ECOLOGICAL PATTERNS OF OCCUPANCY AND USE: NEW METHODS FOR ANALYSIS AND APPLICATIONS TO SPECIES AND COMMUNITIES

by

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(Under the Direction of Robert J. Cooper)

ABSTRACT

Explaining patterns of species presence (occupancy) and if that species is present, the proportion of time it spends in an area (use), is typically the first step in understanding how species interact with their environments. I provide the first method (multi-scale occupancy modeling) to simultaneously estimate occupancy and use from detection-nondetection data while accounting for imperfect detection. Simulations with 5 repeated samples at each scale demonstrated that estimates and credible interval coverage are relatively unbiased when the probability of detecting a species at a site given the site is occupied is ≥0.3. Bias could be reduced by increasing the number of repeated samples. Then we apply the newly-developed multi-scale occupancy models to analyze the relationship between snag density, big tree density (>60.96 cm dbh), and acoustic evidence of Ivory-billed Woodpeckers in Arkansas while accounting for the proportion of area surveyed. Density of big trees (AIC weight=0.54) best predicted patch occupancy, percent area surveyed (AIC weight =0.61) best predicted the probability that evidence of Ivory-billed Woodpeckers was available within the patch (use), and density of big trees (AIC weight =0.61) best predicted the probability that evidence was detected given that it was available. The percent patch surveyed likely represented the level of nonrandom sampling within the patch and multi-level occupancy models helped control for that bias. Finally, we analyze the effect of disturbance on occupancy and use by 18 forest birds in northwest Ecuador. Both occupancy and use showed strong threshold responses at 21-40% upper canopy cover with the probability of occupancy increasing from about 0 to 1 and emigration (the probability that a species would stop using the site during the study period) decreasing from about 1 to 0. Patterns of use and occupancy suggest that disturbed habitat in the region (which is primarily abandoned pasture) may only be valuable to forest birds after a specific level of regeneration and during certain times of the season. The novel insights provided throughout this dissertation highlight the value of analyzing both occupancy and use in a variety of ecological contexts.

INDEX WORDS: Multi-scale occupancy, Use, MCMC, Bayesian statistics, Detectability, Ecuador, Bird communities, Tropical ecology, *Campephilus principalis*, Ivory-billed woodpecker, Proportion area surveyed

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INTRODUCTION AND LITERATURE REVIEW

PREFACE

A large portion of ecological research revolves around two fundamental questions: 1) is a species present in an area (occupancy) and 2) if it is present, how often does it use that area (use). Addressing these two questions is typically the first step in understanding how species interact with their environments.

THE ROLE OF DETECTABILITY

If a species were always detected when present, than estimating occupancy and use would be relatively easy. Detecting a species at least once would mean a site is occupied and the number of detections would indicate how often the site is used. Unfortunately, few species are always detected when present and detectability (the probability of detecting a species given presence) can often vary by abiotic and biotic variables of interest (e.g., Wintle et al. 2005, O'Connell et al. 2006). This can produce misleading results about both use and occupancy (Williams et al. 2002, Gu and Swihart 2004).

Methods to account for detectability in detection-nondetection data began to emerge in the 1980s. Geissler and Fuller (1987) were likely the first to propose that repeat surveys to the same sites could be used to estimate detection probabilities. Azuma et al. (1990) took the next step by using a series of independent Bernoulli trials, with the outcome 1 indicating presence and 0 absence, to describe repeated site visits. They demonstrated that an outcome of independent Bernoulli trials across a series of sites could estimate the proportion of sites occupied while accounting for imperfect detection.

In 2002, there were two major developments in occupancy estimation. Nichols and Karanth (2002) suggested the use of closed capture-recapture models with repeated site visits to estimate site occupancy. In this approach the site is treated as an individual and the pattern of detections and nondetections is treated as capture-recapture data. Also in 2002, MacKenzie et. al (2002) contributed a major advance by showing that detection histories treated as independent Bernoulli trials could be directly incorporated into a maximum likelihood estimation model. The methods of MacKenzie et. al and others have now been expanded to include multiple seasons (MacKenzie et al. 2003), false positives (Royle and Link 2006), and multiple species (Dorazio and Royle 2005, Dorazio et al. 2006)

ESTIMATING USE AND OCCUPANCY

Studies of habitat use commonly rely on radiotelemetry (e.g., Michalski et al. 2006, Matson et al. 2007, Rittenhouse and Semlitsch 2007). Unfortunately, it is often challenging and expensive to get a sufficient sample size to detect differences in use between habitats (Murray 2006). Detection-nondetection data tends to be inexpensive and easy to collect; thus, it may be a more efficient way to analyze patterns of use in many species.

To my knowledge, all studies of use relying on detection-nondetection data have focused on species turnover between years (e.g., Doherty et al. 2003, Huste et al. 2006, Huste and Boulinier 2007). Both site occupancy (MacKenzie et al. 2003) and mark-recapture models (Boulinier et al. 1998, Nichols et al. 1998b, a) have been expanded to analyze multiple seasons. Year-to-year patterns of colonization and extinction can be used to make inference about metapopulation processes, population viability, and may be related to overall habitat quality (Boulinier et al. 1998, MacKenzie et al. 2003). Applying these approaches within a single season, however, provides a unique challenge. In a single-season context, these models can only estimate the probability of a species moving in and out of a site and not the probability a site is occupied during that season. Although the probability of occupancy in these models (the probability that a species occupies the site irregardless of whether it uses the site in a given season) may be of lesser interest when each year of a multi-year study is treated as a season, understanding why a site is occupied will likely be fundamental to any investigation within a season.

INTRODUCTION TO MCMC AND BAYESIAN STATISTICS

Bayesian statistics

Dramatic increases in computing power and the development of more user friendly software such as WinBUGS have made Bayesian statistics more accessible to a wide variety of conservation biologists. Although frequentist (i.e., non-Bayesian) statistics still dominate ecological research, Bayesian approaches are becoming increasingly popular when analyzing complex and hierarchical models, making decisions, and incorporating expert opinion (e.g., Sauer and Link 2002, Martin et al. 2005, Wintle and Bardos 2006).

The fundamental difference between Bayesian statistics and the more traditional frequentist statistics is how they view parameters to be estimated (Gelman et al. 2003). Frequentist statistics supposes that parameters are fixed and that given enough data they could be known without error (Link et al. 2002, Gelman et al. 2003). They essentially rely on what could have happened given an infinite sample size and not what actually happened given the data.

This can lead to confusing interpretations of the summary statistics from frequentist analysis. For example, a 95% confidence interval in frequentist statistics does not state that there is a 95% chance the true value is in that interval. There is only one true value and it is either inside or outside of that interval. The correct interpretation is that in an infinite number of studies the true value would be in that confidence interval 95% of the time (Gelman et al. 2003). Bayesian statistics, however, makes direct probability statements on what actually happened given the data. A 95% credible interval (a Bayesian confidence interval) actually means that there is a 95% chance that the value is in that interval (Gelman et al. 2003).

Bayesian analysis is based on three distributions: the prior, the sampling distribution, and the posterior. The prior summarizes all relevant information about the parameter not contained in the data in the form of a probability distribution. Prior information usually comes from results of other related studies (e.g., McCarthy and Parris 2004, McCarthy and Masters 2005) or expert opinion (e.g., Martin et al. 2005). The sampling distribution (distribution of data given the parameters) summarizes the information in the data in a probability distribution. The prior and the sampling distribution are then combined using Bayes Theorem to get the posterior. The posterior thus summarizes all available information about a parameter. An agreement between previous information (the prior) and information in the data (sampling distribution) reduces the uncertainty about parameter estimates while disagreement between the prior and the likelihood will increase that uncertainty (Gelman et al. 2003). When using uniform priors (thus assuming that all parameters have an equal probability of occurring) the posterior distribution is proportional to the likelihood function.

MCMC: a brief description

Markov chain Monte Carlo (MCMC) has become the dominant tool for implementing Bayesian statistics in conservation biology. Although many authors have commented on the complexity of mathematical ideas behind Bayesian analysis and MCMC, the way MCMC estimates parameters is fairly simple. The equation describing the posterior distribution in Bayesian analysis is usually complex and often cannot be solved directly; therefore, MCMC uses a simulation approach. It proposes values for all parameters to use in the equation. It keeps proposed values that fit in the equation, throws out those that do not, then proposes a new set of values. Once the means and summary statistics from the saved sets of values change very little with more iterations of the simulator, the model is said to have converged and the summary statistics can now be used for inference.

MCMC in more detail

Markov chain Monte Carlo solves a complex equation using simulation (Monte Carlo) through a series of values that are only dependent on the value one time step before (a Markov chain). At each iteration of the simulation, the sampler proposes a set of values. If a value fits into the equation, the result is saved and the chain moves to that point. If the value does not fit, the value is not retained and the chain does not move. This process of either accepting or rejecting values is known as rejection sampling (Gelman et al. 2003). Gibbs sampling, one of the most popular samplers in the program WinBUGS, is a special case of MCMC in which the posterior is structured so that all proposed values can be accepted (Gelman et al. 2003).

Two of the most important decisions when using MCMC are: 1) the number of iterations to run and 2) the number of the initial iterations to ignore. MCMC uses simulation to generate parameter estimates; therefore, determining the number of iterations required to estimate a parameter at a desired level of accuracy is essential. After running a sufficient number of iterations (to achieve the desired accuracy) a parameter is said to have converged (Raftery and Lewis 1992a, b). There are many methods to assess whether parameters have converged (reviewed in Cowles and Carlin 1996) and evaluation of these methods (e.g., Cowles et al. 1999, Sinharay 2004) and development of new approaches (e.g., Hjorth and Vadeby 2005, Nur et al. 2005, De la Rosa et al. 2006) is ongoing.

MCMC requires initial values for all parameters to begin the simulation and one fundamental assumption of MCMC is that accepted values do not depend on those initial values (Gelman et al. 2003). For this reason, values from early iterations, which may still be dependent, are typically ignored (also known as burn-in). Although there are methods to evaluate the optimal burn-in period (e.g., Raftery and Lewis 1992a, Raftery and Lewis 1992b), many researchers also rely on ad-hoc methods such as visual inspection of the chain's values.

OVERVIEW OF REMAINING CHAPTERS

Chapter 2 (Multi-scale occupancy models for imperfectly detected species) introduces a new method, multi-scale occupancy modeling, that uses detection-nondetection data to simultaneously estimate use and occupancy while accounting for detectability. We provide simulation results and an example analysis with green frog (*Lithobates clamitans*) data from Louisiana.

Chapter 3 (Correcting for the proportion area sampled: a case study of Ivory-billed Woodpecker evidence in Arkansas) uses the newly-developed multi-scale occupancy models of Chapter 2 to examine the relationship between habitat and acoustic evidence of Ivory-billed Woodpeckers. We estimate the relationship between use and the proportion of a patch surveyed to correct for unequal sampling coverage between patches.

