



## AN ABSTRACT OF THE DISSERTATION OF

Jonathon J. Valente for the degree of Doctor of Philosophy in Forest Ecosystems and Society presented on May 31, 2017.

Title: Identifying Factors Driving Sensitivity to Fragmentation in Forest Breeding Songbirds

Abstract approved: \_\_\_\_\_

Matthew G. Betts

Habitat loss and fragmentation are the greatest threats to biodiversity worldwide. Fragmentation impacts landscape configuration, resulting in a larger number of patches that are smaller in size and further apart from one another. Island biogeography and metapopulation theory predict populations in these remnant patches should be smaller, have higher extinction rates, and be less likely to receive immigrants from other populations. However, empirical data frequently do not conform with these theoretical predictions, leading to assertions that this model is too simplistic to describe distributions and dynamics of fragmented populations. However, others believe that landscape configuration effects have been poorly tested and modeled to date. In this dissertation, I use breeding bird data collected in a fragmented forest landscape to explore this lack of congruence between theory and reality. I first test the hypothesis that heterogeneity in the detectability of mobile species due to temporary emigration from sample sites can produce biased estimates of metapopulation rates. Next, I test for idiosyncrasies in the effects of forest loss and fragmentation on species belonging to different ecological trait groups. Lastly, I examine whether fragmentation actually reduces the functional connectivity of landscapes for species identified as fragmentation-sensitive.

Dynamic occupancy models are popular for estimating metapopulation dynamic rates (colonization and extinction) from repeated presence/absence surveys of unmarked animals. This approach assumes closure among repeated samples within primary periods, allowing estimation of dynamic rates between these periods. However, the impact of temporary emigration (reversible changes in sampling availability) on dynamic rate estimates has not been tested. In Chapter 2, I use simulated data to investigate the degree to which temporary emigration could mislead researchers interested in quantifying metapopulation rates. I then compared results from three avian point count datasets to evaluate the likelihood that temporary emigration confounds estimates of dynamics for 19 species under a popular sampling protocol. Simulated experiments indicated that when secondary periods were open to temporary emigration, presence of dynamics was identified  $\geq 95.1\%$  of the time, and dynamic rate estimates were accurate. However, dynamic rates were biased when secondary periods were closed to temporary emigration. In empirical datasets, dynamic occupancy models had greater support than closed models for all species when secondary sampling periods occurred in immediate succession (i.e., 3 samples within 10 minutes); however, my results suggest that this is because these estimates were heavily influenced by temporary emigration. When counts within a primary period were separated by 24-48 hours, I found evidence of dynamics for less than half of these species. I recommend an alternative sampling approach that allows accurate estimation of dynamic rates when temporary emigration is of no interest, and introduce a novel model for estimating both processes simultaneously in rare cases where they are both of biological interest. Concern for violating the occupancy modeling closure assumption has led to widespread recommendations that samples within primary periods be conducted extremely close in time. However, these results indicate this is not the best approach when interest is in quantifying

dynamic rates. While dynamic occupancy models provide estimates of ‘colonization’ and ‘extinction,’ these values do not inherently represent dynamics unless temporary emigration has been explicitly modeled or accounted for with sampling design. Naivete to this fact can result in incorrect conclusions about biological processes.

While theory predicts that fragmentation should negatively influence biodiversity, empirical support of this idea is weak in terrestrial systems. However, tests of fragmentation effects are typically confounded with landscape composition and potentially obscured by imperfect detection. In Chapter 3, I used multi-species occupancy models and a mensurative experimental design to test competing hypotheses about how forest fragmentation influences distributions of breeding forest bird species and communities. During the breeding seasons of 2011-2013, we recorded over 80,000 bird detections in 202 forest fragments using a sampling design that isolated the effects of patch size per se from the effects of forest amount (2 km), edge, local vegetation, and sample area. I modeled the effects of these covariates on distributions of individual species categorized by ecological trait groups (i.e., forest, forest interior, or forest edge). Though my results indicated little effect of patch size on total species richness, increasing patch size tended to have a positive effect on interior species, and a negative effect on edge species. The effects of total forest amount were much more variable, and actually had a negative influence on many species, particularly cavity nesters. My results do not support theoretical predictions that forest patch size should positively influence bird species richness. However, composition of bird communities does shift toward edge species from interior species with decreasing patch size. Maintaining large forest patches is thus critical for supporting forest interior species, which tend to be of greater conservation concern.

Maintenance of metapopulations requires movement of dispersers among resource patches. The degree to which a landscape facilitates or impedes such movements is defined as *functional connectivity*. Habitat fragmentation may reduce the functional connectivity of a landscape, but empirical linkages between distribution patterns and movement ability are lacking. In Chapter 4, I use experimental translocations to test whether forest fragmentation impedes movement of two species identified as fragmentation-sensitive in Chapter 3: Wood Thrush (*Hylocichla mustelina*) and Ovenbirds (*Seiurus aurocapilla*). I also tested for behavioral changes in translocated birds and evaluated whether fragmentation effects differed between behavioral modes. Over two breeding seasons, we translocated 35 Wood Thrush and 19 Ovenbirds (1-1.2 km) across landscapes spanning a fragmentation gradient and recorded their movement paths using VHF transmitters and receivers. Eighty-seven percent of individuals returned successfully, taking as long as 72.2 hours. Movement patterns of 96% of successful birds indicated two distinct behavioral modes: *exploring*, characterized by short, undirected movements and course reversals; and *homing*, characterized by large, fast steps towards their home territories. Forest composition and configuration had no effect on homing time or path straightness for either species. However, at a finer scale, I found that both preferred to take steps that minimized their exposure to non-forested gaps. My results demonstrate that movement limitation could drive or exacerbate fragmentation sensitivity for these birds. Further, while fragmentation effects did not differ between behavioral modes, my results highlight the need to link the dichotomous behaviors of translocated animals with natural movement processes. Despite this knowledge gap, results from our study suggest that maintaining contiguous habitat or corridors may improve functional connectivity for fragmentation-sensitive birds.

©Copyright by Jonathon J. Valente  
May 31, 2017  
All Rights Reserved

Identifying Factors Driving Sensitivity to Fragmentation in Forest Breeding Songbirds

by  
Jonathon J. Valente

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Doctor of Philosophy

Presented May 31, 2017  
Commencement June 2017

Doctor of Philosophy dissertation of Jonathon J. Valente presented on May 31, 2017

APPROVED:

---

Major Professor, representing Forest Ecosystems and Society

---

Head of the Department of Forest Ecosystems and Society

---

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

---

Jonathon J. Valente, Author



## ACKNOWLEDGEMENTS

First and foremost, I thank Kelsey McCune for being by my side through this whole process. The most valuable thing I gained from this PhD is you. I thank my parents for being there at every tee ball game, grade school function, and now for traveling across the country for my PhD defense. I am extremely fortunate to have that kind of support. I thank Matt Betts for being probably the most brilliant person I have ever worked with, and for giving me something to aspire to. I thank Richard Fischer for hiring me many years ago, and for continuing to find ways to keep us working together. I hope the projects never end. I thank T. Brandt Ryder for too many things to count, but particularly for his confidence in me, and for always being just a phone call away.

I thank Peter Marra, and Scott Sillett for all of their financial, logistical, and intellectual support. The original ideas and funding for this project began with them, and I hope I have met their expectations. I also thank Calandra Stanley for being such a great colleague and friend in the field. I thank Rebecca Hutchinson, Adam Hadley, Sarah Frey, Joe Northrup, Urs Kormann, Jim Rivers, and all of the other lab mates I have shared time and space with over the last few years. I am fortunate that Matt has chosen to surround himself with such smart, talented, and helpful people.

I have received substantial additional support from the other members of my committee as well. I thank Lisa Ganio for the long hours spent helping me develop and implement the analyses in this document, Nathan Schumaker for making me think outside the box, and John Simonsen for his willingness to serve as my Graduate Council Representative. I also owe a great debt of gratitude to the support staff in the College of Forestry, including Jessica Bagley, Patricia

Cordova, Meghan Foster, Megan Hickman, Misty Magers, Melora Park, Alan Rudisill, Justin Schaffer, Kristie Williams, and Penny Wright. You all pulled me out of a number of holes, and kept me from falling into many others. Thank you.

None of this would have been possible without the help of our dedicated field technicians, and my friends: Megan Arias, Carl Bochmann, Sean Campbell, Ellen Comeau, Shawn Duncan, Rachel Gardner, Lauren Gillespie, Gordon Gover, Vinnie Johnson, Ryan Lancour, Nolan Lancaster, Abby Lanham, Christa LeGrande, Sonia Levitt, Brian Slaby, Christina Slover, Robert Snowden, Josh Suich, Rachel Tamulonis, Anna Tucker, Ryan Ubias, Marcel Villar, Rachel Wadleigh, Chris Winter, and Samantha Wolfe. I spent many arduous hours working in the forests of southern Indiana, and I'm glad you were with me. In many ways, this work represents more of your blood, sweat, and tears than my own.

Over six years of working in southern Indiana, I received logistical support from far too many people to count. I greatly appreciate the friendship and support we received from the staff at West Boggs Park in Loogootee, Indiana, especially Mike Axsom, Debbie Crays, Susan Harrawood, and Jameson Hibbs. In addition, Steve Andrews (Naval Surface Warfare Center Crane) and Joe Robb (Big Oaks National Wildlife Refuge) endured more than a few of headaches in dealing with this project, but never failed to provide the resources we needed to be successful. I also thank Chris Schmitt for giving me a place to come back to in Louisville, and for hosting some pretty outstanding 'bird people' parties.

I've made many additional friends along the way, and I appreciate everyone's support. I particularly thank Evan Bredeweg, Arianne Eason, and Burke Greer, for talking with me about science, or anything but science, when necessary.

Lastly, my work would not have been possible without extensive financial assistance, and I am tremendously grateful to all who supported me. Funding for this research was provided by the Department of Defense Strategic Environmental Research and Development Program (grant number RC-2121), and the Environmental Quality and Installations mission through the U.S. Army Engineer Research and Development Center. I also received support from the Oregon State University Graduate School (Provost's Distinguished Graduate Fellowship, Oregon Lottery Graduate Scholarship, and Targeted Graduate Tuition Scholarship), the Smithsonian Conservation Biology Institute's Migratory Bird Center (Smithsonian Pre-doctoral Fellowship), the Oregon State University College of Forestry (Alfred W. Moltke Memorial Scholarship, Dorothy D. Hoener Memorial Fund Fellowship, and Doctoral Student Fellowship), and the Oregon State University Department of Forest Ecosystems and Society (James H. Dukes Jr. Graduate Fellowship). Thank you.

## CONTRIBUTION OF AUTHORS

Matthew G. Betts and Rebecca A. Hutchinson helped conceive the ideas and develop the study design in Chapter 2. Both also contributed substantial edits to the many iterations of this manuscript.

Matthew G. Betts provided substantial input on the design, collection, and analysis of the data in Chapter 3. He also provided edits and comments on numerous drafts.

Richard A. Fischer provided financial and logistical support for Chapter 4. He, along with T. Brandt Ryder and Matthew G. Betts, helped develop the study design, acquire permits, and provided substantial feedback on manuscript drafts.

## TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION.....	1
DISTINGUISHING DISTRIBUTION DYNAMICS FROM TEMPORARY EMIGRATION USING DYNAMIC OCCUPANCY MODELS.....	6
INTRODUCTION.....	6
MATERIALS AND METHODS.....	10
Simulated Data.....	10
Dynamic, Multi-Scale Occupancy Model.....	12
Empirical Case Study.....	13
RESULTS.....	15
Simulated Data.....	15
Dynamic, Multi-Scale Occupancy Model.....	16
Empirical Case Study.....	16
DISCUSSION.....	17
RESPONSE TO FRAGMENTATION BY AVIAN COMMUNITIES IS MEDIATED BY SPECIES TRAITS.....	28
INTRODUCTION.....	28
MATERIALS AND METHODS.....	31
Sampling Design.....	31
Bird and Vegetation Sampling.....	34
Data Analyses.....	35
RESULTS.....	40
Detection Probability.....	42

## TABLE OF CONTENTS (Continued)

	<u>Page</u>
DISCUSSION.....	42
FOREST GAPS REDUCE LANDSCAPE CONNECTIVITY FOR FRAGMENTATION- SENSITIVE BIRDS IN MULTIPLE BEHAVIORAL STATES.....	52
INTRODUCTION.....	52
MATERIALS AND METHODS.....	55
Study Species and Sites.....	55
Translocations and Tracking.....	56
Behavioral Change Point Analysis.....	58
Landscape Effects on Movement.....	60
Path-Level Analyses.....	61
Step-Level Analyses.....	62
RESULTS.....	64
Behavioral Change Point Analysis.....	64
Path-Level Analyses.....	65
Step-Level Analyses.....	65
DISCUSSION.....	66
CONCLUSION.....	81
BIBLIOGRAPHY.....	85
APPENDICES.....	96

## LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
2.1	When practitioners of dynamic occupancy models ensure complete site closure within primary periods, changes in sampling availability stemming from temporary emigration may not be distinguishable from distributional changes in territory locations.....23
2.2	A schematic outlining the structure of the three occupancy datasets constructed from repeated point counts at 193 locations in southern Indiana in the summer of 2014.....24
2.3	A comparison of the parameter estimates generated by open occupancy models fit to the confounded TE/dynamics and isolated TE empirical datasets for 19 forest-breeding songbirds.....25
2.4	A comparison of the parameter estimates generated by open occupancy models fit to the confounded TE/dynamics and isolated dynamics datasets for nine forest-breeding songbirds.....26
2.5	To quantify distribution dynamics independently from temporary emigration, secondary samples should be spaced far enough apart in time that probability of availability is independent on each repeated visit, but true changes in site use are negligible.....27
3.1	A map of the study region in which we conducted breeding bird point counts between 2011 and 2013.....47
3.2	Posterior means and 95% credible intervals for the effects of a) edge distance, b) amount of forest within 2 km, and c) log-transformed patch size on probability of occupancy for breeding forest bird communities.....48
3.3	Predicted richness ( $\pm$ 95% credible intervals) of breeding forest birds occupying a 50 m radius forest plot varies as a function of forest patch size (left) local forest cover (right), and ecological trait group.....49
3.4	The inverse logit of the detection probability intercept for 52 species classified as edge specialists, forest generalists, or interior specialists.....50
3.5	The distribution of conservation concern scores for 52 species classified as edge specialists, forest generalists, or interior specialists (NABCI 2016).....51
4.1	Locations of field sites (Naval Surface Warfare Center Crane and Glendale Fish and Wildlife Area) used for experimental translocations of Ovenbirds and Wood Thrush in southern Indiana.....78

## LIST OF FIGURES (Continued)

<u>Figure</u>		<u>Page</u>
4.2	Kaplan-Meier homing success curves for translocated Wood Thrush and Ovenbirds.....	79
4.3	A comparison of the distribution of turning and deviation angles between exploring and homing phases for translocated Wood Thrush (WOTH) and Ovenbirds (OVEN).....	80



## LIST OF TABLES

<u>Table</u>		<u>Page</u>
2.1	A comparison of static and dynamic occupancy models fit to simulated presence-absence survey data where distribution dynamics were absent.....	22
4.1	Competing models developed to evaluate the effects of exposure to non-forested habitat on step selection decisions by translocated Wood Thrush and Ovenbirds.....	71
4.2	Results from linear mixed effects models testing for differences in median step distance and speed between exploratory and homing phases for translocated Wood Thrush and Ovenbirds.....	72
4.3	A comparison of models that explore effects of forest loss and fragmentation on homing time and path straightness of translocated Wood Thrush and Ovenbirds.....	73
4.4	Results from mixed conditional logistic regression models evaluating factors influencing movement decisions of translocated Wood Thrush and Ovenbirds.....	75
4.5	Parameter estimates from the top step-level models explaining movement decisions of translocated Wood Thrush and Ovenbirds.....	77

## LIST OF APPENDICES

<u>Appendix</u>	<u>Page</u>
A	SUPPLEMENTARY TABLES AND FIGURES.....97
B	R CODE USED FOR SIMULATION AND ANALYSIS OF OCCUPANCY AND USE SAMPLING DATA..... 129
C	A DYNAMIC, MULTI-SCALE OCCUPANCY MODEL FOR ESTIMATING BOTH TEMPORARY EMIGRATION AND DYNAMIC DISTRIBUTION RATES FROM REPEATED PRESENCE-ABSENCE SURVEYS..... 133
	Sampling Situation.....133
	Statistical Model and Likelihood..... 134
	Model Extensions.....136
	Simulation Study.....137
	Simulation Results..... 137
	R Code for Simulation and Analysis of Dynamic, Multi-Scale Occupancy Models.....139
D	COMMUNITY OCCUPANCY MODEL SPECIFICATION..... 142
	R and JAGS Code..... 142

## LIST OF APPENDIX FIGURES

<u>Figure</u>		<u>Page</u>
A1	A comparison of the posterior means and credible intervals of the parameter estimates from a community occupancy model that did (solid lines) and did not (dashed lines) include an interaction term between patch size and forest amount.....	125
A2	A comparison of three measures of patch size for the 202 forest patches we sampled.....	126
A3	Plots showing distance from home as a function of time for the 32 translocated Wood Thrush that homed successfully.....	127
A4	Plots showing distance from home as a function of time for the 15 translocated Ovenbirds that homed successfully.....	128

## LIST OF APPENDIX TABLES

<u>Table</u>	<u>Page</u>
A1	The 19 species for which site closure was evaluated under 3 different sampling scenarios (confounded TE/dynamics, isolated TE, and isolated dynamics).....97
A2	A comparison of static and dynamic occupancy models fit to simulated presence-absence survey data where distribution dynamics were present..... 98
A3	Results from the principal components analysis of local vegetation variables recorded at 490 point count stations in southern Indiana between 2011 and 2013..... 99
A4	All species detected at 490 point count stations in southern Indiana during the breeding seasons of 2011-2013 in taxonomic order..... 100
A5	Pearson’s correlation coefficients for the six explanatory variables measured at 490 point count stations between 2011 and 2013..... 103
A6	Means and 95% credible intervals for the posterior distributions of covariate effects on occupancy probabilities of 52 breeding bird species..... 104
A7	Means and 95% credible intervals for the posterior distributions of covariate effects on detection probabilities of 52 breeding bird species.....106
A8	Full results from the behavioral change point analysis for 47 translocated Wood Thrush and Ovenbirds that successfully homed.....108
A9	Full results from models fit in the first phase of path-level model building.....116
A10	Full results from models fit in the second phase of path-level model building..... 118
A11	Full results from all mixed conditional logistic regression models fit to step level data for translocated Wood Thrush and Ovenbirds.....120
C1	Results from dynamic, multi-scale occupancy models fit to simulated datasets..... 138

## INTRODUCTION

Habitat loss and degradation are considered the greatest threats to biodiversity worldwide (Pimm & Raven 2000, Pereira et al. 2010, Rands et al. 2010), and one major impact of habitat destruction is fragmentation, the breaking apart of contiguous habitat (Fahrig 2003). The process of fragmentation usually alters the configuration of the remnant habitat, resulting in smaller habitat patches, an increase in the number of patches, and increased distance between those patches (Fahrig 2003). Early developments in island biogeography (MacArthur & Wilson 1967) and metapopulation (Levins 1969) theory have historically framed the way ecologists conceptualize fragmented landscapes: as patchy distributions of resources bounding subpopulations that are characterized by idiosyncratic population parameters (Fretwell & Lucas 1970, Wiens 1976, Pulliam 1988, Pulliam & Danielson 1991, Hanski 1991, 1998, Fahrig & Merriam 1994). These theories predict that patch occupancy rates for individual species should decrease as a function of fragmentation due to demographic processes. Smaller patches should contain smaller populations that are more likely to go extinct due to stochastic events, and less likely to be re-colonized from other patches due to isolation.

Yet, whether fragmented habitat patches can or should be viewed analogously to islands remains controversial. For instance, it is the basis of a decades long debate over whether large patches have greater conservation value than small patches (Terborgh 1974, Diamond 1975, May 1975, Wilson & Willis 1975, Simberloff & Abele 1976, Fahrig 2013,2015, Hanski 2015). Increased patchiness can actually have positive effects on population demography by creating temporary refuges from predators (Huffaker 1958), promoting coexistence of competitive species (Levins & Culver 1971), and spatially spreading the risk of extinction (Den Boer 1968).

Fragmentation also increases landscape heterogeneity, which can promote biodiversity. Not only does it lead to more diversity of habitat types, but also to heterogeneity in biophysical properties around the edges of remnant habitat (Ries et al. 2004, Fischer & Lindenmayer 2007, Fletcher et al. 2007). Finally, unlike in island-ocean systems, terrestrial landscapes are often characterized by biotic and abiotic gradients, and the assumption of homogeneity within patch or matrix habitat is likely poor in many cases (Austin 1985, McIntyre & Barrett 1992, Wiens 1994, McIntyre & Hobbs 1999, Manning et al. 2004, Fischer & Lindenmayer 2006).

Results from empirical studies on fragmentation effects are mixed. Experimental efforts reveal strong, consistent negative impacts on abundance, richness, connectivity, ecosystem services, and ecosystem function (reviewed by Haddad et al. 2015). Results from observational studies, on the other hand, tend to demonstrate little congruency between theory and reality (Fahrig 2003, 2013, 2017, Prugh et al. 2008, Betts et al. 2014). For instance, in their review of patch size and isolation effects, Prugh et al. (2008) found that both were poor predictors of species occupancy patterns across taxa. In another review of landscape scale studies, Fahrig (2017) actually concluded that fragmentation rarely has significant effects on species distribution patterns, and when it does, they are typically positive. This has led some researchers to recommend dropping the patch-island paradigm in favor of a suite of alternative theoretical models (McIntyre & Barrett 1992, Wiens 1994, Baguette 2004, Manning et al. 2004, Fischer & Lindenmayer 2006, Didham et al. 2012, Fahrig 2013, Mendenhall et al. 2014).

Nonetheless, debate over the importance of patch configuration in promoting conservation continues (Fahrig 2013, Hanski 2015, Fahrig 2015), in large part due to widespread assertions that configuration effects have been poorly tested. For instance, despite repeated calls to design studies that disentangle the effects of fragmentation from loss, most still fail to do so

(Fahrig 2003, Hadley & Betts 2016). Thus, while some argue that fragmentation has no effect on species distributions beyond habitat loss (Fahrig 2003, 2013), others contend that this has not been settled (Hanski 2015, Hadley & Betts 2016). Even studies with well-designed sampling schemes often fail to acknowledge heterogeneity in the way species perceive landscapes (Betts et al. 2014). Theoretically, two species should never have identical niches (Gause 1934), and species' perceptions of the landscape should be more important than human perceptions in conservation planning (McIntyre & Hobbs 1999). Thus, others hypothesize that poorly defined patch delineations explain the lack of generalizable results (Betts et al. 2014).

In addition, most fragmentation studies rely on richness as a response variable (Fahrig 2013), ignoring heterogeneity in the way fragmentation affects individual species, and in detectability among species (Kéry & Royle 2008, Zipkin et al. 2009, Iknayan et al. 2014, Yamaura et al. 2016). Treating all species equally may mask life history characteristics that could be linked to fragmentation sensitivity (Bender et al. 1998, Henle et al. 2004, Ewers & Didham 2006), and neglecting to account for imperfect detection can produce demonstrably biased results (e.g., Boulinier et al. 1998, Gu & Swihart 2004, Kéry et al. 2008). Further, multiple processes can impact detection probability, including temporary changes in sampling availability (temporary emigration; Nichols et al. 2009). Studies attempting to quantify metapopulation dynamics in fragmented systems often fail to acknowledge this (Betts et al. 2008, Rota et al. 2009, Gould et al. 2012, McClure & Hill 2012, Otto & Roloff 2012), and it is unclear how that impacts estimates of dynamic rates.

Thus, many questions remain about the impact of fragmentation per se on animal distribution patterns. Birds are excellent study organisms for answering such questions in terrestrial systems. Birds can be identified both visually and aurally, and because they utilize

song in territorial displays and mate attraction, distributional information about a large number of species can be gathered with relatively little effort. In addition, birds can be used as indicators of habitat condition (Bock & Webb 1984, Canterbury et al. 2000), quality (Powell & Powell 1986), and community assemblages for multiple taxonomic groups (Fleishman et al. 2005, Roberge & Angelstam 2006). Yet most importantly, many North American bird species are in decline (Robbins et al. 1989, Askins 1993, James et al. 1996, Holmes & Sherry 2001, Sauer & Link 2002, Lloyd-Evans & Atwood 2004), and habitat loss and fragmentation have been implicated as major causes (Andr en 1994, Robinson et al. 1995, Donovan & Flather 2002). Thus, it is critical that we develop effective tools for sampling and modeling bird distributions in order to implement effective conservation and management strategies in disturbed systems.

In this dissertation, I use occupancy models and translocation experiments to investigate the effects of fragmentation on breeding forest bird communities in southern Indiana. In Chapter 2, I explore the impacts of temporary changes in sampling availability on estimates of colonization and extinction rates from dynamic occupancy models (MacKenzie et al. 2003). Because theory predicts that fragmentation should influence these rates, it is imperative that we develop sound sampling and modeling techniques to appropriately test these predictions. In Chapter 3, I test for the effects of patch size (an indicator of fragmentation) on species distribution patterns while accounting for the confounding effects of habitat amount, edge distance, vegetation heterogeneity, and sample area. I used a sampling scheme that accounts for temporary emigration, and analyzed the data using community occupancy models (K ery & Royle 2008, Zipkin et al. 2009, Iknayan et al. 2014) to quantify detection rates (and factors influencing them) in all species of interest. I then compared the effects of landscape features among species in different ecological trait groups (i.e., forest, forest interior or forest edge specialists). This



approach explicitly acknowledges heterogeneity in species perceptions of the landscape, and highlights traits linked to fragmentation sensitivity. In Chapter 4, I use translocation experiments to test the hypothesis that fragmentation reduces the functional connectivity of a landscape for species identified as fragmentation sensitive. Because, the translocation process itself can impact animal behavior, I also test for behavioral shifts in homing birds, and whether landscape connectivity differs between behavioral modes. Collectively this work represents a substantial step forward in our understanding of how and why fragmentation influences animal distributions, and how to construct appropriate sampling and modeling schemes for identifying those effects.

## DISTINGUISHING DISTRIBUTION DYNAMICS FROM TEMPORARY EMIGRATION USING DYNAMIC OCCUPANCY MODELS

### INTRODUCTION

Many ecological studies rely on presence-absence surveys to identify species distribution patterns and how they vary in space and time. Failing to account for individuals that are present but undetected leads to underestimated distributions, biased estimates of colonization and extinction probabilities, and poor parameterization of resource use models (e.g., Moilanen 2002, Tyre et al. 2003, Gu & Swihart 2004, Kéry et al. 2005, MacKenzie 2005). This realization led to development of a landmark occupancy modeling framework (MacKenzie et al. 2002, Tyre et al. 2003) wherein occupancy and detection probability can be simultaneously estimated from repeated samples of sites that are assumed closed to changes in occupancy. Since its inception, there has been an explosion in use and development of these models to meet numerous estimation needs (Bailey et al. 2014).

Because the *closure assumption* is one of the most important and criticized requirements of occupancy models, much effort has been dedicated to identifying and modeling closure violations. In the strictest interpretation of closure, it is assumed that presence of the species within spatially discrete sampling units does not change between repeated sampling occasions, resulting in an instantaneous “snapshot” of a species’ distribution (MacKenzie & Royle 2005, Latif et al. 2016). Several recent studies have demonstrated that common sampling protocols for birds (Rota et al. 2009, McClure & Hill 2012), salamanders (Otto et al. 2013), anurans (Kendall et al. 2013), and insects (Bried & Pellet 2012) violate the closure assumption, leading some to consider abandoning the method altogether (Hayes & Monfils 2015, Hutto 2016).

Under this strict interpretation, there are two processes that could cause closure violations, the first stemming from temporary changes in sampling availability. A site may be considered *used* (even if not occupied at some instant) if one or more individuals have non-zero probability of being exposed to sampling (MacKenzie & Royle 2005, Nichols et al. 2008, Latif et al. 2016). *Temporary emigration* occurs when all individuals using the site are unavailable for sampling at an instant, and violates the closure assumption when changes in availability occur between sampling visits. Often this arises from a mismatch between the spatial scales of sampling units and animal territories (Nichols et al. 2009, Chandler et al. 2011, Efford & Dawson 2012). For example, if spatially discrete avian point count stations are considered sites, individual territories may only partly overlap the sample space resulting in species presence during only some sampling occasions (Nichols et al. 2009; Fig. 2.1). Similar spatial mismatches can result from any stationary sampling of mobile organisms, such as camera, net, or hair snare trapping (Kendall et al. 1997, Chandler et al. 2011, Efford & Dawson 2012). However, temporary emigration can also arise when at least one individual is spatially present, but otherwise unavailable for detection (Kendall et al. 1997, O'Donnell et al. 2015, Kéry & Royle 2016), for example, due to vertical migration into burrows or below the water surface (O'Donnell et al. 2015). Critically, in each of these scenarios, temporary emigration is a reversible process that results in changes to the occupancy state, but not site use.

Several methods have been proposed for accommodating availability changes in occupancy models. Researchers have made use of multiple detection methods or sampling time scales to simultaneously estimate occupancy and use (Nichols et al. 2008, Mordecai et al. 2011). When site occupancy changes in a non-Markovian way between samples, others recommend simply relaxing the closure assumption and re-interpreting the occupancy parameter as

probability of site use (MacKenzie et al. 2004, MacKenzie & Royle 2005, Latif et al. 2016). In these cases, the detection parameter is also re-interpreted as the product of the probability of availability ( $p_a$ ; the complement of the temporary emigration rate) and probability of detection given availability ( $p_d$ ; Kendall 1999, Nichols et al. 2009). Yet because the number of used sites will always be greater than or equal to the number of occupied sites, site use rates are often considered inferior estimates of a species' distribution (MacKenzie 2005, MacKenzie & Royle 2005, Latif et al. 2016). Thus, others recommend conducting repeated samples simultaneously, or over extremely short time intervals, creating estimates of occupancy not confounded by temporary emigration (MacKenzie & Royle 2005, MacKenzie 2005, Rota et al. 2009, Kendall et al. 2013).

Distribution dynamics can also result in closure violations. We define *distribution dynamics* (henceforth, *dynamics*) as distributional shifts resulting from dispersal or other demographic processes (i.e., births, deaths) that lead to unused sites becoming used, or vice versa. In occupancy models, dynamics can also be accommodated by reducing the interval between sampling periods, or acknowledged by altering the interpretation of occupancy. Alternatively, MacKenzie et al. (2003), developed a dynamic occupancy model that explicitly estimates dynamic rates by utilizing Pollock's robust sampling design (Pollock 1982). This model assumes site closure over repeated secondary sampling periods nested within primary periods, between which dynamic rates are modeled as colonization and extinction. Since development, dynamic occupancy models have been used to test the predictions of island biogeography and metapopulation theory (Ferraz et al. 2007, Pellet et al. 2007), validate metapopulation models (Ozgul et al. 2006), identify source and sink populations (Kerbioui et al. 2012, Peterman et al. 2013, Fisher et al. 2014), estimate population growth rates (Kéry et al.

2010, Kerbiriou et al. 2012), and model biological invasions (Yackulic et al. 2012, Fisher et al. 2014).

Inherent in each of these applications of the dynamic occupancy model is an implicit assumption that the rates modeled between primary periods represent shifting distributions, rather than temporary changes in sampling availability. Yet there is nothing explicit in the model itself that guarantees this. Combining a dynamic occupancy model with a sampling window that ensures complete site closure within primary periods, means that both dynamics and temporary emigration only occur between primary periods. Therefore, both processes may influence colonization and extinction estimates (Fig. 2.1). Numerous recent studies have taken this type of sampling approach. For instance, Otto et al. (2013) estimated salamander extinction rates from secondary periods occurring within 24 hours. In more extreme cases, estimates of amphibian (Gould et al. 2012) and avian (Rota et al. 2009, Betts et al. 2008, McClure & Hill 2012, Otto & Roloff 2012) dynamic rates were generated from secondary periods occurring within minutes of one another. In these scenarios, dynamics may not be distinguishable from temporary emigration (Fig. 2.1); yet tests comparing static and dynamic occupancy models, and the colonization and extinction estimates generated by dynamic models, are frequently assumed to represent distribution dynamics (Rota et al. 2009, Betts et al. 2008, Gould et al. 2012, McClure & Hill 2012, Otto & Roloff 2012). While some authors have acknowledged this potential confounding (Betts et al. 2008, Rota et al. 2009), there has been no evaluation of how temporary emigration might impact model results. Here we use simulated and empirical data to test the hypothesis that failing to account for temporary emigration via sampling design results in misleading comparisons of static and dynamic occupancy models, and biased estimates of distribution dynamics. We then provide recommendations for unbiased sampling and modeling

schemes for estimating dynamic rates of unmarked populations in the presence of temporary emigration.

