOH) in Maryland, USA, recognized that increasing urbanization in the surrounding region, combined with regional predictions of future climate change, may decrease the suitability of wetland breeding habitats within the park that are necessary for population persistence.

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 predicting probabilities of species occupancy in unsampled wetlands and in future years. Here, we evaluate the ability of multispecies 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 data 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 obtain 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 during 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 \times 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* (northern green frog; total of 441 observations at 31 different wetlands), *Ambystoma maculatum* (spotted salamander; 347, 24), *Lithobates sylvaticus* (wood frog; 227, 23), *Lithobates catesbeianus* (American bullfrog; 149, 25), *Anaxyrus americanus/fowleri* (American/Fowler’s toad; 146, 24), *Lithobates palustris* (pickerel frog; 134, 15), *Pseudacris crucifer* (spring peeper; 125, 21), *Notopthalmus viridescens* (red-spotted newt; 111, 8), *Lithobates sphenoccephalus* (southern leopard frog; 100, 17), *Hyla versicolor/chrysocelis* (gray treefrog complex; 53, 17), *Ambystoma opacum* (marbled salamander; 41, 8), and *Hemidactylum scutatum* (four-toed salamander; 11, 3). We analyzed two species complexes (*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

$$\text{conn}_i = \ln \left(\sum_{j \neq i} \exp(-\theta d_{ij}) \text{area}_j \right)$$

where $1/\theta$ 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 750 m 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 multispecies hierarchical modeling framework (Dorazio and Royle 2005, Gelfand et al. 2005, Dorazio et al. 2006), 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 is drawn from a common distribution (for more details also see 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/nondetection records of all 12 species/species complexes across all life stages. The observations, $x_{i,j,t,k}$, denote detection ($x = 1$) or nondetection ($x = 0$) 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, $z_{i,j,t} \sim \text{Bern}(\Psi_{i,j,t})$ 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: $x_{i,j,t,k} \sim \text{Bern}(p_{i,j,t,k} z_{i,j,t})$, 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 nondetection 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) an autologistic model that accounts for the effects of hydroperiod on species colonization and persistence that also includes wetland area and connec-

tivity. For the first three versions, we modeled $\Psi_{i,j,t}$ for each species i using the logit link function:

$$\text{logit}(\Psi_{i,j,t}) = \alpha 1_{i,\text{hydro}_j} + \alpha 2_{i,\text{area}_j} + \alpha 3_{i,\text{conn}_j} + \alpha 4_i \text{trend}_t + \alpha 5_i \text{precip}_t$$

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 parameter $\alpha 4_i$ is an annual trend (standardized so that year 2007 is zero), and $\alpha 5_i$ is the effect of precipitation (standardized to have a mean of zero and standard deviation of one). The parameters $\alpha 4_i$ and $\alpha 5_i$ are included in only one version of the model (e.g., the second and third versions, respectively). For the fourth version, the autologistic model, we estimated $\Psi_{i,j,t}$ such that the intercept term was dependent both on the wetland hydroperiod and on whether or not the species was present in the previous year:

$$\text{logit}(\Psi_{i,j,t}) = \alpha 1_{i,\text{hydro}_j, z_{i,j,t-1}} + \alpha 2_{i,\text{area}_j} + \alpha 3_{i,\text{conn}_j}$$

Thus the autologistic model allows us to specifically examine the colonization (when $z_{i,j,t-1} = 0$) and persistence (when $z_{i,j,t-1} = 1$) probabilities for each species in relation to wetland hydroperiod (similar to the dynamic occupancy models described in Kéry et al. 2009, Dorazio et al. 2010, Ruiz Gutierrez et al. 2010). In fitting the autologistic model based on latent species occurrences (the elements of the \mathbf{z} matrix), our model accounts for imperfect detection rather than simply using observed species occurrences, which likely contain false negative errors.