Chapter 4 (A threshold response to habitat disturbance by forest birds in northwest Ecuador) analyzes the relationship between habitat disturbance and occupancy and use in northwest Ecuador. We use patterns of occupancy and use to make initial recommendations for conservation planning and future monitoring in the region.

Chapter 5 (Conclusion) synthesizes the results from Chapters 1-4.

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CHAPTER 2

MULTI-SCALE OCCUPANCY MODELS FOR IMPERFECTLY-DETECTED SPECIES[1]

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ABSTRACT: Explaining patterns of species presence (occupancy) and if that species is present, the proportion of time it spends in an area (use), is typically the first step in understanding how species interact with their environments. Despite the inherent relationship between occupancy and use, current methods that account for detectability can only estimate one or the other. We propose a multi-scale occupancy model that simultaneously estimates use and occupancy for species with imperfect detection. This approach uses a 3-point binomial mixture, allowing for separate modeling of the probability of occupancy at a large scale and use and detection a smaller scale. We separate use and detectability through repeated samples at each scale. Simulations with 5 repeated samples at each scale demonstrated that estimates and credibility interval (a Bayesian confidence interval) coverage are relatively unbiased when the probability of detecting a species at a site given the site is occupied is ≥0.3. Bias could be reduced by increasing the number of repeated samples. We provide an example analysis using green frog (*Lithobates clamitans*) data collected by the Louisiana Amphibian Monitoring Program to demonstrate how covariates could affect use and detectability in different ways. Multi-scale occupancy modeling can accommodate all recent extensions to single-season occupancy models such as multi-species interactions, community metrics, false positives, and multi-season modeling.

INTRODUCTION

A large portion of ecological research revolves around two fundamental questions: 1) is a species present in an area (occupancy) and 2) if it is present, how often does it use that area (use). Addressing these two questions is typically the first step in understanding how species interact with their environments.

If species were always detected when present, than estimating occupancy and use would be relatively easy. Detecting a species at least once would demonstrate that a site is occupied and the number of detections would indicate how often that site is used. Unfortunately, few species are always detected when present and detectability (the probability of detecting a species given presence) can vary as a result of abiotic and biotic variables of interest (e.g., Wintle et al. 2005, O'Connell et al. 2006). This can produce misleading results about both use and occupancy (Williams et al. 2002, Gu and Swihart 2004).

Although there have been many recent advances in using detection-nondetection data to estimate occupancy while accounting for imperfect detection (MacKenzie et al. 2002, Nichols and Karanth 2002, Williams et al. 2002), most studies of habitat use still rely on radiotelemetry (e.g., Michalski et al. 2006, Matson et al. 2007, Rittenhouse and Semlitsch 2007).Unfortunately, it is often challenging and expensive to get a sufficient sample size to detect differences in use between habitats when using radiotelemetry (Murray 2006). Detection-nondetection data tends to be inexpensive and easy to collect; thus, it may be a more efficient way to analyze patterns of use in many species.

Both mark-recapture (Boulinier et al. 1998, Nichols et al. 1998b, a) and site-occupancy models (MacKenzie et al. 2003) for detection-nondetection data have been adapted to estimate immigration and emigration at a site between seasons. This approach has numerous applications to population viability analysis, metapopulation dynamics, and may be a useful indicator of habitat quality (Boulinier et al. 1998, MacKenzie et al. 2003). These models essentially estimate the probability of use, and of transitions between use and nonuse (emigration and immigration) but not occupancy. Although the probability of occupancy in these models (the probability that a species occupies the site irregardless of whether it uses the site in a given season) may be of lesser interest when each year of a multi-year study is treated as a season, understanding why a site is occupied will likely be fundamental to any investigation within a season.

In this paper, we describe a multi-scale site occupancy model which simultaneously estimates occupancy (Ψ) and use (u) within a single season while accounting for detectability. We begin by presenting a multi-scale occupancy model which relies on a 3-point binomial mixture. Then we present simulation results and an example analysis of green frog (*Lithobates clamitans*) data in Louisiana from the North American Amphibian Monitoring Program. We used the freely available program PyMC (Markov chain Monte Carlo for Python, http://code.google.com/p/pymc/) to perform all analyses.

MULTI-SCALE OCCUPANCY MODEL

Definitions

Let Ψ_i be the probability that site i is occupied, u_{ij} be the probability that site i is used during visit j given the site is occupied, and p_{ijk} be the probability that a species is detected given presence in site i, visit j, during subsample k. A subsample is a repeated sample within a visit. Occupancy is the probability that a species is present at a site, use is the probability that a species is present during a visit to that site given the site is occupied, and detection is the probability that a species is detected given use. We use N to denote the total number of sites, V to denote the total number of visits to a site, and S to denote the total number of subsamples within a visit. As in MacKenzie et al. (2003), we define the detection history, T vectors of 1's or 0's representing the detection or nondetection of a species at site i, as X_{it}.

Sampling design

We envision a design in which repeated samples occur at two different scales within a site. The replication in these samples could be spatial (Fig. 2.1), temporal, or both. We assume that detection of a species at a site, visit, or subsample is independent of the detection of that species in another respective site, visit, or subsample.

The model

When simultaneously estimating occupancy and use, there are two levels of detectability involved: use and detection. The probability of detection can be used to correct the probability of use for situations in which a species uses a site but is not detected. The corrected probability of use can then be used to correct the probability of occupancy for situations in which a site is occupied but not used during the sample period.

Suppose a site is visited 2 times with 3 subsamples at each visit. The species is only detected on the 3rd subsample of the first visit thus producing the detection history of 001 000. The probability of the detection history from the first visit is similar to the single season model of MacKenzie et al. (2002) with *u* replacing Ψ.

$$\Pr(X_{i,1} = 001) = u_{i,1}(1 - p_{i,1,1})(1 - p_{i,1,2})(p_{i,1,3}) \tag{1}$$

We then expand the single season model to estimate *u* as a second level of detectability. Here we know the site is occupied from the first visit but do not know whether the site is used during the second visit. The probability of the detection history from the second visit is then:

$$\Pr(X_{i,2} = 000 \mid X_{i,1}) = u_{i,2}\prod_{k=1}^{3}(1-p_{i,2}) + (1-u_{i,2}) \tag{2}$$

Finally, suppose no individuals were detected during the 2 visits to the site (i.e., 000 000). In this case, the site was not occupied, occupied but not used during the 2 visits, or occupied, used during at least one of the visits, and not detected during the expected number of visits in which the site would have been used. The probability of the detection history is:

$$\Pr(X_i = 000\ 000) = (1-\Psi) + \Psi\prod_{j=1}^{2}(1-u) + \Psi(1-\prod_{j=1}^{2}(1-u))(\prod_{k=1}^{3}(1-p))^{uk} \tag{3}$$

The sampling distribution of the model is then:

$$\Pr(X_1,\ldots,X_N \mid \Psi,u,p) = \prod_{i=1}^{N}\Pr(X_i) \tag{4}$$

Parameters can be estimated by either maximum likelihood or Bayesian techniques.

Covariates and missing data

Both covariates and missing data can be easily incorporated into multi-scale occupancy models in the same way as other occupancy models. Effects of covariates on Ψ, u, and p can be modeled by the logistic model given in MacKenzie et al. (2002), where θ is the parameter of interest, X is the covariate information, and B is the vector of model parameters.

$$\theta = \frac{\exp(XB)}{1+\exp(XB)} \tag{5}$$

Missing data can be accommodated by removing parameters corresponding to those data. Incorporation of covariates and missing values in occupancy models have been discussed at length by MacKenzie et al. (2002, 2003).

SIMULATION STUDY

Simulation methods

We evaluated the performance of multi-scale occupancy models under 28 likely scenarios. We randomly drew a sample size of 50 sites with 5 visits and 5 subsamples per visit and all possible combinations of $\Psi = 0.9, 0.7, 0.5$, $u = 0.9, 0.7, 0.5$, and $p = 0.9, 0.4, 0.1$. We developed a Bayesian implementation of the multi-scale occupancy models using Markov chain Monte Carlo (MCMC). Although it can be relatively simple to implement complex models in MCMC, it is also computationally intensive, thus we used 40 repetitions per scenario in the simulation with enough iterations to achieve convergence within each run. For each scenario, we calculated the bias of the mean estimate and the percent of time the 95% credibility interval (a Bayesian confidence interval) contained the true value. We used the methods of Raftery and Lewis (1992a, 1992b) with the default methods implemented in CODA (Plummer et al. 2006) to assess model convergence.

Bayesian statistics require the specification of any information relevant to the problem not included in the data. This information is summarized as prior distributions around all parameters. In this simulation, all parameters were estimated on the logit scale, which only allows values to asymptotically approach 0 or 1, so we used a uniform prior distribution of -20 to 20 (or effectively 0 to 1 for the real parameters) on Ψ, u, and p.

Simulation results

Simulation results provided relatively unbiased estimates except in situations with low detectability in relation to the number of repeated samples. These results are similar to those reported by MacKenzie et al. (2002). However, in multi-scale occupancy models, biased estimates are not necessarily caused by low detectability at only one scale, as all scenarios with use of 0.9 and detectability of 0.1 were relatively unbiased. Model performance best related to the overall probability of detecting a species at an occupied site. This quantity is the probability that a species is detected at least once during a subsample, $1-(1-p)^S$, times the probability of use, and is equivalent to the p in a single season occupancy model without subsamples. Models began to underestimate parameters and credibility interval coverage once the probability of detecting a species at an occupied site was <0.3. At low probability of detection (given occupancy), when Ψ was high (0.9), u was the most biased (Fig. 2.2), whereas when Ψ was low (0.5), Ψ was the most biased (Fig. 2.3). In all cases, the bias could be removed by increasing the number of repeated visits and subsamples.

BRIEF EXAMPLE WITH GREEN FROGS IN LOUISIANA

Example methods

We provide a brief example of multi-scale occupancy modeling with data on green frogs collected in 2005 by the Louisiana Amphibian Monitoring Program (LAMP). The LAMP follows the protocol of the North American Amphibian Monitoring Program where a set of sites is visited multiple times (visits) each year. Detections of frogs are predominately auditory so visits are spaced out across the season to accommodate differences in singing phenology between species. Each visit is a transect with a subsample of 10 stops along that transect.

In this example, u more closely represents availability for detection than actual use by an individual, because we would expect frogs to not be vocalizing at certain sites if it is either too early or too late in the season. Therefore, Ψ is the probability that the route is occupied, u is the probability green frogs are available for detection given the site is occupied, and p is the probability of detecting a green frog given they are available for detection. Temperature and the time of season can influence detectability (e.g., Weir et al. 2005) while regional variation can influence occupancy (Manley et al. 2005) in many species of frogs. Therefore, we compared 18 models comprised of all possible combinations of a temperature or visit effect on *u* and *p* and a region effect of Ψ. We separated Louisiana into 2 regions: North and South. All sampling sites from Vernon, Rapides, and Avoyelles parishes and North were considered in the North Region while all other counties were in the South region.