## MATERIALS AND METHODS

### Simulated Data

We simulated presence/absence datasets under two different robust-design sampling scenarios (Pollock 1982), one where the strict closure assumption is met within primary periods (*occupancy* scenario), and one where primary periods were closed to dynamics, but availability changes could occur between secondary samples (*use* scenario). The *occupancy* scenario allowed us to evaluate how temporary emigration influences colonization and extinction estimates, while the *use* scenario allowed us to test whether a simple sampling alteration could improve those estimates. Our simulations explicitly assume that availability changes occur over finer time scales than dynamics, and that the researcher is interested in estimating dynamic rates, rather than changes in sampling availability.

Each simulated dataset contained 500 sites and nine sampling occasions, where three secondary samples were nested within each of three primary periods. We simulated initial site use from a Bernoulli distribution with probabilities of  $\psi_0 = 0.3$  or  $0.7$ . We simulated dynamics as transitions in site use between primary sampling periods to represent distributional shifts. Transitions from used to unused were simulated from a Bernoulli distribution with probabilities of  $\epsilon_0 = 0.0, 0.2, \text{ or } 0.4$ . Transitions from unused to used were simulated similarly with probabilities of  $\gamma_0 = 0.0, 0.09, 0.17, 0.47, \text{ or } 0.93$ , where  $\gamma_0$  was calculated so the site use rate remained constant across primary periods. We use  $\psi_0$ ,  $\epsilon_0$ , and  $\gamma_0$  to distinguish probability of site

use and probability of changes in site use from the occupancy ( $\psi$ ), extinction ( $\epsilon$ ), and colonization ( $\gamma$ ) notation used in dynamic occupancy models (MacKenzie et al. 2003).

Given a site was used, we simulated sampling availability from a Bernoulli distribution with probabilities of  $p_a = 0.5$ , or  $0.8$ . In *occupancy* sampling scenarios, availability could only change every third visit, allowing instantaneous estimates of the species' distribution within primary periods. Thus, the occupancy state of a site could change between subsequent primary periods via changes in availability, even if the site was used during both. In the *use* scenarios, availability was simulated independently on each sampling occasion. Finally, given that the species was available for sampling, detection during each secondary period was simulated from a Bernoulli distribution with probabilities of  $p_d = 0.5$  or  $0.8$ . We generated 1000 datasets for each combination of 24 parameter values under each sampling scenario using R (v. 3.1.2).

We fit static (MacKenzie et al. 2002) and dynamic (MacKenzie et al. 2003) occupancy models to each of the respective 24,000 datasets using the *unmarked* R package (v. 0.10-6; Fiske & Chandler 2011). Static models assumed no occupancy changes between any visits and open models allowed distributions to change every third visit. Because multiple studies (e.g., Rota et al. 2009, McClure & Hill 2012) compare static and dynamic occupancy models to test for evidence of dynamics, we compared model pairs with a common approach (Self & Liang 1987, Rota et al. 2009, Dail & Madsen 2011). Static occupancy models are special cases of their dynamic counterparts where dynamic parameters are constrained to be zero. To test for dynamics, we calculated a test statistic as  $T = -2\ln(\Lambda)$ , where  $\Lambda$  is the ratio of the maximized likelihood for the static model to that of the dynamic model. Because the null hypothesis is that the dynamic parameters are on the boundaries of their parameter spaces, this test does not meet the likelihood ratio test regularity conditions. Instead, this test statistic asymptotically

approaches a mixture  $\chi_0^2$ ,  $\chi_1^2$ , and  $\chi_2^2$  distributions with mixing proportions equal to  $0.5-\delta$ ,  $0.5$ , and  $\delta$ , with  $\delta$  calculated from the dynamic model's Hessian matrix (Self & Liang 1987, Dail & Madsen 2011). When  $\delta$  could not be estimated ( $< 1\%$  of comparisons), it was fixed at  $0.5$  to minimize the probability of rejecting the null (static) model. We accepted a P-value of  $< 0.05$  as evidence for dynamic distributions.

For each parameter combination under each sampling scenario we calculated the percentage of correct models selected. Again, we assumed interest is in quantifying dynamics, so the dynamic model was deemed “incorrect” when the simulation parameters  $\gamma_0$  and  $\epsilon_0$  equaled zero. We compared estimates of occupancy, colonization, extinction, and detection with the simulation parameters, and specifically compared estimates of colonization and extinction with those used to simulate dynamics ( $\gamma_0$  and  $\epsilon_0$ ). We estimated bias by subtracting the simulation parameter from each estimate and averaging these values over all 1000 datasets. We calculated variance among the estimates themselves, and mean squared error (MSE) as the sum of the variance and the squared bias. We disregarded parameter estimates from models with non-invertible Hessian matrices ( $< 2\%$  of fitted models). Full simulation and analysis code is provided in Appendix B.

### **Dynamic Multi-Scale Occupancy Model**

When a researcher is interested in quantifying temporal dynamics in both use and occupancy, the simple design-based solution simulated above (*'use'* scenarios) would not be sufficient. At present, we are unaware of any models that explicitly estimate both temporary emigration and dynamic rates simultaneously. Thus, we developed one that relies on an extension of Pollock's robust design (Pollock 1982) to include tertiary sampling periods closed



to both temporary emigration and dynamics, and secondary periods closed only to dynamics. Note that sampling considerations for this model are nearly identical to those described in the *use* sampling scenario above. In both cases, all secondary samples within a primary period must be closed to dynamics, but open to changes in availability. Thus, this model provides no benefit for estimating dynamic rates. Instead, it imposes additional burden by requiring more frequent sampling within secondary periods to estimate ‘availability’, and ‘detection given availability’ separately, rather than estimating their product as a single parameter (Nichols et al. 2009, Schmidt et al. 2013). Use of this model is thus unnecessary in most cases, but we refer interested readers to Appendix C for full model development and testing.

### **Empirical Case Study**

In the summer of 2014, we established 193 point count stations ( $\geq 200$  m apart) in the central hardwoods region of southern Indiana. We used a popular sampling protocol (e.g., Betts et al. 2008, Rota et al. 2009, McClure & Hill 2011, Otto & Roloff 2012) where trained observers conducted three 3:20 point counts during each of three 10-minute site visits (9 total point counts). We recorded all birds within 50 m, and counts took place between sunrise and 10:00 am from 16 June to 16 July in suitable weather conditions (i.e., no rain and minimal wind). For clarity, we will refer to 10-minute site visits as *visits* and repeated 3:20 point counts within each visit as *intervals*. The first two visits to each station were conducted within two mornings of each other, and the third visit was conducted 15 to 19 (median 17) days after the first.

This sampling scheme was designed under three assumptions. First, because repeated intervals within a visit occurred over 10 minutes, it is reasonable to assume complete site closure within visits. Second, because survey sites were stationary (50 m radius circles), but birds are

mobile, availability changes could occur between site visits due to individuals moving in and out of the sample space (Fig. 2.1). Lastly, dynamic rates should be approximately zero over the 24-48 hour period between our first and second site visits, but changes in site use may occur over the 19 days between the first and third visits (Rota et al. 2009, McClure & Hill 2012). Using these assumptions, we constructed three unique presence/absence datasets from the point count data (Fig. 2.2) and label them with the processes being modeled by dynamic occupancy model colonization and extinction parameters.

The first dataset treated the first and third visits as primary periods, and intervals as secondary periods (visit two ignored). Multiple researchers have compared static and dynamic occupancy models fit to data collected analogously, and concluded there was evidence for within-breeding season territorial changes in bird communities (e.g., Betts et al. 2008, Rota et al. 2009, McClure & Hill 2012). Analyzing this dataset allowed us to replicate such results. Under our assumptions, both dynamics and temporary emigration (TE) could only occur between primary periods, and we refer to this as the *confounded TE/dynamics* dataset.

The second dataset was similar to the first, except that the first and second visits were considered primary periods (visit three ignored). Under our assumptions, any closure violations detected could be explained primarily by changes in availability. Thus, analyzing this dataset allowed us to evaluate the impacts of temporary emigration on tests of within-breeding season territorial shifts. We refer to this as the *isolated TE* dataset.

The final dataset combined all three visits and ignored the repeated intervals. We treated the first two visits as a single primary period containing two secondary periods. The third visit was a unique primary period containing only one secondary period. While the first two datasets were designed to generate estimates of instantaneous occupancy within primary periods (by

assuring complete site closure), this dataset is designed to estimate site use within primary periods (by allowing availability changes between secondary samples). Thus, the temporary emigration rate should be estimated with detection in the dynamic occupancy model (Nichols et al. 2009), and colonization/extinction estimates should only be influenced by distribution dynamics. We refer to this as the *isolated dynamics* dataset.

We limited analyses to the 19 species detected on > 20% of sample sites (Appendix A, Table A1). Using the approach described above, we tested for distribution dynamics in each of these 57 datasets (three per species) by comparing static occupancy models that assumed site closure over all samples (MacKenzie et al. 2002) to dynamic occupancy models allowing colonization and extinction between primary periods (MacKenzie et al. 2003). In each model, time of day and observer were included as covariates for detection probability, but for simplicity, initial occupancy, colonization, and extinction were modeled as constants. All analyses were conducted using the *unmarked* package (v. 0.10-6) in R (v. 3.1.2).

## RESULTS

### Simulated Data

In the *use* sampling scenarios, site closure tests performed very well. Where distribution dynamics did not occur, the static occupancy models were appropriately selected  $\geq 95.1\%$  of the time (Table 2.1), and when dynamics were present, the dynamic occupancy model was selected  $\geq 97.2\%$  of the time (Appendix A, Table A2). In both cases, the estimates of initial occupancy approximated  $\psi_0$  while detection estimates approximated  $p_a p_d$ . Accordingly, dynamic parameter estimates were highly accurate and precise estimates of the dynamic rates.

When secondary sampling periods were closed to availability changes (*occupancy* scenarios), site closure tests and dynamic parameter estimates resulted in misleading conclusions about dynamic rates. Where dynamics were absent, the closed models were appropriately selected  $\leq 1.3\%$  of the time (Table 2.1), and when dynamics were present, the dynamic model was selected 100% of the time (Appendix A, Table A2). In both cases, estimates of initial occupancy tended to approximate  $\psi_0 p_a$  while the detection estimate approximated  $p_d$ . However, the dynamic occupancy models tended to underestimate  $\gamma_0$  and overestimate  $\epsilon_0$ .

### **Dynamic, Multi-Scale Occupancy Model**

By augmenting the dynamic occupancy model to include tertiary sampling periods, we were able to estimate temporary emigration and dynamic rates simultaneously (Appendix C). This extended model performed well under simulated sampling scenarios that involved three primary, three secondary, and three tertiary periods (Appendix C, Table C1). However, dynamic rate estimates showed no accuracy improvements over those generated by combining *use* sampling with a dynamic occupancy model, as described above. Therefore, we chose not to pursue further testing.

### **Empirical Case Study**

Results from the analysis of our confounded TE/dynamics and isolated TE datasets were very similar. The null hypothesis (i.e. that closure could be assumed among site visits) was rejected for all 19 species using both datasets ( $P < 0.02$ ; Appendix A, Table A1). That is, the dynamic occupancy models had greater support for all species even when the interval between primary sampling periods was limited to 24-48 hours. Estimates of extinction probability from

the confounded TE/dynamics datasets tended to be greater than the estimates from the isolated TE datasets (Fig. 2.3), as might be expected if multiple processes influenced the former but not the latter. However, estimates of detection, initial occupancy, and colonization were similar between these models. Therefore, in most cases, the parameter estimates generated by dynamic models were extremely similar when primary periods were separated by two days versus 17 days. This suggests that the colonization and extinction estimates were heavily influenced by temporary emigration when all secondary samples occurred within 10 minutes.

In contrast, we only found evidence for closure violations for nine species using the isolated dynamics datasets (Appendix A, Table A1). That is, for most species there was no evidence for dynamics over the ~17 day period when the effects of temporary emigration were excluded. Though some parameter estimates from isolated dynamics models had poor precision due to a smaller number of secondary periods, strong patterns emerged. Estimates of detection and extinction tended to be greater, while initial occupancy tended to be lower in models fit to the confounded TE/dynamics datasets than when fit to the isolated dynamics datasets (Fig. 2.4). In our simulation study, we saw a similar pattern when we compared the *occupancy* and *use* scenarios (Appendix A, Table A2). This supports our assumption that the colonization and extinction parameters from the isolated dynamics models are likely quantifying changes in site use between primary periods, while estimates generated from the other two datasets are likely measuring changes in instantaneous occupancy.

## DISCUSSION

Concern about overestimating species distributions due to closure assumption violations has led to widespread recommendations that secondary samples be conducted extremely close in

time (MacKenzie & Royle 2005, MacKenzie 2005, Rota et al. 2009, Kendall et al. 2013). This enables instantaneous estimates of species occupancy patterns, which are valuable for generating a snapshot of the species' distribution at a moment in time. However, as our simulations demonstrate, this may be a poor sampling approach for quantifying distributional shifts. When instantaneous occupancy is estimated within primary periods, dynamic occupancy models estimate colonization and extinction rates as changes in instantaneous occupancy, which can be influenced by both distribution dynamics and temporary emigration; naiveté to this fact could mislead interpretations of the biological process being modeled.

Results from our empirical data analysis demonstrate how this problem could emerge in observational studies. By varying the temporal duration between primary and secondary periods, we demonstrated that colonization and extinction estimates generated using a popular avian sampling technique are potentially heavily influenced by temporary emigration. Nevertheless, numerous studies have interpreted these dynamic rates as evidence of within-season dispersal (e.g., Betts et al. 2008, Rota et al. 2009, McClure & Hill 2012, Otto & Roloff 2012). Indeed, Rota et al. (2009) thoroughly considered the influence temporary emigration had on their results, and concluded that it was likely not the process being modeled between their 10-minute primary periods. Yet, our results indicate temporary emigration may be the only process being modeled between primary periods for some species. Note, that sequential surveys may additionally violate the assumption that detections are independent (MacKenzie et al. 2002), which could also explain the inflated detection and deflated occupancy estimates observed under this protocol (Fig. 2.4). Regardless of the mechanism, this sampling approach is poorly adapted for modeling distribution dynamics.

Designing sampling schemes for dynamic occupancy modeling requires a more nuanced consideration of the closure assumption; researchers must also consider the biological process being modeled by the colonization and extinction parameters. In cases where temporary emigration is the only process occurring between primary periods (e.g. in our isolated TE datasets), models that explicitly estimate this parameter (Nichols et al. 2008, Mordecai et al. 2011) may be more appropriate than the dynamic occupancy model. Estimating temporary emigration rates directly may be valuable for designing survey protocols (Riddle et al. 2010), or for generating instantaneous occupancy estimates (Nichols et al. 2008). Yet, for many research questions, interest lies in distributional changes in space use rather than short-term, reversible changes in availability. Applications of dynamic occupancy models for quantifying dispersal (Betts et al. 2008, Rota et al. 2009), metapopulation dynamics (Ferraz et al. 2007, Pellet et al. 2007), or source/sink rates (Kerbyriou et al. 2012, Peterman et al. 2013) all seek colonization and extinction estimates representing distribution dynamics. In these cases, temporary emigration is a nuisance parameter that should be accounted for to estimate dynamics accurately.

As demonstrated in Appendix C, by extending the dynamic occupancy model to include tertiary sampling periods, rates of dynamics and temporary emigration can be estimated simultaneously. However, for all parameters to be identifiable, the model requires collecting additional data (tertiary samples) that contribute no information to dynamic rate estimates. Therefore, when researchers wish to estimate distribution dynamics, and temporary emigration is of no interest, we strongly recommend adjusting the sampling design rather than fitting a more complex model. Nevertheless, the model performed well in initial simulations, and we encourage further testing to more thoroughly explore its utility and limitations.

As we and others (e.g., Kendall 1999, Schmidt et al. 2013) have demonstrated, dynamic rates can be isolated simply by designing studies to estimate site use within primary periods, rather than instantaneous occupancy. This approach requires estimating detection probability as  $p_d p_a$ , and therefore that the probability the species is available for sampling is random and independent during each secondary period (MacKenzie 2005, Nichols et al. 2009). Where there is a spatial mismatch between the size of sample sites and the space used by targeted individuals (e.g., Fig. 2.1), this means allowing time for spatial redistribution of individuals such that their locations during two sampling events are uncorrelated (Fig. 2.5). Spatial autocorrelation in such within-home range locations should decrease over time, but the length of time required to achieve statistical independence will be longer for slower moving species (Swihart & Slade 1985). When the sampling technique itself is destructive or induces a “trap response” (e.g., Otto et al. 2013), the duration between samples may need to be further extended to ensure that availability on each sampling occasion is not negatively influenced by a previous sampling event. Indeed, in all situations, increasing the time between samples should reduce correlation in availability (e.g., the likelihood that an animal is vocalizing); yet critically, the total time interval within a primary period must be sufficiently short that dynamic rates are negligible. Otherwise, these processes will also be estimated as a component of detection probability (Kendall 1999, Rota et al. 2009).

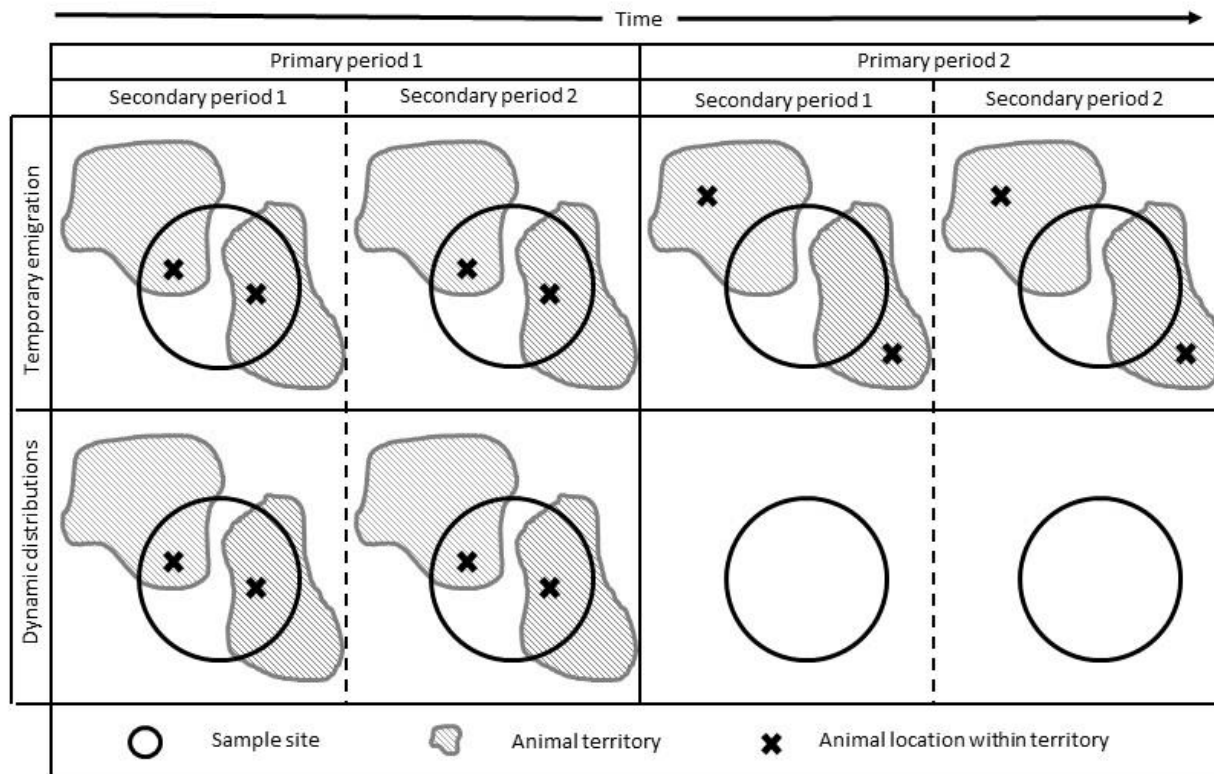
Importantly, these recommendations assume a study system in which temporary emigration occurs over a finer time scale than distribution dynamics, and that the two are sufficiently distinguishable (Fig. 2.5). Designing an appropriate sampling scheme thus requires substantial knowledge about the study system and species. In our empirical study of territorial breeding birds, we assumed 24-48 hour periods were long enough to ensure independence among



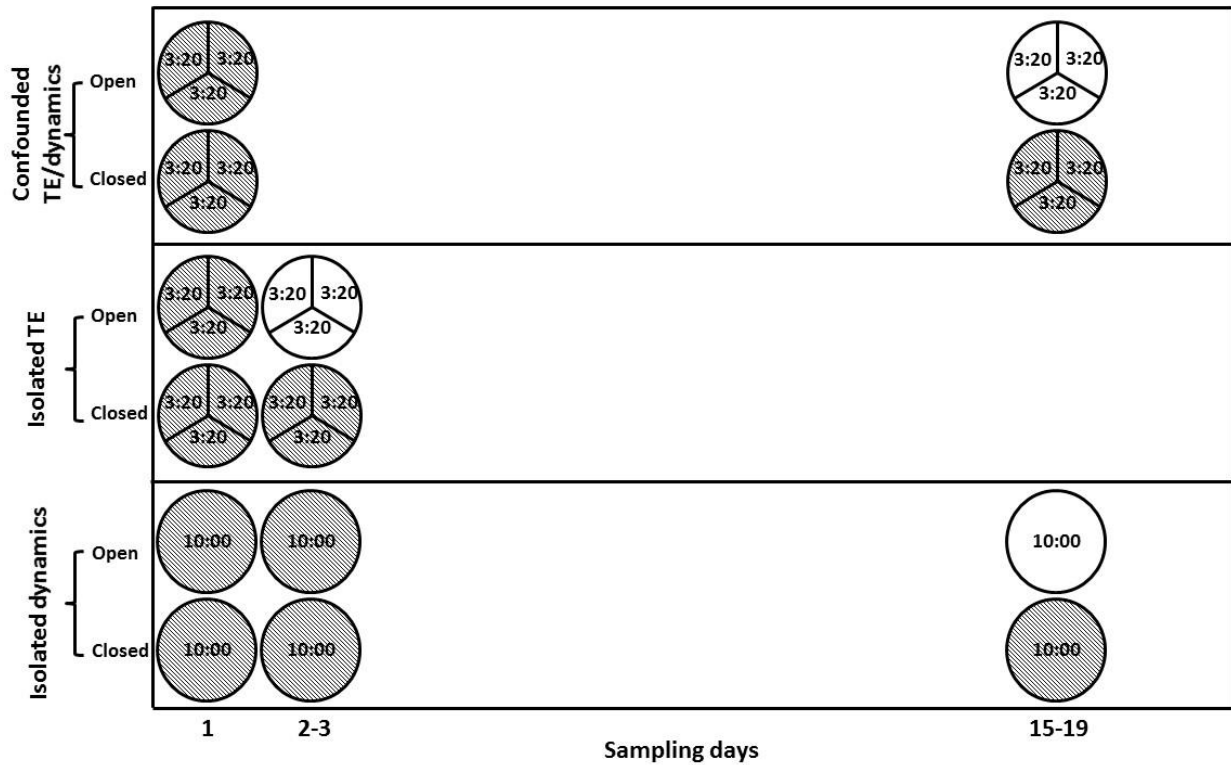
successive individual bird locations within territories, yet short enough that dynamic rates were negligible. Although we did not evaluate this assumption in the field, a two-day period should allow ample movement for highly vagile species like birds, while substantial changes in site use are unlikely. In other sampling scenarios, however, these processes may not be uniquely identifiable, even with a robust sampling design. For instance, Kendall et al. (1997) noted that non-nesting birds could be considered temporary emigrants when sampling techniques focus on nesting individuals (e.g., Spendelov & Nichols 1989). However, the temporal scale of mating and nest-building may not be distinguishable from that of changes in population distributions. Similarly, for species with poorly defined territories or home ranges, temporary emigration and dynamics may not be biologically distinct processes. Future work should identify appropriate temporal sampling scales for different species and sampling techniques to help separate temporary emigration from dynamic rates.

**Table 2.1.** A comparison of static and dynamic occupancy models fit to simulated presence-absence survey data where distribution dynamics were absent. For each set of simulation parameters, we generated 1000 datasets. In *use* sampling, availability was independent during each sampling period. As a result, the static models were chosen the majority of the time. In *occupancy* sampling, availability could only change between primary periods, and the dynamic models were selected nearly 100% of the time. Metrics provided are on the original parameter scale.

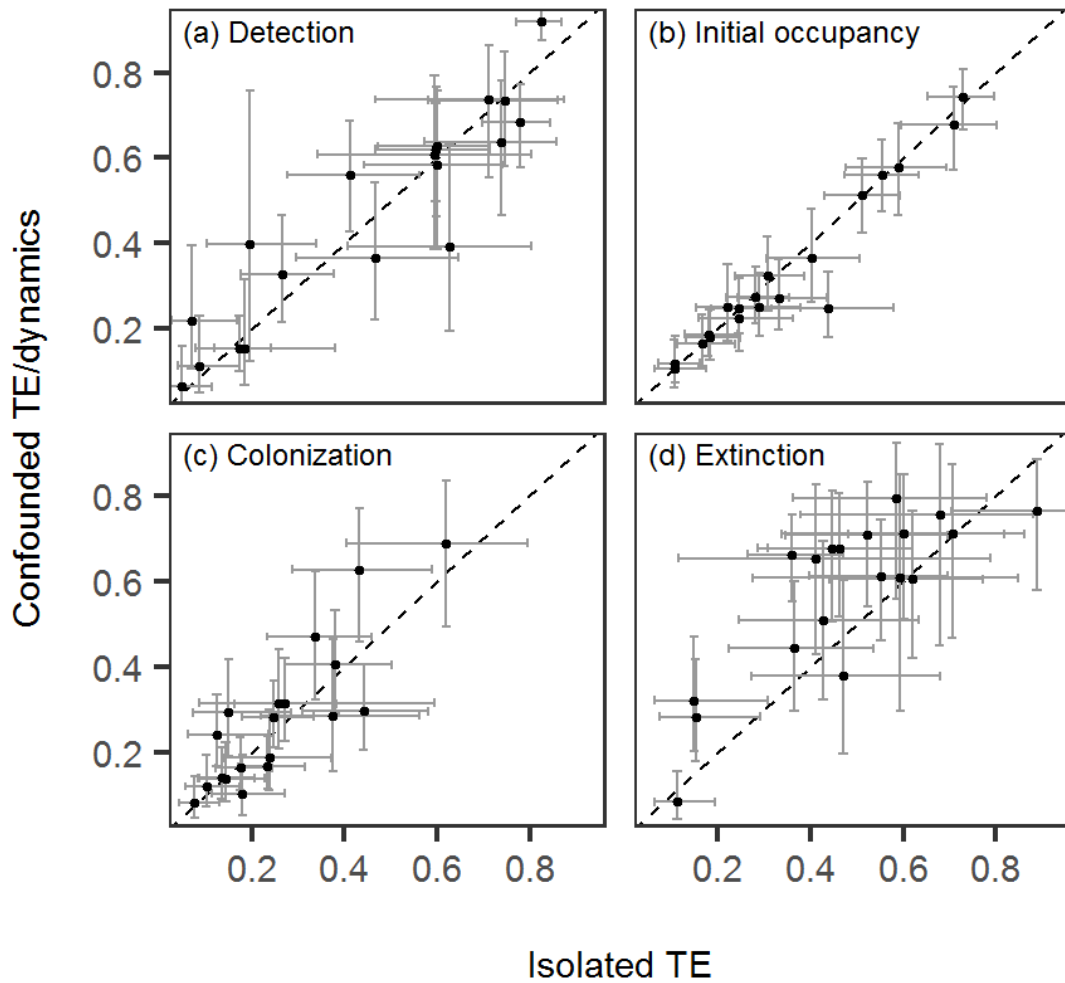
<u>Simulation parameters</u>					% open selected	<u>Occ (<math>\psi</math>)</u>		<u>Det (p)</u>		<u>Colonization (<math>\gamma</math>)</u>			<u>Extinction (<math>\epsilon</math>)</u>		
$\psi_0$	$p_a$	$p_d$	$\gamma_0$	$\epsilon_0$		Mean	Var	Mean	Var	Mean/Bias	Var	MSE	Mean/Bias	Var	MSE
Use scenarios															
0.3	0.5	0.5	0.00	0	3.9	0.30	0.00	0.25	0.00	---	---	---	---	---	---
0.3	0.5	0.8	0.00	0	4.1	0.30	0.00	0.40	0.00	---	---	---	---	---	---
0.3	0.8	0.5	0.00	0	4.9	0.30	0.00	0.40	0.00	---	---	---	---	---	---
0.3	0.8	0.8	0.00	0	3.3	0.30	0.00	0.64	0.00	---	---	---	---	---	---
0.7	0.5	0.5	0.00	0	3.8	0.70	0.00	0.25	0.00	---	---	---	---	---	---
0.7	0.5	0.8	0.00	0	4.2	0.70	0.00	0.40	0.00	---	---	---	---	---	---
0.7	0.8	0.5	0.00	0	4.7	0.70	0.00	0.40	0.00	---	---	---	---	---	---
0.7	0.8	0.8	0.00	0	3.7	0.70	0.00	0.64	0.00	---	---	---	---	---	---
Occupancy scenarios															
0.3	0.5	0.5	0.00	0	100	0.16	0.00	0.47	0.00	0.07	0.00	0.01	0.39	0.00	0.15
0.3	0.5	0.8	0.00	0	100	0.15	0.00	0.80	0.00	0.09	0.00	0.01	0.49	0.00	0.24
0.3	0.8	0.5	0.00	0	98.7	0.26	0.00	0.46	0.00	0.03	0.00	0.00	0.08	0.00	0.01
0.3	0.8	0.8	0.00	0	99.9	0.24	0.00	0.78	0.00	0.05	0.00	0.00	0.15	0.00	0.02
0.7	0.5	0.5	0.00	0	100	0.35	0.00	0.50	0.00	0.26	0.00	0.07	0.48	0.00	0.24
0.7	0.5	0.8	0.00	0	100	0.35	0.00	0.80	0.00	0.27	0.00	0.07	0.50	0.00	0.25
0.7	0.8	0.5	0.00	0	99.6	0.58	0.00	0.47	0.00	0.17	0.00	0.03	0.11	0.00	0.01
0.7	0.8	0.8	0.00	0	100	0.56	0.00	0.80	0.00	0.25	0.00	0.06	0.19	0.00	0.04



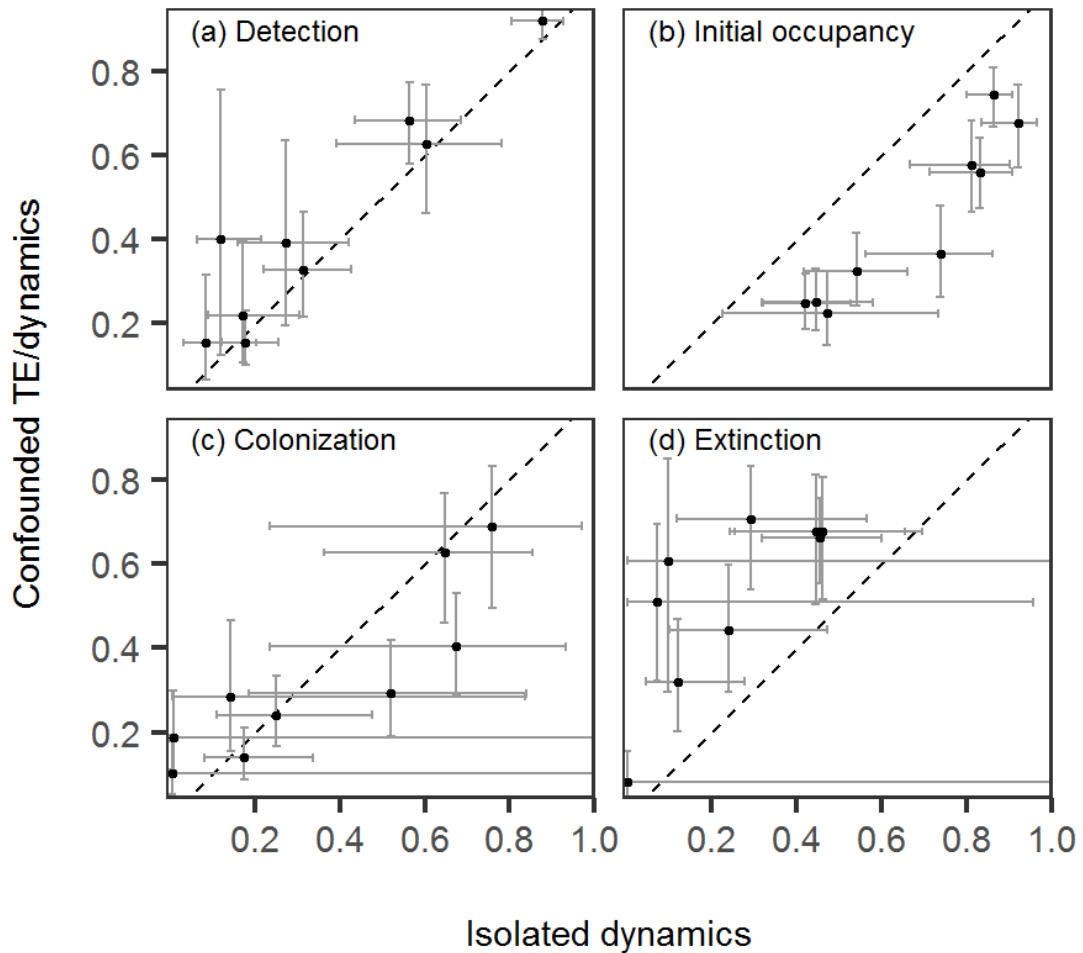
**Figure 2.1.** When practitioners of dynamic occupancy models ensure complete site closure within primary periods, changes in sampling availability stemming from temporary emigration may not be distinguishable from distributional changes in territory locations. In the two scenarios depicted, there is some probability of detecting the species during both samples in the first primary period, but no possibility of detecting it during either sample in the second. Yet only in the bottom scenario does the actual distribution of the species change.