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 2009). We note that in specifying the model this way, we effectively averaged over both any existing observer effects and temporal variation in detection probability. 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 because 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), although they may be used for foraging or breeding by others. Although 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*, *Hemidactylum scutatum*, *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 (Whitehead and Jones 1969, Haddad and Baum 1999, Armstrong 2005). 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 uncertainty 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 predictions using AUC and accounting for imperfect detection

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 esti-

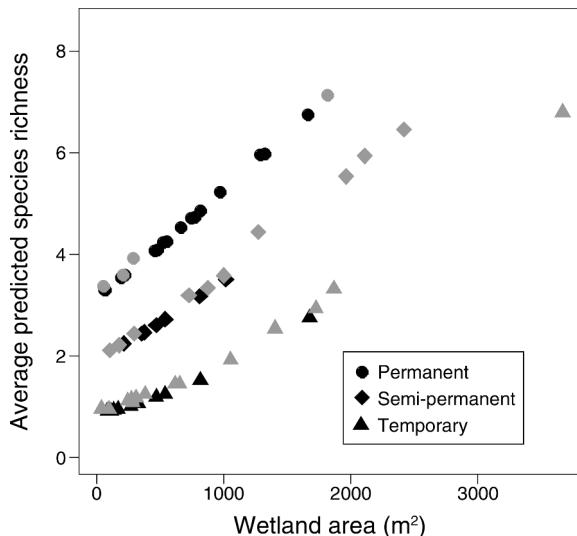


FIG. 1. Average predicted wetland richness (number of species, estimated using the habitat-only model with data from 2005–2009) for each of the 63 wetlands, by type, plotted against wetland area. The gray symbols are wetlands with below-average connectivity.

mates for both (1) the 33 sites that had previously been sampled and (2) the 30 new sites that were sampled only in 2010. For the autologistic model, we used the latent occupancy states generated by WinBUGS for each species at each wetland (sampled and unsampled) in 2009 (observation data for the 30 newly sampled wetlands were entered as NA for 2005–2009, allowing WinBUGS to estimate those missing values based on covariate information). 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 discriminatory ability 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 multispecies modeling approach allowed us to use all of the available data and estimate the occurrence probabilities and covariate effects for each of the 12 species and species complexes. For all species, hydroperiod was the most significant wetland covariate affecting occurrence probabilities (Fig. 1). This result was fairly consistent across all models (see Tables 1 and 2 for species-specific covariate estimates for the habitat-only and autologistic models). Occurrence probabilities for all species were generally lowest in temporary wetlands and highest in permanent wetlands (Table 1). In the autologistic model, which allowed us to examine colonization and persistence probabilities, mean species-specific colonization ranges were 0.01–0.09 in temporary, 0.02–0.29 in semi-permanent, and 0.03–0.31 in permanent wetlands, whereas persistence ranges were 0.10–0.44 in temporary, 0.11–0.66 in semi-permanent, and 0.19–0.84 in permanent wetlands (when other covariates were at their average values). This suggests that persistence was generally higher than colonization in all wetland types and that colonization probabilities increased with hydroperiod (Table 2). Area had a significant positive effect on the occupancy probabilities of almost all species in the habitat-only, precipitation, and trend models (except for *Hemidactylum scutatum*, possibly because of its small sample size). In the autologistic model, area had a significant positive effect on all but five species and species complexes (*Ambystoma maculatum*, *Ambystoma opacum*, *Hemidactylum scutatum*, *Hyla versicolor/chrysoceles*, and *Notophthalmus viridescens*). Connectivity was not significant for any of the species except for *Lithobates sylvaticus*, which surprisingly showed a negative effect (Table 1).

The observed number of species per wetland was lower in 2010 compared to the average number of observed species per wetland in 2005–2009 (Fig. 2a). Thus, predicted wetland richness was generally overestimated in 2010 using the habitat-only model (Fig. 2b) and, to a lesser extent, with the autologistic model (Fig. 2c). 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

TABLE 1. Parameter estimates from habitat-only models: occupancy probabilities for each species in temporary (Temp), semi-permanent (Semi), and permanent (Perm) wetlands, as well as the effects of area and connectivity.