In 2005, there were 3 visits performed in Louisiana. The first visits occurred between January 10 and March 9, the second visits were from March 21 to May 9, and the third visits were from April 29 to July 16. The visits represented sampling done progressively later in the season so we estimated the visit effect as a separate u for each visit. Temperature was the mean temperature recorded during each visit. There was also a large amount of missing data in 2005 with only 7 out of 18 sites having information for all 3 visits. Just as in the simulations, we used the MCMC toolkit PyMC with a uniform prior of -20 and 20 on the logit scale for Ψ, u, and p. We also used a uniform prior of -10 and 10 on the logit scale for the effect of covariates. We assessed convergence by the methods of Raftery and Lewis (1992a, 1992b) using the default values implemented in CODA (Plummer et al. 2006) and compared all models using the Akaike's Information

Criterion (AIC, Burnham and Anderson 2002). To facilitate comparison of AIC values we constructed AIC weights as described by Burnham and Anderson (2002).

Example results

Three models had substantial empirical support (ΔAIC<2, Burnham and Anderson 2002) with a combined Akaike weight of 0.67 (Table 2.1). Two of these models included visit-specific effects on both u and p and one included a positive effect on occupancy of being in the northern region (1.14, BCI: -3.9 - 5). Estimates from one of these models suggested that use, representing the availability for detection, increased across time (from visit 1 to 3, Fig. 2.4) while the probability of detection peaked during visit 2 (Fig. 2.5).

DISCUSSION

Questions about occupancy and use dominate much of the ecological literature. Despite the inherent relationship between occupancy and use, existing approaches that account for detectability only estimate either one or the other. Here we presented the first approach to simultaneously estimate occupancy and use from detection-nondetection data while accounting for detectability.

The simulation study suggested that 5 visits with 5 subsamples within each visit provides relatively unbiased estimates and credibility interval coverage when the probability of detecting a species at a site given occupancy is ≥0.3. This directly corresponds to the detectability (<0.3) at which single season occupancy models become biased at 5 visits (MacKenzie et al. 2002). When designing a multi-scale occupancy study for species which may have a low combined probability of detection and use it will be important to ensure that there are enough visits and subsamples to provide unbiased estimates.

Detectability is often thought of as a nuisance parameter which must be modeled to get unbiased estimates of another quantity of interest. If a species is always using a site (or always available for detection), this is generally not a problem; however, in many situations this is not true. The probability of detection would then combine the probability of use (*u*), something potentially of interest, and the probability of detection given use (*p*).

There are many ways multi-scale occupancy modeling can be used to separate *u* and *p* in contemporary ecological problems. One common example involves large-ranging organisms which are not present during all visits to the site. In this scenario, an investigator may want to model patterns of occupancy at the site-level and patterns of use within the site. Another common situation, as illustrated by the green frog analysis, involves a species that can be present during all visits to a site but is not always available for detection. Separately modeling *u* and *p* would be particularly informative when, as was the case with the green frog example, there can be different patterns in *u* and *p* in relation to a factor of interest.

Covariates may even affect *u* and *p* in completely different ways when a species is not always available for detection. Imagine a forest-associated species which rarely uses non-forested habitat but is easier to detect in areas with no forest. A single-season occupancy model could estimate occupancy in forested and non-forested habitat to be roughly equal and there would be no way to separate the contribution of use versus detectability.

Multi-scale occupancy modeling could be expanded in numerous ways. Current extensions to single-season occupancy models such as species interactions (MacKenzie et al. 2004), community-level metrics (Dorazio and Royle 2005, Dorazio et al. 2006), multi-season models (MacKenzie et al. 2003), and false positives (Royle and Link 2006) could all be applied to multi-scale occupancy models. Additionally, detection probability at any scale could be estimated with double-observer sampling (Cook and Jacobson 1979), removal models (Moran 1951, Seber 1982), or distance sampling (Reynolds et al. 1980, Buckland et al. 1993). Incorporating both removal models and distance sampling is an active area of ongoing research.

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TABLE 2.1. Model selection results for the effect of temperature (temp) and visit on use (u) and detection (p), and region on occupancy (Ψ) for green frogs (*Lithobates clamitans*) in Louisiana. Models are ordered by the difference in Akaike Information Criterion (ΔAIC) and Akaike weights (w_i). Only models with ΔAIC < 10 are shown.

Model	ΔAIC	w_i	k	deviance
Ψ(.) *u*(.) *p*(visit)	0.0	0.28	5	127.6
Ψ(.) *u*(visit) *p*(visit)	0.3	0.24	7	123.9
Ψ(region) *u*(visit) *p*(visit)	1.2	0.15	8	122.8
Ψ(region) *u*(visit) *p*(.)	2.1	0.10	6	128.4
Ψ(.) *u*(visit) *p*(.)	2.6	0.08	5	130.2
Ψ(region) *u*(temp) *p*(visit)	3.0	0.06	7	126.6
Ψ(.) *u*(temp) *p*(visit)	3.5	0.05	6	129.1
Ψ(region) *u*(visit) *p*(temp)	4.8	0.03	7	128.4
Ψ(.) *u*(visit) *p*(temp)	8.2	0.00	6	133.8

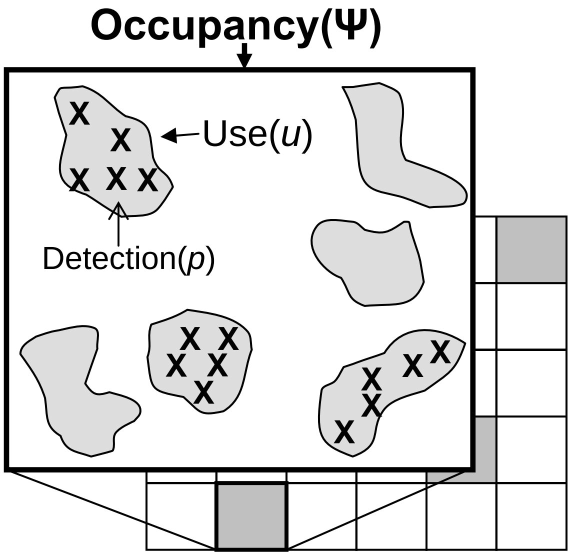

Fig. 2.1. Example multi-scale occupancy design with only spatial replication. The probability of detection is calculated using subsamples within a patch (denoted by Xs). Use is the probability that the species is present in a patch and occupancy is the probability that a species is present in at least one of the patches within the square.

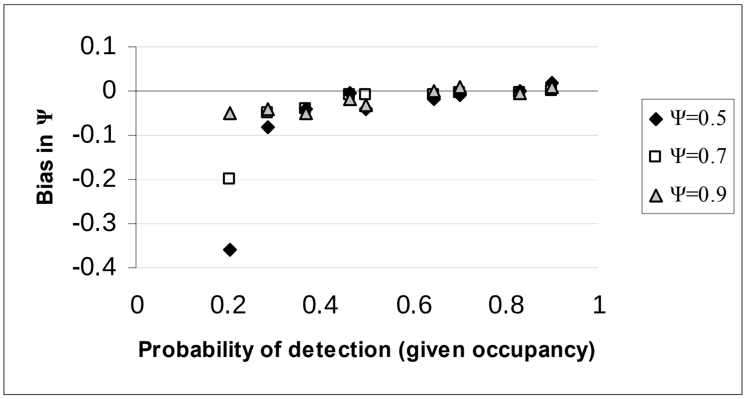

Fig. 2.2. Bias in estimated Ψ in relation to an interaction between simulated Ψ and the probability of detecting a species given occupancy.

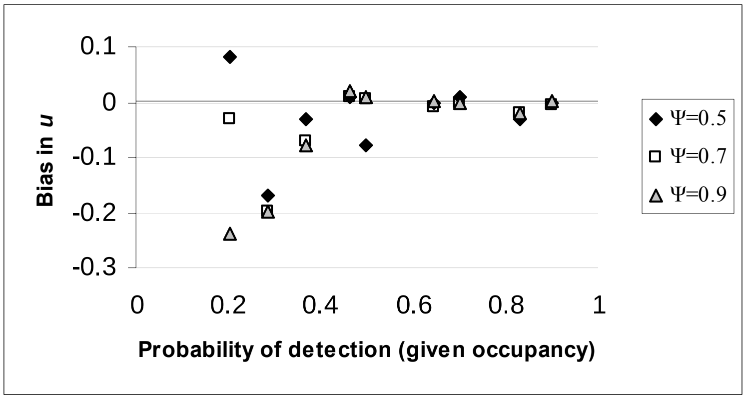

Fig. 2.3. Bias in estimated *u* in relation to an interaction between simulated Ψ and the probability of detecting a species given occupancy.

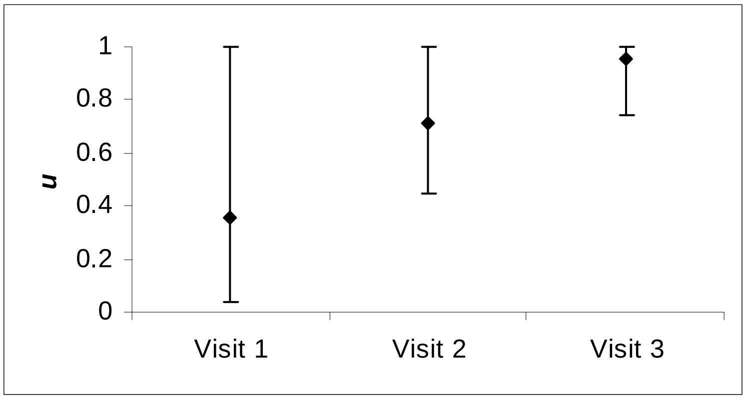

Fig. 2.4. Visit-specific availability for detection (u) in green frog (*Lithobates clamitans)* example based on one of the top models (Ψ(.) u(visit) p(visit)). Error bars indicate 95% credibility intervals (Bayesian confidence intervals)

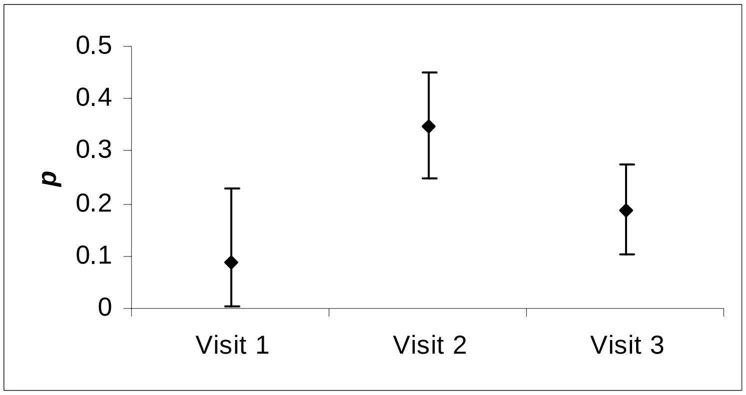

Fig. 2.5. Visit-specific detectability (*p*) in green frog (*Lithobates clamitans)* example based on one of the top models (Ψ(.) *u*(visit) *p*(visit)). Error bars indicate 95% credibility intervals (Bayesian confidence intervals)

CHAPTER 3

CORRECTING FOR THE PROPORTION OF AREA SAMPLED: A CASE STUDY OF IVORY-BILLED WOODPECKER EVIDENCE IN ARKANSAS[1]

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[1] Mordecai, R. S., R. W. Rohrbaugh Jr., J. T. Peterson, C. T. Moore, B. J. Mattsson, R. J. Cooper, and M. J. Conroy. To be submitted to Auk.