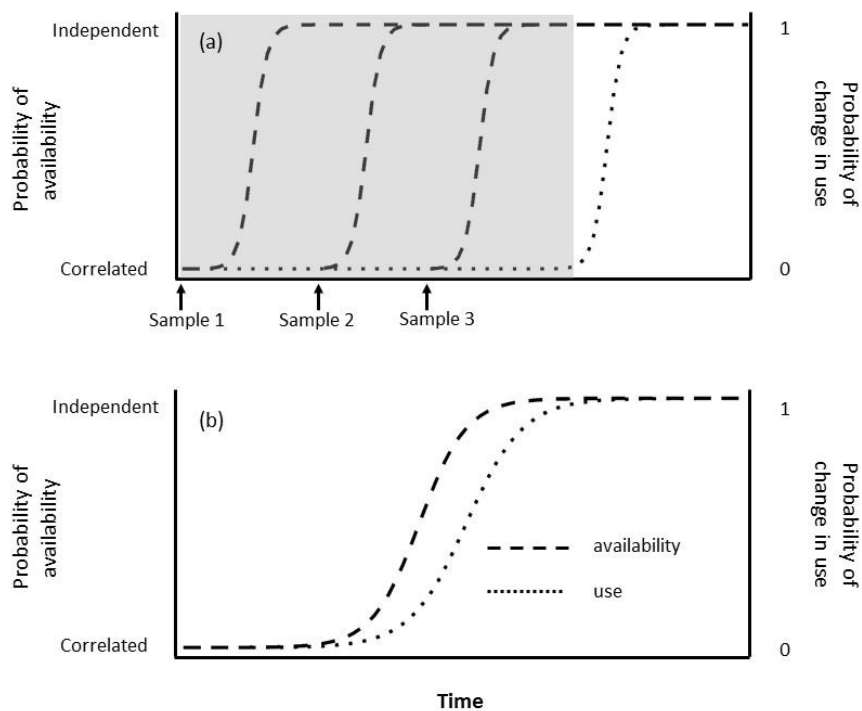
**Figure 2.2.** A schematic outlining the structure of the three occupancy datasets constructed from repeated point counts at 193 locations in southern Indiana in the summer of 2014. Circles represent 10-minute site visits, some of which were split into 3:20 subintervals. Circles, and circle parts shaded similarly were included in the same primary period. Datasets were designed to quantify either distribution dynamics, temporary emigration (TE), or both between primary periods.



**Figure 2.3.** A comparison of the parameter estimates generated by open occupancy models fit to the confounded TE/dynamics and isolated TE empirical datasets for 19 forest-breeding songbirds. Error bars represent 95% Wald confidence intervals and the dashed line indicates no difference in estimates. Most parameter estimates were similar under this sampling scheme when primary periods were separated by 2 days versus 17 days.



**Figure 2.4.** A comparison of the parameter estimates generated by open occupancy models fit to the confounded TE/dynamics and isolated dynamics datasets for nine forest-breeding songbirds. Error bars represent 95% Wald confidence intervals and the dashed line indicates no difference in estimates. Detection and extinction estimates tended to be larger, while initial occupancy estimates tended to be lower in the confounded TE/dynamics models.



**Figure 2.5.** To quantify distribution dynamics independently from temporary emigration, secondary samples should be spaced far enough apart in time that probability of availability is independent on each repeated visit, but true changes in site use are negligible. In (a), the gray box represents the maximum length of a primary sampling period, and three secondary samples are spaced so that probability of availability is independent on each occasion. If samples are conducted closer together in time, dynamic rates will be confounded by temporary emigration. If secondary samples occur outside of the gray box, dynamic rates will be confounded with detection probability. In (b), temporary emigration and dynamics occur at similar rates, and the two processes cannot be distinguished using Pollock's (1982) robust sampling design.

## RESPONSE TO FRAGMENTATION BY AVIAN COMMUNITIES IS MEDIATED BY SPECIES TRAITS

### INTRODUCTION

The notion that the size of an environmental patch should influence community structure and composition has been one of the most persistent and controversial doctrines in landscape ecology and fragmentation research (Haila 2002, Laurance 2008, Fahrig 2013). Rooted in island biogeography (IBT; MacArthur & Wilson 1967) and metapopulation theory (Levins 1969), smaller fragments are hypothesized to support smaller populations, which results in higher extinction probabilities (Hanski 1998, Hanski & Ovaskainen 2002) and lower colonization rates (Gilpin & Diamond 1976, Lomolino 1990) than larger patches. Yet empirical studies tend to report weak or inconsistent patch size effects on distributions of diverse taxonomic groups (Debinski & Holt 2000, Prugh et al. 2008). This juxtaposition of theory and reality has been the catalyst for an unresolved debate about whether larger habitat patches have greater conservation value than small patches (Laurance 2008, Fahrig 2013, Hanski 2015, Fahrig 2015). While some argue that the disagreement is trivial (Didham et al. 2012), science examining the effects of landscape composition and configuration on biodiversity shapes land-use policy (Fahrig 2017), and influences land acquisition and management strategies (Villard & Metzger 2014, Hadley & Betts 2016).

Central to the debate is whether the reduction in patch size per se – stemming from landscape fragmentation – has any influence on species distribution patterns beyond what can be explained by the habitat lost. Unfortunately, because patch size and habitat amount tend to be highly correlated (Andrén 1994, Fahrig 2003, Didham et al. 2012), their independent effects are rarely discernable, despite repeated calls to separate them (Fahrig 2003, Hadley & Betts 2016).



Yet evidence is mounting that habitat loss has a much greater influence on biodiversity than fragmentation per se. While habitat loss tends to have strong negative effects (Andren 1994, Trzcinski et al. 1999, McGarigal & Cushman 2002, Fahrig 2003, 2013, 2017), patch size effects tend to be weak (Debinski & Holt 2000, Prugh et al. 2008), and dependent on landscape context (Andren 1994, Betts et al. 2006, Villard & Metzger 2014, Bartlett et al. 2016).

Even where patch size effects do seem to exist, evidence suggests they can often be explained by a sample area effect (Cam et al. 2002, Fahrig 2013), or variability stemming from edge effects (Ries et al. 2004, Fletcher et al. 2007). As a result, many researchers have criticized the patch-matrix habitat model as overly simplistic, and questioned whether the debate should be abandoned (Baguette 2004, Manning et al. 2004, Fahrig 2013, Mendenhall et al. 2014). In fact, Fahrig (2013) provided evidence that patch size per se has no influence on species distribution patterns beyond the amount of habitat it contributes to the local landscape. These results suggest there may be no conservation value in large habitat patches beyond the fact that they contain more habitat.

Theoretical predictions about patch size effects relate to species richness (MacArthur & Wilson 1967), and consequently most patch-size studies examine species richness (Fahrig 2013). This approach typically ignores species identities, and may paint an incomplete picture about how patch size influences communities (Kéry & Royle 2008, Zipkin et al. 2009, Iknayan et al. 2014). For instance, treating all species equivalently can mask important trait groupings that could predict sensitivity to fragmentation (Bender et al. 1998, Henle et al. 2004, Dondina et al. 2017). Niche theory (Grinnell 1917, Hutchinson 1957) emphasizes that habitat requirements differ among species, and studies acknowledging this tend to find habitat specialists are more sensitive to fragmentation effects than habitat generalists (Bender et al. 1998, Cook et al. 2002,

Betts et al. 2007, Püttker et al. 2013, Carrara et al. 2015, Dondina et al. 2017; but see Fahrig 2017).

Additionally, richness summaries typically ignore variability in detection probability among species, sites, and surveys (Kéry & Royle 2008, Zipkin et al. 2009, Iknayan et al. 2014). While comparisons between richness metrics that do, and do not explicitly model detectability are lacking (Iknayan et al. 2014), ignoring such factors can produce demonstrably biased or misleading results (e.g., Boulinier et al. 1998, Kéry et al. 2008). For example, detectability is often associated with conspecific (Dorazio 2007) or heterospecific (e.g., Bailey et al. 2009) abundance; thus, richness metrics that fail to account for that may disproportionately represent common species (Zipkin et al. 2009) at the expense of the rare or cryptic species of greater conservation concern (Samu et al. 2008).

During the breeding seasons of 2011-2013, we sampled bird communities in 202 unique forest fragments in southern Indiana. We used a mensurative experimental design (Hadley & Betts 2016) that isolated the effects of patch size per se from the effects of confounding variables such as habitat amount, edge, local vegetation, and sample area. Here, we use those data to compare four hypotheses about the influence of landscape composition and configuration on breeding bird distribution patterns. The *random sample hypothesis* posits that distributions are only influenced by habitat variables at the scale of the animal territory (Haila 1983). The *landscape composition hypothesis* states that distributions are influenced by the amount of habitat at broader spatial scales (Fahrig 2003, 2013), while the *landscape fragmentation hypotheses* implies a linear decline with decreasing patch size, beyond what can be explained by habitat loss (Villard et al. 1999). Finally, the *fragmentation threshold hypothesis* posits that

patch size only influences distributions below critical thresholds in landscape habitat amount (Andrén 1994, Betts et al. 2006).

We analyzed the data using a community occupancy modeling approach (Kéry & Royle 2008, Zipkin et al. 2009, Iknayan et al. 2014) that allowed us to test these hypotheses for all species of interest, while accounting for imperfect detection. In addition, we grouped species according to ecological traits a priori and tested the hypotheses that 1) interior forest specialists are negatively associated with decreasing patch size, 2) forest edge specialists are positively influenced by decreasing patch size, and 3) the effects of patch size on forest generalists are weak or non-existent. This study represents one of the most comprehensive efforts to disentangle the independent effects of habitat amount and fragmentation per se, shining new light on an age-old debate.

## **MATERIALS AND METHODS**

### **Sampling Design**

Our study area spanned approximately 1.6 million ha of land in the central hardwoods region of southern Indiana (Fig. 3.1). The area is dominated by corn and soybean agriculture and remnant tracts of temperate broadleaf and mixed forests. Mean annual rainfall is approximately 119 cm (Indiana State Climate Office 2002), and mean annual temperatures range from 6° C in winter to 18° C in summer (National Climatic Data Center 2011). Dominant tree species include oaks (*Quercus spp.*), hickories (*Carya spp.*), tulip poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), American beech (*Fagus grandifolia*), maples (*Acer spp.*) and black walnut (*Juglans nigra*). Dominant understory shrubs include spicebush (*Lindera benzoin*), multiflora rose (*Rosa multiflora*), and berry bushes (*Rubus spp.*).

The United States Department of Defense (DoD) operates two large military installations in the region, Naval Surface Warfare Center Crane (NSWCC), and Big Oaks National Wildlife Refuge (BONWR). Both installations encompass large contiguous forest tracts surrounded by forest plots that vary substantially in size, isolation, and ownership. In the spring of 2011 we used ArcMap (v. 9.3.1) to digitize the boundaries of all mature forest patches on lands owned by the DoD, Indiana Department of Natural Resources, U.S. Forest Service, and The Nature Conservancy that were within 50 km of NSWCC or BONWR boundaries. Patch delineations were based on aerial images collected for the National Agriculture Imagery Program (USDA 2010); we considered patches discrete if separated by canopy gaps greater than 30 m. We also separated patches if connected by forest corridors narrower than 100 m, as these would not be wide enough to contain territories for most targeted species (Rodewald 2015).

We removed patches that were not accessible within 250 m of a road to help standardize edge distances of sampling points in large and small patches. We then classified patches into five size categories: 1) 1-3 ha, 2) 3-10 ha, 3) 10-20 ha, 4) 20-100 ha, and 5) > 100 ha. We randomly placed up to three potential point count stations in category 1, 2, or 3 patches while ensuring a minimum distance of 50 m from the nearest edge, and 250 m between any two points. For patches >20 ha, random point placement often resulted in inaccessible sampling locations. For these, we randomly located a single accessible point 50 m from the patch edge as the beginning of a 4 or 5 point transect (with 250 m spacing) stretching toward the patch interior. We then centered a 2 km radius circle on each point and quantified the proportion of the circle dominated by mature forest (forest amount) using the National Land Cover Database (NLCD; Fry et al. 2011). We chose this radius because it is likely to include the spatial extent relevant to habitat use (Mitchell et al. 2001), natal dispersal (Bowman 2003), and extra-territorial

movements (Norris & Stutchbury 2001) for most the species we examined. We calculated mean forest amount values among the points within a patch, and classified patches into four forest amount categories; 1) 0-40%, 2) 40-60%, 3) 60-80%, and 4) 80-100%. We attempted to randomly select 10 patches from each of the resulting 20 size-by-amount patch groupings. When there were not enough patches available in a group (e.g., size > 100 ha, amount < 40%), we moved the transect starting locations, or chose patches from other groupings that were close in size and amount. Although not completely random, these decisions were based on aerial imagery, and are unlikely to have introduced bias because we had no a priori knowledge about species composition or forest structure on the ground. In all, we selected 490 point count stations for sampling in 202 unique forest patches.

Our study design achieved one of our primary goals of minimizing point-level correlation between patch size and forest amount (Pearson's correlation,  $r = 0.22$ ), allowing us to separate their independent effects on occupancy patterns. While others have argued that focal patch studies such as ours do not truly test fragmentation effects (McGarigal & Cushman 2002, Fahrig 2003, 2017), these are ideal for distinguishing among the relative effects of within-patch, patch, and landscape variables (Thornton et al. 2011). Moreover, theory (MacArthur & Wilson 1967, Levins 1969, Hanski 1998) predicts that the size of the patch itself should influence distribution patterns, rather than the mean size of the patch in a landscape. Finally, focal patch size should be a reasonable proxy for fragmentation given that these variables tend to be highly correlated at the landscape scale (Andr en 1994, Fahrig 2003, Didham et al. 2012).

## **Bird and Vegetation Sampling**

Trained observers conducted three avian point counts per year (2011, 2012, and 2013) at each station between 29 May and 18 July. Repeated visits to a single site within a year were separated by approximately two weeks, and surveys were conducted between sunrise and 1030 in suitable weather conditions (i.e., no rain and minimal wind). Each count lasted 10 minutes and observers recorded all birds seen or heard within 50 m, though birds seen flying overhead were excluded.

Because our points fell along a gradient in edge distances, and because edge effects can substantially alter vegetation characteristics (Ries et al. 2004, Fletcher et al. 2007) we conducted two or three local vegetation surveys at each point count station. We sampled vegetation in 2011 and 2013 at all sites, and a third time in 2012 in cases where the site had been visibly disturbed. During each survey we established one 5 m radius circle (subplot) centered on the point count station itself, and another centered 30 m from the point count station in a randomly chosen cardinal direction. Within each subplot we recorded: an ocular estimate of shrub cover; canopy cover using 10 samples from a vertical viewing tube (Emlen 1967); tree basal area using a 2 basal-area factor forester's prism (Cruise Master, Forestry Suppliers, Jackson, MS) at the center of the plot; and leaf litter depth and vertical foliage density (VFD) from four points on the periphery of the subplot (one in each cardinal direction). We estimated VFD as the proportion of  $\frac{1}{4}$  m sections of a 5 m retractable painter's pole (Mr. LongArm #6618, A & M Products, Pleasant Hill, MO) contacted by live vegetation. We averaged all variables across the two subplots in each year.

## Data Analyses

We were not explicitly interested in the effects of any particular local vegetation variable on bird communities, but rather in accounting for the potential confounding effects of local variability. To that end, we conducted a principal component analysis (PCA) on our 5 local vegetation metrics to reduce the number of covariates in our models. We treated each year-by-point combination as a unique observation in the PCA, and results from the 2011 vegetation survey were applied to 2012 for sites where vegetation was not sampled that year. The first three principal components represented 77% of the total variance (Appendix A, Table A3) and we thus chose these to represent local vegetation in our models.

Over the three breeding seasons, we recorded over 80,000 detections of 114 unique bird species (Appendix A, Table A4). We processed these data by removing all species that do not breed in the region (i.e., transient migrants), and those species poorly sampled by the point count methodology (i.e., raptors, waterbirds, swifts and swallows, nocturnal and crepuscular species, hummingbirds, and game birds). We classified the remaining 74 species into four ecological trait groups: forest interior specialists (8), forest edge specialists (21), forest generalists (23), and habitat generalists (22). We made classifications a priori based on previous studies (*e.g.*, Lynch & Whigham 1984, Robbins et al. 1989, Villard 1998), and by consultation with the Birds of North America species accounts (Rodewald 2015). For habitat generalists (i.e., species regularly occurring outside of forest), forest amount and forest patch sizes are not biologically relevant metrics of available habitat, and we had no other a priori reason to expect these metrics would influence generalist distribution patterns. Thus, we excluded these species from further analyses.

We fit a temporally-dependent, Bayesian community occupancy model to the point count data for the remaining, 52 forest-associated, species. Community occupancy models estimate

species-specific occupancy and detection parameters within a hierarchical framework where estimates are related through community-level hyperparameters (Kéry & Royle 2008, Zipkin et al. 2009). The full advantages of such a modeling approach are detailed elsewhere (Kéry & Royle 2008, Royle & Dorazio 2008, Zipkin et al. 2009, Iknayan et al. 2014), but we chose this approach for three primary reasons. First, it allows explicit modeling of detection probabilities. Second, we could include all rare species in the analysis because the community hyperparameters borrow information from more common species (Royle & Dorazio 2008, Zipkin et al. 2009, Iknayan et al. 2014). Lastly, we were interested in the community hyperparameters estimates themselves to summarize differences in mean response between trait groups.

In our model  $y_{hijklm}$  represents the observed detection information, taking a value of 1 if species  $i$  in trait group  $h$  was detected in patch  $j$  at site  $k$  during survey  $m$  of year  $l$ , and 0 otherwise. We assumed  $y_{hijklm} \sim \text{Bernoulli}(Z_{hijkl} * p_{hijklm})$  where  $Z_{hijkl}$  represents the true species-specific occurrence state, and  $p_{hijklm}$  represents the species-specific probability of detection at the site during the sampled time. While detection probability can vary within a single year, this model assumes sites are closed to changes in occupancy within a breeding season (about 7 weeks in our study). This assumption is standard in occupancy modeling, and is likely reasonable for most of our breeding species (Chapter 2). We assumed that  $Z_{hijkl} \sim \text{Bernoulli}(\psi_{hijkl})$ , and incorporated covariate effects on occupancy ( $\psi_{hijkl}$ ) and detection ( $p_{hijklm}$ ) probabilities into the model on the logit scale.

We expected detection probability for most species would decline with increasing Julian date (JULIAN), and that increasing tree basal area (TREE) would reduce the ability of observers to see and hear birds. Thus, we modeled detection probabilities as



$$\text{logit}(p_{hijklm}) = \alpha_{0hi} + \alpha_{1hi}JULIAN_{jklm} + \alpha_{2hi}TREE_{jkl}$$

We modeled occupancy probability as a function of the local vegetation principal components (PC1, PC2, and PC3), edge distance (EDGE), log-transformed patch size (SIZE), amount of forest within 2 km (AMNT), and an interaction between SIZE and AMNT. To account for autocorrelation between points within the same patch, we also included a unique patch effect (PATCH) for each trait group in each year. For the first year, we specified the occupancy model as

$$\begin{aligned} \text{logit}(\psi_{hijk1}) = & \beta_{0hi} + PATCH_{hj1} + \beta_{1hi}PC1_{jk1} + \beta_{2hi}PC2_{jk1} + \beta_{3hi}PC3_{jk1} + \beta_{4hi}EDGE_{jk} \\ & + \beta_{5hi}SIZE_{jk} + \beta_{6hi}AMNT_{jk} + \beta_{7hi}SIZE_{jk}AMNT_{jk} \end{aligned}$$

In subsequent years, we assumed that the covariate effects remained constant, but that occupancy probability was dependent on occupancy in the previous year. Thus, for  $l > 1$ ,

$$\begin{aligned} \text{logit}(\psi_{hijkl}) = & \gamma_{0hi} + \gamma_{1hi}Z_{hijk(l-1)} + PATCH_{hjl} + \beta_{1hi}PC1_{jkl} + \beta_{2hi}PC2_{jkl} + \beta_{3hi}PC3_{jkl} \\ & + \beta_{4hi}EDGE_{jk} + \beta_{5hi}SIZE_{jk} + \beta_{6hi}AMNT_{jk} + \beta_{7hi}SIZE_{jk}AMNT_{jk} \end{aligned}$$

where  $\gamma_{1hi}$  is a species-specific autologistic parameter (Royle & Dorazio 2008); this term represents the change in the occupancy intercept if the site was occupied the previous year. We chose this model specification over a dynamic model that estimates colonization and extinction

rates (e.g., MacKenzie et al. 2003) because we were not explicitly interested in distributional changes through time but rather community structure in each year. We standardized all covariates with a mean of zero and standard deviation of one before inclusion to assist with model convergence. Although SIZE and EDGE did have a relatively strong positive relationship ( $r = 0.62$ ), the Pearson's correlation coefficient between all other variable pairs was weak ( $|r| < 0.25$ ; Appendix A, Table A5).

We expected that species in the same trait group would respond to occupancy covariates similarly. However, we did not expect random patch effects or detection covariates to vary systematically between these groups. Thus, we specified parameter-specific hyperdistributions for the effects of each covariate in the following way:

$$\theta_{hi} \sim \text{Normal}(\mu_{\theta,h}, \sigma_{\theta,h}^2), \quad \text{for } \theta = \beta_0 - \beta_7, \gamma_0, \text{ and } \gamma_1$$

$$\theta_{hi} \sim \text{Normal}(\mu_{\theta}, \sigma_{\theta}^2), \quad \text{for } \theta = \alpha_0 - \alpha_2$$

$$\text{PATCH}_{hjl} \sim \text{Normal}(0, \sigma_{patch}^2)$$

Because our initial model indicated only weak support for a significant SIZE-by-AMNT interaction for most species, we also fit a second model as described above that excluded this interaction term. We fit both models in JAGS (Plummer 2003) using the jagsUI v 1.4.2 package (Kellner 2016) within the R v 3.1.2 programming language. We specified vague priors for all community hyperparameters;  $\mu$  values were distributed normally with a mean of 0 and variance of 1000;  $\sigma^2$  values had a uniform (0, 5) distribution. For each model we ran three MCMC chains for 400,000 iterations with a burn-in of 200,000 and thinned by 100. This left us with 6,000

estimates from the posterior distribution across all chains. We assessed model convergence by visually inspecting traceplots, and ensuring the Gelman-Rubin statistic for all monitored parameters was less than 1.1 (Gelman et al. 2004). The full model specification, including a description of our model fit assessment, is found in Appendix D.

We evaluated support for our hypotheses for each species and each trait group mean based on 95% posterior credible intervals for the landscape variables (SIZE and AMNT). We deemed effects significant if the intervals did not overlap zero. Because SIZE and AMNT were only weakly correlated, we interpreted a significant SIZE effect as support for the *landscape fragmentation hypothesis*, and a significant AMNT effect as support for *the landscape composition hypothesis*. A significant SIZE\*AMNT term supported the *fragmentation threshold hypothesis*, and the *random sample hypothesis* was supported if credible intervals overlapped zero for all landscape terms.

Because all species are detected imperfectly, point-level species richness could not be directly observed. As a result, our model does not explicitly examine the relationship between richness and covariates. Following Zipkin et al. (2009), we instead inferred these relationships by examining predicted species richness as an emergent value from the model. For each of the 6,000 posterior draws, we first calculated predicted probability of occupancy for each species by varying the values of SIZE or AMNT, and holding all other covariates constant at their means. We then calculated predicted richness for the entire community and for each trait group separately by summing these values at each iteration, resulting in 6,000 estimates of predicted richness for each SIZE or AMNT value.

## RESULTS

We found very little support for the *fragmentation threshold hypothesis*. The SIZE-by-AMNT interaction term was only significantly negative for a single species (Hooded Warbler). For 46 species (88%), this term was non-significant, and for five species (10%) it was significantly positive, indicating that fragmentation effects increase with increasing habitat amount (Appendix A, Fig. A1). We found no evidence for lack of fit in the model that included the interaction term ( $p = 0.571$ ), nor in the model that excluded this term ( $p = 0.568$ ). In fact, the posterior distributions for all parameters shared between the two models were nearly identical (Appendix A, Fig. A1). Therefore, we present the results from the more parsimonious model below. Full results from this model are presented in Appendix A, Tables A6 and A7.

Based on our criteria, we found evidence for the *random sample hypothesis* (*i.e.*, no significant SIZE or AMNT effect) for one interior species (13%), 11 edge species (52%), and 8 forest generalists (35%). Note, however, that we had very few detections for most of these species, resulting in large posterior credible intervals for the effects of SIZE and AMNT (Fig. 3.2). At the fine scale, one or more local habitat covariates (edge distance, PC1, PC2, or PC3) influenced the probability of occupancy for 26 (50%) species (Appendix A, Table A6). In fact, the estimates of the effects of edge distance confirmed our trait group classifications. On average, probability of occupancy was greater at points further from the edge for interior specialists, and greater at points close to the edge for edge specialists; for all 23 forest generalists, the credible intervals for the edge distance effect overlapped zero (Fig. 3.2).

Our test of the *landscape fragmentation hypothesis* revealed substantial differences in the response by ecological trait groups. The estimate of the mean patch size effect was significantly positive for interior specialists, significantly negative for edge specialists, and approximately

zero for habitat generalists (Fig. 3.2), supporting our hypotheses about how fragmentation influences these groups. Indeed, 78% of species that were significantly positively associated with patch size were interior specialists, and 86% that were significantly negatively associated with patch size were edge specialists. These results were also reflected in emergent patterns of species richness. Predicted richness values increased with patch size for interior specialists, and decreased with patch size for edge specialists. We saw no strong trend for forest generalists or for all species combined (Fig. 3.3).

Support for the *landscape composition hypothesis* was much more variable within trait groups. Credible intervals for the average effect of forest amount overlapped zero for all groups (Fig. 3.2). Nevertheless, a much greater proportion of interior species were significantly positively associated with forest amount (50%), when compared to the generalist (13%) and edge (14%) groups. Surprisingly, 16 total species were significantly negatively associated with the amount of forest within 2 km, including over half of the forest generalists. Of these 16 species, 11 (69%) are obligate primary (Downy Woodpecker, Hairy Woodpecker, Red-bellied Woodpecker, Red-headed Woodpecker, and Northern Flicker) or secondary (Carolina Chickadee, Prothonotary Warbler, Tufted Titmouse, White-breasted Nuthatch, Carolina Wren, and Great Crested Flycatcher) cavity nesters (Rodewald 2015). Again, these results were reflected in emergent richness patterns; while predicted richness of interior species increased with increasing forest cover, predicted richness of edge specialists, forest generalists, and all species combined was actually greatest at low forest cover values (Fig. 3.3).

## Detection Probability

Detection probability, and the factors influencing it, varied widely among species. Although we initially assumed detection probabilities would not systematically differ among ecological trait groups, interior specialists did tend to be more detectable. The average detection intercept for interior specialists was 2.5 times larger than the average intercept for forest generalists, and over 4 times larger than the average intercept for edge specialists (Fig. 3.4). In addition, detectability of 31 species (60%) was significantly influenced by at least one modeled covariate (Appendix A, Table A7). The effects of tree basal area tended to be weak and insignificant, (posterior community mean = 0.02; 95% CI = -0.02, 0.06) while the effects of Julian date tended to be strong and negative (posterior community mean = -0.16; 95% CI = -0.26, -0.06).

## DISCUSSION

In this study, we tested for the independent effects of patch size and habitat amount on the distribution of forest breeding birds while accounting for the confounding effects of, edge distance, sample area, and imperfect detection. Although we found little evidence for the *fragmentation threshold hypothesis*, both the *landscape composition* and *landscape fragmentation* hypotheses were supported for numerous species. These results bolster the growing body of research highlighting the importance of landscape features in driving species distribution patterns. Moreover, our results unequivocally demonstrate that patch size per se has a significant influence on the distribution pattern of many species, beyond the amount of forest it contributes to the local landscape. Although our results show that species richness varies little

with patch size, community composition changes in ways that can be predicted by general ecological traits.

We found that the average patch size effect was significantly positive for interior specialists, significantly negative for edge specialists, and approximately zero for forest generalists (Fig. 3.2). Bender et al. (1998) identified a similar pattern in their review of patch size effects on animal densities and pointed out that the amount of habitable area is overestimated for interior species at low patch sizes, and for edge species at large patch sizes. Our results may have been driven by a similar geometric pattern, because the size of a contiguous habitable interior patch would increase with forest patch size, while small patches have a greater edge-to-area ratio. This prompted us to test whether interior and edge species distributions were positively associated with core patch size and edge patch size, respectively. However, our results did not differ markedly from the model presented, likely because all three measures of patch size were highly correlated (Appendix A, Fig. A2). A more adequate test would require defining habitat uniquely for each species (Fahrig 2013, Betts et al. 2014, Hanski 2015), which was beyond the scope of this study.

Contrary to the results from other studies (Andren 1994, Trzcinski et al. 1999, McGarigal & Cushman 2002, Fahrig 2003, 2013, 2017), we did not find that a reduction in the amount of forest cover was overwhelmingly detrimental to bird distributions in our study area. In fact, we found the opposite pattern for many species, particularly cavity nesters (Fig. 3.2). We speculate that availability of cavity trees is somehow inversely related to forest cover in our study region. Tree mortality tends to be greater near forest edges (e.g., Esseen et al. 1994), and it is possible that landscapes with lower forest cover tended to have greater edge-to-area ratios. Regardless of the mechanism, failure to account for the distribution of cavity trees at the landscape scale likely

meant that forest cover was a poor measure of habitat amount, even for many of our forest generalist species.

Similar to others, we did not find that total species richness increased with increasing patch size (Fahrig 2013). Such evidence has led to calls to dismiss patch size as a useful landscape metric because it does not conform with island biogeography (MacArthur & Wilson 1967) or metapopulation theory (Levins 1969, Hanski 1998). Yet the pattern of our results implies that equating ‘forest’ with ‘habitat’ was likely imprecise for most species. Thus, our study does not constitute a rigorous, ‘species-centered’ test of these ideas (Fahrig 2013, Betts et al. 2014, Hanski 2015). Unfortunately, designing multi-species studies that both account for idiosyncrasies in habitat requirements, and minimize correlation between composition and configuration variables for all species would require an extraordinary financial and logistical effort. Thus, while our results do not conform with established theory, they do have practical implications for conservation and land management; forest patch size per se influences the distribution of many species, particularly interior and edge specialists.