Species	Occupancy probability									
	Temp		Semi		Perm		Area (logit scale)		Connectivity (logit scale)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Ambystoma maculatum</i>	0.20	0.05	0.19	0.05	0.51	0.06	0.45	0.19	-0.06	0.19
<i>Ambystoma opacum</i>	0.03	0.02	0.05	0.02	0.11	0.04	0.59	0.23	-0.02	0.29
<i>Anaxyrus americanus/fowleri</i>	0.15	0.05	0.52	0.09	0.44	0.08	0.54	0.22	0.26	0.21
<i>Hemidactylum scutatum</i>	0.02	0.01	0.02	0.02	0.07	0.03	0.45	0.29	0.02	0.33
<i>Hyla versicolor/chrysoceles</i>	0.10	0.04	0.21	0.07	0.42	0.09	0.54	0.23	-0.14	0.23
<i>Notophthalmus viridescens</i>	0.05	0.02	0.06	0.03	0.29	0.06	0.57	0.22	0.42	0.29
<i>Pseudacris crucifer</i>	0.11	0.03	0.23	0.06	0.38	0.07	0.60	0.20	-0.32	0.22
<i>Lithobates catesbeianus</i>	0.17	0.05	0.50	0.08	0.53	0.08	0.73	0.22	0.31	0.21
<i>Lithobates clamitans</i>	0.31	0.07	0.51	0.07	0.72	0.06	0.67	0.20	-0.05	0.19
<i>Lithobates palustris</i>	0.08	0.03	0.25	0.06	0.43	0.07	0.86	0.22	-0.20	0.21
<i>Lithobates sphenoccephalus</i>	0.08	0.03	0.21	0.06	0.38	0.07	0.56	0.21	-0.08	0.22
<i>Lithobates sylvaticus</i>	0.13	0.04	0.31	0.06	0.40	0.07	0.94	0.21	-0.51	0.21

Note: For area and connectivity, boldface values indicate a significant effect (i.e., the 95% posterior interval did not overlap with zero).

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 occurrence probabilities in the following year, with higher probabilities of persistence, compared to colonization, in all wetland types (temporary, semi-permanent, and permanent). The differences between colonization and persistence probabilities were generally larger than the differences in occupancy among hydroperiod types (Table 2), suggesting that knowing a species occupancy status at a given wetland is

a better indicator of future occurrence than even wetland hydroperiod.

Evaluating model predictions

The AUC was virtually identical in the habitat-only, trend, and precipitation models. 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) and autologistic (AUC: mean 0.73; 95% PI 0.68–0.77) 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

TABLE 2. Parameter estimates from autologistic models: occupancy probabilities for each species in temporary (Temp), semi-permanent (Semi), and permanent (Perm) wetlands, as well as the effects of area and connectivity; values are means with SD in parentheses.

Species	Colonization probability			Persistence probability			Area (logit scale)	Connectivity (logit scale)
	Temp	Semi	Perm	Temp	Semi	Perm		
<i>Ambystoma maculatum</i>	0.03 (0.02)	0.06 (0.03)	0.08 (0.04)	0.42 (0.08)	0.49 (0.10)	0.78 (0.06)	0.39 (0.21)	0.00 (0.20)
<i>Ambystoma opacum</i>	0.02 (0.01)	0.04 (0.03)	0.03 (0.02)	0.10 (0.05)	0.13 (0.07)	0.27 (0.10)	0.42 (0.23)	-0.01 (0.26)
<i>Anaxyrus americanus/fowleri</i>	0.09 (0.04)	0.29 (0.12)	0.31 (0.10)	0.25 (0.08)	0.60 (0.11)	0.51 (0.10)	0.45 (0.21)	0.26 (0.21)
<i>Hemidactylum scutatum</i>	0.01 (0.01)	0.02 (0.02)	0.03 (0.02)	0.10 (0.05)	0.11 (0.07)	0.19 (0.10)	0.34 (0.28)	0.05 (0.28)
<i>Hyla versicolor/chrysoceles</i>	0.07 (0.04)	0.17 (0.08)	0.29 (0.13)	0.17 (0.07)	0.32 (0.12)	0.50 (0.13)	0.45 (0.22)	-0.10 (0.22)
<i>Notophthalmus viridescens</i>	0.01 (0.01)	0.03 (0.02)	0.03 (0.03)	0.17 (0.06)	0.20 (0.09)	0.59 (0.10)	0.42 (0.24)	0.34 (0.29)
<i>Pseudacris crucifer</i>	0.05 (0.03)	0.13 (0.06)	0.26 (0.09)	0.20 (0.07)	0.39 (0.10)	0.46 (0.10)	0.54 (0.20)	-0.22 (0.21)
<i>Lithobates catesbeianus</i>	0.05 (0.03)	0.16 (0.08)	0.19 (0.10)	0.36 (0.09)	0.66 (0.09)	0.68 (0.09)	0.53 (0.22)	0.24 (0.21)
<i>Lithobates clamitans</i>	0.09 (0.04)	0.27 (0.09)	0.18 (0.09)	0.44 (0.09)	0.62 (0.08)	0.84 (0.05)	0.58 (0.20)	0.00 (0.18)
<i>Lithobates palustris</i>	0.02 (0.01)	0.06 (0.04)	0.07 (0.05)	0.23 (0.08)	0.50 (0.11)	0.66 (0.09)	0.72 (0.23)	-0.10 (0.22)
<i>Lithobates sphenoccephalus</i>	0.04 (0.02)	0.15 (0.06)	0.22 (0.08)	0.20 (0.07)	0.34 (0.10)	0.54 (0.10)	0.50 (0.20)	-0.08 (0.21)
<i>Lithobates sylvaticus</i>	0.03 (0.02)	0.10 (0.05)	0.12 (0.06)	0.34 (0.08)	0.57 (0.10)	0.65 (0.08)	0.78 (0.22)	-0.31 (0.22)