ABSTRACT: Initial surveys for rare and elusive species often utilize ad hoc schemes for the selection of temporal and spatial sampling units in an effort to maximize the total number of species detections. The resulting variations in area sampled and time spent in each area can strongly bias results, and controlling for that bias can be particularly challenging. We use newly-developed multi-scale occupancy models to relate the density of big trees (>60.96 cm dbh) and density of snags to high interest acoustic evidence (hereafter; evidence) of Ivory-billed Woodpeckers from Arkansas in 2004 and 2005 while controlling for the proportion of area sampled and time spent in that area. Density of big trees (AIC weight=0.54) best predicted patch occupancy, percent area surveyed (AIC weight =0.61) best predicted the probability that evidence was available within the patch (use), and density of big trees (AIC weight =0.61) best predicted the probability that evidence was detected given that it was available. Model-averaged predictions correctly classified 68% of 22 patches. The number of 14-day sessions of acoustic sampling required to be 90% confident that evidence would be detected given that it was present ranged from 7.4 (95% Bayesian credible interval (BCI): 3-12) in low densities of big trees to 360.8 (95% BCI: 3-1158) in high densities of big trees. The negative relationship between percent area surveyed and the availability of evidence to an ARU likely resulted from a pattern of nonrandom sampling. In "hot spots" with much additional evidence of Ivory-billed Woodpecker presence (e.g., sightings, feeding sign), recording units were generally placed near such evidence rather than in a random or evenly-distributed sampling design. In patches with little or no previous evidence, recording units were more evenly distributed in an ad-hoc fashion. Thus, the percent

patch surveyed represents the level of nonrandom sampling within the patch. Multi-scale occupancy models effectively controlled for proportion area surveyed and can be an important tool to account for sampling bias in occupancy studies.

INTRODUCTION

Species of greatest conservation concern tend to be rare and elusive. Initial sampling effort for these species is often distributed in an ad hoc manner in both space and time with the ultimate goal of documenting species presence. Unfortunately, the difficulty in detecting many of these species will likely lead to several areas in which the species is present but is not detected (a false absence). Moreover, the proportion of the total area surveyed (hereafter; proportion area surveyed) and the sampling effort at each survey location will likely impact the probability of a false absence (MacKenzie et al. 2002, Williams et al. 2002)

The Ivory-billed Woodpecker may be the most rare and elusive bird species in the United States and thus presents a great challenge for designing efficient and effective surveys. The species once existed at low densities in the southeastern U.S. from Florida to Texas and as far North as Illinois and Indiana and are thought to have used extensive forested areas with very large trees and many dead trees (Jackson 2002). In 1938, Tanner (1942) took the last universally accepted photograph of this species in the U.S.; however, intriguing sightings continued throughout the 20th century (Jackson 2002, Fitzpatrick et al. 2005, Hill et al. 2006). Recent evidence that the Ivory-billed Woodpecker (*Campephilus principalis*) persists in both Arkansas (Fitzpatrick et al. 2005) and Florida (Hill et al. 2006) has reinvigorated the hope that this species can be saved from extinction.

Despite historic records and the contributions of Allen and Kellogg (1937), Tanner (1942), and others, we still know very little about Ivory-billed Woodpeckers. Most of the historic information on habitat associations comes from one site (the Singer Tract in Louisiana), which may not be representative of typical Ivory-billed Woodpecker habitat and may poorly reflect historical or current habitat associations. We know even less about the survey effort required to be relatively confident that the bird is not there; although it is probably high given the expected density of the species (1 pair per 16-44 km^2, Tanner 1942).

We use newly-developed multi-scale occupancy models (Chapter 1) and audio evidence to estimate the relationship between habitat and patterns of occupancy and detectability of Ivory-billed Woodpecker evidence while controlling for the proportion of patch sampled at the Cache and White River National Wildlife Refuges in Arkansas from 2004-2005. Although there is not yet consensus about the persistence of the Ivory-billed Woodpecker in North America (Jackson 2006, Collinson 2007, Sibley et al. 2007), the relationship between habitat and "high interest" evidence (hereafter; evidence) can provide valuable guidance for ongoing search efforts. To further inform these search efforts we also use the estimated habitat relationships to determine the sampling effort required to be 90% confident that not detecting evidence indicates a true absence of evidence in a patch.

METHODS

Study site

Our study area encompassed 22 stands, ranging in size from 1.2 to 7 km^2 (mean = 2 km^2), within the Cache (35.06°N, 91.33°W) and White River National Wildlife Refuge in Arkansas (34.29°N, 90.08°W). We used existing stand boundaries delineated by the Lower Mississippi Valley Joint Venture (Lower Mississippi Joint Venture *unpubl. data*). The Joint Venture delineated these boundaries to construct stands averaging roughly 2-km^2 using natural features and management history.

Acoustic sampling

Autonomous recording units (ARUs) recorded 16,248 hours (2,031 days) of ambient sound using throughout the Cache and White River National Wildlife Refuge from December 18, 2004 to May 31, 2005. Each ARU recorded sound for two 4 hr periods, the first from 30-45 min before sunrise and the second terminating 30-45 min after sunset. ARU deployments lasted between 6 and 41 days. Recording sites were selected based on perceived habitat quality (i.e. many large and dead trees) and prior evidence of Ivory-billed Woodpecker presence such as sightings, acoustic encounters, and feeding sign.

Acoustic analysis

There are two commonly described sounds produced by Ivory-billed Woodpeckers: a kent call and a double knock (Jackson 2002). In 1935, Arthur Allen made the only known recording of a kent call (Allen and Kellogg 1937), a call often described as sounding like a toy trumpet or clarinet. There is no known recording of the Ivory-billed Woodpecker double knock; however, historic descriptions of “double resounding whacks” produced by Ivory-billed Woodpeckers (Allen and Kellogg 1937) agree well with double knocks produced by other woodpeckers in the genus *Campephilus*.

We first used the XBAT software system (http://xbat.org/) to identify sounds similar to Arthur Allen's recordings of Ivory-billed Woodpecker kent calls and double knocks from Pale-billed Woodpeckers (*Campephilus guatemalensis*) and Powerful Woodpeckers (*Campephilus pollens*). XBAT compares spectrogram cross-correlations between a template and unclassified sounds and retains only sounds with correlations above a specified threshold (henceforth, signals). We used a conservatively low threshold (0.25) to insure that signals were not prematurely removed from consideration. This threshold, however, resulted in hundreds of thousands of signals that were obviously not produced by an Ivory-billed Woodpecker.

In an attempt to exclude false detections, we then subjected signals identified by the XBAT system to a 3-stage expert review process. First, one of six acoustic analysts reviews the signals and easily removes most of them (>99%) from consideration due to a strong dissimilarity from historical records of Ivory-billed Woodpecker sounds. Then at least five acoustic analysts vote on whether the remaining signals are potentially produced by Ivory-billed Woodpeckers. Signals accepted by at least 60% of analysts reach the next level of review (henceforth, detections). A panel of at least three experts outside the acoustic analysis team perform the final review and classify (by consensus) these detections as A2 (rejected), A3 (moderate interest), or A4 (high interest). A3 detections lack "a compelling qualitative resemblance" to Ivory-billed Woodpecker sounds but could not be confidently rejected based on quantitative evidence. A4 detections could not be separated from template sounds based on qualitative or quantitative criteria. Quantitative criteria included double knock interval and fundamental frequency (for kent calls). Qualitative criteria involved the absence of a probable alternative sound source and the general impression of a human observer that a signal sounded like a *Campephilus* woodpecker. We used only detection classified as A4 (high interest) in this analysis.

Vegetation sampling

We used stand-level estimates of big trees/ha (>60.96 cm dbh) and snags/ha from the Lower Mississippi Valley Joint Venture Ivory-billed Woodpecker habitat inventory and assessment. Historic accounts of Ivory-billed Woodpeckers typically mention a strong association with many big trees and many dead trees (e.g. Allen and Kellogg 1937, Tanner 1942). In each stand, the Joint Venture randomly selected four 322m transects. Every 80.5m on those transect they estimated the number of big trees and the number of snags within a 16m radius. Detailed methods for this habitat inventory are available at http://www.lmvjv.org/IBWO_habitat_inventory_&_assessment.htm.

Statistical analysis

We used multi-scale occupancy modeling (Chapter 1) to accommodate the hierarchical nature of the data. These models estimate three parameters based on repeated visits at two scales: occupancy (probability of species presence in an area), use (probability of species presence at a smaller scale within that area given occupancy), and detection (probability of detecting a species given use). As we could not confirm with certainty whether Ivory-billed Woodpeckers were present in any of the patches, we define occupancy as the probability that putative acoustic evidence (hereafter; evidence) was present in a stand. We then defined use as the probability that evidence was available within the stand, given it is present, during the deployment of an ARU, and detectability as the probability of detecting such evidence on a given day of the ARU deployment given use.

We corrected for the proportion area sampled by modeling the effect of percent patch surveyed on use; thus linking the availability of evidence to the total area sampled. We used ArcGIS 9.1 (Environmental Systems Research Institute, Redland, California) to place 200m buffers around all ARU locations and calculated percent patch surveyed as the percent of each patch covered by at least one buffer. Buffers of 200m roughly correspond to the suspected distance at which a signal from an Ivory-billed Woodpecker would likely be detected by an ARU (Ron Rohrbaugh, Jr. *unpubl. data*)

We identified 32 candidate models using all possible combinations of density of big trees and density of snags to explain occupancy and detection, and percent area surveyed to explain use. We compared models using mean Akaike's information criterion (AIC) and interpreted parameter estimates using model averaging (Burnham and Anderson 2002) . To estimate the relative importance of each parameter we summed the Akaike weight of all models in which the parameter occurs (importance weight (w), Burnham and Anderson 2002). To test model fit, we compared model-averaged predictions from all models with AIC<4 to stand-level patterns of detections. If the model-averaged prediction of occupancy was greater that 0.5, and there was at least one detection in that stand, the stand was considered classified correctly.

Using the model with the lowest AIC value, we also calculated the number of 14-day sampling periods required to be 90% confident that a stand was not occupied. The probability of no detections after 14-days of sampling (period_{14}), given presence, is the probability that evidence is available during the sampling period (use) times the probability that the species is not detected over the 14 days ($(1-p)^{14}$). We solve for the number of sampling periods (X) required to be 90% confidence that a stand is not occupied by setting the equation $1-(1-\text{period}_{14})^X$, the probability that at least one of the sampling periods produces a detection given presence, equal to .90.