Fahrig (2017) recently noted that the vast majority (76%) of significant fragmentation effects found in the literature are positive. That is, the distributions of individual species are far more likely to increase, rather than decrease, with fragmentation. We found a similar pattern, yet our results notably contrast with one of Fahrig’s (2017) main conclusions that “there is no justification for assigning lower conservation value to a small patch than to an equivalent area within a large patch...” We fit a linear model to compare conservation concern scores (NABCI 2016) among our ecological trait groups; we found that occupancy probability was not only higher for interior species in large forest patches, but members of this group also tend to be of significantly greater conservation concern than forest edge ( $t = 2.92, p = 0.005$ ) or generalist ( $t =$



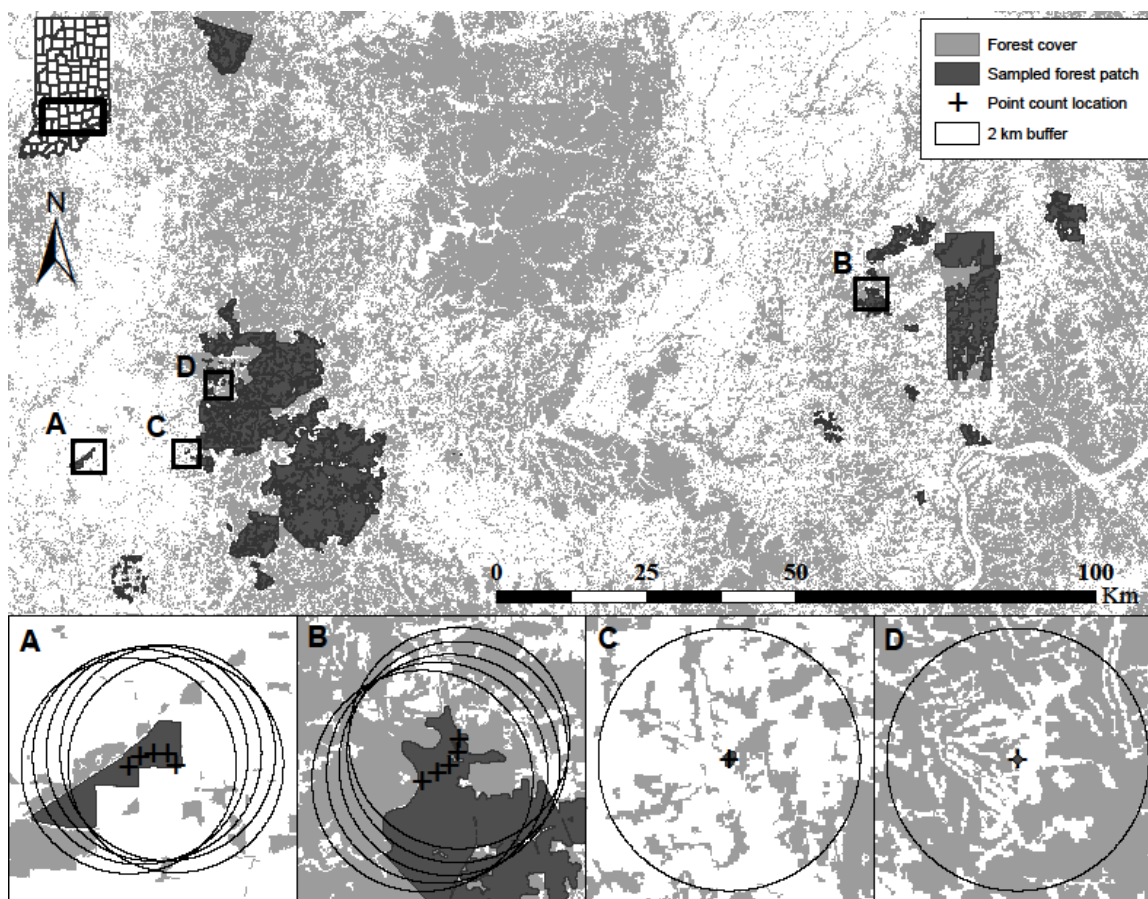
2.81,  $p = 0.007$ ) species (Fig. 3.5). Indeed, the ratio of interior to edge specialists in our study region may help explain the overwhelming majority of positive fragmentation effects; if species that prefer edge habitat are simply more common, one would expect to find positive effects of reduced patch size more often.

There are numerous potential mechanisms that could explain the sensitivity of interior specialists to forest patch size. Villard (1998) cautions against confusing interior preference with area sensitivity, and these potential drivers are notably confounded in our habitat classifications, which we based on previously observed patterns. Studies that document active edge avoidance are rare (Villard 1998), and apparent sensitivity to patch size could be driven by edge-interior vegetation or microclimatic gradients, or by densities of predators, prey, or nest parasites (reviewed by Stratford & Robinson 2005). Although we did not attempt to isolate the mechanism driving patch sensitivity, our results clearly demonstrate that larger forest patches do, in fact, have greater conservation value for many species.

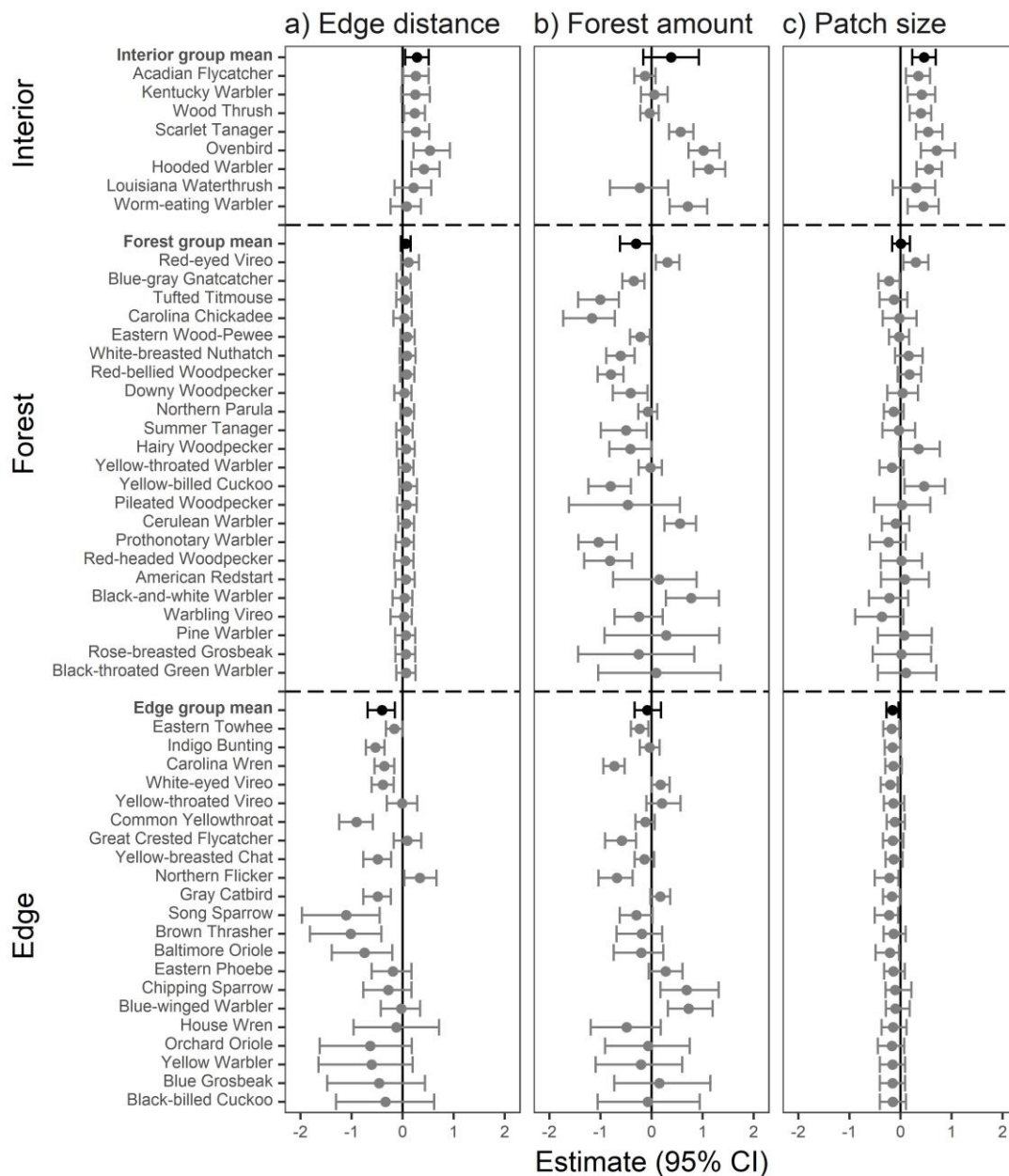
Finally, our results demonstrate the benefit of a hierarchical approach to modeling community structure, rather than focusing exclusively on richness. In our study, species which tended to be negatively associated with patch size (edge specialists) also tended to have lower probabilities of detection than those positively associated with patch size (interior specialists, Fig. 3.4). In other words, when patch sizes were large, we were likely detecting a greater proportion of the species in the community during a survey than when patch size was small. Failing to account for this could have resulted a biased relationship between patch size and species richness, resulting in a more positive association. This implies that variability in detection rates may not explain the general lack of empirical support for fragmentation effects (Fahrig 2013, 2017). Regardless, modeling occupancy probabilities for each species individually

allowed us to not only identify shifts in community composition, but also to account for the potential confounding effects of imperfect detection.

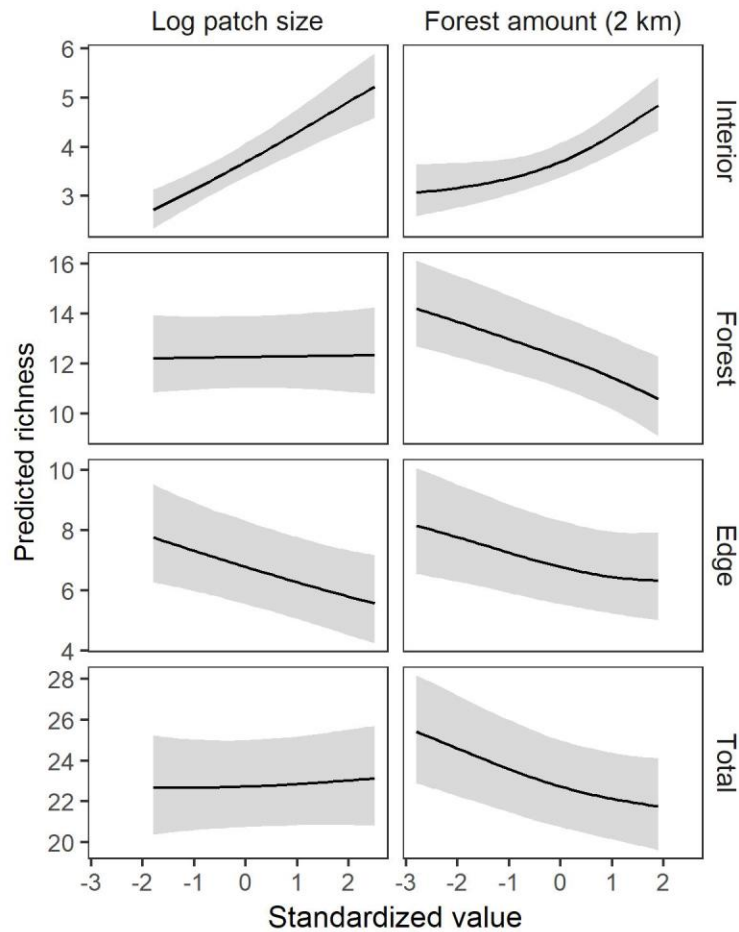
Those who argue for abandoning the patch-island paradigm in fragmentation research do so on the grounds that patch boundaries and matrix characteristics do not conform with existing theory. That is, larger patches do not tend to have higher species richness as predicted by IBT (e.g., Fahrig 2013, Mendenhall et al. 2014), boundaries between patches and matrix are blurry and do not delineate demographically distinct units as required in a metapopulation framework (Baguette 2004, Manning et al. 2004, Fahrig 2013), and the amount of habitat is vastly more important than the size of any given patch (Andren 1994, Trzcinski et al. 1999, McGarigal & Cushman 2002, Fahrig 2003, 2013, 2017). Yet some species require large forest patches in order to have any habitat available to them at all. A conservation strategy focused on maintaining large forest patches will not necessarily be beneficial for all or even most species (Fahrig in). Yet given that core forest area has become extremely scarce worldwide (Haddad et al. 2015), and that many species of conservation concern depend upon it, protecting large forest patches may provide additional benefit above and beyond the conservation of habitat amount.



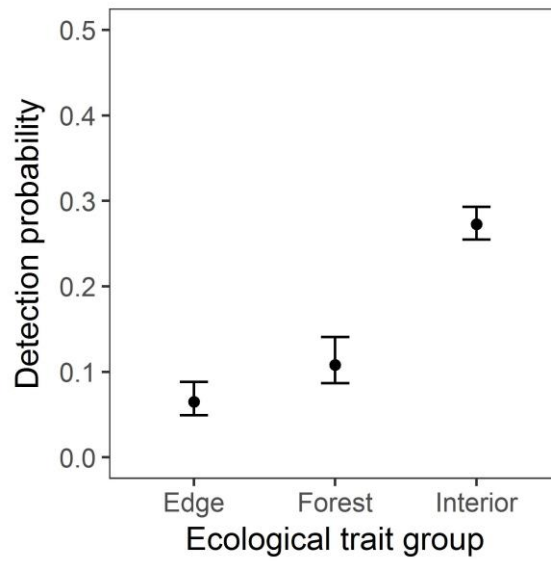
**Figure 3.1.** A map of the study region in which we conducted breeding bird point counts between 2011 and 2013. Gray areas represent forest cover (National Land Cover Database; Fry et al. 2011), and the darker gray areas highlight the 202 unique forest patches sampled. We designed our study to minimize correlation between patch size and the amount of forest within 2 km at the point level. Thus, we sampled A) large patches with low forest amount, B) large patches with high forest amount, C) small patches with low forest amount, and D) small patches with high forest amount. Larger patches (A and B) contained more point count stations to ensure we sampled the gradient in edge distance.



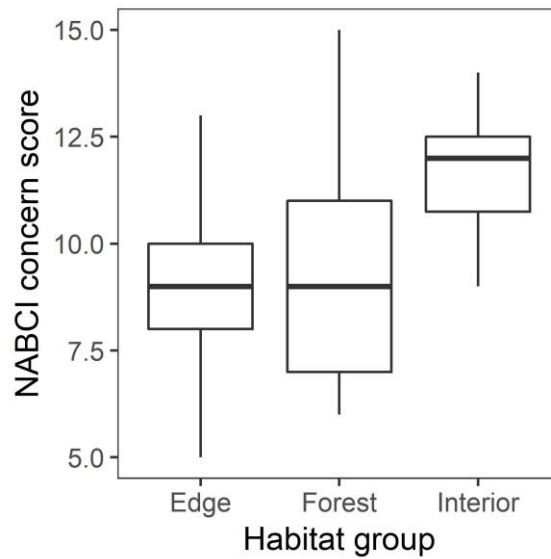
**Figure 3.2.** Posterior means and 95% credible intervals for the effects of a) edge distance, b) amount of forest within 2 km, and c) log-transformed patch size on probability of occupancy for breeding forest bird communities. Species were divided into three ecological trait groups (interior specialist, forest generalist, or edge specialist), and the mean effect of the covariate on members of each group was estimated along with individual effects. Within each trait group, species are listed from most common (top) to least common, or equivalently, from most influential on the group mean estimate, to least. Note that all covariates were standardized with a mean of 0 and standard deviation of 1 prior to model fitting.



**Figure 3.3.** Predicted richness ( $\pm$  95% credible intervals) of breeding forest birds occupying a 50 m radius forest plot varies as a function of forest patch size (left) local forest cover (right), and ecological trait group. Predicted richness values were calculated from each of 6,000 draws from the posterior distributions of a community occupancy model, and represent the sum of the predicted occupancy probabilities of species when all other local and landscape variables are held constant at their means.



**Figure 3.4.** The inverse logit (and 95% credible interval) of the average detection probability intercept for species classified as edge specialists ( $n = 21$ ), forest generalists ( $n = 23$ ), and interior specialists ( $n = 8$ ). The values plotted are the means of the posterior distributions from a community occupancy model in which detection intercepts represent the probability of detecting the species at a site with average tree basal area, sampled on the mean Julian date.



**Figure 3.5.** The distribution of conservation concern scores for 52 species classified as edge specialists, forest generalists, or interior specialists (NABCI 2016). Results from a linear model indicated that interior specialists, which tend to be positively associated with forest patch size, are also of greater conservation concern than forest edge ( $t = 2.92$ ,  $p = 0.005$ ) or generalist ( $t = 2.81$ ,  $p = 0.007$ ) species.

## FOREST GAPS REDUCE LANDSCAPE CONNECTIVITY FOR FRAGMENTATION-SENSITIVE BIRDS IN MULTIPLE BEHAVIORAL STATES

### INTRODUCTION

Habitat loss and fragmentation pose major threats to biodiversity worldwide (Rands et al. 2010, Haddad et al. 2015). Such alterations can reduce the functional connectivity of a landscape (i.e., the propensity for movement; Taylor et al. 1993) by decreasing the size of remnant patches and increasing the distance between them (Fahrig 2003), or by altering the quality and utility of the intervening matrix (Ricketts 2001, Kennedy & Marra 2010). Metapopulation theory predicts that maintaining functional connectivity is critical for ensuring species persistence in fragmented systems (Hanski 1998, Hanski & Ovaskainen 2002). Thus, understanding how animal movements are influenced by landscape structure is one of the most important challenges facing ecologists (Taylor et al. 1993, Bélisle 2005).

Unfortunately, progress in this field has been hampered due to disagreements over how to define and measure functional connectivity (Bélisle 2005), and the complexities of analyzing spatial movement data (Kadoya 2009). Further, comparative studies are complicated by heterogeneity at the level of both the species and the individual. Species can vary in terms of perceptual ranges (Lima & Zollner 1996), inclination to explore (e.g., Greenberg 1983, Mettke-Hoffman & Gwinner 2004), or the way they perceive landscapes (Betts et al. 2015); all of these factors can influence the propensity for movement. At the individual level, idiosyncrasies in past experiences, as well as localized predator densities, food availability, and habitat quality can alter the motivation or willingness to move (Bélisle 2005, Betts et al. 2015). This implies that just because an individual chooses not to move between two patches, does not mean it is incapable of doing so. As such, observational studies are likely to be inadequate for quantifying functional



connectivity, and there is a need to utilize experimental procedures to properly evaluate if an individual can move among habitat patches (Bélisle 2005, Betts et al. 2015).

In recent years, researchers have used translocation experiments to help standardize some of these variables among experimental trials (Bélisle 2005). By translocating territorial individuals across landscapes, the researcher can provide motivation to move towards a specific destination (i.e., their home territory). This minimizes the influence of individual experiences on the propensity to move in different landscapes, and allows for comparison of the movements of different species in the same landscape (Betts et al. 2015). This technique has proved useful for evaluating connectivity for a wide variety of taxonomic groups (see Betts et al. 2015).

Importantly, these studies rely on an assumption that behaviors and choices exhibited by translocated individuals reflect those made by conspecifics under natural conditions (Volpe et al. 2014, Betts et al. 2015). Volpe et al. (2014) demonstrated that translocated hummingbirds made similar habitat choices to individuals moving within their territories. However, numerous other studies have shown that exposure to novel environments can substantially alter movement behavior. For instance, longer movements and altered trajectories have been documented in spatially relocated insects (Heidinger et al. 2009, Watts et al. 2012), mammals (Jacquot & Solomon 1997), reptiles (Reinert & Rupert 1999, Rittenhouse et al. 2007) and birds (Kesler et al. 2012, Kemink & Kesler 2013). Further, several studies have documented behavioral shifts in movement patterns of translocated individuals; this indicates that the translocation itself may induce atypical behaviors (Heidinger et al. 2009). Translocated animals often transition from exploratory movements immediately post-release to either directional homing, or patterns resembling those of residents (Reinert & Rupert 1999, Tsoar et al. 2011, Kesler et al. 2012,

Watts et al. 2012). Thus, experimental translocations may provide the opportunity to investigate limitations to functional connectivity under multiple behavioral states.

Habitat loss and fragmentation have been implicated as a major cause of population decline for many North American bird species (Andr n 1994, Robinson et al. 1995, Donovan & Flather 2002). Because both migrants and residents exhibit some propensity for homing (e.g., Keiser et al. 2005, Kennedy & Marra 2010) there has been a rise in use of translocation experiments to examine the role of functional connectivity in these declines. Results from these studies highlight the importance of maintaining land cover (B lisle et al. 2001, Gobeil & Villard 2002, Castell n & Sieving 2006, Hadley & Betts 2009), corridors and stepping stones (Castell n & Sieving 2006, Gillies et al. 2011, Vergara et al. 2013), and permeable matrix (Gobeil & Villard 2002, Kennedy & Marra 2010) for improving connectivity. However, many of these studies relate landscape features to measures of homing success or homing time (e.g., B lisle et al. 2001, Gobeil & Villard 2002, Kennedy & Marra 2010), limiting inference that can be drawn about particular movement barriers. Though technological (Bridge et al. 2011) and statistical (Jonsen et al. 2005, Fortin et al. 2011) advancements have improved our ability to evaluate fine-scale movement decisions (e.g., Hadley & Betts 2009, Castell n & Sieving 2006, Gillies et al. 2011, Vergara et al. 2013, Volpe et al. 2014), variation in behavior exhibited by translocated birds has largely been ignored.

In this study, we use experimental translocations to evaluate the effects of forest fragmentation on multi-scaled movement patterns of Ovenbirds (*Seiurus aurocapilla*) and Wood Thrush (*Hylocichla mustelina*) in southern Indiana. Previously collected data in our study region indicated that the distributions of both species are limited by decreasing patch size and forest cover (Chapter 3), and our study seeks to test the hypothesis that these patterns could be

explained by movement limitation. If true, we would expect that movements should be more constrained as fragmentation increases, leading to longer, more tortuous homing paths, with individuals showing reluctance to cross forest gaps. We additionally test the hypothesis that our focal species exhibit multiple behavioral modes in their movement patterns, and evaluate whether the effects of fragmentation on movement differ between these modes. These results will be valuable for helping land managers to understand if, when, and how promoting functional connectivity may be beneficial to fragmentation-sensitive species.

## **MATERIALS AND METHODS**

### **Study Species and Sites**

During the breeding seasons of 2011-2013 we conducted avian point counts in 202 forest patches across southern Indiana to evaluate the effects of forest loss and fragmentation on breeding bird distributions (Chapter 3). Results indicated that forest interior specialists tended to be particularly sensitive to these landscape variables, and thus we chose two of these species to evaluate how landscape structure limits connectivity. Ovenbird distributions were heavily limited by forest cover, and showed greater sensitivity to patch size than any of the other 51 species examined. Wood Thrush were similarly influenced by patch size, but showed no response to decreasing forest cover. Thus, a comparison of these two species also provided the opportunity to qualitatively relate distribution patterns to movement processes.

We chose two properties in southern Indiana, USA for our experimental translocations (Fig. 4.1). Naval Surface Warfare Center Crane (hereafter Crane) is owned by the Department of Defense, and provides operational support and weapons storage for the U.S. military. Crane spans over 25,000 ha, and is dominated by large, contiguous tracts of forest. Glendale Fish and

Wildlife Area (hereafter Glendale) is owned by the Indiana Department of Natural Resources, and focuses on providing hunting and fishing opportunities. Glendale spans just over 3,000 ha, which are dominated by small forest fragments interspersed with active and fallow agricultural fields. Annual rainfall averages 119 cm (Indiana State Climate Office 2002) in the region, and temperatures average between 6° C in winter to 18° C in summer (National Climatic Data Center 2011). Dominant trees in these temperate hardwood forests include tulip poplar (*Liriodendron tulipifera*), white ash (*Fraxinus americana*), American beech (*Fagus grandifolia*), black walnut (*Juglans nigra*), and various species of oak (*Quercus spp.*), hickory (*Carya spp.*), and maple (*Acer spp.*).

We chose specific landscapes for our translocation experiments that spanned the range of forest cover and fragmentation represented in the region. We overlaid a grid with a grain of 2 km<sup>2</sup> on each property and eliminated all cells that were inaccessible due to private property rights or safety concerns. Within the remaining cells, we quantified the number of unique forest patches and the proportion of forest cover. We then used a stratified random design to select 17 landscapes that spanned the combination of the two gradients. Forest cover in the selected landscapes ranged from 39% to 93% (mean = 66%) and the number of patches ranged from 2 to 55 (mean = 21.47).

### **Translocations and Tracking**

During the breeding seasons of 2015 and 2016 we conducted initial surveys of each landscape to locate breeding, territorial male Wood Thrush and Ovenbirds. When we located individuals, we conducted behavioral observations to confirm breeding behavior. Individuals were only considered for a translocation experiment if we found evidence of breeding; thus

translocated birds had motivation to return home. Evidence of breeding constituted either the presence of a nest, or that individuals were found singing on the same territory for three consecutive days. We were concerned that birds living in highly fragmented systems may have lower initial fitness than those in more contiguous areas, inhibiting us from separating the effects of initial fitness from landscape structure on movement patterns (Bélisle 2005, Betts et al. 2015). To limit this confounding, we attempted to translocate two birds (from the same patch, where possible) of the same species in each landscape; one individual was challenged by having to cross multiple large gaps to return home (fragmentation treatment), while the other had predominantly contiguous forest between the release site and its home territory (control treatment; Fig. 4.1). In cases where we were unable to identify two conspecifics in the same landscape, we assigned the single individual to the fragmentation treatment to maximize the information we could gather on gap crossing behavior.

Once breeding was confirmed, we chose release sites to (1) ensure one fragmentation treatment and one control treatment per species in the landscape (where possible), (2) maintain standard translocation distances of 1-1.2 km, (3) assure likely homing routes avoided inaccessible private or military lands, and (4) minimize travel time between capture and release sites, limiting the stress on translocated birds. Target birds were captured using mist nets and conspecific playback. Once captured, we measured the bird's mass and tarsus length to assess body condition, and affixed a USGS aluminum bands and unique set of color bands to the legs. We then attached a 0.7 g Pip Ag376 VHF transmitter (Biotrack Ltd., Wareham, UK) using a leg loop harness (Rappole & Tipton 1991), and translocated the bird to its pre-determined release site. Mean time between capture and release was 59.85 minutes.

After release, trained technicians tracked movements of translocated birds continuously using handheld TRX-1000S telemetry receivers (Wildlife Materials, Inc., Murphysboro, IL) for four days, or until the bird returned home (i.e., when it was recorded within 100 m of its capture location). Birds that did not return home within four days were located daily, and deemed a homing failure if they did not return by the tenth day. Logistical constraints prevented us from tracking birds between sundown and sunrise, and during 2015, between approximately 1200 h and 1600 h. Technicians were instructed to stay within 50 m of the bird at all times and record GPS and directional compass bearings every 20 minutes, or more frequently when birds were moving quickly. In some instances, technicians were unable to stay within 50 m, and instead recorded an estimated distance to the bird based on telemetry receiver strength calibrated through field tests. GPS points were discarded if the distance estimate was >100 m due to accuracy concerns. In all, we translocated 36 Wood Thrush and 19 Ovenbirds, though one Wood Thrush dropped its transmitter soon after release and was excluded from all analyses.

### **Behavioral Change Point Analysis**

Based on previous literature (e.g., Kesler et al. 2012), we expected that movements for translocated birds might occur in two phases, the first comprised of *exploratory* foraging and orientation movements, and the second comprised of directed *homing* movements once the individual had recovered from translocation stress and become reoriented (Kemink & Kesler 2013). To test for and separate these two potential phases, we conducted a behavioral change point analysis (BCPA) on the temporal series of persistence velocities for each individual (Gurarie et al. 2009). Persistence velocity ( $V_p$ ), is a measure of the tendency and magnitude of movements to persist in the same direction (Gurarie et al. 2009), and thus should be useful for

separating these two phases. We defined a *step* for each bird as the incremental movement made between two subsequently recorded GPS points, and characterized it by time  $t$ , representing the time at which the step endpoint was recorded. We calculated persistence velocity for each step as

$$Vp_t = V_t * \cos(\theta_t)$$

where  $V_t$  represents the speed of the movement, and  $\theta_t$  represents the angular change in trajectory from the previous step. For each bird, which took a total of  $T$  steps, we iteratively split the time series at every  $Vp_t$ , and fit the following autocorrelated time series model to each half of the data:

$$Vp_{i,j} = \mu_i + \rho_i^{\tau_{i,j}} (Vp_{i,j-1} - \mu_i) + \varepsilon_{i,j}$$

$$\varepsilon_{i,j} \sim N\left(0, \sigma_i^2 (1 - \rho_i^{2\tau_{i,j}})\right)$$

Here,  $\mu$  represents the mean persistence velocity, and  $\rho$  represents the autocorrelation between two observations, which decreases exponentially as a function of the time interval between them ( $\tau$ ). The subscript  $i = 1, 2$  represents the behavioral mode, and  $j = 1, 2, \dots, t$  when  $i = 1$ , and  $j = t+1, t+2, \dots, T$  when  $i = 2$ .

For each iteration, we recorded the likelihood of the model, and chose the value of  $t$  where the likelihood was maximized as the most likely behavioral change point (Gurarie et al. 2009). While BCPA can be used to identify multiple behavioral shifts (e.g., Gurarie et al. 2016), we chose to split the data for each individual into only two periods (i.e., one change point) to objectively identify the most likely point at which individuals switched from exploring to homing. Once we had identified the most likely BCP, we fit a null model to the data that assumed all parameters ( $\mu$ ,  $\rho$ , and  $\sigma$ ) were identical on both sides of the BCP, along with seven

additional models that allowed one, two, or three of the parameters to vary. We compared among these models using AICc, and concluded there was no evidence for a behavioral change if the null model had the most support.

We then pooled steps taken by all individuals to test for differences in step length, step speed, turning angle, and deviation angle between the exploratory and homing phases. We measured deviation angle as the angular difference between the step trajectory and a direct line path towards the capture location. We compared log-transformed step length and step speed using linear mixed effects models that included a random intercept for ‘individual’. Because angular data have circular distributions, we compared the distribution of turning and deviation angles between behavioral modes using a Kolmogorov-Smirnov test. All analyses were conducted in R (v. 3.3.3), and mixed effects models were fit using the `lme` function in the *nlme* package (Pinheiro et al. 2017).

### **Landscape Effects on Movement**

We analyzed the effects of fragmentation on movement at two spatial scales representing movement paths and step-level decisions. We defined the bird’s *path* as the entirety of the route taken from the time it was released until it returned home. In all path- and step-level analyses, we chose to use only data from the individuals that successfully homed for three reasons. First, identifying BCPs to distinguish between exploratory and homing movements did not make sense for birds that did not home. Second, we could not be certain that individuals that failed to home were motivated to do so. Lastly, some unsuccessful individuals were predated or dropped their transmitters, and the precise timing of those events was unclear.



### *Path-Level Analyses*

At the path level, we identified the *local landscape* to which each individual was exposed by drawing an ellipse using the capture and release locations as foci. The minor axis was 500 m wide, and the major axis was 1.4 times the distance between the capture and release sites (Fig. 4.1). Local landscapes encompassed, on average, 90.4% of all points recorded on an individual. We used ArcMap v. 10.2.2 (ESRI, Redlands, CA) to digitize all forest in the region by referencing aerial images from the National Agriculture Imagery Program (USDA 2014). Within each ellipse, we quantified landscape composition as the proportion covered by digitized forest (PROP.FOR), and fragmentation by the number of unique forest patches (PATCHES). PROP.FOR ranged from 0.52 to 0.96, with a mean value of 0.78. PATCHES ranged from 1 to 25 with a mean of 8.82. The Pearson's correlation between PROP.FOR and PATCHES was -0.66. Because other studies have found that translocated birds tend to follow riparian corridors (Gillies & St. Clair 2008, Volpe et al. 2014), we also quantified the total length of rivers and streams within each ellipse using the USGS National Hydrography Dataset.

We evaluated the effects of fragmentation on bird homing time and path straightness for the entire homing process, and in each of the behavioral phases separately. We chose not to model homing success because most translocated individuals returned successfully, and thus there was little variability to explore. We calculated straightness by dividing the length of the straight-line path between the start and end points by the total distance traveled. Start and end points for total path straightness were the release and capture sites, respectively. The end point for the exploring phase, and starting point for the homing phase was the spatial location where the BCPA indicated the bird's behavior changed.

For each response variable, we used a two-stage model building approach. We began with a null model (homing time responses) or one that included the number of steps recorded (straightness responses). In the first stage, we tested for effects of covariates unrelated to fragmentation, but that have potential to influence homing (Bélisle 2005, Betts et al. 2015): body condition (CONDITION), the ratio of body size to tarsus length; total time from capture to release (CAPTIVITY); and total river/stream length in the local landscape (RIPARIAN). We compared the null model to models containing these covariates individually. Due to our small sample sizes, we wanted to minimize the number of explanatory variables, and thus we created a baseline model for stage two comprised of variables that improved the null model by greater than two AICc units (Burnham & Anderson 2002). In stage two, we compared the baseline model with four additional models containing linear predictors for 1) PATCHES, 2) PROP.FOR, 3) additive effects of PATCHES and PROP.FOR, and 4) additive effects of PATCHES and PROP.FOR plus their interaction.

### *Step-Level Analyses*

At the step level, we used step selection functions to model movement decisions conditional on the bird's location at each moment in time (Fortin et al. 2005). Following precedence (Gillies et al. 2011, Volpe et al. 2014), we eliminated all steps where start and end points were recorded over 20 minutes apart, or that were less than 25 m in length. This helped ensure that steps represented relatively straight line movements, and were not dominated by telemetry error, respectively. This left us with 372 exploring and 382 homing steps for Wood Thrush, and 286 exploring and 260 homing steps for Ovenbirds. For each used step, we generated 20 unused steps by randomly drawing independent turning angles and step lengths.

The distributions from which we drew these values differed between behavioral modes, and were constructed uniquely for individuals based on the mean distribution of all other individuals. We ensured that all unused steps were realistic by mandating endpoints landed in forest.