Note: For area and connectivity, boldface values indicate a significant effect (i.e., the 95% posterior interval did not overlap with zero).

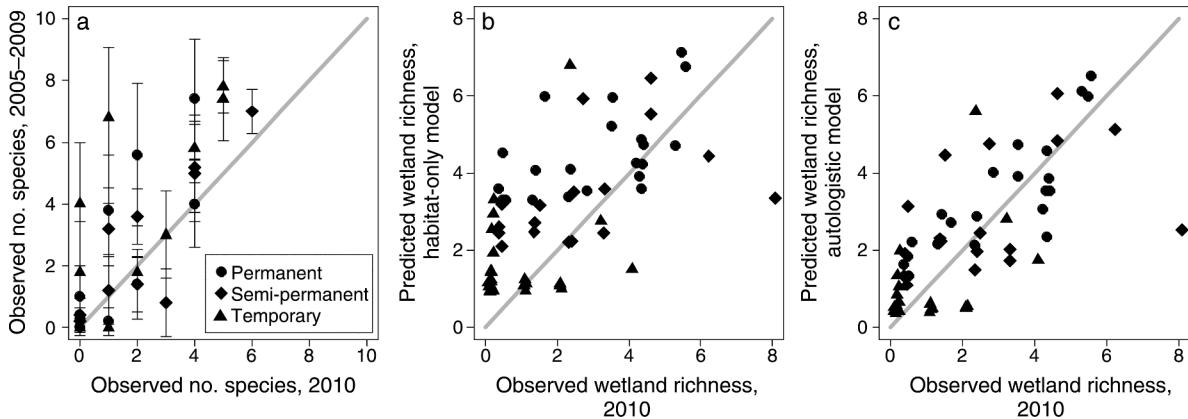


FIG. 2. Observed and predicted species richness for different years and models. In all panels the gray line is the one-to-one line, circles represent permanent wetlands, diamonds are semi-permanent wetlands, and triangles are temporary wetlands. (a) Observed number of species in 2010 plotted against the average number of observed species in 2005–2009 for the 33 wetlands that were sampled continuously over the duration of the study. (b) Species richness (accounting for detection errors) in 2010 for all 63 wetlands plotted against predicted wetland species richness as estimated using the habitat model for the 2005–2009 data. (c) Species richness (accounting for detection errors) in 2010 for all 63 wetlands plotted against predicted wetland species richness as estimated using the autologistic model for the 2005–2009 data.

sampled from 2005–2009 (AUC: mean 0.79; 95% PI: 0.76–0.83) 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 performed poorly in predicting occupancy in unsampled wetlands (AUC: mean 0.68; 95% PI: 0.61–0.74) compared to wetlands that had been sampled, but was not significantly worse than the habitat-only model in the newly sampled wetlands.

To examine 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 data sets generated using the model results. As an illustration, we used the habitat-only model to simulate ten data sets 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 data set (10 replicate trials). We calculated the AUC values using these new covariate estimates and a similar data set 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 10 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 > 0.6 for all species, except in some instances for *Ambystoma opacum*, *Lithobates sylvaticus*, and *Hemidactylum scutatum*; Table 3), with nine species having overall mean AUC values > 0.7 in one or both of the habitat-only and autologistic models. Although 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 *Notophthalmus viridescens*.