We analyzed candidate models with moBayes (http://code.google.com/p/mobayes/). moBayes uses the Markov chain Monte Carlo (MCMC) toolkit PyMC (http://code.google.com/p/pymc/) to estimate multi-scale occupancy models. This program uses a Bayesian approach to estimation and thus requires the specification of all information relevant to the problem in the form of a prior distribution around all parameters (Link et al. 2002, Gelman et al. 2003). There was scant prior information regarding occupancy, use or detection for this species, so we used a uniform distribution from -20 to 20 on the logit scale for all intercepts and -10 to 10 for all covariates. We used PyMC to estimate the number of 14-day sampling periods required to be 90% confident the species was not present.

MCMC uses simulation to generate parameter estimates; therefore, determining the number of iterations required to estimate a parameter at a desired level of accuracy is essential. After running a sufficient number of iterations (to achieve the desired accuracy) a parameter is said to have converged (Raftery and Lewis 1992a, Raftery and Lewis 1992b). To ensure convergence of model parameters, we used both visual inspection of simulation values and the methods of Raftery and Lewis (1992a, 1992b) with the default options in CODA (Plummer et al. 2006).

MCMC requires initial values for all parameters to begin the simulation and one fundamental assumption of MCMC is that accepted values do not depend on those initial values (Gelman et al. 2003). Typically, values from early iterations, which may still be dependent, are ignored (also known as burn-in). We used a burn-in period of 5,000 iterations and tested its adequacy using visual inspection and the methods of Raftery and Lewis (1992a, 1992b) with the default options in CODA (Plummer et al. 2006).

RESULTS

Four models had a mean ΔAIC < 2 (Table 3.1). The null model had a ΔAIC of 4.54 and an Akaike weight of 0.02. Model-averaged predictions classified 68% of 22 stands correctly with 5 false positives and 2 false negatives. Percent patch surveyed (w=0.61) and the effect of density of big trees on detection (w=0.61) had the greatest importance weights followed by the effect of big tree density on occupancy (w=0.54), snag density on occupancy (w=0.35), and sang density on detection (w=0.23). Although 95% credible intervals (a Bayesian confidence interval, BCI) did not overlap zero for the effect of big tree density on occupancy or detection in most of the top models (Table 3.1), model-averaged BCIs for the effect of big tree density on occupancy (-0.35, 0.09) and detection (-.68, .60) did. The model-averaged BCI for the effect of percent patch surveyed on use was between -2.33 and 2.23.

Model-averaged predictions of occupancy declined with greater big tree density (Fig. 3.1), use declined with greater percent patch surveyed (Fig. 3.2), and detection was relatively unaffected by big tree density (Fig. 3.3). The number of 14-day acoustic sampling periods required for 90% confidence in detecting evidence given that it is present ranged from 7.4 (95% BCI: 3-12) in low densities of big trees to 360.8 (95% BCI: 3-1158) in high densities of big trees (Fig. 3.4).

DISCUSSION

The probability that Ivory-billed Woodpecker evidence was available to an individual ARU increased as the percent patch surveyed declined, while holding survey effort constant. One likely explanation for this relationship is nonrandom sampling. In "hot spots" with much evidence of Ivory-billed Woodpecker presence (e.g. sightings, feeding sign), recording units were generally placed near such evidence. In patches with little evidence, recording units were more evenly distributed; thus, the percent patch surveyed also represents the level of nonrandom sampling within the patch. Although multi-scale occupancy modeling allowed us to control for this bias, there was a large amount of uncertainty introduced by statistically controlling it.

The best way to control for sampling bias is to include some random sampling in the design of surveys for rare and elusive species. Such randomization is important even for preliminary or initial surveys. The ideal form of randomization depends on the ecology of the species. While a completely randomized or stratified random design may work best for more evenly dispersed species, newer methods such as adaptive cluster sampling may be better for highly clustered populations (Thompson 1990, 1991, Thompson and Seber 1996).

Even without sampling bias, interpretation of occupancy surveys for large-ranging organisms can be particularly challenging. Researchers are often interested in patterns of occupancy at scales much smaller than the species' typical range of movement. In this situation, the probability of detection in occupancy models is a combination of the probability that a species is present during the sample period and the probability that it is detected given presence. The probability of detection given presence, generally thought of as a nuisance parameter to be statistically controlled, is now confounded by the probability that the species was present during the sample, something potentially of interest.

Previously published estimates of Ivory-billed Woodpecker density are far greater than the roughly 2-km^2 patches in which we analyzed acoustic evidence. We used each day of recording from an ARU as a repeated sample to estimate the probability of detection. Therefore, because the woodpecker could potentially leave and/or return to the patch during those days, the probability of detection combines the probability of detection given presence and the probability of presence during the sample. As we can not separate these two probabilities, we cannot determine whether habitat influences the actual use of the area, our ability to detect that use, or both.

Our finding that the probability of evidence being present and/or detection of such evidence increased with declining big tree density may seem counterintuitive. Ivory-billed Woodpeckers are historically associated with areas of large trees, and one might expect dense stands of large trees to attract this woodpecker. Density of big trees (>60.96 cm dbh) in this area, however, decreases with increasing density of even bigger trees (>91.44 cm dbh, M. Lammertink pers. obs.), so the decrease in big tree density probably represents an ecological transition to fewer, but even larger, trees. Unfortunately, we did not have data on the density of trees >91.44 cm for our study area. As all of the stands in our study were older and dominated by big or even bigger trees, further study is needed in younger stands dominated by smaller trees.

A decrease in big tree density may also have increased the probability of detection by allowing acoustic signals to travel farther. Fewer trees could have resulted in fewer obstructions for kent calls and double knocks, thus increasing the probability that a signal would be detected.

There remains much uncertainty as to whether density of big trees affects presence of evidence for Ivory-billed Woodpecker, detection of that evidence, or both. Much of this uncertainty probably results from very low detectability in areas with a high density of big trees making it hard to separate species absence from species that are simple difficult to detect.

Information on detectability, and particularly how it responds to habitat variables, is extremely valuable in the design of bird surveys. Mackenzie and Royle (2005) discuss how estimates of occupancy and detectability can be used to estimate the optimal number of repeated visits for an occupancy survey. The optimal number of repeated visits decreases with higher detectability and lower occupancy (Mackenzie and Royle 2005). For situations in which occupancy and detectability vary with habitat, such as this study, the optimal number of repeated visits will also likely vary by habitat.

Detectability can also be used to estimate the amount of effort required to demonstrate that a species is not present at a certain level of confidence. When working with endangered species, this quantity can be very important, as it allows natural resource professionals to adopt consistent standards for determining the presence/absence of a species. When using acoustic surveys for evidence of Ivory-billed Woodpecker, our results suggest that demonstrating absence at a 90% confidence level, even at low densities of big trees, would be difficult. In particular, the lowest estimated effort would require more than 100 days of acoustic sampling per patch and thus analysis of more than 800 hours of recordings. The intensive sampling required and potentially costly analysis of acoustic data suggests that demonstrating absence of evidence at a 90% confidence level within a 2-km^2 patch will not be feasible without more efficient survey methods (i.e., methods with a higher probability of detection).

Multi-scale occupancy models effectively controlled for the proportion area surveyed. While in some cases a larger area sampled may have a positive effect on the availability of the species, in situations where sample locations are clustered around specific prior information of species presence the trend may be reversed. Regardless of the relationship with proportion area surveyed, the approach appears to be a valuable tool to account for sampling bias in occupancy studies.

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Table 3.1. Model selection results for the effect of big tree (B) and snag (S) density on occupancy (ψ) and detection (p), and percent patch surveyed (Sur) on use. Models are ordered by the difference in Akaike Information Criterion (ΔAIC) and Akaike weights (w_i). Superscripts of + or – indicate the direction of the estimate and * indicates 95% credible intervals (Bayesian confidence intervals) that do not overlap zero. Only models with ΔAIC < 4 are shown.

ψ	**Use**	$\boldsymbol{p}$	**Deviance**	**K**	**ΔAIC**	$\boldsymbol{w_i}$
.	$\mathrm{Sur}^{(-)}$	$B^{(-)*}$	106.67	5	0	0.20
$B^{(-)*}$	.	.	109.7	4	1.03	0.12
$S^{(-)}$	$\mathrm{Sur}^{(-)}$	$B^{(-)*}$	106.05	6	1.38	0.10
$B^{(-)}$	$\mathrm{Sur}^{(-)}$	$B^{(-)*}$	106.53	6	1.86	0.08
$B^{(-)*}S^{(-)}$	.	.	109.27	5	2.6	0.05
.	$\mathrm{Sur}^{(-)}$	$B^{(-)*}S^{(-)}$	107.69	6	3.02	0.04
$B^{(-)*}$	.	$S^{(-)}$	109.68	5	3.01	0.04
$B^{(-)*}$	$\mathrm{Sur}^{(-)}$	.	109.76	5	3.09	0.04
$B^{(-)*}$	.	$B^{(-)}$	109.8	5	3.13	0.04
$B^{(-)}S^{(-)}$	$\mathrm{Sur}^{(-)}$	$B^{(-)*}$	105.98	7	3.31	0.04
$S^{(-)}$	$\mathrm{Sur}^{(-)}$	$B^{(-)*}S^{(+)}$	106.6	7	3.93	0.03

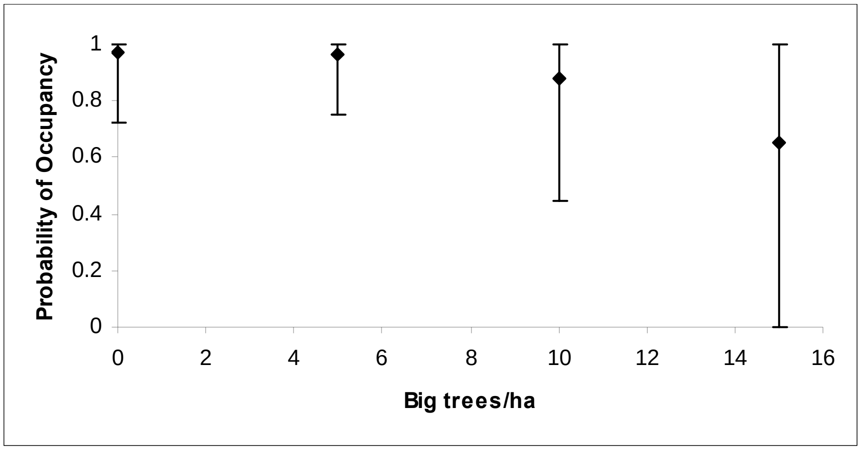

FIG 3.1. Model-averaged association between big trees/ha and the probability of occupancy by Ivory-billed Woodpecker (i.e., probability that evidence was present in a stand). Observed values of big tree density ranged from 1-14.5. Error bars indicate 95% credible intervals (Bayesian confidence intervals).