We then used mixed conditional logistic regression (Duchesne et al. 2010) to model factors influencing the probability of taking a step given the options available. Because we had multiple steps for each bird, the effects of all explanatory variables were modeled with random, individual-specific regression coefficients. We assumed that the distance from a step endpoint to the capture site (CAPDIST) would have substantial influence on movement decisions. Thus, we began with a null model that only included CAPDIST and an interaction between CAPDIST and behavioral mode (BEHAV). Once again, we used a two-stage model-building process. In the first stage, we compared the null model to models that included distance from the step endpoint to the nearest river or stream (RIPDIST) with and without an interaction between RIPDIST and BEHAV. We compared among these initial three models for each species using AICc, and chose the top model as the baseline for stage two.

In stage two, we identified three variables to characterize steps in terms of exposure to non-forested habitat. These included the number of forest gaps in the step (GAPS), the proportion of the step contained in forest (FOR%), and the total distance of forest gaps in the step (GAPDIST). We also quantified the forested proportion of a 50 m radius circle around the step start points (FOR50) to evaluate whether landscape context influences movement decisions. We chose 50 m to reasonably approximate the birds' perceptual range, as the median length of used steps was 45.84 m. We constructed five competing models (Table 4.1) for each exposure variable and compared them using AICc. Because all exposure variables were highly correlated (Pearson's correlation:  $|r| > 0.7$ ), we chose not to include them in any models simultaneously.

## RESULTS

Of the 35 Wood Thrush we translocated, 32 (91%) returned home. Of those that did not, all made some attempt to home. One refused to cross a road gap of approximately 500 m, while the other two returned within several hundred meters of their capture sites. Of the 19 translocated Ovenbirds, 15 (79%) returned home. Two of those that did not home were predated at approximately 70 hours post-release. One refused to cross the same 500 m road gap as the Wood Thrush, and one made no substantial directional movements toward home in 10 days. Among all birds that returned, homing times ranged between 3.1 and 72.2 hours, and Wood Thrush tended to return more rapidly than Ovenbirds (Fig. 4.2).

### Behavioral Change Point Analysis

The BCPA identified two distinct movement phases for 45 of the 47 birds that homed successfully (see Table A8 and Figs. A3, A4 in Supplementary material). Both Wood Thrush that did not exhibit dichotomous behavior appeared to start homing immediately after release, skipping the exploring phase (Fig. A3). However, rather than assume all movements for these birds represented homing, we chose to exclude their data from all analyses that required behavioral classification.

The proportion of the time spent in the exploring phase ranged from 0.23 to 0.89, and averaged 0.46 and 0.47 for Wood Thrush and Ovenbirds, respectively. Movement steps during the exploring phase were significantly shorter and slower than during homing for both species (Table 4.2). In addition, the distribution of turning (Wood Thrush,  $D = 0.11$ ,  $p < 0.01$ ; Ovenbird,  $D = 0.09$ ,  $p = 0.01$ ) and deviance (Wood Thrush,  $D = 0.08$ ,  $p < 0.01$ ; Ovenbird,  $D = 0.09$ ,  $p = 0.01$ ) angles significantly differed between phases. Exploratory movements had more random

orientations, and consisted of a large amount of course reversal. Homing movements tended to be straighter and oriented towards the bird's capture location (Fig. 4.3).

### **Path-Level Analyses**

Neither number of patches, nor forest cover improved the baseline model for any response variable of either species (Table 4.3; see Tables A9 and A10 for parameter estimates). Thus, there was little evidence for an effect of landscape composition or configuration on homing time or path straightness in any behavioral mode. The baseline model for Wood Thrush homing time did include body condition (Table A9), though counterintuitively, its effect was positive. That is, birds in better condition took longer to home once they entered the homing phase. The baseline models for Ovenbird total return time and path straightness during homing included captivity time. Parameter estimates indicated that longer captivity times led to increased return times and more tortuous routes (Table A9). For all other response variables, the null model was selected.

### **Step-Level Analyses**

At the step level, distance from the step endpoint to the nearest stream was included in all exposure models for Ovenbirds, but not for Wood Thrush (see Table A11 for full step level modeling results). On average, individual Ovenbirds did not prefer steps near streams ( $Z = -0.93$ ,  $p = 0.352$ ), but the variability among individuals was significant ( $Z = 3.11$ ,  $p = 0.002$ ), indicating birds differed greatly in their fidelity to riparian zones. We found strong evidence that both species were deterred from choosing steps that increased exposure to non-forested habitat. The effects of GAPS and GAPDIST were both negative, while the effects of FOR% were

positive in every model in which they were included (Table A11). Further, the baseline model had the least support when compared to the 15 exposure models for both species (Table 4.4). However, we found little evidence that the effects of exposure on step selection differed between behavioral modes, or with landscape context. In nearly every case, the model assuming a constant effect of each exposure variable had greater support than model allowing the effect of the variable to change with behavior or context (Table 4.4).

Of the three exposure variables, GAPS appeared to have the greatest influence on step selection. The relative influence (i.e., summed AICc weights of models including the covariate) of GAPS on step selection was 0.72 for Wood Thrush and 0.94 for Ovenbirds; the relative influence of the other two exposure variables was  $\leq 0.2$  for both species. The top model for both species included only GAPS, in addition to the baseline covariates (see Table 4.5 for parameter estimates).

## **DISCUSSION**

Uncovering the mechanisms driving fragmentation sensitivity is the first step in developing conservation and management schemes (Lindenmayer et al. 2008, Hadley & Betts 2016). Previous research has demonstrated that the distribution patterns of both Wood Thrush and Ovenbirds are both limited by forest loss and fragmentation (Chapter 2). Here, we found strong gap-crossing reluctance in both species, and this effect was stronger in the more fragmentation-sensitive Ovenbird. These results suggest potential mechanisms driving or exacerbating fragmentation sensitivity. These species may be purposefully choosing habitat surrounded by contiguous forest so that they can more easily (1) upgrade their territories through breeding dispersal, or (2) increase their fitness through access to mates or extra-pair copulations

(Banks et al. 2007). Alternatively, fragmentation may disrupt metapopulation dynamics by rendering small, isolated fragments inaccessible. Theory predicts that small patches should have higher extinction rates (MacArthur & Wilson 1967, Hanski 1998), and forest gaps could prevent dispersers from recolonizing unused patches or rescuing dwindling populations (Brown & Kodrick-Brown 1977). Of course, other explanations of the observed distribution patterns exist. For instance, these species may avoid fragmented landscapes due to altered biophysical properties in the remnant forest (e.g., Ries et al. 2004). Thus, while our results are consistent with the hypothesis that movement limitation may drive fragmentation sensitivity, we cannot exclude other alternatives.

Interestingly, the negative effects of gaps on fine-scale movement decisions did not scale up to the path level, as we saw no effects of forest cover or fragmentation on homing time and path straightness. We also saw no evidence that gap-crossing probability differed as a function of landscape context (i.e., forest within 50 m). We posit that these results reflect the high motivation to home induced by our experimental translocations, as homing failure would result in loss of a partner, territory, and potentially offspring. For many individuals, avoiding gaps was not an option in order to home successfully. In fact, we often observed that when birds encountered a forest gap, they would move along its edge for several steps before eventually crossing out of necessity. It is possible then, that the birds in our sample may have preferred routes that avoid gaps (e.g., Hadley & Betts 2009), but that given limited options for such avoidance, the most direct line home was the best choice.

Our results thus highlight several important questions regarding the nature of observed movement patterns, and their relationship to natural behavior. First, it is unclear how motivation interacts with inclination to cross barriers. Numerous studies have demonstrated that forest

specialist birds tend to be reluctant, though willing, to cross gaps when motivated (e.g., Castellón & Sieving 2006, Gillies & St. Clair 2010, Gillies et al. 2011, Ibarra-Macias et al. 2011).

However, the hesitation we observed at forest boundaries could translate into complete refusal to cross those gaps in the absence of strong motivation. If true, then the results of studies such as ours would have the tendency to overestimate landscape functional connectivity.

Volpe et al. (2014) showed similarities between movement decisions of translocated and non-translocated hummingbirds. However, the relationship between movement behaviors of translocated versus dispersing animals remains untested. Gap crossing may in fact be common for forest-dependent birds moving in familiar habitats if it increases access to resources or extra-pair copulations (Norris & Stutchbury 2001, Fraser & Stutchbury 2004, MacIntosh et al. 2011). Yet birds moving in novel environments may be more reluctant to expose themselves to adverse conditions (Gillies et al. 2011). There is thus a critical need to compare results from translocation experiments to movement behaviors of dispersing animals to evaluate their utility for understanding metapopulation processes.

Translating information from translocation studies into useful management strategies requires an understanding of how well the data represent true biological processes (Betts et al. 2015). Our results demonstrate a clear dichotomy in the movement behaviors of translocated birds, suggesting that such data may capture information about multiple processes simultaneously. Though we found no difference in the effects of fragmentation on movement patterns between these behavioral modes, this may not always be the case. If animals are more willing to move in certain contexts (e.g., Gillies et al. 2011) it may not be prudent to assume uniformity in the way landscape connectivity is perceived among behavioral modes (e.g., Hadley & Betts 2009, Castellón & Sieving 2006, Gillies et al. 2011, Vergara et al. 2013, Volpe et al.



2014). Further examination of what processes these behavioral modes represent will be critical to understanding how functional connectivity differs among times of year and life stages.

Immediately after release, translocated birds exhibited exploratory behavior, characterized by short, undirected movements and frequent returns to their release sites (Table 4.2, Fig. 4.3). Similar behaviors have been demonstrated by other species translocated to novel environments (e.g., Reinert & Rupert 1999, Tsoar et al. 2011, Kesler et al. 2012). In their study of Tuamotu Kingfishers (*Todiramphus gambieri gertrudae*), Kesler et al. (2012) noted that these movement patterns resembled those made by post-natal dispersing juveniles. Vega Rivera et al. (1998) also noted a high frequency of exploratory forays by juvenile Wood Thrush, described as a > 300 m movement from a dispersal site followed by a return. This pattern was not noted, however, until after birds had arrived at a dispersal site, as much as 5 km from their natal territories. Thus, the relationship between the exploratory movements we observed and juvenile dispersal patterns is speculative and requires further testing.

Eventually, most birds in our study exhibited homing behavior, in which they appeared to recognize where they were, and take larger, faster steps oriented towards home (Table 4.2, Fig. 4.3). These behaviors may thus more closely reflect movement decisions made by adults moving or dispersing in familiar areas (Gillies et al. 2011). Yet while we found both species exhibited reluctance to cross gaps, adults often do not. For instance, MacIntosh et al. (2011) found that territorial Wood Thrush regularly crossed forest gaps, and Bayne & Hobson (2001) found no effect of fragmentation on dispersal of adult Ovenbirds. However, these studies did not compare fine-scale movement decisions in the context of available options. It is possible that these adult birds also prefer to avoid gaps in their natural movements when given the choice, but this too requires further study.

Because the translocation procedure influences movement behavior, and studies linking translocation and natural movements are lacking, it is unclear how well these results translate to conservation planning. Future studies should compare natural and translocation movements across species that span a gradient in fragmentation sensitivity to truly test whether metapopulation processes drive these patterns. Nevertheless, we have demonstrated a clear link between fragmentation sensitivity and gap crossing behavior in two territorial birds. Preliminary evidence thus suggests that maintaining contiguous habitat, or corridors between habitat patches (Castellón & Sieving 2006, Gillies et al. 2011, Vergara et al. 2013) can improve the functional connectivity of fragmented landscapes for sensitive species.

**Table 4.1.** Competing models developed to evaluate the effects of exposure to non-forested habitat on step selection decisions by translocated Wood Thrush and Ovenbirds. We developed these five models and compared them for each of three exposure variables separately: total number of forest gaps in the step; proportion of the step contained in forest, and total distance of forest gaps in the step. FOR50 is the forested proportion of a 50 m radius circle around the step start point, and BEHAV represents behavioral mode (exploring versus homing).

Model	Hypothesis
Exposure	Exposure influences step decisions
Exposure + Exposure*BEHAV	The effect of step exposure differs among behavioral modes
Exposure + Exposure*FOR50	The effect of step exposure changes with landscape context
Exposure + Exposure*BEHAV + Exposure*FOR50	The effect of step exposure differs among behavioral modes and changes with landscape context
Exposure + Exposure*BEHAV + Exposure*FOR50 + Exposure*BEHAV*FOR50	The effect of step exposure changes with landscape context, and that change differs among behavioral modes

**Table 4.2.** Results from linear mixed effects models testing for differences in median step distance and speed between exploratory and homing phases for translocated Wood Thrush and Ovenbirds.

Species	Exploring (95% CI)	Homing (95% CI)	df	t-value	p-value
Wood Thrush					
Distance	20.20 (17.19, 23.73)	38.92 (32.98, 45.93)	1937	13.65	< 0.001
Speed	1.96 (1.60, 2.40)	5.05 (4.12, 6.21)	1937	16.36	< 0.001
Ovenbird					
Distance	20.54 (18.11, 23.30)	30.08 (26.40, 34.28)	1397	6.39	< 0.001
Speed	1.82 (1.41, 2.35)	3.37 (2.59, 4.37)	1397	7.89	< 0.001

**Table 4.3.** A comparison of models that explore effects of forest loss and fragmentation on homing time and path straightness of translocated Wood Thrush and Ovenbirds. In each model table, the baseline model was chosen in a previous step (Table A9) to determine whether effects of body condition (CONDITION) or captivity time (CAPTIVITY) should be included. For each response variable, this baseline model had greater support than models that built on it with covariates for forest cover (PROP.FOR) and number of patches (PATCHES) in the local landscape. All models of straightness included a covariate for number of recorded steps. Parameter estimates for these models can be found in Table A10.

Species	Response	Model	DF	LogLik	AICc	Delta AICc	Weight
Wood Thrush							
	Total time						
		NULL	2	-36.37	77.15	0.00	0.45
		PATCHES * PROP.FOR	5	-33.27	78.85	1.70	0.19
		PATCHES	3	-36.26	79.38	2.23	0.15
		PROP.FOR	3	-36.32	79.49	2.34	0.14
		PATCHES + PROP.FOR	4	-35.82	81.12	3.97	0.06
	Exploring time						
		NULL	2	-108.25	220.95	0.00	0.54
		PATCHES	3	-108.10	223.12	2.17	0.18
		PROP.FOR	3	-108.20	223.32	2.37	0.17
		PATCHES + PROP.FOR	4	-107.57	224.74	3.79	0.08
		PATCHES * PROP.FOR	5	-107.16	226.82	5.87	0.03
	Homing time						
		CONDITION	3	-100.37	207.67	0.00	0.41
		PROP.FOR	4	-99.57	208.74	1.07	0.24
		PATCHES	4	-99.60	208.79	1.12	0.23
		PATCHES + PROP.FOR	5	-99.45	211.40	3.73	0.06
		PATCHES * PROP.FOR	6	-98.11	211.87	4.20	0.05
	Total straightness						
		NULL	3	21.49	-36.11	0.00	0.46
		PROP.FOR	4	22.12	-34.77	1.34	0.24
		PATCHES	4	21.93	-34.37	1.74	0.19
		PATCHES + PROP.FOR	5	22.14	-31.97	4.14	0.06
		PATCHES * PROP.FOR	6	23.43	-31.51	4.60	0.05
	Exploring straightness						
		NULL	3	20.75	-34.58	0.00	0.60
		PATCHES	4	20.85	-32.10	2.48	0.17
		PROP.FOR	4	20.80	-32.00	2.58	0.17
		PATCHES + PROP.FOR	5	20.85	-29.20	5.38	0.04
		PATCHES * PROP.FOR	6	21.36	-27.08	7.50	0.01
	Homing straightness						
		NULL	3	13.82	-20.71	0.00	0.61
		PROP.FOR	4	13.85	-18.09	2.62	0.17
		PATCHES	4	13.82	-18.04	2.67	0.16
		PATCHES + PROP.FOR	5	13.85	-15.20	5.51	0.04
		PATCHES * PROP.FOR	6	14.66	-13.67	7.04	0.02

Table 4.3 (Continued)

Species	Response	Model	DF	LogLik	AICc	Delta AICc	Weight
Ovenbird	Total time	CAPTIVITY	3	-10.99	30.17	0.00	0.58
		PATCHES + PROP.FOR	5	-8.12	32.92	2.75	0.15
		PROP.FOR	4	-10.48	32.95	2.78	0.15
		PATCHES	4	-10.71	33.42	3.25	0.11
		PATCHES * PROP.FOR	6	-7.83	38.17	8.00	0.01
	Exploring time	NULL	2	-61.95	128.89	0.00	0.56
		PATCHES	3	-61.23	130.63	1.74	0.23
		PROP.FOR	3	-61.94	132.05	3.16	0.12
		PATCHES + PROP.FOR	4	-60.66	133.33	4.44	0.06
		PATCHES * PROP.FOR	5	-59.08	134.82	5.93	0.03
	Homing time	NULL	2	-60.74	126.47	0.00	0.69
		PATCHES	3	-60.72	129.62	3.15	0.14
		PROP.FOR	3	-60.73	129.65	3.18	0.14
		PATCHES + PROP.FOR	4	-60.67	133.35	6.88	0.02
		PATCHES * PROP.FOR	5	-60.61	137.89	11.42	0.00
	Total straightness	NULL	3	13.49	-18.80	0.00	0.76
		PATCHES	4	13.51	-15.02	3.78	0.11
		PROP.FOR	4	13.51	-15.01	3.79	0.11
		PATCHES + PROP.FOR	5	13.51	-10.36	8.44	0.01
		PATCHES * PROP.FOR	6	14.19	-5.88	12.92	0.00
	Exploring straightness	NULL	3	8.89	-9.60	0.00	0.65
		PROP.FOR	4	9.43	-6.87	2.73	0.17
		PATCHES	4	9.41	-6.81	2.79	0.16
		PATCHES + PROP.FOR	5	9.49	-2.32	7.28	0.02
		PATCHES * PROP.FOR	6	9.82	2.86	12.46	0.00
	Homing straightness	CAPTIVITY	4	8.46	-4.93	0.00	0.81
		PATCHES	5	8.71	-0.76	4.17	0.10
		PROP.FOR	5	8.51	-0.36	4.57	0.08
		PATCHES + PROP.FOR	6	9.32	3.86	8.79	0.01
		PATCHES * PROP.FOR	7	9.36	11.28	16.21	0.00

**Table 4.4.** Results from mixed conditional logistic regression models evaluating factors influencing movement decisions of translocated Wood Thrush and Ovenbirds. We designed these models to test how step choice was influenced by number of gaps (GAPS), gap distance (GAPDIST), the proportion of the step in forest (FOR%), and whether these effects were mediated by landscape context (FOR50) and behavioral mode (BEHAV). BEHAV was an indicator variable equal to one if the step occurred during the exploring phase.

Species	Model	DF	LogLik	AICc	Delta AICc	Weight
Wood Thrush						
	GAPS	7	-2235.47	4485.09	0.00	0.46
	GAPS + GAPS*FOR50	9	-2234.58	4487.41	2.32	0.14
	GAPDIST	7	-2236.71	4487.57	2.48	0.13
	GAPS + GAPS*BEHAV	9	-2235.21	4488.67	3.58	0.08
	FOR% + FOR%*FOR50	9	-2235.59	4489.43	4.33	0.05
	GAPS + GAPS*BEHAV + GAPS*FOR50	11	-2233.96	4490.27	5.18	0.03
	GAPDIST + GAPDIST*FOR50	9	-2236.11	4490.47	5.37	0.03
	GAPDIST + GAPDIST*BEHAV	9	-2236.18	4490.59	5.50	0.03
	FOR%	7	-2239.14	4492.43	7.34	0.01
	FOR% + FOR%*BEHAV + FOR%*FOR50	11	-2235.47	4493.29	8.20	0.01
	GAPDIST + GAPDIST*BEHAV + GAPDIST*FOR50	11	-2235.47	4493.29	8.20	0.01
	GAPS + GAPS*BEHAV + GAPS*FOR50 + GAPS*BEHAV*FOR50	13	-2233.86	4494.22	9.13	0.00
	GAPDIST + GAPDIST*BEHAV + GAPDIST*FOR50 + GAPDIST*BEHAV*FOR50	13	-2234.63	4495.74	10.65	0.00
	FOR% + FOR%*BEHAV + FOR%*FOR50 + FOR%*BEHAV*FOR50	13	-2234.79	4496.06	10.97	0.00
	FOR% + FOR%*BEHAV	9	-2238.97	4496.18	11.09	0.00
	Baseline†	5	-2244.45	4498.97	13.88	0.00

**Table 4.4 (Continued)**

Species	Model	DF	LogLik	AICc	Delta AICc	Weight
Ovenbird	GAPS	9	-1594.41	3207.16	0.00	0.57
	GAPS + GAPS*BEHAV	11	-1593.27	3209.04	1.87	0.22
	GAPS + GAPS*FOR50	11	-1593.96	3210.41	3.25	0.11
	FOR%	9	-1597.01	3212.35	5.19	0.04
	GAPS + GAPS*BEHAV + GAPS*FOR50	13	-1593.35	3213.38	6.21	0.03
	FOR% + FOR%*BEHAV	11	-1596.66	3215.82	8.65	0.01
	FOR% + FOR%*FOR50	11	-1596.92	3216.34	9.18	0.01
	GAPS + GAPS*BEHAV + GAPS*FOR50 + GAPS*BEHAV*FOR50	15	-1592.73	3216.37	9.21	0.01
	GAPDIST	9	-1599.82	3217.98	10.82	0.00
	FOR% + FOR%*BEHAV + FOR%*FOR50	13	-1596.59	3219.87	12.70	0.00
	GAPDIST + GAPDIST*BEHAV	11	-1598.88	3220.25	13.08	0.00
	GAPDIST + GAPDIST*FOR50	11	-1599.69	3221.87	14.71	0.00
	GAPDIST + GAPDIST*BEHAV + GAPDIST*FOR50 + GAPDIST*BEHAV*FOR50	15	-1595.75	3222.40	15.24	0.00
	FOR% + FOR%*BEHAV + FOR%*FOR50 + FOR%*BEHAV*FOR50	15	-1596.21	3223.33	16.17	0.00
	GAPDIST + GAPDIST*BEHAV + GAPDIST*FOR50	13	-1598.65	3223.98	16.82	0.00
	Baseline††	7	-1613.19	3240.59	33.42	0.00

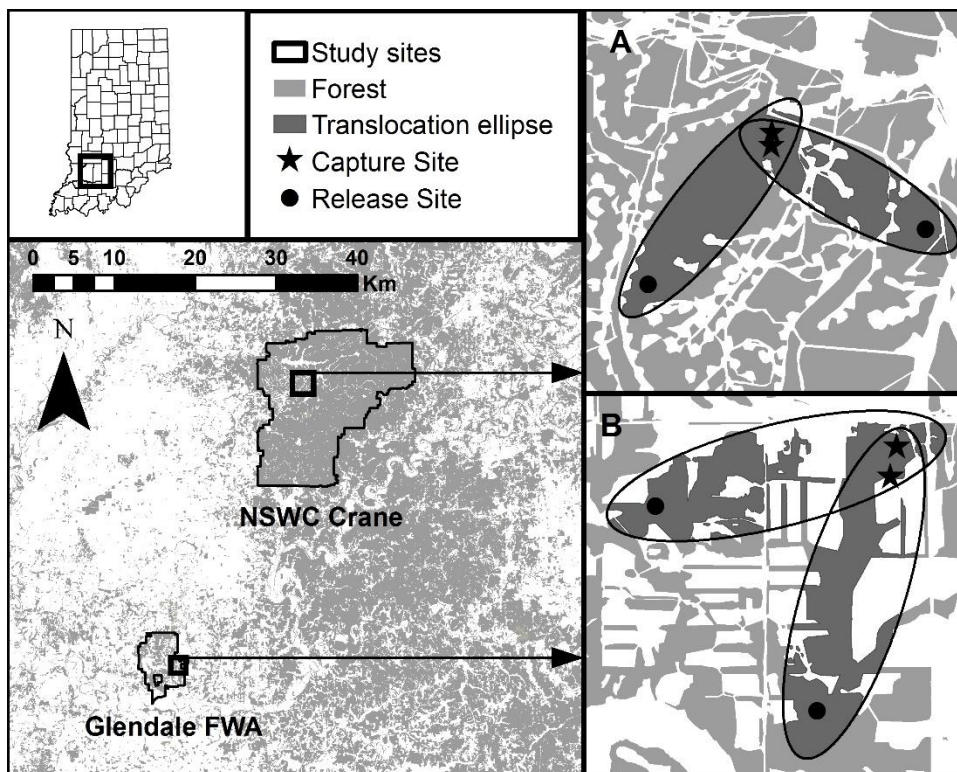
†All models for Wood Thrush contained linear effects of CAPDIST and CAPDIST\*BEHAV

††All models for Ovenbirds contained linear effects of CAPDIST, CAPDIST\*BEHAV, and RIPDIST

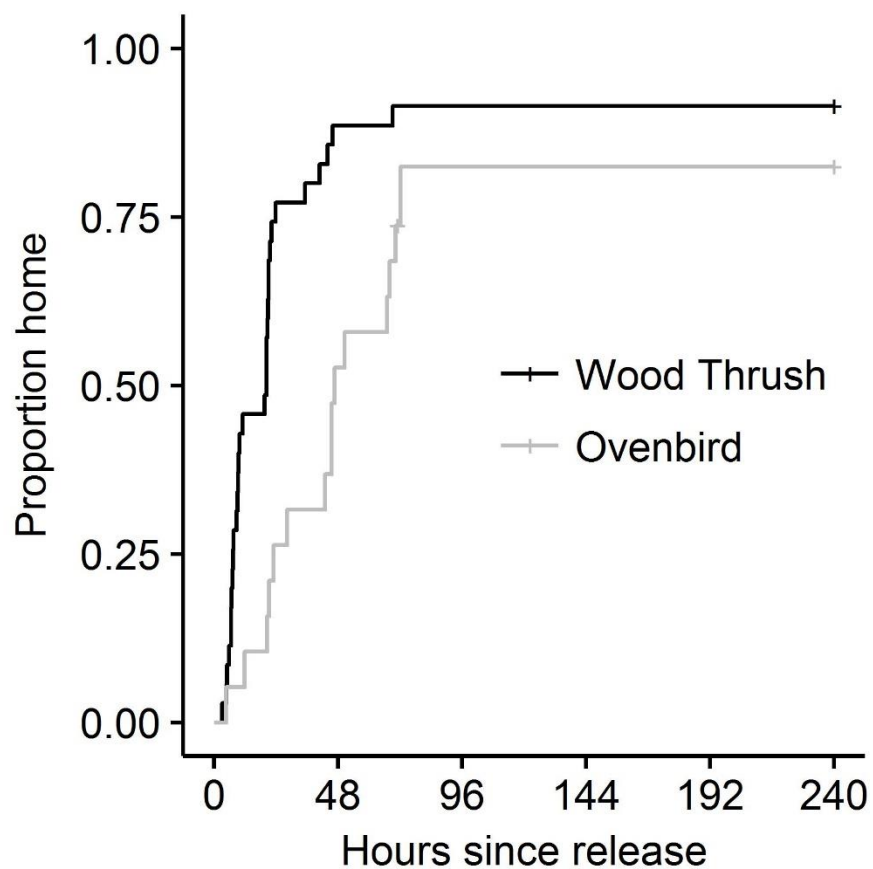


**Table 4.5.** Parameter estimates from the top step-level models explaining movement decisions of translocated Wood Thrush and Ovenbirds. Variables include distance from the step endpoint to home (CAPDIST) or the nearest stream (RIPDIST), number of gaps in the step (GAPS), and an indicator variable for behavioral mode (BEHAV) equal to one if the step occurred during exploring. We modeled all effects with random, bird-specific coefficients. Thus, we report the estimated mean effect size, and estimated standard deviation in effect size among individuals.

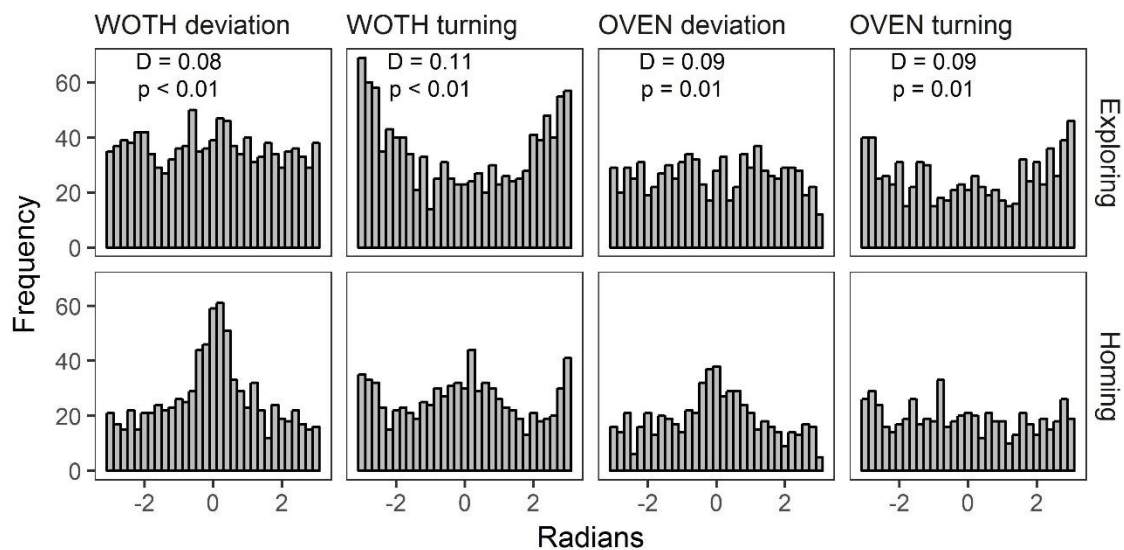
Species	Variable	Mean						SD					
		Est	SE	Z	p	lcl	ucl	Est	SE	Z	p	lcl	ucl
Wood Thrush													
	CAPDIST	-2.10	0.29	-7.24	0.00	-2.66	-1.53	0.78	0.32	2.45	0.01	0.16	1.40
	CAPDIST*BEHAV	0.07	0.77	0.09	0.93	-1.45	1.58	2.55	0.71	3.61	0.00	1.17	3.94
	GAPS	-0.23	0.08	-3.02	0.00	-0.39	-0.08	0.21	0.08	2.49	0.01	0.04	0.37
Ovenbird													
	CAPDIST	-4.67	0.52	-9.01	0.00	-5.68	-3.65	0.70	0.64	-1.10	0.27	1.96	0.56
	CAPDIST*BEHAV	2.64	0.81	3.25	0.00	1.05	4.23	0.35	1.61	0.21	0.83	2.82	3.51
	RIPDIST	-0.13	0.13	-0.98	0.33	-0.38	0.13	0.39	0.13	3.02	0.00	0.14	0.65
	GAPS	-0.47	0.12	-3.89	0.00	-0.71	-0.23	0.17	0.20	0.83	0.41	0.23	0.56



**Figure 4.1.** Locations of field sites (Naval Surface Warfare Center Crane and Glendale Fish and Wildlife Area) used for experimental translocations of Ovenbirds and Wood Thrush in southern Indiana. Crane was dominated by large contiguous forest tracts, separated by small road gaps (A), while Glendale was a more heterogeneous mix of forest and agricultural fields (B). We chose multiple landscapes on each site and attempted to translocate two conspecifics from the same forest patch across local landscapes (ellipses) that varied in terms of the amount of forest and number of forest patches.



**Figure 4.2.** Kaplan-Meier homing success curves for translocated Wood Thrush and Ovenbirds. Tick marks on the curves indicate censored data (i.e., birds that were predated or that we stopped following after 10 days).



**Figure 4.3.** A comparison of the distribution of turning and deviation angles between exploring and homing phases for translocated Wood Thrush (WOTH) and Ovenbirds (OVEN). Deviation angles were more concentrated around zero for both species during homing, indicating directed movement towards capture locations. Turning angles were concentrated near  $\pi$  and  $-\pi$  radians during exploring, indicating a large amount of course reversal. Test statistics and p-values represent results from a Kolmogorov-Smirnov test examining whether the data come from the same distribution.

## CONCLUSION

Island biogeography (MacArthur & Wilson 1967) and metapopulation (Levins 1969, Hanski 1998) theory predict fragmentation should negatively impact species distribution patterns by increasing patch extinction rates and decreasing colonization rates. Thus, one of the original goals of this dissertation was to test the effects of forest patch size on breeding bird colonization and extinction rates. Because many of the species we sampled are migratory, I expected landscape structure to have little influence on inter-annual distribution shifts, and instead planned to model dynamics within breeding seasons. Thus, I employed a widely used sampling protocol (as described in Chapter 2) intended to allow estimation of distributional shifts between 10-minute primary sampling periods. Rather than make assumptions about the biological process being modeled using this protocol, I found in Chapter 2 that our estimates of colonization and extinction were heavily influenced by temporary changes in sampling availability. Unfortunately, the implication of this was that I was unable to confidently estimate within-season dynamic rates with the data we collected. Nonetheless, these findings represent an important step forward in our understanding of how to appropriately sample and model dynamic distributions of unmarked animals.