DISCUSSION

Value of AUC in evaluating model predictions and quantifying uncertainty in discrimination

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, Peterson et al. 2008). Although 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 and Jones 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). This can lead to erroneous inferences on which models are best able to predict true species distributions, confounding the selection of optimal conservation and management strategies (Ruiz Gutierrez and Zipkin 2011). 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

TABLE 3. Species-specific AUC values (mean of the posterior distributions and 95% posterior intervals) for the habitat-only and autologistic models for 33 wetlands sampled continuously in 2005–2009 and for 30 wetlands unsampled in 2005–2009.

Species	Habitat-only model						Autologistic model					
	Sampled wetlands			Unsampled wetlands			Sampled wetlands			Unsampled wetlands		
	Mean	Low	High									
<i>Ambystoma maculatum</i>	0.60	0.54	0.65	0.64	0.48	0.78	0.89	0.86	0.93	0.70	0.48	0.84
<i>Ambystoma opacum</i>	0.75	0.43	0.91	0.41	0.31	0.56	0.57	0.16	0.88	0.46	0.33	0.62
<i>Anaxyrus americanus/fowleri</i>	0.82	0.66	0.92	0.77	0.54	0.91	0.78	0.62	0.91	0.75	0.51	0.93
<i>Hemidactylum scutatum</i>	NA	NA	NA	0.51	0.10	0.88	NA	NA	NA	0.64	0.21	0.94
<i>Hyla versicolor/chrysoceles</i>	0.64	0.46	0.80	0.77	0.54	0.91	0.65	0.42	0.87	0.76	0.52	0.94
<i>Notophthalmus viridescens</i>	0.74	0.64	0.79	0.80	0.73	0.88	0.97	0.84	0.99	0.69	0.21	0.91
<i>Pseudacris crucifer</i>	0.68	0.57	0.78	0.82	0.68	0.92	0.77	0.63	0.87	0.82	0.68	0.92
<i>Lithobates catesbeianus</i>	0.78	0.59	0.92	0.82	0.63	0.93	0.79	0.59	0.96	0.78	0.58	0.94
<i>Lithobates clamitans</i>	0.71	0.61	0.79	0.86	0.77	0.92	0.81	0.71	0.89	0.80	0.61	0.93
<i>Lithobates palustris</i>	0.84	0.72	0.90	0.64	0.56	0.74	0.83	0.68	0.91	0.60	0.44	0.76
<i>Lithobates sphenoccephalus</i>	0.79	0.64	0.90	0.79	0.54	0.94	0.83	0.69	0.92	0.79	0.55	0.96
<i>Lithobates sylvaticus</i>	0.41	0.32	0.52	0.63	0.57	0.70	0.51	0.44	0.60	0.61	0.52	0.72

Note: NA means not available.

was truly present, but overlooked during sampling, leading to a more inclusive picture of the variability and transient use of habitat that is 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.

It has been noted before that the AUC depends on prevalence and that the maximum achievable AUC may be less than 1.0 as a result of low prevalence (Lobo et al. 2007, Liu et al. 2011, Jiménez-Valverde 2012). We discovered that the AUC ceiling for our models was less than 1.0. By this we mean that if the actual data-generating model is known and the AUC is computed, then the expected AUC value would still be less than 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 the model with an AUC value that is closest to its particular ceiling (for predictive purposes). There is no generally accepted approach for model selection in 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, Phillips 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 autologistic models (Appendix: Tables A1 and A2). Comparison of these results shows that the two models are comparable, except that the autologistic model is somewhat better at estimating the true negative rate at the community level. 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 recommend calculating these quantities when interest lies in knowing the relative contributions of omission and commission errors (Jiménez-Valverde 2012).

Management implications for CHOH

In establishing the utility of our multispecies 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 both for 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. Although 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 (Table 3). In wetlands where previous amphibian use is unknown, the results demonstrate that our approach to using the autologistic model is no more informative than simply using the habitat-only model. This is, of course, an intuitive result; nonetheless, it highlights that in extrapolating results to the hundreds of unsampled wetlands, the simplest model works best in this scenario.