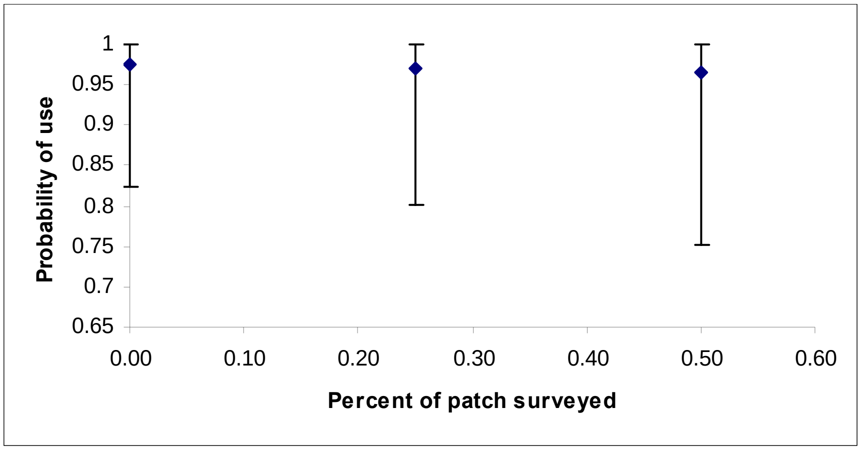

FIG 3.2. Model-averaged association between percent of patch surveyed and the probability of use by Ivory-billed Woodpecker (i.e., probability that evidence was present during the deployment of an autonomous recording unit). Observed values of percent patch surveyed ranged from 4.8-47.2. Error bars indicate 95% credible intervals (Bayesian confidence intervals).

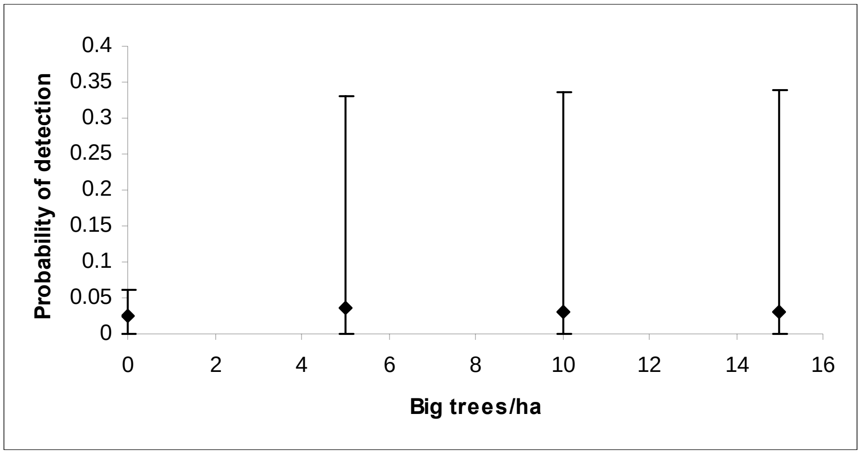

FIG 3.3. Model-averaged association between big trees/ha and detectability of evidence for Ivory-billed Woodpecker (i.e., probability of detecting evidence during a one-day deployment of an autonomous recording unit). Observed values of big tree density ranged from 1-14.5. Error bars indicate 95% credible intervals (Bayesian confidence intervals).

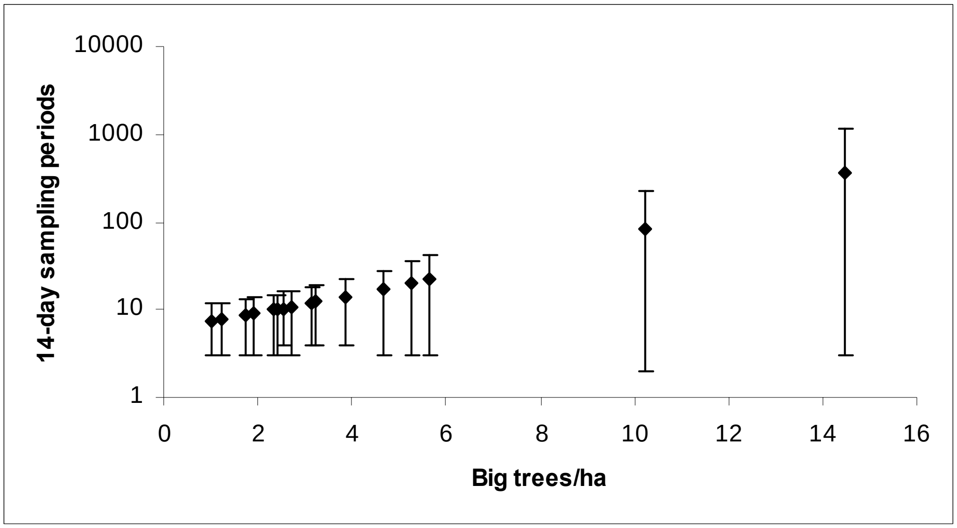

FIG 3.4. Number of 14-day sampling periods required to be 90% confident that evidence of Ivory-billed Woodpecker is absent from a stand based on the model with the lowest AIC value. Points correspond to observed values of big trees/ha. Error bars indicate 95% credible intervals (Bayesian confidence intervals). Number of sampling periods is plotted on the log scale.

CHAPTER 4

A THRESHOLD RESPONSE TO HABITAT DISTURBANCE BY FOREST BIRDS IN NORTHWEST ECUADOR[1]

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[1] Mordecai, R. S., R. J. Cooper, and R. Justicia. To be submitted to Conservation Biology.

ABSTRACT: Understanding how organisms use disturbed habitats and how that use can be increased is a pivotal question in conservation biology. We analyzed the relationship between upper canopy cover, an indicator of disturbance, and occupancy and use by 18 forest bird species in northwest Ecuador. From May 22 to June 28, 2006 we conducted five, 10-min 50m-radius point counts at 28 sites (140 total) representing a gradient of habitat disturbance from 1285 – 1787m in elevation. Both occupancy and use showed strong threshold responses at 21-40% upper canopy cover with the probability of occupancy increasing from roughly 0 to 1 and emigration (the probability that a species would stop using the site during the study period) decreasing from roughly 1 to 0. Bird surveys ended near the beginning of the dry season and high levels of emigration in more disturbed areas imply that forest birds stopped using these areas as the dry season approached, possibly due to a shift in food resources. Patterns of use and occupancy suggest that disturbed habitat in the region (which is primarily abandoned pasture) may only be valuable to forest birds after a specific level of regeneration and during certain times of the season.

INTRODUCTION

With the increasing evidence that protected areas alone are not enough to conserve most of the world's biodiversity (Liu et al. 2001, Dirzo and Raven 2003), many authors are highlighting the importance of disturbed habitats in tropical bird conservation (e.g. Welford 2000, Peh et al. 2006, Sekercioglu et al. 2007). Disturbed habitats, which range from regenerating pastures (Welford 2000) to agricultural systems such as coffee (e.g. Mas and Dietsch 2003, Bhagwat et al. 2005), cacao (e.g. Greenberg et al. 2000, Verea and Solozano 2005), and cardamom (Raman 2006), can contain many of the forest-associated species found in nearby mature forests and can provide important buffers around, or connections between, forested areas (Castellon and Sieving 2006).

The time spent in disturbed habitat by forest birds, however, may be short-lived (DaSilva et al. 1996, but see Sekercioglu et al. 2007) and highly-dependent on the distance to the nearest forest patch (DaSilva et al. 1996). For example, DaSilva et al. (1996) observed 18 species of frugivorous forest birds flying from secondary forest to abandoned pastures in eastern Amazonia. These species spent only a few minutes in the pastures and rarely traveled more than 80 m from the forest patch. Therefore, although these frugivorous birds were present in the abandoned pasture, their limited use of this habitat suggests that it is of lesser importance than the secondary forest.

The Choco-Andean corridor was initiated by Fundación Maquipucuna and numerous nongovernmental partners in 1992. Its goal is to create a network of protected areas and managed human landscapes that extend from the western crest of the Andes Mountains in northwestern Ecuador to the coastal mangroves of the Pacific Ocean. To date, most of the efforts to connect protected areas have focused on promoting shade-grown cacao, shade-grown coffee, reforestation, and strategic land purchases. Understanding how forest birds use these disturbed habitats and how those habitats can be manipulated to increase that use will be essential in conservation planning throughout the corridor.

We examine the association between upper canopy cover and patterns of occupancy (the probability of species presence) and use (proportion of time spent in an area given presence) for 18 forest interior species (hereafter; forest species) in the tropical Andes region of northwest Ecuador. We use an information-theoretic approach (Burnham and Anderson 2002) to evaluate 3 hypotheses about the relationship between occupancy and increasing upper canopy cover (greater occupancy, greater use, and greater occupancy and use) and 5 hypotheses about the relationship between use and increasing canopy cover (greater use, lower emigration, higher immigration and lower emigration, no effect: emigration, and no effect: stable).

METHODS

Study area

We sampled birds in regenerating and mature forests in the Pichincha province of northwest Ecuador (0.1°N, 78.6°W) from 1285 – 1787m in elevation. This area is part of the Tropical Andes biodiversity hotspot which is the richest and most diverse hotspot on earth (Myers et al. 2000). Average daily minimum and maximum air temperature ranges from 17-26°C with little seasonal change (Rhoades and Coleman 1999). Average annual precipitation is 3200 mm with a distinct dry period in August and September when monthly precipitation drops to less than 100 mm (Rhoades and Coleman 1999).

Sampling

From May 22 to June 28, 2006 one observer conducted five, 10-min 50m-radius point counts from 6:15 to 10:00 a.m. at 28 sites (140 total) representing a gradient of habitat disturbance. Each site was separated by at least 150 meters to reduce the likelihood that individual birds were detected in more than one count. We recorded all birds seen or heard during the count and the time interval in which it was first detected (first 3 min, middle 2 min, or final 5 min, Ralph et al. 1995). We visited sites in order so that the first count at all sites occurred during roughly the same date then the second, third, fourth, and fifth counts at all sites occurred during subsequent and roughly equivalent dates, respectively. This design allowed us to look at patterns of occupancy and use over time within each site.

We measured the percent of total canopy cover and upper canopy cover (trees >5m, Gale 2000) through ocular estimation within the 50m count radius in 5 categories: 0, 1-10, 11-20, 21-40, 41-60, 61-80, and >80%. We used ocular estimation to measure the average percent epiphyte cover for trees within the 50m count radius in 3 categories: 0,1-40, and >40%. We estimated elevation at each site using a Garmin GPS12XL GPS unit.