Despite this setback, I was still able to test for the effects of fragmentation on species distribution patterns. To date, our work in Chapter 3 represents one of the most comprehensive efforts to disentangle the independent effects of fragmentation from habitat loss. Moreover, these results contribute to a growing body of knowledge indicating that fragmentation tends to have strong negative effects on interior specialists, and positive effects on edge specialists (Bender et al. 1998, Henle et al. 2004). Though this may seem intuitive, it is a critical step

towards viewing landscapes from the species' perspectives (Betts et al. 2014), and reconciling theory and reality. Fragmentation of forest habitat likely increases connectivity among habitats preferred by edge specialists; measures of forest patch size and amount are thus poor explanatory variables for testing fragmentation effects on these species. Future work should focus on redefining patch and matrix boundaries for edge specialists to truly evaluate how fragmentation influences this group.

Our patch size measurements were likely much more relevant for forest interior and forest generalist species. As our results demonstrated, interior specialists tended to be particularly sensitive to fragmentation, while forest generalists were not. However, we note that these species were assigned to habitat groupings based predominantly on distribution patterns observed in other studies. In most cases, it remains to be tested whether these patterns indicate choice, habitat quality, or true sensitivity to metapopulation processes (Villard 1998). This distinction has important implications for conservation efforts for fragmentation sensitive species; if these species are able to access fragmented patches, and either choose not to settle, or have poor success, then local habitat may drive distributions (i.e., *random sample hypothesis*) and management efforts could focus on improving within-patch characteristics. However, if sensitivity is driven by colonization and extinction dynamics, then the focus should be on conserving large patches and improving landscape connectivity.

In Chapter 4, we took a step towards identifying why interior specialists exhibit sensitivity to fragmentation. Using experimental translocations, we found that both Wood Thrush and Ovenbirds show reluctance to cross forest gaps. In fact, Ovenbirds were both more reluctant to cross gaps, and more limited by fragmentation (in terms of their distribution) than Wood Thrush. Because we did not replicate across multiple fragmentation-sensitive and

fragmentation-resilient species we cannot infer beyond these species to others having similar traits; we would need to conduct similar experiments with many more species to truly test for a relationship between distributions and movement behavior. Nonetheless, our results suggest a potential link between distribution patterns and dispersal limitation that should be addressed in future work.

During the field work associated with Chapter 4, we noticed that translocated birds were exhibiting peculiar behavior in which they would move very little, sometimes for days at a time, before eventually making large, quick movements homeward. In many cases, individuals covered over 90% of the distance home in less than 10% of their travel time (Figs. A3 and A4). These observations led us to explicitly test for behavioral shifts, and our study now represents one of the first to do so for translocated birds or any other animals. These results have raised important questions about the relationship between the behavior of translocated animals and those moving under natural conditions. Further, these results highlight the need to consider that movement patterns of translocated individuals may not be uniform, and thus may reflect multiple natural (or unnatural) behavioral phases or life stages. Unfortunately, we did not have the ability to link these behavioral modes to those exhibited by non-translocated individuals, and this is a critical area for future research. Until we can clearly link these behaviors with true biological processes, the application of the results from translocation experiments to conservation will be speculative.

Despite thousands of studies investigating the ecological ramifications of habitat fragmentation (Hadley & Betts 2016), there are still many questions left to answer. Ultimately, the most important lesson I learned from this dissertation may be that our understanding of the impacts of fragmentation on animal distribution patterns is heavily dependent on methodology

and human perspective. It is true that theory implies fragmentation should negatively impact species distribution patterns. However, our understanding of whether fragmentation influences any particular species depends both on the species, and what is being fragmented. Truly testing theoretical predictions will likely require more intensive methods of quantifying species-specific habitat (e.g., Shirley et al. 2013, Betts et al. 2014). Yet our results show that fragmentation of forests does affect the distribution (both positively and negatively) and movement patterns of many species. Given the extent to which forests are influenced by fragmentation worldwide, (Haddad et al. 2015), we hope these findings will help generate practical approaches to conservation and management.



## BIBLIOGRAPHY

- Andrén H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355–366.
- Askins R.A. (1993) Population trends in grassland, shrubland, and forest birds in eastern North America. *Current Ornithology*, **11**, 1-34.
- Austin M.P. (1985) Continuum concept, ordination methods and niche theory. *Annual Review of Ecology and Systematics*, **16**, 39-61.
- Baguette M. (2004) The classical metapopulation theory and the real, natural world: a critical appraisal. *Basic and Applied Ecology*, **5**, 213–224.
- Bailey L.L., MacKenzie D.I. & Nichols J.D. (2014) Advances and applications of occupancy models. *Methods in Ecology and Evolution*, **5**, 1269–1279.
- Bailey L.L., Reid J.A., Forsman E.D., & Nichols J.D. (2009) Modeling co-occurrence of northern spotted and barred owls: accounting for detection probability differences. *Biological Conservation*, **142**, 2983-2989.
- Banks S.C., Piggott M.P., Stow A.J., & Taylor A.C. (2007) Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. *Canadian Journal of Zoology*, **85**, 1065-1079.
- Bartlett L.J., Newbold T., Purves D.W., Tittensor D.P., & Harfoot M.B.J. (2016) Synergistic impacts of habitat loss and fragmentation on model ecosystems. *Proceedings of the Royal Society B*, **283**, 20161027.
- Bayne E.M. & Hobson K.A. (2001) Movement patterns of adult male Ovenbirds during post-fledging period in fragmented and forested boreal landscapes. *The Condor*, **103**, 343-351.
- Bélisle M. (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology*, **86**, 1988-1995.
- Bélisle M., Desrochers A., & Fortin M.-J. (2001) Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology*, **82**, 1893-1904.
- Bender D.J., Contreras T.A., & Fahrig L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology*, **79**, 517–533.
- Betts M.G., Fahrig L., Hadley A.S., Halstead K.E., Bowman J., Robinson W.D., Wiens J.A., & Lindenmayer D.B. (2014) A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography*, **37**, 517–527.
- Betts M.G., Forbes G.J., & Diamond A.W. (2007) Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology*, **21**, 1046–58.
- Betts M.G., Forbes G.J., Diamond A.W., & Taylor P.D. (2006) Independent effects of fragmentation on forest songbirds: an organism-based approach. *Ecological Applications*, **16**, 1076–1089.
- Betts M.G., Gutzwiller K.J., Smith M.J., Robinson W.D., & Hadley A.S. (2015) Improving inferences about functional connectivity from animal translocation experiments. *Landscape Ecology* **30**, 585-593.
- Betts M.G., Rodenhouse, N.L., Sillett, T.S., Doran, P.J. & Holmes, R.T. (2008) Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. *Ecography*, **31**, 592–600.

- Bock C.E. & Webb B. (1984) Birds as grazing indicator species in southeastern Arizona. *The Journal of Wildlife Management*, **48**, 1045-1049.
- Boulinier T., Nichols J.D., Sauer J.R., Hines J.E., & Pollock K.H. (1998) Estimating species richness: the importance of heterogeneity in species detectability. *Ecology*, **79**, 1018-1028.
- Bowman J. (2003) Is dispersal distance of birds proportional to territory size? *Canadian Journal of Zoology*, **81**, 195-202.
- Bridge E.S., Thorup K., Bowlin M.S., Chilson P.B., Diehl R.H., Fléron R.W., Hartl P., Kays R., Kelly J.F., Robinson W.D., Wikelski M. (2011) Technology on the move: recent and forthcoming innovations for tracking migratory birds. *BioScience*, **61**, 689-698.
- Bried J.T. & Pellet J. (2012) Optimal design of butterfly occupancy surveys and testing if occupancy converts to abundance for sparse populations. *Journal of Insect Conservation*, **16**, 489-499.
- Brown J.H. & Kodric-Brown A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445-449.
- Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodel Inference*. Springer-Verlag, New York, New York.
- Cam E., Nichols J.D., Sauer J.R., & Hines J.E. (2002) On the estimation of species richness based on the accumulation of previously unrecorded species. *Ecography*, **25**, 102-108.
- Canterbury G.E., Martin T.E., Petit D.R., Petit L.J., & Bradford D.F. (2000) Bird communities and habitat as ecological indicators of forest condition in regional monitoring. *Conservation Biology*, **14**, 544-558.
- Carrara E., Arroyo-Rodríguez V., Vega-Rivera J.H., Schondube J.E., de Freitas S.M., & Fahrig L. (2015) Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. *Biological Conservation*, **184**, 117-126.
- Castellón T.D. & Sieving K.E. (2006) An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation Biology*, **20**, 135-145.
- Chandler R.B., Royle J.A. & King D.I. (2011) Inference about density and temporary emigration in unmarked populations. *Ecology*, **92**, 1429-1435.
- Cook W.M., Lane K.T., Foster B.L., & Holt R.D. (2002) Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters*, **5**, 619-623.
- Dail D. & Madsen L. (2011) Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics*, **67**, 577-587.
- Debinski D.M. & Holt R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342-355.
- den Boer P.J. (1968) Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica*, **18**, 165-194.
- Diamond J.M. (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, **7**, 129-146.
- Didham R.K., Kapos V., & Ewers R.M. (2012) Rethinking the conceptual foundations of habitat fragmentation research. *Oikos*, **121**, 161-170.
- Dondina O., Orioli V., D'Occhio P., Luppi M., & Bani L. (2017) How does forest species specialization affect the application of the island biogeography theory in fragmented landscapes? *Journal of Biogeography*, **44**, 1041-1052.

- Donovan T.M. & Flather C.H. (2002) Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications*, **12**, 364-374.
- Dorazio R.M. (2007) On the choice of statistical models for estimating occurrence and extinction from animal surveys. *Ecology*, **88**, 2773-2782.
- Duchesne T., Fortin D., & Courbin N. (2010) Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology*, **79**, 548-555.
- Efford M.G. & Dawson D.K. (2012) Occupancy in continuous habitat. *Ecosphere*, **3**, 32.
- Emlen J.T. (1967) A rapid method for estimating arboreal canopy cover. *Ecology*, **48**, 158-160.
- Esseen P.-A. (1994) Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. *Biological Conservation*, **68**, 19-28.
- Ewers R.M. & Didham R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117-142.
- Fahrig L. (2003) Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487-515.
- Fahrig L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, **40**, 1649-1663.
- Fahrig L. (2015) Just a hypothesis: a reply to Hanski. *Journal of Biogeography*, **42**, 993-994.
- Fahrig L. (2017) Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, **48**.
- Fahrig L. & Merriam G. (1994) Conservation of fragmented populations. *Conservation Biology*, **8**, 50-59.
- Ferraz G., Nichols J.D., Hines J.E., Stouffer P.C., Bierregaard R.O., & Lovejoy T.E. (2007) A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. *Science*, **315**, 238-241.
- Fischer J. & Lindenmayer D.B. (2006) Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos*, **112**, 473-480.
- Fischer J. & Lindenmayer D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265-280.
- Fisher A.C., Volpe J.P., & Fisher J.T. (2014) Occupancy dynamics of escaped farmed Atlantic salmon in Canadian Pacific coastal salmon streams: implications for sustained invasions. *Biological Invasions*, **16**, 2137-2146.
- Fiske I.J., & Chandler R.B. (2011) unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, **43**, 1-23.
- Fleishman E., Thomson J.R., Nally R.M., Murphy D.D., & Fay J.P. (2005) Using indicator species to predict species richness of multiple taxonomic groups. *Conservation Biology*, **19**, 11215-1137.
- Fletcher R.J., Ries L., Battin J., & Chalfoun A.D. (2007) The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? *Canadian Journal of Zoology*, **85**, 1017-1030.
- Fortin D., Beyer H.L., Boyce M.S., Smith D.W., Duchesne T., & Mao J.S. (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320-1330.
- Fraser G. & Stutchbury B.J.M. (2004) Area-sensitive songbirds move extensively among forest patches. *Biological Conservation*, **118**, 377-387.

- Fretwell S.D. & Lucas H.L. (1970) On territorial behavior and other factors influencing distribution in birds: theoretical development. I. Theoretical development. *Acta Biotheoretica*, **19**, 16-36.
- Fry J., Zian G., Jin S., Dewitz, J., Homer C., Yang L., Barnes C., Herold N., & Wickham J. (2011) Completion of the 2006 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing*, **77**, 858-864.
- Gause G.F. (1934) *The Struggle for Existence*. Williams and Wilkins, Baltimore, Maryland.
- Gelman A., Carlin J.B., Stern H.S., & Rubin D.B. (2004) *Bayesian Data Analysis, Second Edition*. CRC/Chapman and Hall, Boca Raton, Florida.
- Gelman A., Meng X.-L., & Stern H. (1996) Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica*, **6**, 733-760.
- Gillies C.S., Beyer H.L., & St. Clair C.C. (2011). Fine-scale movement decisions of tropical forest birds in a fragmented landscape. *Ecological Applications*, **21**, 944-954.
- Gillies C.S. & St. Clair C.C. (2008) Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Sciences*, **105**, 19774-19779.
- Gillies C.S. & St. Clair C.C. (2010) Functional responses in habitat selection by tropical birds moving through fragmented forest. *Journal of Applied Ecology*, **47**, 182-190.
- Gilpin M.E. & Diamond J.M. 1976. Calculation of immigration and extinction curves from the species area distance relation. *Proceedings of the National Academy of Sciences*, **73**, 4130-4134.
- Gobeil, J.-F. & Villard M.-A. (2002) Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos*, **98**, 447-458.
- Gould W.R., Patla D.A., Daley R., Corn P.S., Hossack B.R., Bennetts R., & Peterson C.R. (2012) Estimating occupancy in large landscapes: evaluation of amphibian monitoring in the greater Yellowstone ecosystem. *Wetlands*, **32**, 379-389.
- Greenberg R. (1983) The role of neophobia in determining the degree of foraging specialization in some migrant warblers. *American Naturalist*, **122**, 444-453.
- Grinnell J. (1917) The niche-relationships of the California Thrasher. *Auk*, **34**, 427-433.
- Gu W. & Swihart R.K. (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation*, **116**, 195-203.
- Gurarie E., Andrews R.D., & Laidre K.L. (2009) A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, **12**, 395-408.
- Gurarie E., Bracis C., Delgado M., Meckley T.D., Kojola I., & Wagner C.M. (2016) What is the animal doing? Tools for exploring behavioural structure in animal movements. *Journal of Animal Ecology*, **85**, 69-84.
- Haddad N.M., Brudvig L.A., Clobert J., Davies K.F., Gonzalez A., Holt R.D., Lovejoy T.E., Sexton J.O., Austin M.P., Collins C.D., Cook W.M., Damschen E.I., Ewers R.M., Foster B.L., Jenkins C.N., King A.J., Laurance W.F., Levey D.J., Murgueles C.R., Melbourne B.A., Nicholls A.O., Orrock J.L., Song D.-X., & Townshend J.R. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, **1**, e1500052.
- Hadley A.S. & Betts M.G. (2009) Tropical deforestation alters hummingbird movement patterns. *Biology Letters*, **5**, 207-210.

- Hadley A.S. & Betts M.G. (2016) Refocusing habitat fragmentation research using lessons from the last decade. *Current Landscape Ecology Reports*, **1**, 55–66.
- Haila Y. (1983) Land birds on northern islands: a sampling metaphor for insular colonization. *Oikos*, **41**, 334–351.
- Haila Y. (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications*, **12**, 321–334.
- Hanski I. (1991) Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society*, **42**, 17–38.
- Hanski I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Hanski I. (2015) Habitat fragmentation and species richness. *Journal of Biogeography*, **42**, 989–994.
- Hanski I. & Ovaskainen (2002) Extinction debt at extinction threshold. *Conservation Biology*, **16**, 666–673.
- Hayes D.B. & Monfils M.J. (2015) Occupancy modeling of bird point counts: Implications of mobile animals. *The Journal of Wildlife Management*, **79**, 1361–1368.
- Heidinger I.M.M., Poethke H.-J., Bonte D., & Hein S. (2009) The effect of translocation on movement behavior – a test of the assumptions of behavioural studies. *Behavioural Processes*, **82**, 12–17.
- Henle K., Davies K.F., Kleyer M., Margules C., & Settele J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207–251.
- Holmes R.T. & Sherry T.W. (2001) Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *The Auk*, **118**, 589–609.
- Huffaker C.B. (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia*, **27**, 795–835.
- Hutchinson G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.
- Hutto R.L. (2016) Should scientists be required to use a model-based solution to adjust for possible distance-based detectability bias? *Ecological Applications*, **26**, 1287–1294.
- Ibarra-Macias A., Robinson W.D., & Gaines M.S. (2011) Experimental evaluation of bird movements in a fragmented Neotropical landscape. *Biological Conservation*, **144**, 703–712.
- Iknayan K.J., Tingley M.W., Furnas B.J., & Beissinger S.R. (2014) Detecting diversity: emerging methods to estimate species diversity. *Trends in Ecology and Evolution*, **29**, 97–106.
- Indiana State Climate Office (2002) About Indiana climate.  
<https://climate.agry.purdue.edu/climate/narrative.asp>. Accessed 24 September 2013.
- Jacquot J.J. & Solomon N.G. (1997) Effects of site familiarity on movement patterns of male prairie voles *Microtus ochrogaster*, **138**, 414–417.
- James F.C., McCulloch C.E., & Wiedenfeld D.A. (1996) New approaches to the analysis of population trends in land birds. *Ecology*, **77**, 13–27.
- Jonsen I.D., Flemming J.M., & Myers R.A. (2005) Robust state-space modeling of animal movement data. *Ecology*, **86**, 2874–2880.
- Kadoya T. (2009) Assessing functional connectivity using empirical data. *Population Ecology*, **51**, 5–15.

- Keiser J.T., Ziegenfus C.W.S., & Cristol D.A. (2005) Homing success of migrant versus nonmigrant Dark-Eyed Juncos (*Junco hyemalis*). *The Auk*, **122**, 608-617.
- Kellner K. (2016) jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses. R package version 1.4.2. <http://CRAN.R-project.org/package=jagsUI>.
- Kemink K.M. & Kesler D.C. (2013) Using movement ecology to inform translocation efforts: a case study with an endangered lekking bird species. *Animal Conservation*, **16**, 449-457.
- Kendall W.L. (1999) Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology*, **80**, 2517-2525.
- Kendall W.L., Hines J.E., Nichols J.D. & Grant E.H.C. (2013) Relaxing the closure assumption in occupancy models: staggered arrival and departure times. *Ecology*, **94**, 610-617.
- Kendall W.L. Nichols J.D. & Hines J.E. (1997) Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology*, **78**, 563-578.
- Kennedy C.M. & Marra P.P. (2010) Matrix mediates avian movements in tropical forested landscapes: Inference from experimental translocations. *Biological Conservation*, **143**, 2136-2145.
- Kerbiriou C., Le Viol I., Bonnet X., & Robert A. (2012) Dynamics of a northern fulmar (*Fulmarus glacialis*) population at the southern limit of its range in Europe. *Population Ecology*, **54**, 295-304.
- Kéry M. & Royle J.A. (2008) Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology*, **45**, 589-598.
- Kéry M. & Royle J.A. (2016) *Applied Hierarchical Modeling in Ecology, Volume 1*. Elsevier Inc., London.
- Kéry M., Royle J.A. & Schmid H. (2005) Modeling avian abundance from replicated counts using binomial mixture models. *Ecological Applications*, **15**, 1450-1461.
- Kéry M., Royle J.A., & Schmid H. (2008) Importance of sampling design and analysis in animal population studies: a comment on Sergio et al. *Journal of Applied Ecology*, **45**, 981-986.
- Kéry M., Royle J.A., Schmid H., Schaub M., Volet B., Häfliger G., & Zbinden N. (2010) Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. *Conservation Biology*, **24**, 1388-1397.
- Kesler D.C., Cox A.S., Albar G., Gouni A., Mejeur J., & Plassé C. (2012) Translocation of Tuamotu Kingfishers, postrelease exploratory behavior, and harvest effects on the donor population. *Pacific Science*, **66**, 467-480.
- Latif Q.S., Ellis M.M. & Amundson C.L. (2016) A broader definition of occupancy: Comment on Hayes and Monfils. *Journal of Wildlife Management*, **80**, 192-194.
- Laurance W. (2008) Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation*, **141**, 1731-1744.
- Levins R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237-240.
- Levins R. & Culver D. (1971) Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences*, **68**, 1246-1248.
- Lima S.L. & Zollner P.A. (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution*, **11**, 131-135.
- Lindenmayer D., Hobbs R.J., Montague-Drake R., Alexandra J., Bennett A., Burgman M., Cale P., Calhoun A., Cramer V., Cullen P., Driscoll D., Fahrig L., Fischer J., Franklin J., Haila Y., Hunter M., Gibbons P., Lake S., Luck G., MacGregor C., McInyre S., Mac Nally R.,

- Manning A., Miller J., Mooney H., Noss R., Possingham H., Saunders D., Schmiegelow F., Scott M., Simberloff D., Sisk T., Tabor G., Walker B., Wiens J., Woinarski J., & Zavaleta E. (2008) A checklist for ecological management of landscapes for conservation. *Ecology Letters*, **11**, 78-91.
- Lloyd-Evans T.L. & Atwood J.L. (2004). 32 years of changes in passerine numbers during spring and fall migrations in coastal Massachusetts. *Wilson Bulletin*, **116**, 1-16.
- Lomolino M.V. (1990) The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. *Oikos*, **57**, 297-300.
- Lynch J.F. & Whigham D.F. (1984) Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation*, **28**, 287-324.
- MacArthur R.G. & Wilson E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- MacIntosh T., Stutchbury B.J.M., & Evans M.L. (2011) Gap-crossing by Wood Thrushes (*Hyllocichla mustelina*) in a fragmented landscape. *Canadian Journal of Zoology*, **89**, 1091-1097.
- MacKenzie D.I. (2005) What are the issues with presence-absence data for wildlife managers? *Journal of Wildlife Management*, **69**, 849-860.
- MacKenzie D.I., Bailey L.L., & Nichols J.D. (2004) Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, **73**, 546-555.
- MacKenzie D.I., Nichols J.D., Hines J.E., Knutson M.G., & Franklin A.B. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, **84**, 2200-2207.
- MacKenzie D.I., Nichols J.D., Lachman G.B., Droege S., Royle J.A. & Langtimm C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248-2255.
- MacKenzie D.I. & Royle J.A. (2005) Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, **42**, 1105-1114.
- Manning A.D., Lindenmayer D.B., & Nix H.A. (2004) Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos*, **104**, 621-628.
- May R.M. (1975) Island biogeography and the design of wildlife preserves. *Nature*, **254**, 177-178.
- McClure C.J.W. & Hill G.E. (2012) Dynamic versus static occupancy: How stable are habitat associations through a breeding season? *Ecosphere*, **3**, 1-13.
- McGarigal K. & Cushman S.A. (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications*, **12**, 335-345.
- McIntyre S. & Barret G.W. (1992) Habitat variegation, an alternative to fragmentation. *Conservation Biology*, **6**, 146-147.
- McIntyre S. & Hobbs R.J. (1999) A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology*, **13**, 1282-1292.
- Mendenhall C.D., Karp D.S., Meyer C.F.J., Hadly E.A., & Daily G.C. (2014) Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature*, **509**, 213-217.
- Mettke-Hofmann C. & Gwinner E. (2004) Differential assessment of environmental information in a migratory and nonmigratory passerine. *Animal Behaviour*, **68**, 1079-1086.

- Mitchell M.S., Lancia R.A., & Gerwin J.A. (2001) Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. *Ecological Applications*, **11**, 1692-1708.
- Moilanen A. (2002) Implications of empirical data quality for metapopulation model parameter estimation and application. *Oikos*, **96**, 516-530.
- Mordecai R.S., Mattsson B.J., Tzilkowski C.J. & Cooper R.J. (2011) Addressing challenges when studying mobile or episodic species: hierarchical Bayes estimation of occupancy and use. *Journal of Applied Ecology*, **48**, 56–66.
- National Climatic Data Center. 2011. NOAA's 1981-2010 climate normals. <http://www.ncdc.noaa.gov/oa/climate/normal/usnormals.html>. Accessed 24 September 2013.
- Nichols J.D., Bailey L.L., O'Connell A.F., Talancy N.W., Grant E.H.C., Gilbert A.T., Annand E.M., Husband T.P. & Hines J.E. (2008) Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology*, **45**, 1321–1329.
- Nichols J.D., Thomas L. & Conn P.B. (2009) Inferences about landbird abundance from count data: recent advances and future directions. *Modeling Demographic Processes in Marked Populations* (eds D.L. Thomson, E.G. Cooch & M.J. Conroy), pp. 201–235. Springer Science+Business Media, LLC, New York.
- Norris D.R. & Stutchbury B.J.M. (2001) Extraterritorial movements of a forest songbird in a fragmented landscape. *Conservation Biology*, **15**, 729-736.
- North American Bird Conservation Initiative (2016) *The State of North America's Birds 2016*. Environment and Climate Change Canada, Ottawa, Ontario.
- O'Donnell K.M., Thompson F.R. & Semlitsch R.D. (2015) Partitioning detectability components in populations subject to within-season temporary emigration using binomial mixture models. *Plos One*, **10**, e0117216.
- Otto C.R.V., Bailey L.L. & Roloff G.J. (2013) Improving species occupancy estimation when sampling violates the closure assumption. *Ecography*, **36**, 1299–1309.
- Otto C.R.V., & Roloff G.J. (2012) Songbird response to green-tree retention prescriptions in clearcut forests. *Forest Ecology and Management*, **284**, 241-250.
- Ozgul A., Armitage K.B., Blumstein D.T., Vanvuren D.H., & Oli M.K. (2006) Effects of patch quality and network structure on patch occupancy dynamics of a yellow-bellied marmot metapopulation. *Journal of Animal Ecology*, **75**, 191-202.
- Pellet J., Fleishman E., Dobkin D.S., Gander A., & Murphy D.D. (2007) An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. *Biological Conservation*, **136**, 483-495.
- Pereira H.M., Leadley P.W., Proença V., Alkemade R., Scharlemann J.P.W., Fernandez-Manjarrés J.F., Araújo M.B., Balvanera P., Biggs R., Cheung W.W.L., Chini L., Cooper H.D., Gilman E.L., Guénette S., Hurtt G.C., Huntington H.P., Mace G.M., Oberdorff T., Revenga C., Rodrigues P., Scholes R.J., Sumaila U.R., & Walpole M. (2010) Scenarios for global biodiversity in the 21<sup>st</sup> century. *Science*, **330**, 1496-1501.
- Peterman W.E., Rittenhouse T.A.G., Earl J.E., & Semlitsch R.D. (2013) Demographic network and multi-season occupancy modeling of *Rana sylvatica* reveal spatial and temporal patterns of population connectivity and persistence. *Landscape Ecology*, **28**, 1601-1613.
- Pimm S.L. & Raven P. (2000) Extinction by numbers. *Nature*, **403**, 843-845.



- Pinheiro J., Bates D., DebRoy S., Sarkar D., & R Core Team (2017) nlme: Linear and Nonlinear Mixed Models. R package version 3.1-131. <https://CRAN.R-project.org/package=nlme>.
- Plummer M. (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3<sup>rd</sup> International Workshop on Distributed Statistical Computing* (ed. by K. Hornik, F. Leisch and A. Zeileis), pp. 1-10. Technische Universität Wien, Vienna, Austria.
- Pollock K.H. (1982) A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management*, **46**, 752–757.
- Powell G.V.N. & Powell A.H. (1986) Reproduction by Great White Herons *Ardea Herodias* in Florida bay as an indicator of habitat quality. *Biological Conservation*, **36**, 101-113.
- Prugh L.R., Hodges K.E., Sinclair A.R.E., & Brashares J.S. (2008) Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences*, **105**, 20770–20775.
- Pulliam H.R. (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652-661.
- Pulliam H.R. & Danielson B.J. (1991) Sources, sinks, and habitat selection – a landscape perspective on population dynamics. *The American Naturalist*, **137**, S50-S66.
- Püttker T., Bueno A.A., de Barros C.S., Sommer S., & Pardini R. (2013) Habitat specialization interacts with habitat amount to determine dispersal success of rodents in fragmented landscapes. *Journal of Mammalogy*, **94**, 714-726.
- Rands M.R.W., Adams W.M., Bennun L., Butchart S.H.M., Clements A., Coomes D., Entwistle A., Hodge I., Kapos V., Scharlemann J.P.W., Sutherland W.J., & Vira B. (2010) Biodiversity conservation: challenges beyond 2010. *Science*, **329**, 1298-1303.
- Rappole J.H. & Tipton A.R. (1991) New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology*, **62**, 335-337.
- Reinert H.K. & Rupert R.R. (1999) Impacts of translocation on behavior and survival of Timber Rattlesnakes, *Crotalus horridus*. *Journal of Herpetology*, **33**, 45-61.
- Ricketts T.H. (2001) The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist*, **158**, 87-99.
- Riddle J.D., Stanislav S.J., Pollock K.H., Moorman C.E. & Perkins F.S. (2010) Separating components of the detection process with combined methods: an example with northern bobwhite. *Journal of Wildlife Management*, **74**, 1319–1325.
- Ries L., Fletcher R.J., Battin J., & Sisk T.D. (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 491-522.
- Rittenhouse C.D., Millspaugh J.J., Hubbard M.W., & Sheriff S.L. (2007) Movements of translocated and resident three-toed Box Turtles. *Journal of Herpetology*, **41**, 115-121.
- Robbins C.S., Dawson D.K., & Dowell B.A. (1989) Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs*, **103**, 3–34.
- Roberge J.M. & Angelstam P. (2006) Indicator species among resident forest birds – a cross-regional evaluation in northern Europe. *Biological Conservation*, **130**, 134-147.
- Robinson S.K., Thompson F.R., Donovan T.M., Whitehead D.R., & Faaborg J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987-1990.
- Rodewald P. (2015) *The Birds of North America*: <https://birdsna.org>. Cornell Lab of Ornithology, Ithaca, NY.

- Rota C.T., Fletcher R.J., Dorazio R.M. & Betts M.G. (2009) Occupancy estimation and the closure assumption. *Journal of Applied Ecology*, **46**, 1173–1181.
- Royle J.A. & Dorazio R.M. (2008) *Hierarchical Modeling and Inference in Ecology*. Academic Press, Boston.
- Samu F., Csontos P., & Szinetar C. (2008) From multi-criteria approach to simple protocol: assessing habitat patches for conservation value using species rarity. *Biological Conservation*, **141**, 1310-1320.
- Sauer J.R. & Link W.A. (2002) Hierarchical modeling of population stability and species group attributes from survey data. *Ecology*, **83**, 1743-1751.
- Schmidt J.H., McIntyre C.L. & MacCluskie M.C. (2013) Accounting for incomplete detection: What are we estimating and how might it affect long-term passerine monitoring programs? *Biological Conservation*, **160**, 130–139.
- Self S.G. & Liang K. (1987) Asymptotic properties of maximum likelihood estimators and likelihood ratio tests under nonstandard conditions. *Journal of the American Statistical Association*, **82**, 605–610.
- Shirley S.M., Yang Z., Hutchinson R.A., Alexander J.D., McGarigal K., & Betts M.G. (2013) Species distribution modelling for the people: unclassified landsat TM imagery predicts bird occurrence at fine resolutions. *Diversity and Distributions*, **19**, 855-866.
- Simberloff D.S. & Abele L.G. (1976) Island biogeography and conservation: strategy and limitations. *Science*, **193**, 1032.
- Spendelov J.A., & Nichols J.D. (1989) Annual survival rates of breeding adult Roseate Terns (*Sterna dougalii*). *The Auk*, **106**, 367-374.
- Stratford J.A. & Robinson W.D. (2005) Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. *Frontiers in Ecology and the Environment*, **3**, 91-98.
- Swihart R.K., & Slade N.A. (1985) Testing for independence of observations in animal movements. *Ecology*, **66**, 1176-1184.
- Taylor P.D., Fahrig L., Henein K., & Merriam G. (1993) Connectivity is a vital element of landscape structure. *Oikos*, **68**, 571-573.
- Terborgh J. (1974) Faunal equilibria and the design of wildlife preserves. *Tropical Ecological Systems* (ed. by F.B. Golley and E. Medina), pp. 369-380. Springer-Verlag, New York.
- Thornton D.H., Branch L.C., & Sunquist M.E. (2011) The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. *Landscape Ecology*, **26**, 7–18.
- Trzcinski M.K., Fahrig L., & Merriam G. (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications*, **9**, 586–593.
- Tsoar A., Nathan R., Bartan Y., Vyssotski A., Dell’Omo G., & Ulanovsky N. (2011) Large-scale navigational map in a mammal. *Proceedings of the National Academy of Sciences*, **108**, E718-E724.
- Tyre A.J., Tenhumberg B., Field S.A., Niejalke D., Parris K., & Possingham H.P. (2003) Improving precision and reducing bias in biological surveys by estimating false negative error rates in presence-absence data. *Ecological Applications*, **13**, 1790-1801.
- Vega Rivera J.H., Rappole J.H., McShea W.J., & Haas C.A. (1998) Wood Thrush postfledging movements and habitat use in northern Virginia. *The Condor*, **100**, 69-78.