The habitat and autologistic models had fairly high predictive abilities for most species (Table 3). In some instances (e.g., *Lithobates sylvaticus* in the previously sampled locations and *Ambystoma opacum* in the wetlands that had not been previously sampled), 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, toward the community mean). It is also possible 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 are 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 (Manley et al. 2004, Weir et al. 2005, DeWan and Zipkin 2010), 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 (Fig. 2b). The autologistic model was better at predicting richness for wetlands that had been previously sampled, but it was unable to improve estimates in unsampled wetlands (an entirely expected result; see Fig. 2b). The breeding season in 2010 had lower cumulative precipitation (9.32 inches [23.67 cm]) in CHOH compared to any of the other years of the survey (mean, 45.44 cm; range, 26.64–58.88 cm), which could help to explain why the observed number of species was lower in 2010 compared to previous years (Fig. 2a), 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

Based on the AUC results from our models, we believe that managers could use the habitat-only model 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. All amphibian species had higher occurrence probabilities at semi-permanent or permanent than at temporary wetlands (Tables 1 and 2). 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, our habitat-only model 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 to 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). However, it is important to first assess whether model predictions are reliable. Our approach for evaluating the predictive power of multispecies 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 requires a clear understanding of species–habitat relationships and the potential trade-offs associated with alternative management actions.

ACKNOWLEDGMENTS

We thank Andy Royle, Marc Kéry, Bob Dorazio, and an anonymous reviewer for many useful suggestions that greatly improved the final product. We also thank several people at the National Park Service including Scott Bell (CHOH), Shawn Carter, Patrick Campbell, Geoff Sanders, J. P. Schmit (Inventory and Monitoring program), and Paul Geisler, as well as the National Park Monitoring Program for funding this project. Larissa Bailey, Adrienne Brand, Eric Dallalio, and a slew of technicians collected the data and provided invaluable technical support. This is contribution number 397 of the U.S. Geological Survey Amphibian Research and Monitoring Initiative (ARMI). Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The manuscript has Bureau Approval (17Nov11).

LITERATURE CITED

- Anderson, R. P., and A. Raza. 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.
- Cowardin, L., V. Carte, F. Golet, and E. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.
- Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* 128:231–240.
- DeWan, A. A., P. J. Sullivan, A. J. Lembo, C. R. Smith, J. C. Maerz, J. P. Lassoie, and M. E. Richmond. 2009. Using occupancy models of forest breeding birds to prioritize conservation planning. *Biological Conservation* 142:982–991.
- DeWan, A., and E. F. Zipkin. 2010. An integrated sampling and analysis approach for improved biodiversity monitoring. *Environmental Management* 45:1223–1230.
- Dorazio, R. M., M. Kéry, J. A. Royle, and M. Plattner. 2010. Models for inference in dynamic metacommunity systems. *Ecology* 91:2466–2475.
- Dorazio, R. M., and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association* 100:389–398.
- Dorazio, R. M., J. A. Royle, B. Söderström, and A. Glimskär. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842–854.
- Elith, J., et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Gelfand, A. E., and S. K. Ghosh. 1998. Model choice: a minimum posterior predictive loss approach. *Biometrika* 85:1–11.
- Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York, New York, USA.
- Gelfand, A. E., A. M. Schmidt, S. Wu, J. A. Silander, A. Latimer, and A. G. Rebelo. 2005. Explaining species diversity through species-level hierarchical modeling. *Applied Statistics* 65:1–20.
- Green, D. M. 2003. The ecology of extinction: population fluctuation and decline in amphibians. *Biological Conservation* 111:331–343.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Haddad, N. M., and K. A. Baum. 1999. An experimental test of corridor effects on butterfly densities. *Ecological Applications* 9:623–633.
- Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199:142–152.
- Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. Wiley, New York, New York, USA.
- Jiménez-Valverde, A. 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography* 21:498–507.
- Kéry, M., and J. A. Royle. 2008. Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology* 45:589–598.
- Kéry, M., and J. A. Royle. 2009. Inference about species richness and community structure using species-specific occupancy models in the National Swiss Breeding Bird Survey MHB. Pages 639–656 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer, New York, New York, USA.
- Kéry, M., J. A. Royle, M. Plattner, and R. M. Dorazio. 2009. Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology* 90:1279–1290.
- Kharouba, H. M., and J. T. Kerr. 2010. Just passing through: Global change and the conservation of biodiversity in protected areas. *Biological Conservation* 143:1094–1101.
- Liu, C., M. White, and G. Newell. 2011. Measuring and comparing the accuracy of species distribution models with presence-absence data. *Ecography* 34:232–243.
- Lobo, J. M., A. Jiménez-Valverde, and R. Real. 2007. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17:145–151.
- Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS—A Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* 10:325–337.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38:921–931.
- Manley, P. N., W. J. Zielinski, M. D. Schlesinger, and S. R. Mori. 2004. Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. *Ecological Applications* 14:296–310.
- Mattfeldt, S. D., L. L. Bailey, and E. H. C. Grant. 2009. Monitoring multiple species: estimating state variables and