To represent the gradient of habitat disturbance, we considered total canopy cover, upper canopy cover, and an interaction between canopy cover and epiphytes. Once total canopy cover reached 41-60% only epiphyte cover could distinguish primary from secondary forest; therefore, an interaction between total canopy cover and epiphytes would also represent the transition from secondary to primary forest (Mordecai *unpubl. data*). All 3 representations of habitat disturbance were highly correlated (Pearson Correlation coefficients >0.72), so we chose to only include the measurement of disturbance which was easiest to take in the field, upper canopy cover, in the analysis.

Data analysis

We examined support for 3 hypotheses about the association between forest bird occupancy and upper canopy cover: 1) greater occupancy, 2) greater use, and 3) greater occupancy and use. The greater occupancy hypothesis predicts that forest birds are more likely to occupy sites with greater canopy cover. The greater use hypothesis predicts that the time a forest bird spends in the site is positively related to upper canopy cover. The greater occupancy and use hypothesis is a combination of the first two hypotheses. We defined forest birds as birds either not described as using forest edge or open habitats or described as rarely using forest edge in Ridgely and Greenfield (2001b).

We began by using the detection or nondetection of individual forest species over multiple visits to each site, occupancy modeling (MacKenzie et al. 2002), and program PRESENCE (available at www.mbr-pwrc.usgs.gov/software.html) to analyze the relationship between occupancy and detectability of forest bird species and upper canopy cover. This allowed us to evaluate the greater occupancy hypothesis.

We also indirectly evaluated the greater use hypothesis through the probability of detection. In this study some forest birds will probably leave the 50m radius of a point count between repeated visits to a site; therefore, the probability of detecting a species given that it occupies the site (i.e., detectability) is a combination of the probability that the species is detected given that it is in the 50m radius and the probability that it is inside that radius and thus available to be detected. The probability of being inside the radius would be a direct measure of use; however, it is confounded by the probability of detecting the species when it is inside that radius.

Although we cannot explicitly separate these two quantities at this first stage, there are certain situations in which the relationship between the estimated detection probability and upper canopy cover can be highly suggestive of a relationship driven by amount of use. For example, as canopy cover increases, the greater amount of vegetation potentially between the bird and the observer should make birds within the count radius harder to detect by both sight and sound. Therefore, if the probability of detection increases with upper canopy cover, it suggests that availability for detection (i.e., time spent) in the count is also increasing.

Then, we directly investigated the relationship between upper canopy cover and use by examining support for 5 hypotheses: 1) Greater use, 2) Lower emigration, 3) Higher immigrations and lower emigration, 4) No effect: emigration, and 5) No effect: stable. The greater use hypothesis predicts that use of habitat by forest species increases with upper canopy cover. The lower emigration hypothesis predicts that the probability of a forest species leaving the site over the sampling period declines with increasing canopy cover. This hypothesis represents an interaction between season and use where, as the season progresses, the relationship between upper canopy cover and use changes. The higher immigration and lower emigration hypothesis predicts that the probability of a forest species leaving the site over the sampling period declines while the probability that a new forest species enters the site increases with increasing canopy cover. The no effect: stable hypothesis predicts that use does not change over sampling period and is not related to canopy cover while the no effect: emigration hypothesis predicts that although use is not related to canopy cover it still declines over the sample period.

We used time of first detection during multiple visits to each site, multi-season occupancy models (MacKenzie et al. 2003), and program PRESENCE to separate level of use and detectability. To analyze time of first detection data in program PRESENCE, we treated all periods after a detection as missing data. We assumed that species do not leave the count radius during the 10 min count but can leave and reenter between visits. This species turnover between counts allowed us to directly estimate patterns of use.

We tested 4 structural models for each occupancy hypothesis: main effects alone, main effects and an influence of elevation on occupancy and detection, main effects and species-specific detectability, and main effects, elevation, and species specific detectability. This resulted in 12 total models for the analysis of occupancy. We tested 5 structural models for each use hypothesis: main effects alone, main effects and an influence of elevation on the main effects, main effects and species-specific detectability, main effects and an influence of upper canopy cover on detectability, and main effects, elevations, upper canopy cover on detectability, and species-specific detectability. This resulted in 30 total models for the analysis of use.

RESULTS

We detected 18 species of forest birds during point count surveys (Table 4.1). One of these species is primarily frugivorous, six are omnivorous, and the rest are insectivorous (Ridgely and Greenfield 2001a). All sites, with the exception of one with no upper canopy cover, had forest bird detections.

One model, representing the greater occupancy hypothesis, best fit patterns of forest bird detections (AIC weight = .84, all other models with ΔAIC>4.26, Table 4.2). Occupancy was very low (0.001 to 0.033) from 0-10% upper canopy cover with a sharp increase from 11-40%, which then leveled off to almost 1 at >41% (Fig. 4.1). Species-specific detectability ranged from 0.01 (CI: 0.001-0.07) for the Ochre-breasted Antpitta and Collared Trogon to 0.49 (CI: 0.39-0.59) for the Orange-billed Euphonia (scientific names appear in Table 4.1). Elevation had a negative but non significant association with occupancy (CI: -3.7-0.23) and a significant positive association with detectability (CI 0.16-0.50) on the logit scale.

Models using all three time periods within a count (first 3 min, middle 2 min, and final 5 min) to examine forest bird use failed to converge so we limited our analysis to only the first two time periods. Even after focusing only on the first two time periods, models with species-specific detectability and those controlling for elevation failed to converge so we only considered models without species-specific detectability and elevation. This resulted in 2 structural models for each of the 5 use-related hypotheses. Two models, both representing the lower emigration hypothesis, had good empirical support (ΔAIC<4, Burnham and Anderson 2002, Table 4.3). The model-averaged estimate of emigration was essentially 1 from 0 to 10% upper canopy cover with a sharp decrease from 11 to 20%, which then leveled off to almost 0 for >21% upper canopy cover (Fig. 4.2). Estimates of detectability from the best model (All other models with ΔAIC>2, Burnham and Anderson 2002) was 0.19 (CI: 0-.99) for the first 3 min and 0.07 (CI: 0-0.99) for the middle 2 min.

DISCUSSION

Forest birds exhibited a strong threshold response to disturbance in both occupancy and use. When upper canopy cover decreased below 21-40%, there was a sharp decline in both forest bird occupancy and the probability that a forest bird would continue to use the area as the season progressed. This suggests that disturbed habitat in the region (which is primarily abandoned pasture) may only be valuable to forest birds after a certain level of regeneration.

To our knowledge, this is the first study to demonstrate a threshold response to disturbance in both occupancy and within-year use. An ecological threshold is a region or point where an abrupt change occurs from one ecosystem condition to another (Luck 2005, Groffman et al. 2006, Denoel and Ficetola 2007). Although the use of thresholds in conservation and management holds great promise (Drinnan 2005, Guenette and Villard 2005, Denoel and Ficetola 2007), empirical studies have shown mixed results (reviewed in Huggett 2005). For example, while bird, frog, plant, and fungi richness show a threshold response to habitat fragmentation in urban areas of Sydney, Australia (Drinnan 2005), an examination of the response of mammal, reptile and bird communities in southeastern Australia to variation in patterns of native and exotic vegetation cover found no evidence of a threshold (Lindenmayer et al. 1999, Lindenmayer et al. 2002, Lindenmayer et al. 2005).

To our knowledge, this is also the first study to demonstrate a threshold response to disturbance in the tropics while quantitatively accounting for differences in detectability. The issue of detectability further complicates not only the investigation of ecological thresholds but any analysis of species-habitat relationships. Few species are always detected when present and if detectability varies with habitat than estimated relationships can be biased (reviewed in Thompson 2002). Although accounting for detectability in estimation of species-habitat relationships is becoming more common (e.g. O'Connell et al. 2006, Yates and Muzika 2006, Huste and Boulinier 2007), existing studies investigating ecological thresholds have not (e.g. Drinnan 2005, Guenette and Villard 2005, Lindenmayer et al. 2005).

The threshold level identified in this study corresponds well with management recommendations for another disturbed habitat of potential conservation value, coffee. Certification guidelines by the Smithsonian Institution for “bird friendly” coffee (available at http://nationalzoo.si.edu/ConservationAndScience/MigratoryBirds/Coffee/Certification/criteria.cfm) and by the Rainforest Alliance for “sustainable” coffee (available at http://www.rainforest-alliance.org/programs/agriculture/certifiedcrops/standards_2005.html) require at least 40% total canopy cover. Of the 6 sites with an upper canopy cover of 21-40% (the identified threshold), 3 sites had a total canopy cover of 41-60% and 1 site had a total canopy cover of 61-80% (Mordecai *unpubl. data*). The agreement between our results and management recommendations from these two organizations suggests that there may be consistent threshold responses to disturbance by forest birds in a variety of tropical areas.

This threshold response probably occurs only in disturbed areas near forest. All of our study sites were adjacent to forested areas and thus our results only apply to disturbed areas near forests; however, many studies have shown that the distance to nearby forest can strongly affect bird communities (e.g. Luck and Daily 2003, Perfecto et al. 2003). The importance of nearby forest in previous studies further supports the contention that the primary value of disturbed habitats is as a buffer around, or a connector between, protected forests.

Aside from providing preliminary guidance for conservation planning, our results also demonstrate the value of investigating patterns of both use and occupancy across ecological gradients. While forest bird occupancy showed a relatively simple threshold response to upper canopy cover, the analysis of use revealed a more complex pattern. The negative relationship between upper canopy cover and emigration during the study period suggests that use of disturbed habitats by forest birds can be strongly seasonal.

The desertion of more disturbed habitats in this study corresponds with the onset of the dry season. During the wet and dry season in Panama, Richards and Windsor (2007) compared arthropod abundance between canopy gaps and nearby understory. During the wet season they found 34% more arthropods in canopy gaps but in the dry season they found 32% more arthropods in nearby understory. Arthropods comprise at least part of the diet of 17 of the 18 forest birds examined in this study and it is possible that the shift in use away from disturbed habitat leading up to the dry season may be driven by concurrent changes in food resources (i.e. arthropods).

The threshold identified in this study will provide a preliminary quantitative target for conservation planning throughout the Choco-Andean Corridor. This target, however, is only preliminary and we have established a long-term bird monitoring program throughout the corridor to examine numerous unresolved issues. These issues include: potential threshold responses to canopy cover and tree diversity in shade-grown coffee and shade-grown cacao, seasonal trends in occupancy and use, and the influence of landscape context on regional bird communities.

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Table 4.1. Forest species detected during point count surveys from May 22 to June 28, 2006 at 1285 – 1787m in elevation. Association with forest and diet (F = frugivorous, O = omnivorous, I = insectivorous) from Ridgely and Greenfield (2001b, 2001a).