- Vergara P.M., Pérez-Hernández C.G., Hahn I.J., & Jiménez J.E. (2013) Matrix composition and corridor function for austral thrushes in a fragmented temperate forest. *Landscape Ecology*, **28**, 121-133.
- Villard M.-A. (1998) On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *The Auk*, **115**, 801–805.
- Villard M.-A. & Metzger J.P. (2014) Beyond the fragmentation debate : a conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology*, **51**, 309–318.
- Villard M.-A., Trzcinski M.K., & Merriam G. (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology*, **13**, 774-783.
- Volpe N.L., Hadley A.S., Robinson W.D., & Betts M.G. (2014) Functional connectivity experiments reflect routine movement behavior of a tropical hummingbird species. *Ecological Applications*, **24**, 2122-2131.
- Watts C., Empson R., Thornburrow D., & Rohan M. (2012) Movements, behavior and survival of adult Cook Strait giant weta (*Deinacrida rugosa*; Anostostomatidae: Orthoptera) immediately after translocation as revealed by radiotracking. *Journal of Insect Conservation*, **16**, 763-776.
- Wiens J.A. (1976) Population responses to patch environments. *Annual Review of Ecology, Evolution, and Systematics*, **7**, 81-120.
- Wiens J.A. (1994) Habitat fragmentation: island vs landscape perspectives on bird conservation. *Ibis*, **137**, S97-S104.
- Wilson E.O. & Willis E.O. (1975) Applied biogeography. *Ecology and Evolution of Communities* (ed. by M.L. Cody and J.M. Diamond), pp.522-534. Belknap Press, Cambridge, Massachusetts.
- Yackulic C.B., Reid J., Davis R., Hines J.E., Nichols J.D., & Forsman E. (2012) Neighborhood and habitat effects on vital rates: expansion of the Barred Owl in the Oregon Coast Ranges. *Ecology*, **93**, 1953-1966.
- Yamura Y., Connor E.F., Royle J.A., Itoh K., Sato K., Taki H., & Mishima Y. (2016) Estimating species-area relationships by modeling abundance and frequency subject to incomplete sampling. *Ecology and Evolution*, **6**, 4836-4848.
- Zipkin E.F., DeWan A., & Royle J.A. (2009) Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *Journal of Applied Ecology*, **46**, 815-822.

APPENDICES

## APPENDIX A: SUPPLEMENTARY TABLES AND FIGURES

**Table A1.** The 19 species for which site closure was evaluated under 3 different sampling scenarios (confounded TE/dynamics, isolated TE, and isolated dynamics). The data were based on repeated visits to 193 point count locations in southern Indiana in the summer of 2014.

Species	Scientific name*	Naïve occupancy	Occ. closure test p-values		
			confounded	TE	dynamics
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	0.37	< 0.001	0.006	0.01
Downy Woodpecker	<i>Picoides pubescens</i>	0.53	< 0.001	< 0.001	0.36
Eastern Wood-Pewee	<i>Contopus virens</i>	0.44	< 0.001	0.01	0.18
Acadian Flycatcher	<i>Empidonax vireescens</i>	0.92	< 0.001	< 0.001	< 0.001
Yellow-throated Vireo	<i>Vireo flavifrons</i>	0.25	< 0.001	< 0.001	0.31
Red-eyed Vireo	<i>Vireo olivaceus</i>	0.88	< 0.001	< 0.001	0.02
Carolina Chickadee	<i>Poecile carolinensis</i>	0.44	< 0.001	< 0.001	0.63
Tufted Titmouse	<i>Baeolophus bicolor</i>	0.60	< 0.001	< 0.001	0.07
White-breasted Nuthatch	<i>Sitta carolinensis</i>	0.48	< 0.001	< 0.001	0.17
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	0.79	< 0.001	< 0.001	< 0.001
Wood Thrush	<i>Hylocichla mustelina</i>	0.69	< 0.001	< 0.001	0.07
Ovenbird	<i>Seiurus aurocapilla</i>	0.41	< 0.001	< 0.001	< 0.001
Kentucky Warbler	<i>Geothlypis Formosa</i>	0.41	< 0.001	< 0.001	0.01
Hooded Warbler	<i>Setophaga citrina</i>	0.28	< 0.001	< 0.001	0.27
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	0.38	< 0.001	< 0.001	0.79
Scarlet Tanager	<i>Piranga olivacea</i>	0.47	< 0.001	< 0.001	0.03
Northern Cardinal	<i>Cardinalis cardinalis</i>	0.42	< 0.001	< 0.001	0.03
Indigo Bunting	<i>Passerina cyanea</i>	0.22	< 0.001	< 0.001	0.17
Brown-headed Cowbird	<i>Molothrus ater</i>	0.69	< 0.001	< 0.001	0.03

\*Citations for scientific names can be found on Avibase (<http://avibase.bsc-eoc.org/>).

**Table A2.** A comparison of static and dynamic occupancy models fit to simulated presence-absence survey data where distribution dynamics were present. For each set of simulation parameters, we generated 1000 datasets. In *use* scenarios, availability for sampling was independent during each sampling period. Thus, the detection estimates tend to approximate  $p_{apd}$ , the occupancy parameters approximate the rate of site use ( $\psi_0$ ), and the colonization and extinction parameters provided accurate and precise estimates of dynamic rates. In *occupancy* sampling, availability for sampling could only change every third visit (between primary periods). Here, the detection estimates tend to approximate  $p_d$ , the occupancy parameters approximate the instantaneous occupancy rate ( $\psi_{0pa}$ ), and the colonization and extinction parameters overestimate dynamic rates because they are confounded with temporary emigration. Metrics provided are on the original parameter scale.

Simulation parameters					% open selected	Occ ( $\psi$ )		Det (p)		Colonization ( $\gamma$ )				Extinction ( $\epsilon$ )			
$\psi_0$	$p_a$	$p_d$	$\gamma_0$	$\epsilon_0$		Mean	Var	Mean	Var	Mean	Var	Bias	MSE	Mean	Var	Bias	MSE
Use scenarios																	
0.3	0.5	0.5	0.09	0.2	97.2	0.30	0.00	0.25	0.00	0.08	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.3	0.5	0.5	0.17	0.4	100	0.32	0.01	0.25	0.00	0.17	0.00	0.00	0.00	0.39	0.01	-0.01	0.01
0.3	0.5	0.8	0.09	0.2	100	0.30	0.00	0.40	0.00	0.08	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.3	0.5	0.8	0.17	0.4	100	0.30	0.00	0.40	0.00	0.17	0.00	0.00	0.00	0.40	0.00	0.00	0.00
0.3	0.8	0.5	0.09	0.2	100	0.30	0.00	0.40	0.00	0.09	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.3	0.8	0.5	0.17	0.4	100	0.30	0.00	0.40	0.00	0.17	0.00	0.00	0.00	0.40	0.00	0.00	0.00
0.3	0.8	0.8	0.09	0.2	100	0.30	0.00	0.64	0.00	0.09	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.3	0.8	0.8	0.17	0.4	100	0.30	0.00	0.64	0.00	0.17	0.00	0.00	0.00	0.40	0.00	0.00	0.00
0.7	0.5	0.5	0.47	0.2	100*	0.70	0.00	0.25	0.00	0.45	0.01	-0.01	0.01	0.20	0.00	0.00	0.00
0.7	0.5	0.5	0.93	0.4	100†	0.70	0.00	0.25	0.00	0.92	0.01	-0.01	0.01	0.40	0.00	0.00	0.00
0.7	0.5	0.8	0.47	0.2	100	0.70	0.00	0.40	0.00	0.47	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.7	0.5	0.8	0.93	0.4	100	0.70	0.00	0.40	0.00	0.94	0.00	0.01	0.00	0.40	0.00	0.00	0.00
0.7	0.8	0.5	0.47	0.2	100	0.70	0.00	0.40	0.00	0.47	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.7	0.8	0.5	0.93	0.4	100	0.70	0.00	0.40	0.00	0.95	0.00	0.01	0.00	0.40	0.00	0.00	0.00
0.7	0.8	0.8	0.47	0.2	100	0.70	0.00	0.64	0.00	0.47	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.7	0.8	0.8	0.93	0.4	100	0.70	0.00	0.64	0.00	0.93	0.00	0.00	0.00	0.40	0.00	0.00	0.00
Occupancy scenarios																	
0.3	0.5	0.5	0.09	0.2	100	0.15	0.00	0.49	0.00	0.10	0.00	0.02	0.00	0.57	0.00	0.37	0.14
0.3	0.5	0.5	0.17	0.4	100	0.15	0.00	0.50	0.00	0.12	0.00	-0.05	0.00	0.70	0.00	0.30	0.09
0.3	0.5	0.8	0.09	0.2	100	0.15	0.00	0.80	0.00	0.11	0.00	0.02	0.00	0.60	0.00	0.40	0.16
0.3	0.5	0.8	0.17	0.4	100	0.15	0.00	0.80	0.00	0.12	0.00	-0.05	0.00	0.70	0.00	0.30	0.09
0.3	0.8	0.5	0.09	0.2	100	0.24	0.00	0.49	0.00	0.10	0.00	0.02	0.00	0.32	0.00	0.12	0.02
0.3	0.8	0.5	0.17	0.4	100	0.24	0.00	0.50	0.00	0.16	0.00	-0.01	0.00	0.52	0.00	0.12	0.01
0.3	0.8	0.8	0.09	0.2	100	0.24	0.00	0.80	0.00	0.11	0.00	0.03	0.00	0.36	0.00	0.16	0.03
0.3	0.8	0.8	0.17	0.4	100	0.24	0.00	0.80	0.00	0.16	0.00	-0.01	0.00	0.52	0.00	0.12	0.02
0.7	0.5	0.5	0.47	0.2	100	0.35	0.00	0.50	0.00	0.32	0.00	-0.14	0.02	0.60	0.00	0.40	0.16
0.7	0.5	0.5	0.93	0.4	100	0.35	0.00	0.50	0.00	0.38	0.00	-0.55	0.31	0.70	0.00	0.30	0.09
0.7	0.5	0.8	0.47	0.2	100	0.35	0.00	0.80	0.00	0.32	0.00	-0.14	0.02	0.60	0.00	0.40	0.16
0.7	0.5	0.8	0.93	0.4	100	0.35	0.00	0.80	0.00	0.38	0.00	-0.56	0.31	0.70	0.00	0.30	0.09
0.7	0.8	0.5	0.47	0.2	100	0.56	0.00	0.50	0.00	0.46	0.00	-0.01	0.00	0.36	0.00	0.16	0.03
0.7	0.8	0.5	0.93	0.4	100	0.56	0.00	0.50	0.00	0.66	0.00	-0.27	0.07	0.52	0.00	0.12	0.02
0.7	0.8	0.8	0.47	0.2	100	0.56	0.00	0.80	0.00	0.46	0.00	-0.01	0.00	0.36	0.00	0.16	0.03
0.7	0.8	0.8	0.93	0.4	100	0.56	0.00	0.80	0.00	0.66	0.00	-0.27	0.07	0.52	0.00	0.12	0.02

Percentages for \* and † are based on 997 and 936 comparisons, respectively, because closed models could not be fit to some datasets.

**Table A3.** Results from the principal components analysis of local vegetation variables recorded at 490 point count stations in southern Indiana between 2011 and 2013. We sampled each station two or three times, and considered each year-by-point combination a unique observation.

Variable	PC1	PC2	PC3	PC4	PC5
<b>Loadings</b>					
Tree basal area	-0.39	-0.45	0.44	-0.65	0.16
% shrub cover	0.57	-0.39	0.08	-0.19	-0.69
% canopy cover	-0.43	-0.45	0.28	0.69	-0.26
Vertical foliage density	0.55	-0.44	0.15	0.24	0.66
Leaf litter depth	-0.19	-0.50	-0.84	-0.08	0.05
<b>Summary</b>					
Standard deviation	1.34	1.08	0.95	0.85	0.65
Proportion of variance	0.36	0.23	0.18	0.14	0.08
Cumulative variance	0.36	0.59	0.77	0.92	1.00

**Table A4.** All species detected at 490 point count stations in southern Indiana during the breeding seasons of 2011-2013 in taxonomic order. Species which do not breed in the region and species that are poorly sampled with point count methodology were placed in the “Other” habitat group and eliminated from analyses. The remaining species were classified as forest edge specialists (Edge), forest interior specialists (Interior), forest generalists (Forest), or habitat generalists (Non-forest). There was a maximum of 1470 site-year combinations in which each species could be detected. Species detected in 0 site-years were recorded during at least one point count survey, but not close enough (within 50 m) to be considered using the site.

Common name	Scientific name	Habitat group	Detected	% detected
Canada Goose	<i>Branta canadensis</i>	Other	3	0.20
Wood Duck	<i>Aix sponsa</i>	Other	1	0.07
Mallard	<i>Anas platyrhynchos</i>	Other	0	0.00
Northern Bobwhite	<i>Colinus virginianus</i>	Non-forest	18	1.22
Ruffed Grouse	<i>Bonasa umbellus</i>	Other	1	0.07
Wild Turkey	<i>Meleagris gallopavo</i>	Other	25	1.70
Common Loon	<i>Gavia immer</i>	Other	0	0.00
Great Blue Heron	<i>Ardea herodias</i>	Other	7	0.48
Great Egret	<i>Ardea alba</i>	Other	0	0.00
Green Heron	<i>Butorides virescens</i>	Other	0	0.00
Black Vulture	<i>Coragyps atratus</i>	Other	0	0.00
Turkey Vulture	<i>Cathartes aura</i>	Other	6	0.41
Sharp-shinned Hawk	<i>Accipiter striatus</i>	Other	0	0.00
Cooper's Hawk	<i>Accipiter cooperii</i>	Other	3	0.20
Red-shouldered Hawk	<i>Buteo lineatus</i>	Other	16	1.09
Broad-winged Hawk	<i>Buteo platypterus</i>	Other	2	0.14
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Other	8	0.54
American Kestrel	<i>Falco sparverius</i>	Other	0	0.00
American Coot	<i>Fulica americana</i>	Other	0	0.00
Killdeer	<i>Charadrius vociferus</i>	Other	2	0.14
American Woodcock	<i>Scolopax minor</i>	Other	5	0.34
Mourning Dove	<i>Zenaida macroura</i>	Non-forest	92	6.26
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	Forest	155	10.54
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	Edge	0	0.00
Eastern Screech-Owl	<i>Megascops asio</i>	Other	2	0.14
Great Horned Owl	<i>Bubo virginianus</i>	Other	1	0.07
Barred Owl	<i>Strix varia</i>	Other	4	0.27
Common Nighthawk	<i>Chordeiles minor</i>	Other	1	0.07
Eastern Whip-poor-will	<i>Caprimulgus vociferus</i>	Other	0	0.00
Eastern Whip-poor-will	<i>Caprimulgus vociferus</i>	Non-forest	4	0.27
Chimney Swift	<i>Chaetura pelagica</i>	Other	9	0.61
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	Other	73	4.97
Belted Kingfisher	<i>Megaceryle alcyon</i>	Non-forest	13	0.88
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	Forest	32	2.18
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	Forest	638	43.40
Downy Woodpecker	<i>Picoides pubescens</i>	Forest	615	41.84
Hairy Woodpecker	<i>Picoides villosus</i>	Forest	230	15.65
Northern Flicker	<i>Colaptes auratus</i>	Edge	211	14.35
Pileated Woodpecker	<i>Dryocopus pileatus</i>	Forest	139	9.46
Eastern Wood-Pewee	<i>Contopus virens</i>	Forest	771	52.45
Acadian Flycatcher	<i>Empidonax virescens</i>	Interior	1240	84.35
Least Flycatcher	<i>Empidonax minimus</i>	Other	2	0.14
Eastern Phoebe	<i>Sayornis phoebe</i>	Edge	40	2.72
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	Edge	252	17.14



Table A4 (Continued)

Common name	Scientific name	Habitat group	Detected	% detected
Eastern Kingbird	<i>Tyrannus tyrannus</i>	Non-forest	11	0.75
White-eyed Vireo	<i>Vireo griseus</i>	Edge	365	24.83
Yellow-throated Vireo	<i>Vireo flavifrons</i>	Edge	335	22.79
Warbling Vireo	<i>Vireo gilvus</i>	Forest	16	1.09
Red-eyed Vireo	<i>Vireo olivaceus</i>	Forest	1257	85.51
Blue Jay	<i>Cyanocitta cristata</i>	Non-forest	252	17.14
American Crow	<i>Corvus brachyrhynchos</i>	Non-forest	156	10.61
Purple Martin	<i>Progne subis</i>	Other	1	0.07
Tree Swallow	<i>Tachycineta bicolor</i>	Other	10	0.68
Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>	Other	2	0.14
Barn Swallow	<i>Hirundo rustica</i>	Other	0	0.00
Carolina Chickadee	<i>Poecile carolinensis</i>	Forest	817	55.58
Tufted Titmouse	<i>Baeolophus bicolor</i>	Forest	957	65.10
White-breasted Nuthatch	<i>Sitta carolinensis</i>	Forest	754	51.29
Carolina Wren	<i>Thryothorus ludovicianus</i>	Edge	696	47.35
House Wren	<i>Troglodytes aedon</i>	Edge	9	0.61
Blue-gray Gnatcatcher	<i>Poliptila caerulea</i>	Forest	1029	70.00
Eastern Bluebird	<i>Sialia sialis</i>	Non-forest	38	2.59
Veery	<i>Catharus fuscescens</i>	Other	1	0.07
Swainson's Thrush	<i>Catharus ustulatus</i>	Other	1	0.07
Wood Thrush	<i>Hylocichla mustelina</i>	Interior	660	44.90
American Robin	<i>Turdus migratorius</i>	Non-forest	289	19.66
Gray Catbird	<i>Dumetella carolinensis</i>	Edge	205	13.95
Northern Mockingbird	<i>Mimus polyglottos</i>	Non-forest	4	0.27
Brown Thrasher	<i>Toxostoma rufum</i>	Edge	49	3.33
European Starling	<i>Sturnus vulgaris</i>	Non-forest	2	0.14
Cedar Waxwing	<i>Bombycilla cedrorum</i>	Non-forest	36	2.45
Ovenbird	<i>Seiurus aurocapilla</i>	Interior	258	17.55
Worm-eating Warbler	<i>Helmitheros vermivorum</i>	Interior	80	5.44
Louisiana Waterthrush	<i>Parkesia motacilla</i>	Interior	91	6.19
Golden-winged Warbler	<i>Vermivora chrysoptera</i>	Other	0	0.00
Blue-winged Warbler	<i>Vermivora cyanoptera</i>	Edge	37	2.52
Black-and-white Warbler	<i>Mniotilta varia</i>	Forest	24	1.63
Prothonotary Warbler	<i>Protonotaria citrea</i>	Forest	73	4.97
Tennessee Warbler	<i>Oreothlypis peregrina</i>	Other	0	0.00
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	Other	1	0.07
Kentucky Warbler	<i>Geothlypis formosa</i>	Interior	674	45.85
Common Yellowthroat	<i>Geothlypis trichas</i>	Edge	260	17.69
Hooded Warbler	<i>Setophaga citrina</i>	Interior	253	17.21
American Redstart	<i>Setophaga ruticilla</i>	Forest	25	1.70
Cerulean Warbler	<i>Setophaga cerulea</i>	Forest	93	6.33
Northern Parula	<i>Setophaga americana</i>	Forest	484	32.93
Blackburnian Warbler	<i>Setophaga fusca</i>	Other	0	0.00
Yellow Warbler	<i>Setophaga petechia</i>	Edge	5	0.34
Blackpoll Warbler	<i>Setophaga striata</i>	Other	1	0.07
Pine Warbler	<i>Setophaga pinus</i>	Forest	10	0.68
Yellow-rumped Warbler	<i>Setophaga coronata</i>	Other	0	0.00
Yellow-throated Warbler	<i>Setophaga dominica</i>	Forest	193	13.13
Prairie Warbler	<i>Setophaga discolor</i>	Non-forest	52	3.54
Black-throated Green Warbler	<i>Setophaga virens</i>	Forest	1	0.07
Yellow-breasted Chat	<i>Icteria virens</i>	Edge	227	15.44
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	Edge	904	61.50
Chipping Sparrow	<i>Spizella passerina</i>	Edge	38	2.59

**Table A4 (Continued)**

Common name	Scientific name	Habitat group	Detected	% detected
Field Sparrow	<i>Spizella pusilla</i>	Non-forest	36	2.45
Song Sparrow	<i>Melospiza melodia</i>	Edge	53	3.61
Summer Tanager	<i>Piranga rubra</i>	Forest	283	19.25
Scarlet Tanager	<i>Piranga olivacea</i>	Interior	516	35.10
Northern Cardinal	<i>Cardinalis cardinalis</i>	Non-forest	1102	74.97
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	Forest	2	0.14
Blue Grosbeak	<i>Passerina caerulea</i>	Edge	1	0.07
Indigo Bunting	<i>Passerina cyanea</i>	Edge	892	60.68
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	Non-forest	15	1.02
Eastern Meadowlark	<i>Sturnella magna</i>	Non-forest	2	0.14
Common Grackle	<i>Quiscalus quiscula</i>	Non-forest	35	2.38
Brown-headed Cowbird	<i>Molothrus ater</i>	Non-forest	979	66.60
Orchard Oriole	<i>Icterus spurius</i>	Edge	5	0.34
Baltimore Oriole	<i>Icterus galbula</i>	Edge	48	3.27
House Finch	<i>Carpodacus mexicanus</i>	Non-forest	0	0.00
American Goldfinch	<i>Spinus tristis</i>	Non-forest	172	11.70
House Sparrow	<i>Passer domesticus</i>	Non-forest	0	0.00

**Table A5.** Pearson's correlation coefficients for the six explanatory variables measured at 490 point count stations between 2011 and 2013. All variables were included in breeding bird community occupancy models. PC1-3 represent values of local vegetation principal components (see Table A3), and forest amount is the proportion of a 2 km radius circle around the point count station dominated by forest.

	PC1	PC2	PC3	Edge distance	Forest amount	Log(patch size)
PC1	1.000	-----	-----	-----	-----	-----
PC2	0.000	1.000	-----	-----	-----	-----
PC3	0.000	0.000	1.000	-----	-----	-----
Edge distance	-0.106	-0.080	-0.036	1.000	-----	-----
Forest amount	0.052	-0.070	-0.233	0.158	1.000	-----
Log(patch size)	-0.063	-0.052	-0.109	0.622	0.218	1.000

**Table A6.** Means and 95% credible intervals for the posterior distributions of covariate effects on occupancy probabilities of 52 breeding bird species. Species were separated into habitat groups (edge specialists, forest generalists, or interior specialists), and rows highlighted in bold represent the estimated mean effect of the covariate on members of the habitat group. Within a habitat group, species are listed from most common (top) to least common (Table A4). The 95% credible intervals did not overlap zero for those entries marked with an asterisk.

Species	Intercept (year = 1)	Intercept (year > 1)	Autologistic	PC1	PC2
<b>Edge community</b>	<b>-1.05 (-1.98, -0.22)*</b>	<b>-1.95 (-2.77, -1.15)*</b>	<b>2.78 (2.16, 3.64)*</b>	<b>0.20 (0.09, 0.30)*</b>	<b>0.10 (0.02, 0.20)*</b>
Eastern Towhee	1.17 (0.88, 1.49)*	-0.41 (-0.79, -0.04)*	2.51 (1.91, 3.10)*	0.42 (0.29, 0.57)*	0.02 (-0.14, 0.15)
Indigo Bunting	1.85 (1.46, 2.28)*	-0.75 (-1.30, -0.25)*	2.63 (1.96, 3.35)*	0.33 (0.18, 0.48)*	0.11 (-0.03, 0.26)
Carolina Wren	0.05 (-0.27, 0.39)	0.30 (-0.06, 0.69)	2.22 (1.33, 3.02)*	0.26 (0.13, 0.41)*	0.12 (-0.02, 0.27)
White-eyed Vireo	-0.95 (-1.23, -0.67)*	-2.13 (-2.48, -1.80)*	3.05 (2.46, 3.76)*	0.25 (0.14, 0.37)*	0.04 (-0.10, 0.16)
Yellow-throated Vireo	0.26 (-0.31, 0.93)	-0.33 (-1.09, 0.72)	3.06 (1.80, 5.33)*	-0.04 (-0.26, 0.20)	0.06 (-0.13, 0.24)
Common Yellowthroat	-1.03 (-1.39, -0.66)*	-2.50 (-2.92, -2.10)*	2.52 (1.87, 3.16)*	0.20 (0.08, 0.33)*	0.14 (0.02, 0.29)*
Great Crested Flycatcher	-0.31 (-0.98, 0.45)	-0.27 (-1.02, 0.77)	2.26 (0.46, 3.87)*	0.03 (-0.20, 0.25)	0.13 (-0.04, 0.33)
Yellow-breasted Chat	-1.04 (-1.41, -0.68)*	-2.57 (-2.97, -2.17)*	2.46 (1.82, 3.08)*	0.33 (0.20, 0.47)*	0.15 (0.02, 0.30)*
Northern Flicker	-0.33 (-1.06, 0.49)	-0.16 (-0.85, 0.75)	2.21 (-0.11, 3.95)	0.10 (-0.12, 0.30)	0.01 (-0.25, 0.18)
Gray Catbird	-1.23 (-1.59, -0.86)*	-2.68 (-3.12, -2.29)*	2.71 (2.02, 3.48)*	0.18 (0.04, 0.31)*	0.13 (0.00, 0.27)*
Song Sparrow	-3.17 (-3.96, -2.39)*	-3.66 (-4.52, -2.89)*	3.65 (2.35, 6.11)*	0.18 (-0.02, 0.37)	0.15 (-0.02, 0.37)
Brown Thrasher	-1.41 (-2.58, -0.07)*	-2.37 (-3.94, -1.04)*	2.99 (1.55, 5.24)*	0.25 (0.00, 0.53)*	0.19 (0.01, 0.48)*
Baltimore Oriole	-1.07 (-2.47, 0.60)	-2.48 (-3.68, -1.14)*	3.01 (1.58, 5.24)*	0.20 (-0.05, 0.46)	0.04 (-0.22, 0.23)
Eastern Phoebe	-2.88 (-3.77, -1.78)*	-3.41 (-4.22, -2.49)*	3.44 (2.23, 5.65)*	0.17 (-0.04, 0.37)	0.05 (-0.17, 0.22)
Chipping Sparrow	-0.20 (-1.92, 1.95)	-2.37 (-3.94, -0.63)*	2.73 (-0.43, 5.23)	0.19 (-0.09, 0.48)	0.15 (-0.04, 0.43)
Blue-winged Warbler	-2.23 (-3.28, -1.03)*	-3.41 (-4.36, -2.36)*	2.68 (1.15, 4.58)*	0.26 (0.05, 0.48)*	0.13 (-0.05, 0.34)
House Wren	-1.52 (-3.88, 1.18)	-1.41 (-3.65, 1.40)	3.07 (1.32, 5.72)*	0.11 (-0.26, 0.43)	0.14 (-0.08, 0.45)
Orchard Oriole	-2.60 (-5.96, 0.31)	-1.85 (-4.07, 0.71)	2.89 (1.07, 5.36)*	0.16 (-0.19, 0.48)	0.11 (-0.13, 0.38)
Yellow Warbler	-1.08 (-3.52, 1.78)	-3.14 (-5.40, -0.40)*	2.66 (0.71, 4.60)*	0.22 (-0.10, 0.56)	0.09 (-0.16, 0.35)
Blue Grosbeak	-2.19 (-5.94, 1.38)	-2.17 (-5.04, 0.66)	2.84 (0.89, 5.13)*	0.18 (-0.17, 0.50)	0.11 (-0.14, 0.37)
Black-billed Cuckoo	-2.22 (-5.74, 1.14)	-3.21 (-6.42, -0.19)*	2.65 (0.47, 4.85)*	0.19 (-0.17, 0.54)	0.10 (-0.14, 0.37)
<b>Forest community</b>	<b>0.11 (-1.29, 1.44)</b>	<b>-1.33 (-2.68, 0.08)</b>	<b>2.93 (1.82, 4.26)*</b>	<b>0.04 (-0.05, 0.12)</b>	<b>-0.12 (-0.20, -0.03)*</b>
Red-eyed Vireo	2.48 (2.12, 2.88)*	1.51 (0.99, 2.06)*	1.24 (0.63, 1.84)*	-0.17 (-0.32, -0.03)*	-0.12 (-0.24, 0.01)
Blue-gray Gnatcatcher	2.02 (1.66, 2.42)*	0.47 (0.01, 0.93)*	1.73 (1.01, 2.49)*	0.13 (0.00, 0.26)*	-0.12 (-0.25, -0.00)*
Tufted Titmouse	2.52 (1.95, 3.22)*	2.24 (1.27, 3.50)*	0.37 (-0.89, 1.52)	0.05 (-0.12, 0.23)	-0.11 (-0.26, 0.04)
Carolina Chickadee	3.33 (2.28, 4.90)*	1.79 (0.59, 3.14)*	1.10 (-0.62, 3.05)	0.10 (-0.08, 0.31)	-0.13 (-0.29, 0.02)
Eastern Wood-Pewee	1.07 (0.70, 1.47)*	-0.49 (-0.96, -0.07)*	2.70 (1.96, 3.56)*	-0.03 (-0.15, 0.09)	-0.15 (-0.29, -0.02)*
White-breasted Nuthatch	1.04 (0.60, 1.53)*	1.04 (0.38, 1.78)*	1.87 (0.65, 3.51)*	-0.10 (-0.27, 0.07)	-0.16 (-0.32, -0.03)*
Red-bellied Woodpecker	0.75 (0.28, 1.30)*	0.53 (-0.11, 1.20)	1.05 (0.13, 2.14)*	0.03 (-0.12, 0.17)	-0.13 (-0.27, -0.01)*
Downy Woodpecker	1.84 (1.05, 2.96)*	0.28 (-1.67, 1.93)	2.20 (-0.12, 5.31)	0.10 (-0.08, 0.29)	-0.11 (-0.27, 0.04)
Northern Parula	0.28 (-0.05, 0.62)	-1.80 (-2.37, -1.32)*	3.15 (2.35, 4.10)*	0.11 (-0.01, 0.23)	-0.03 (-0.16, 0.14)
Summer Tanager	1.23 (0.54, 2.08)*	-2.52 (-5.15, -0.42)*	5.92 (2.49, 10.28)*	0.02 (-0.17, 0.21)	-0.14 (-0.32, -0.00)*
Hairy Woodpecker	-1.96 (-2.66, -1.27)*	1.35 (0.44, 2.81)*	1.25 (-1.14, 5.88)	0.10 (-0.08, 0.32)	-0.15 (-0.34, -0.01)*
Yellow-throated Warbler	-0.16 (-0.70, 0.44)	-2.78 (-4.28, -1.89)*	3.36 (1.83, 5.63)*	0.03 (-0.11, 0.17)	-0.08 (-0.21, 0.07)
Yellow-billed Cuckoo	4.02 (1.90, 7.77)*	-4.56 (-7.15, -2.67)*	4.19 (2.22, 6.85)*	0.07 (-0.11, 0.26)	-0.09 (-0.24, 0.09)
Pileated Woodpecker	4.01 (1.59, 7.99)*	1.25 (-2.95, 6.47)	3.62 (-0.44, 8.38)	0.03 (-0.22, 0.28)	-0.12 (-0.32, 0.07)
Cerulean Warbler	-1.94 (-2.43, -1.44)*	-3.99 (-5.32, -3.11)*	5.24 (3.32, 8.23)*	0.04 (-0.13, 0.20)	-0.13 (-0.29, 0.01)
Prothonotary Warbler	-2.88 (-3.53, -2.25)*	-4.53 (-5.69, -3.70)*	4.11 (2.45, 6.50)*	0.01 (-0.16, 0.19)	-0.10 (-0.25, 0.06)
Red-headed Woodpecker	-1.36 (-2.79, 0.62)	-3.46 (-5.15, -1.90)*	2.45 (0.17, 5.11)*	0.05 (-0.15, 0.27)	-0.10 (-0.26, 0.09)
American Redstart	-0.51 (-3.36, 4.62)	-1.23 (-4.30, 4.93)	3.91 (-0.15, 8.39)	0.05 (-0.18, 0.30)	-0.10 (-0.27, 0.10)
Black-and-white Warbler	-3.30 (-4.68, -1.80)*	-3.84 (-5.24, -2.39)*	4.19 (1.42, 8.37)*	0.10 (-0.10, 0.34)	-0.11 (-0.27, 0.07)
Warbling Vireo	-3.77 (-4.68, -2.80)*	-5.90 (-7.84, -4.45)*	5.16 (2.58, 7.98)*	0.03 (-0.18, 0.25)	-0.13 (-0.31, 0.03)
Pine Warbler	0.17 (-3.50, 4.95)	-1.12 (-4.65, 4.13)	2.56 (-2.39, 7.65)	0.04 (-0.22, 0.29)	-0.12 (-0.30, 0.07)
Rose-breasted Grosbeak	-3.27 (-8.42, 2.28)	-1.71 (-5.92, 3.74)	3.21 (-1.18, 7.88)	0.05 (-0.21, 0.32)	-0.11 (-0.30, 0.08)
Black-throated Green Warbler	-2.95 (-8.78, 2.81)	-2.96 (-7.35, 3.32)	2.93 (-1.42, 7.49)	0.01 (-0.26, 0.27)	-0.11 (-0.30, 0.07)
<b>Interior community</b>	<b>-0.25 (-1.78, 1.27)</b>	<b>-1.85 (-3.58, -0.17)*</b>	<b>3.73 (2.31, 5.38)*</b>	<b>-0.02 (-0.36, 0.30)</b>	<b>-0.17 (-0.34, 0.01)</b>
Acadian Flycatcher	1.88 (1.57, 2.22)*	0.21 (-0.22, 0.63)	3.45 (2.86, 4.08)*	-0.27 (-0.40, -0.13)*	-0.23 (-0.39, -0.08)*
Kentucky Warbler	1.62 (1.13, 2.17)*	-1.78 (-3.11, -0.86)*	4.54 (3.22, 6.38)*	0.48 (0.27, 0.71)*	-0.22 (-0.45, -0.02)*
Wood Thrush	0.49 (0.14, 0.83)*	-0.97 (-1.39, -0.58)*	2.58 (1.93, 3.30)*	0.12 (-0.01, 0.16)	-0.21 (-0.37, -0.06)*
Scarlet Tanager	0.81 (0.33, 1.34)*	-0.20 (-0.82, 0.41)	1.49 (0.41, 2.70)*	-0.03 (-0.20, 0.25)	0.03 (-0.18, 0.27)
Ovenbird	-1.47 (-1.89, -1.06)*	-3.12 (-3.80, -2.54)*	4.18 (3.11, 5.42)*	-0.20 (-0.39, -0.01)*	-0.03 (-0.23, 0.22)
Hooded Warbler	-1.61 (-2.00, -1.20)*	-3.95 (-4.86, -3.27)*	4.46 (3.36, 5.75)*	0.37 (0.19, 0.55)*	-0.23 (-0.45, -0.03)*
Louisiana Waterthrush	-1.27 (-2.30, -0.01)*	-0.68 (-1.78, 0.69)	5.30 (2.80, 8.94)*	-0.25 (-0.60, 0.08)	-0.22 (-0.55, 0.04)
Worm-eating Warbler	-2.30 (-2.91, -1.67)*	-4.36 (-5.71, -3.42)*	3.88 (1.89, 6.56)*	-0.41 (-0.70, -0.13)*	-0.22 (-0.49, 0.00)