- exploring the efficacy of a monitoring program. *Biological Conservation* 142:720–737.
- Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. *Ecology* 83:1131–1145.
- Peterson, A. T., M. Papes, and M. Eaton. 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography* 30:550–560.
- Peterson, A. T., M. Papes, and J. Soberón. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling* 213:63–72.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Rebelo, H., and G. Jones. 2010. Ground validation of presence-only modelling with rare species: a case study on *Barbastella barbastellus* (Chiroptera: Vespertilionidae). *Journal of Applied Ecology* 47:410–420.
- Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology. Academic Press, Amsterdam, The Netherlands.
- Ruiz Gutierrez, V., and E. F. Zipkin. 2011. Detection biases yield misleading patterns of species persistence and colonization in fragmented landscapes. *Ecosphere* 2:art61.
- Ruiz Gutierrez, V., E. F. Zipkin, and A. A. Dhondt. 2010. Occupancy dynamics in a tropical bird community: unexpectedly high forest use by birds classified as non-forest species. *Journal of Applied Ecology* 47:621–630.
- Russell, R. E., J. A. Royle, V. A. Saab, J. F. Lehmkuhl, W. M. Block, and J. R. Sauer. 2009. Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. *Ecological Applications* 19:1253–1263.
- Sing, T., O. Sander, N. Beerenwinkel, and T. Lengauer. 2005. ROCr: visualizing classifier performance in R. *Bioinformatics* 21:3940–3941.
- Smith, M. A., and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* 28:110–128.
- Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: A package for running WinBUGS from R. *Journal of Statistical Software* 12:1–16.
- Suarez-Rubio, M., and J. R. Thomlinson. 2009. Landscape and patch-level factors influence bird communities in an urbanized tropical island. *Biological Conservation* 142:1311–1321.
- Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications* 13:1790–1801.
- Wake, D. B., and V. T. Vrendenburg. 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 USA* 105:11466–11473.
- Walls, S. C., J. H. Waddle, and R. M. Dorazio. 2011. Estimating occupancy dynamics in an anuran assemblage from Louisiana, USA. *Journal of Wildlife Management* 75:751–761.
- Weir, L. A., J. A. Royle, P. Nanjappa, and R. E. Jung. 2005. Modeling anuran site occupancy and detection probability on North American Amphibian Monitoring Program (NAAMP) routes in Maryland. *Journal of Herpetology* 39:627–639.
- Werner, E., K. Yurewicz, D. Skelly, and R. Relyea. 2007. Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos* 116:1713–1725.
- Whitehead, D. R., and C. E. Jones. 1969. Small islands and the equilibrium theory of insular biogeography. *Evolution* 23:171–179.
- Williams, B., J. D. Nichols, and M. Conroy. 2002. Analysis and management of animal populations: modeling, estimation and decision making. Academic Press, San Diego, California, USA.
- Zipkin, E. F., A. DeWan, and J. A. Royle. 2009. Impacts of forest fragmentation on bird species richness: a hierarchical approach to community modelling. *Journal of Applied Ecology* 46:815–822.
- Zipkin, E. F., J. A. Royle, D. K. Dawson, and S. Bates. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation* 143:479–484.

SUPPLEMENTAL MATERIAL

Appendix

Species- and community-level true positive rate (TPR) and true negative rate (TNR) values for the habitat-only and autologistic models (*Ecological Archives* A022-105-A1).