Common Name	**Scientific Name**	**Diet**
Orange-bellied Euphonia	*Euphonia xanthogaster*	F
Broad-billed Motmot	*Electron platyrhynchum*	I
Esmeraldas Antbird	*Myrmeciza nigricauda*	I
Immaculate Antbird	*Myrmeciza immaculata*	I
Ochre-breasted Antpitta	*Grallaricula flavirostris*	I
Plain Antvireo	*Dysithamnus mentalis*	I
Plain-brown Woodcreeper	*Dendrocincla fuliginosa*	I
Rufous-breasted Antthrush	*Formicarius rufipectus*	I
Slaty Antwren	*Mymotherula schisticolor*	I
Strong-billed Woodcreeper	*Xiphocolaptes promeropirhynchus*	I
Three-striped Warbler	*Basileuterus tristriatus*	I
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*	I
Chestnut-capped Brush-Finch	*Atlapetes brunneinucha*	O
Masked Trogon	*Trogon personatus*	O
Orange-billed Sparrow	*Arremon aurantiirostris*	O
Rufous-throated Tanager	*Tangara rufigula*	O
Scaled Fruiteater	*Ampelioides tschudii*	O
Spotted Nightingale-Thrush	*Catharus dryas*	O

Table 4.2. Model selection results and associated hypotheses for the relationship between upper canopy cover (Can) and occupancy (*ψ*) and detection (*p*). Elev indicates a covariate for elevation and Sp indicates species-specific detection probabilities. Models are ordered by the difference in Akaike Information Criterion (Δ_i) and Akaike weights (w_i). Superscripts of + or – indicate the direction of the estimate and * indicates 95% confidence intervals that do not overlap zero. Only models with some empirical support (ΔAIC<10, Burnham and Anderson 2002) are shown.

Hypothesis	Model	Δ_i	w_i	K
↑ occupancy	$\Psi(\text{Can}^{(+)*}, \text{Elev}^{(-)})\ p(\text{Elev}^{(+)*}, \text{Sp})$	0	0.84	22
↑ use	$\Psi(\text{Elev}^{(-)})\ p(\text{Can}^{(+)*}, \text{Elev}^{(+)*}, \text{Sp})$	4.3	0.10	22
↑ occupancy ↑ use	$\Psi(\text{Can}^{(+)}, \text{Elev}^{(-)})\ p(\text{Can}^{(+)}, \text{Elev}^{(+)*}, \text{Sp})$	5.7	0.05	23
↑ occupancy	$\Psi(\text{Can}^{(+)})\ p(\text{Sp})$	9.5	0.01	20
↑ occupancy ↑ use	$\Psi(\text{Can}^{(+)*})\ p(\text{Can}^{(+)*}, \text{Sp})$	9.8	0.01	21

Table 4.3. Model selection results and associated hypotheses for the relationship between upper canopy cover (Can) and initial occupancy (ψ_i), colonization (γ), extinction (ε), and detection (p). Models are ordered by the difference in Akaike Information Criterion (Δ_i) and Akaike weights (w_i). Superscripts of + or – indicate the direction of the estimate and * indicates 95% confidence intervals that do not overlap zero. Only models with some empirical support (ΔAIC<10, Burnham and Anderson 2002) are shown.

Hypothesis	Model	Δ_i	w_i	K
↓Emigration	$\Psi_i(.)\gamma(.)\varepsilon(\mathrm{Can}^{(-)*})p(\mathrm{t})$	0	0.68	6
↓Emigration	$\Psi_i(.)\gamma(.)\varepsilon(\mathrm{Can}^{(-)*})p(\mathrm{Can}^{(+)},\mathrm{t})$	2.0	0.25	8
↑Immigration ↓Emigration	$\Psi_i(\mathrm{Can}^{(+)})\gamma(\mathrm{Can}^{(+)})\varepsilon(\mathrm{Can}^{(-)*})p(\mathrm{Can}^{(+)},\mathrm{t})$	5.6	0.04	10

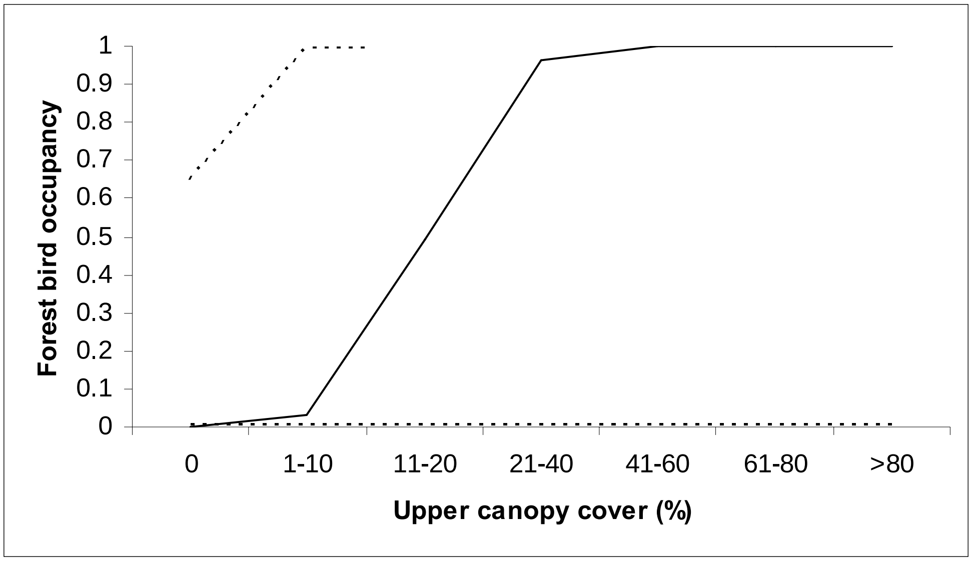

Fig. 4.1. Threshold response in forest bird occupancy to upper canopy cover. Dashed lines indicate a 95% confidence interval for predictions.

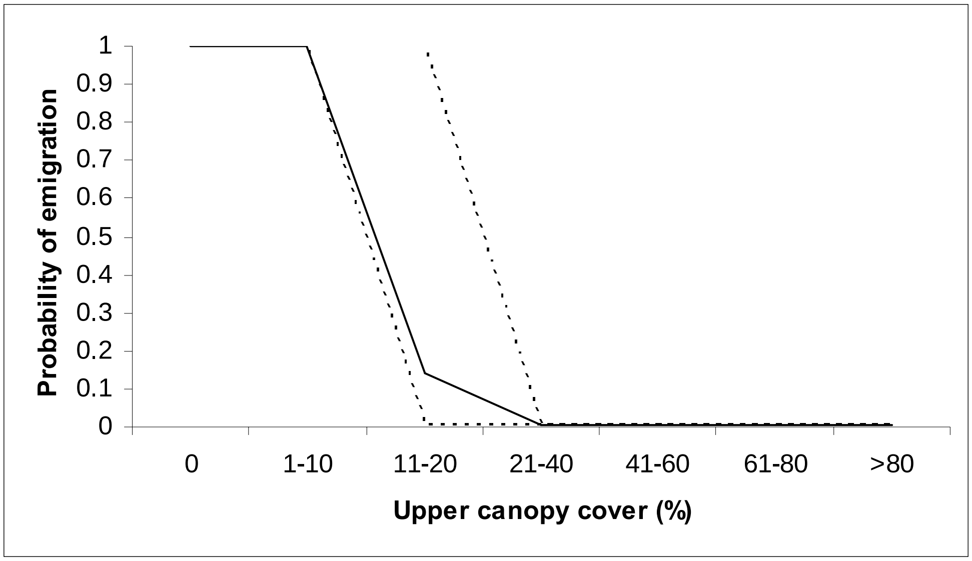

Fig. 4.2. Threshold response in forest bird extinction (i.e. species stops using the patch as the season progresses) to upper canopy cover. Dashed lines indicate a 95% confidence interval for predictions.

CHAPTER 5

SUMMARY AND CONCLUSIONS

SUMMARY AND CONCLUSIONS

In the preceding chapters we provided new methods and unique approaches to the analysis of occupancy and use from detection-nondetection data. Despite the inherent relationship between occupancy and use, these two quantities are usually estimated separately using different data and protocols. Through these new methods and approaches, we demonstrate that occupancy and use can be estimated simultaneously using simple and easy-to-collect data. By leveraging simple and easy to collect data, the techniques described in this dissertation can be applied to projects ranging from large-scale volunteer-driven monitoring programs to small-scale experiments.

In chapter 1, we summarized literature on the estimation of occupancy and use in addition to providing a general introduction to Bayesian statistics and MCMC. In chapter 2, we built on previous methods of Azuma el al. (1990), MacKenzie et al. (2002), and others to construct a model that estimates occupancy and use through repeated visits to a site and two different scales. Simulations with 5 repeated samples at each scale demonstrated that estimates and credible interval coverage are relatively unbiased when the probability of detecting a species at a site given the site is occupied is ≥0.3. Bias could be reduced by increasing the number of repeated samples. An example analysis of green frog (*Lithobates clamitans*) data demonstrated that use and detection can respond differently to a single covariate.

In chapter 3, we applied the newly-developed multi-scale occupancy model of Chapter 2 to examine the relationship between habitat and acoustic evidence of Ivory-billed Woodpeckers while controlling for the proportion of area sampled. We found a negative relationship between either detection or occupancy and density of big trees.

Ivory-billed Woodpeckers are historically associated with areas of large trees, and one might expect dense stands of large trees to attract this woodpecker. Density of big trees (>60.96 cm dbh) in this area, however, decreases with increasing density of even bigger trees, so the decrease in big tree density probably represents an ecological transition to fewer, but even larger, trees. When using acoustic surveys for evidence of Ivory-billed Woodpecker, our results suggest that demonstrating absence at a 90% confidence level, even at low densities of big trees, would be difficult, and more efficient survey techniques will be needed. A negative relationship between percent area surveyed and the availability of evidence to an ARU likely resulted from a pattern of nonrandom sampling. In "hot spots" with much additional evidence of Ivory-billed Woodpecker presence (e.g., sightings, feeding sign), recording units were generally placed near such evidence rather than a random or evenly-distributed sampling design. In patches with little or no previous evidence, recording units were more evenly distributed in an ad-hoc fashion. Thus, the percent patch surveyed represents the level of nonrandom sampling within the patch and the new multi-scale occupancy models allowed us to statistically control for this nonrandom sampling.

In chapter 4, we examined the relationship between habitat disturbance and occupancy and use in northwest Ecuador. Both occupancy and use showed strong threshold responses at 21-40% upper canopy cover with the probability of occupancy increasing from roughly 0 to 1 and emigration (the probability that a species would stop using the site during the study period) decreasing from roughly 1 to 0. Bird surveys ended near the beginning of the dry season and high levels of emigration in more disturbed areas implied that forest birds stopped using these areas as the dry season approached, possibly due to a shift in food resources. Patterns of use and occupancy suggest that disturbed habitat in the region (which is primarily abandoned pasture) may only be valuable to forest birds after a specific level of regeneration and during certain times of the season.

The novel insights provided throughout this dissertation highlight the value of analyzing both occupancy and use in a variety of ecological contexts. Whether analyzing a single species sampling problem (chapter 3), or a multi-species conservation problem (chapter 4), estimation of use and occupancy provides an efficient and unbiased method to understand how species interact with their environment.

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