Table A6 (Continued)

Species	PC3	Edge distance	Patch size	Forest amount
<b>Edge community</b>	<b>0.05 (-0.05, 0.13)</b>	<b>-0.40 (-0.68, -0.15)*</b>	<b>-0.16 (-0.28, -0.04)*</b>	<b>-0.08 (-0.33, 0.18)</b>
Eastern Towhee	0.05 (-0.06, 0.17)	-0.17 (-0.33, -0.00)*	-0.17 (-0.33, -0.02)*	-0.23 (-0.41, -0.06)*
Indigo Bunting	0.04 (-0.08, 0.16)	-0.53 (-0.72, -0.35)*	-0.16 (-0.31, 0.01)	-0.04 (-0.23, 0.16)
Carolina Wren	0.08 (-0.03, 0.25)	-0.36 (-0.55, -0.16)*	-0.14 (-0.29, 0.03)	-0.73 (-0.94, -0.53)*
White-eyed Vireo	0.08 (-0.04, 0.22)	-0.39 (-0.61, -0.17)*	-0.20 (-0.39, -0.05)*	0.18 (0.01, 0.35)*
Yellow-throated Vireo	0.03 (-0.14, 0.16)	-0.01 (-0.31, 0.29)	-0.14 (-0.32, 0.07)	0.20 (-0.10, 0.57)
Common Yellowthroat	0.05 (-0.08, 0.17)	-0.91 (-1.24, -0.59)*	-0.11 (-0.27, 0.08)	-0.12 (-0.31, 0.06)
Great Crested Flycatcher	0.06 (-0.07, 0.21)	0.09 (-0.17, 0.37)	-0.15 (-0.34, 0.06)	-0.59 (-0.91, -0.30)*
Yellow-breasted Chat	0.04 (-0.09, 0.16)	-0.49 (-0.77, -0.22)*	-0.14 (-0.29, 0.04)	-0.14 (-0.33, 0.05)
Northern Flicker	0.04 (-0.13, 0.18)	0.34 (0.03, 0.66)*	-0.22 (-0.51, -0.04)*	-0.68 (-1.04, -0.37)*
Gray Catbird	0.05 (-0.09, 0.17)	-0.49 (-0.77, -0.23)*	-0.17 (-0.34, -0.01)*	0.17 (-0.02, 0.36)
Song Sparrow	0.02 (-0.17, 0.15)	-1.10 (-1.97, -0.45)*	-0.22 (-0.50, -0.04)*	-0.30 (-0.62, 0.02)
Brown Thrasher	0.03 (-0.16, 0.16)	-1.02 (-1.81, -0.41)*	-0.14 (-0.33, 0.10)	-0.19 (-0.68, 0.21)
Baltimore Oriole	0.04 (-0.14, 0.17)	-0.49 (-0.77, -0.23)*	-0.21 (-0.49, -0.02)*	-0.20 (-0.74, 0.23)
Eastern Phoebe	0.04 (-0.11, 0.19)	-0.19 (-0.61, 0.17)	-0.14 (-0.32, 0.09)	0.28 (-0.06, 0.61)
Chipping Sparrow	0.03 (-0.16, 0.18)	-0.28 (-0.77, 0.18)	-0.10 (-0.29, 0.21)	0.68 (0.17, 1.31)*
Blue-winged Warbler	0.05 (-0.12, 0.19)	-0.09 (-0.42, 0.34)	-0.10 (-0.29, 0.18)	0.72 (0.32, 1.20)*
House Wren	0.04 (-0.15, 0.19)	-0.12 (-0.96, 0.72)	-0.14 (-0.37, 0.12)	-0.49 (-1.19, 0.18)
Orchard Oriole	0.06 (-0.10, 0.24)	-0.63 (-1.63, 0.18)	-0.17 (-0.44, 0.08)	-0.07 (-0.91, 0.75)
Yellow Warbler	0.05 (-0.13, 0.21)	-0.61 (-1.65, 0.20)	-0.16 (-0.40, 0.09)	-0.21 (-1.09, 0.60)
Blue Grosbeak	0.05 (-0.13, 0.21)	-0.46 (-1.48, 0.44)	-0.16 (-0.40, 0.09)	0.15 (-0.73, 1.15)
Black-billed Cuckoo	0.05 (-0.13, 0.20)	-0.33 (-1.30, 0.62)	-0.15 (-0.40, 0.11)	-0.07 (-1.06, 0.94)
<b>Forest community</b>	<b>-0.02 (-0.17, 0.13)</b>	<b>0.06 (-0.04, 0.16)</b>	<b>0.01 (-0.16, 0.19)</b>	<b>-0.30 (-0.61, 0.00)</b>
Red-eyed Vireo	-0.32 (-0.55, -0.11)*	0.11 (-0.03, 0.32)	0.30 (0.06, 0.55)*	0.31 (0.09, 0.54)*
Blue-gray Gnatcatcher	0.15 (-0.05, 0.35)	0.04 (-0.12, 0.16)	-0.22 (-0.43, -0.02)*	-0.35 (-0.57, -0.14)*
Tufted Titmouse	0.23 (-0.07, 0.53)	0.04 (-0.12, 0.17)	-0.13 (-0.41, 0.14)	-1.01 (-1.44, -0.64)*
Carolina Chickadee	0.10 (-0.23, 0.44)	0.03 (-0.18, 0.18)	-0.02 (-0.35, 0.31)	-1.17 (-1.73, -0.72)*
Eastern Wood-Pewee	-0.25 (-0.48, -0.04)*	0.09 (-0.04, 0.24)	-0.03 (-0.23, 0.17)	-0.22 (-0.42, -0.03)*
White-breasted Nuthatch	-0.17 (-0.44, 0.09)	0.08 (-0.06, 0.25)	0.16 (-0.10, 0.43)	-0.61 (-0.89, -0.33)*
Red-bellied Woodpecker	0.02 (-0.20, 0.25)	0.08 (-0.05, 0.23)	0.18 (-0.05, 0.40)	-0.80 (-1.06, -0.55)*
Downy Woodpecker	-0.11 (-0.43, 0.20)	0.03 (-0.17, 0.18)	0.04 (-0.26, 0.34)	-0.41 (-0.76, -0.08)*
Northern Parula	-0.01 (-0.19, 0.17)	0.08 (-0.04, 0.23)	-0.13 (-0.32, 0.06)	-0.07 (-0.26, 0.11)
Summer Tanager	-0.29 (-0.66, 0.05)	0.05 (-0.12, 0.20)	-0.03 (-0.35, 0.29)	-0.50 (-0.99, -0.09)*
Hairy Woodpecker	0.11 (-0.24, 0.49)	0.06 (-0.11, 0.24)	0.35 (-0.02, 0.77)	-0.41 (-0.83, -0.01)*
Yellow-throated Warbler	-0.04 (-0.30, 0.21)	0.07 (-0.08, 0.21)	-0.17 (-0.41, 0.07)	-0.02 (-0.25, 0.20)
Yellow-billed Cuckoo	0.17 (-0.15, 0.53)	0.09 (-0.06, 0.28)	0.46 (0.08, 0.87)*	-0.80 (-1.24, -0.40)*
Pileated Woodpecker	-0.02 (-0.53, 0.50)	0.08 (-0.11, 0.28)	0.03 (-0.51, 0.59)	-0.47 (-1.62, 0.56)
Cerulean Warbler	-0.24 (-0.53, 0.04)	0.07 (-0.08, 0.23)	-0.09 (-0.37, 0.17)	0.56 (0.26, 0.87)*
Prothonotary Warbler	0.14 (-0.15, 0.45)	0.05 (-0.14, 0.22)	-0.23 (-0.60, 0.10)	-1.04 (-1.43, -0.68)*
Red-headed Woodpecker	-0.05 (-0.42, 0.30)	0.05 (-0.16, 0.21)	0.02 (-0.39, 0.42)	-0.82 (-1.32, -0.38)*
American Redstart	0.12 (-0.34, 0.63)	0.06 (-0.14, 0.23)	0.08 (-0.38, 0.56)	0.15 (-0.75, 0.88)
Black-and-white Warbler	-0.21 (-0.61, 0.15)	0.04 (-0.20, 0.19)	-0.22 (-0.62, 0.15)	0.78 (0.28, 1.32)*
Warbling Vireo	0.10 (-0.26, 0.51)	0.03 (-0.24, 0.18)	-0.37 (-0.89, 0.06)	-0.24 (-0.73, 0.22)
Pine Warbler	0.06 (-0.43, 0.60)	0.06 (-0.15, 0.25)	0.07 (-0.44, 0.61)	0.29 (-0.92, 1.33)
Rose-breasted Grosbeak	-0.01 (-0.52, 0.52)	0.06 (-0.14, 0.25)	0.02 (-0.54, 0.60)	-0.25 (-1.44, 0.84)
Black-throated Green Warbler	-0.03 (-0.53, 0.49)	0.07 (-0.12, 0.25)	0.11 (-0.44, 0.70)	0.09 (-1.05, 1.36)
<b>Interior community</b>	<b>-0.12 (-0.30, 0.03)</b>	<b>0.28 (0.05, 0.51)*</b>	<b>0.46 (0.23, 0.69)*</b>	<b>0.38 (-0.16, 0.93)</b>
Acadian Flycatcher	-0.07 (-0.25, 0.11)	0.26 (0.01, 0.51)*	0.35 (0.11, 0.58)*	-0.13 (-0.34, 0.08)
Kentucky Warbler	-0.06 (-0.26, 0.20)	0.25 (-0.02, 0.54)	0.42 (0.14, 0.68)*	0.05 (-0.21, 0.32)
Wood Thrush	-0.03 (-0.20, 0.16)	0.24 (0.03, 0.44)*	0.40 (0.18, 0.60)*	-0.04 (-0.22, 0.14)
Scarlet Tanager	-0.22 (-0.48, -0.01)*	0.26 (-0.01, 0.52)	0.54 (0.31, 0.82)*	0.57 (0.34, 0.82)*
Ovenbird	-0.17 (-0.41, 0.04)	0.53 (0.21, 0.93)*	0.71 (0.40, 1.07)*	1.02 (0.72, 1.33)*
Hooded Warbler	-0.20 (-0.46, 0.01)	0.41 (0.17, 0.72)*	0.56 (0.32, 0.81)*	1.12 (0.83, 1.45)*
Louisiana Waterthrush	-0.14 (-0.47, 0.15)	0.21 (-0.16, 0.56)	0.30 (-0.15, 0.68)	-0.23 (-0.81, 0.33)
Worm-eating Warbler	-0.10 (-0.36, 0.15)	0.08 (-0.23, 0.36)	0.45 (0.14, 0.75)*	0.71 (0.36, 1.09)*

**Table A7.** Means and 95% credible intervals for the posterior distributions of covariate effects on detection probabilities of 52 breeding bird species. Species were separated into habitat groups (edge specialists, forest generalists, or interior specialists), but we did not expect detection covariates to vary systematically among habitat groups. Therefore, a single mean effect of each covariate was estimated for the entire bird community. The 95% credible intervals did not overlap zero for those entries marked with an asterisk.

Species	Intercept	Julian date	Tree basal area
Entire community	-2.16 (-2.76, -1.60)*	-0.16 (-0.26, -0.06)*	0.02 (-0.02, 0.06)
Edge community	--	--	--
Eastern Towhee	-0.08 (-0.16, 0.01)	0.10 (0.03, 0.17)*	-0.11 (-0.19, -0.04)*
Indigo Bunting	-0.29 (-0.37, -0.20)*	0.02 (-0.04, 0.09)	-0.02 (-0.10, 0.06)
Carolina Wren	-0.68 (-0.78, -0.58)*	0.18 (0.10, 0.26)*	0.11 (0.03, 0.19)*
White-eyed Vireo	-0.38 (-0.53, -0.22)*	-0.02 (-0.12, 0.09)	-0.16 (-0.28, -0.05)*
Yellow-throated Vireo	-1.87 (-2.10, -1.63)*	-0.01 (-0.11, 0.10)	-0.02 (-0.13, 0.09)
Common Yellowthroat	-1.00 (-1.21, -0.79)*	0.29 (0.16, 0.42)*	-0.09 (-0.22, 0.03)
Great Crested Flycatcher	-2.08 (-2.38, -1.76)*	-0.33 (-0.45, -0.20)*	0.20 (0.07, 0.33)*
Yellow-breasted Chat	-1.01 (-1.22, -0.79)*	0.08 (-0.05, 0.22)	-0.02 (-0.15, 0.10)
Northern Flicker	-2.28 (-2.57, -1.91)*	0.25 (0.11, 0.38)*	0.06 (-0.07, 0.18)
Gray Catbird	-0.95 (-1.20, -0.71)*	-0.11 (-0.25, 0.03)	-0.08 (-0.23, 0.06)
Song Sparrow	-1.84 (-2.43, -1.31)*	-0.01 (-0.26, 0.24)	0.02 (-0.16, 0.21)
Brown Thrasher	-3.25 (-3.96, -2.42)*	-0.48 (-0.76, -0.21)*	-0.07 (-0.27, 0.10)
Baltimore Oriole	-3.34 (-4.13, -2.36)*	-0.65 (-0.96, -0.36)*	0.02 (-0.16, 0.19)
Eastern Phoebe	-2.02 (-2.99, -1.22)*	-0.60 (-0.92, -0.29)*	0.01 (-0.18, 0.20)
Chipping Sparrow	-3.85 (-4.66, -2.89)*	-0.67 (-1.00, -0.36)*	-0.01 (-0.19, 0.16)
Blue-winged Warbler	-2.71 (-3.64, -1.77)*	-0.78 (-1.15, -0.45)*	-0.07 (-0.27, 0.11)
House Wren	-5.13 (-6.34, -3.55)*	-0.50 (-0.99, -0.05)*	0.03 (-0.16, 0.23)
Orchard Oriole	-5.23 (-6.68, -3.29)*	-0.26 (-0.77, 0.25)	0.02 (-0.17, 0.22)
Yellow Warbler	-5.15 (-6.64, -3.26)*	-0.19 (-0.70, 0.31)	0.02 (-0.19, 0.22)
Blue Grosbeak	-6.29 (-8.37, -3.89)*	-0.05 (-0.64, 0.55)	0.01 (-0.19, 0.21)
Black-billed Cuckoo	-6.58 (-9.28, -3.87)*	-0.15 (-0.75, 0.45)	0.02 (-0.19, 0.22)
Forest community	--	--	--
Red-eyed Vireo	0.76 (0.68, 0.83)*	0.02 (-0.04, 0.09)	0.08 (0.00, 0.15)*
Blue-gray Gnatcatcher	-0.14 (-0.23, -0.05)*	-0.51 (-0.58, -0.44)*	0.03 (-0.04, 0.10)
Tufted Titmouse	-0.52 (-0.61, -0.44)*	-0.05 (-0.11, 0.02)	-0.00 (-0.07, 0.07)
Carolina Chickadee	-0.99 (-1.08, -0.89)*	-0.02 (-0.09, 0.05)	-0.00 (-0.07, 0.07)
Eastern Wood-Pewee	-0.54 (-0.64, -0.44)*	0.11 (0.04, 0.18)*	0.05 (-0.04, 0.13)
White-breasted Nuthatch	-0.93 (-1.04, -0.81)*	0.18 (0.11, 0.25)*	0.04 (-0.04, 0.12)
Red-bellied Woodpecker	-0.92 (-1.06, -0.78)*	-0.14 (-0.22, -0.07)*	0.10 (0.01, 0.19)*
Downy Woodpecker	-1.32 (-1.45, -1.17)*	0.04 (-0.04, 0.12)	0.06 (-0.02, 0.15)
Northern Parula	-0.87 (-1.00, -0.72)*	-0.17 (-0.27, -0.08)*	0.05 (-0.05, 0.15)
Summer Tanager	-2.15 (-2.35, -1.94)*	-0.01 (-0.13, 0.10)	0.02 (-0.09, 0.13)
Hairy Woodpecker	-2.20 (-2.46, -1.91)*	0.06 (-0.07, 0.19)	0.01 (-0.11, 0.12)
Yellow-throated Warbler	-1.76 (-2.07, -1.44)*	-0.15 (-0.29, -0.01)*	0.03 (-0.11, 0.17)
Yellow-billed Cuckoo	-2.54 (-2.76, -2.31)*	0.17 (0.02, 0.33)*	0.02 (-0.11, 0.15)
Pileated Woodpecker	-3.32 (-3.51, -3.10)*	-0.20 (-0.36, -0.04)*	0.06 (-0.06, 0.20)
Cerulean Warbler	-1.82 (-2.20, -1.44)*	-0.58 (-0.81, -0.37)*	-0.04 (-0.21, 0.13)
Prothonotary Warbler	-1.38 (-1.80, -0.95)*	-0.30 (-0.52, -0.07)*	0.04 (-0.12, 0.20)

**Table A7 (Continued)**

Species	Intercept	Julian date	Tree basal area
Red-headed Woodpecker	-3.05 (-3.98, -2.13)*	-0.13 (-0.44, 0.18)	0.07 (-0.11, 0.25)
American Redstart	-4.26 (-5.40, -2.64)*	-0.49 (-0.86, -0.14)*	-0.04 (-0.24, 0.13)
Black-and-white Warbler	-2.63 (-3.76, -1.55)*	-0.50 (-0.88, -0.14)*	-0.03 (-0.23, 0.16)
Warbling Vireo	-1.53 (-2.53, -0.67)*	0.13 (-0.26, 0.54)	0.11 (-0.08, 0.33)
Pine Warbler	-5.12 (-6.40, -2.93)*	-0.08 (-0.53, 0.36)	0.06 (-0.13, 0.26)
Rose-breasted Grosbeak	-5.66 (-8.00, -2.25)*	-0.33 (-0.92, 0.23)	-0.00 (-0.20, 0.20)
Black-throated Green Warbler	-5.69 (-8.39, -2.12)*	-0.08 (-0.66, 0.48)	0.02 (-0.18, 0.21)
Interior community	--	--	--
Acadian Flycatcher	1.36 (1.27, 1.44)*	-0.13 (-0.21, -0.05)*	0.04 (-0.04, 0.11)
Kentucky Warbler	-0.95 (-1.06, -0.84)*	-0.01 (-0.09, 0.07)	-0.07 (-0.16, 0.01)
Wood Thrush	-0.48 (-0.60, -0.36)*	0.24 (0.16, 0.33)*	0.14 (0.04, 0.23)*
Scarlet Tanager	-1.12 (-1.27, -0.98)*	0.10 (0.01, 0.19)*	0.09 (-0.02, 0.19)
Ovenbird	-1.10 (-1.27, -0.92)*	-0.64 (-0.78, -0.50)*	0.10 (-0.02, 0.23)
Hooded Warbler	-0.67 (-0.86, -0.48)*	-0.09 (-0.21, 0.03)	-0.06 (-0.19, 0.07)
Louisiana Waterthrush	-3.12 (-3.58, -2.60)*	-0.55 (-0.77, -0.35)*	-0.04 (-0.20, 0.11)
Worm-eating Warbler	-1.76 (-2.21, -1.31)*	-0.43 (-0.65, -0.21)*	0.05 (-0.12, 0.22)

**Table A8.** Full results from the behavioral change point analysis for 47 translocated Wood Thrush and Ovenbirds that successfully homed. For each bird, we iteratively split the time series of persistence velocities at each step and fit a segmented, autocorrelated time series model and compared the likelihoods among these models. We chose a break time corresponding to the most likely model. Using that value, we then fit eight models that allowed 0, 1, 2, or 3 of the model parameters to differ on the two sides of the break point. The models were defined as: Model 0 – all parameters equal; Model 1 –  $\mu_1 \neq \mu_2$ ; Model 2 –  $\sigma_1 \neq \sigma_2$ ; Model 3 –  $\rho_1 \neq \rho_2$ ; Model 4 – only  $\rho_1 = \rho_2$ ; Model 5 – only  $\sigma_1 = \sigma_2$ ; Model 6 – only  $\mu_1 = \mu_2$ ; and Model 7 – all parameters differ. We compared these using AICc, and concluded there was no evidence for a behavioral change if Model 0 had the most support.

Species	ID	Home time (hr)	Steps	Break time (hr)	Model	DF	LogLik	AICc	Delta AICc	Weight
Wood Thrush	1	3.12	9	1.60	0	4	-20.33	68.66	0.00	1.00
					1	5	-15.20	100.40	31.74	0.00
					3	5	-17.27	104.54	35.88	0.00
					4	6	-9.35	114.70	46.05	0.00
					2	5	-28.00	126.00	57.34	0.00
					5	6	-15.67	127.34	58.68	0.00
					7	7	-9.23	144.46	75.80	0.00
					6	6	-66.40	228.80	160.14	0.00
	2	4.92	21	2.03	2	5	-56.82	128.25	0.00	0.70
					6	6	-56.76	132.52	4.27	0.08
					4	6	-56.86	132.72	4.47	0.08
					3	5	-59.28	133.17	4.93	0.06
					1	5	-59.37	133.35	5.10	0.05
					0	4	-62.66	136.17	7.92	0.01
					5	6	-59.31	137.61	9.36	0.01
					7	7	-56.80	137.79	9.54	0.01
	3	4.95	34	2.35	2	5	-122.83	257.97	0.00	0.60
					6	6	-122.53	260.43	2.46	0.18
					4	6	-122.55	260.46	2.49	0.17
					7	7	-122.25	263.17	5.21	0.04
					1	5	-131.05	274.41	16.44	0.00
					3	5	-131.30	274.91	16.94	0.00
					5	6	-130.98	277.32	19.35	0.00
					0	4	-138.05	285.59	27.62	0.00
	4	5.75	38	3.77	3	5	-125.61	263.22	0.00	0.26
					2	5	-125.62	263.24	0.03	0.26
					1	5	-125.88	263.76	0.54	0.20
					6	6	-125.20	265.29	2.08	0.09
					4	6	-125.56	266.01	2.80	0.07
					5	6	-125.62	266.13	2.92	0.06
					0	4	-129.10	267.49	4.27	0.03
					7	7	-125.17	268.34	5.13	0.02
	5	6.58	46	2.80	2	5	-132.32	276.22	0.00	0.40
					4	6	-131.04	276.36	0.14	0.38
					6	6	-132.34	278.95	2.73	0.10
					7	7	-131.02	279.15	2.93	0.09
					1	5	-135.58	282.74	6.52	0.02
					3	5	-136.54	284.65	8.43	0.01
					5	6	-135.57	285.40	9.18	0.00
					0	4	-139.36	287.75	11.53	0.00



Table A8 (Continued)

Species	ID	Home time (hr)	Steps	Break time (hr)	Model	DF	LogLik	AICc	Delta AICc	Weight
Wood Thrush	6	6.60	30	5.38	4	6	-76.22	168.45	0.00	0.77
					7	7	-75.64	170.88	2.43	0.23
					2	5	-88.94	190.61	22.16	0.00
					1	5	-89.80	192.33	23.88	0.00
					5	6	-91.62	199.25	30.80	0.00
					0	4	-96.26	202.27	33.82	0.00
					6	6	-93.49	202.98	34.54	0.00
	3	5	-95.16	203.05	34.61	0.00				
	7	6.70	36	5.60	4	6	-99.46	214.02	0.00	0.82
					7	7	-99.39	217.09	3.07	0.18
					1	5	-139.33	290.80	76.78	0.00
					5	6	-139.32	293.76	79.74	0.00
					3	5	-144.09	300.33	86.31	0.00
					0	4	-147.80	304.98	90.96	0.00
					2	5	-155.62	323.39	109.37	0.00
	6	6	-163.62	342.36	128.34	0.00				
	8	7.10	34	6.28	4	6	-92.85	201.06	0.00	0.65
					7	7	-91.81	202.28	1.22	0.35
					1	5	-108.23	228.76	27.70	0.00
					5	6	-109.97	235.29	34.23	0.00
					3	5	-120.34	252.98	51.92	0.00
					0	4	-123.63	256.74	55.69	0.00
					6	6	-137.67	290.69	89.64	0.00
	2	5	-139.20	290.71	89.65	0.00				
	9	7.45	14	1.43	0	4	-23.95	61.61	0.00	0.69
					1	5	-22.40	64.79	3.18	0.14
					3	5	-22.63	65.26	3.65	0.11
					4	6	-18.83	66.45	4.84	0.06
					2	5	-26.84	73.68	12.07	0.00
					5	6	-22.70	74.19	12.58	0.00
					7	7	-18.29	78.59	16.97	0.00
	6	6	-40.62	110.04	48.43	0.00				
	10	7.62	24	2.42	2	5	-71.20	156.16	0.00	0.34
					1	5	-71.57	156.89	0.73	0.24
					3	5	-71.71	157.17	1.01	0.21
					6	6	-70.70	159.00	2.84	0.08
					4	6	-70.93	159.45	3.29	0.07
					5	6	-71.54	160.68	4.52	0.04
					0	4	-76.29	162.93	6.78	0.01
	7	7	-70.53	163.07	6.91	0.01				
	11	8.63	71	5.95	4	6	-216.85	447.06	0.00	0.77
					7	7	-216.85	449.53	2.47	0.23
2					5	-284.71	580.37	133.31	0.00	
1					5	-286.05	583.05	135.99	0.00	
5					6	-286.18	585.72	138.66	0.00	
3					5	-288.02	586.99	139.93	0.00	
0					4	-291.84	592.31	145.25	0.00	
6	6	-310.35	634.06	187.00	0.00					

Table A8 (Continued)

Species	ID	Home time (hr)	Steps	Break time (hr)	Model	DF	LogLik	AICc	Delta AICc	Weight
Wood Thrush	12	9.08	42	6.63	4	6	-120.24	255.03	0.00	0.81
					7	7	-120.24	257.99	2.95	0.19
					2	5	-132.26	276.29	21.26	0.00
					6	6	-132.26	279.07	24.04	0.00
					1	5	-149.32	310.41	55.38	0.00
					5	6	-149.32	313.19	58.16	0.00
					3	5	-154.64	321.04	66.01	0.00
					0	4	-158.26	325.66	70.63	0.00
	13	9.25	32	2.67	2	5	-91.80	196.11	0.00	0.69
					4	6	-91.79	199.23	3.13	0.14
					6	6	-91.81	199.27	3.16	0.14
					7	7	-91.76	202.60	6.50	0.03
					1	5	-99.40	211.30	15.19	0.00
					3	5	-99.50	211.50	15.40	0.00
					5	6	-99.58	214.80	18.70	0.00
					0	4	-104.12	217.83	21.73	0.00
	14	9.52	67	5.15	4	6	-236.58	486.62	0.00	0.78
					7	7	-236.58	489.13	2.52	0.22
					1	5	-257.43	525.88	39.26	0.00
					5	6	-257.47	528.39	41.77	0.00
					3	5	-258.97	528.96	42.35	0.00
					0	4	-262.68	534.03	47.41	0.00
					6	6	-272.46	558.37	71.75	0.00
					2	5	-274.03	559.08	72.47	0.00
	15	9.88	45	3.45	4	6	-134.62	283.57	0.00	0.72
					7	7	-134.62	286.44	2.87	0.17
					2	5	-138.59	288.80	5.23	0.05
					1	5	-139.28	290.17	6.60	0.03
					6	6	-138.59	291.51	7.94	0.01
					5	6	-139.28	292.88	9.31	0.01
					3	5	-141.89	295.41	11.84	0.00
					0	4	-146.68	302.40	18.83	0.00
	16	10.97	42	9.57	4	6	-101.02	216.59	0.00	0.75
					7	7	-100.62	218.74	2.15	0.25
					1	5	-162.22	336.21	119.62	0.00
					5	6	-166.37	347.28	130.69	0.00
					2	5	-169.62	351.00	134.42	0.00
					3	5	-170.92	353.61	137.02	0.00
					0	4	-173.15	355.44	138.86	0.00
					6	6	-328.92	672.38	455.79	0.00
	17	19.62	68	7.25	4	6	-176.32	366.06	0.00	0.65
					7	7	-175.69	367.32	1.25	0.35
2					5	-211.33	433.66	67.60	0.00	
6					6	-213.04	439.50	73.44	0.00	
1					5	-247.34	505.69	139.63	0.00	
3					5	-248.46	507.91	141.85	0.00	
5					6	-247.56	508.55	142.49	0.00	
0					4	-251.71	512.07	146.01	0.00	

Table A8 (Continued)

Species	ID	Home time (hr)	Steps	Break time (hr)	Model	DF	LogLik	AICc	Delta AICc	Weight
Wood Thrush	18	20.38	66	7.93	7	7	-216.48	448.95	0.00	0.72
					4	6	-218.67	450.81	1.86	0.28
					1	5	-249.54	510.11	61.16	0.00
					5	6	-248.88	511.23	62.27	0.00
					3	5	-250.85	512.74	63.79	0.00
					0	4	-255.59	519.85	70.90	0.00
					6	6	-260.53	534.54	85.59	0.00
					2	5	-271.32	553.68	104.72	0.00
	19	20.42	65	6.53	4	6	-164.14	341.79	0.00	0.76
					7	7	-164.05	344.13	2.34	0.24
					6	6	-177.93	369.37	27.58	0.00
					2	5	-179.86	370.77	28.98	0.00
					1	5	-186.92	384.89	43.10	0.00
					3	5	-187.96	386.97	45.18	0.00
					5	6	-186.90	387.30	45.51	0.00
					0	4	-190.64	389.97	48.18	0.00
	20	20.42	45	5.98	3	5	-144.54	300.69	0.00	0.38
					6	6	-143.75	301.83	1.13	0.21
					2	5	-145.34	302.31	1.62	0.17
					5	6	-144.54	303.42	2.73	0.10
					7	7	-143.78	304.76	4.07	0.05
					1	5	-146.58	304.79	4.10	0.05
					4	6	-145.34	305.01	4.32	0.04
					0	4	-152.38	313.81	13.12	0.00
	21	20.72	84	11.02	4	6	-248.79	510.71	0.00	0.77
					7	7	-248.79	513.10	2.39	0.23
					1	5	-359.88	730.55	219.85	0.00
					5	6	-359.88	732.88	222.18	0.00
					6	6	-363.43	739.98	229.28	0.00
					2	5	-366.45	743.70	232.99	0.00
3					5	-366.75	744.30	233.59	0.00	
0					4	-370.78	750.08	239.37	0.00	
22	20.85	89	5.40	4	6	-246.05	505.16	0.00	0.66	
				7	7	-245.55	506.51	1.35	0.34	
				1	5	-305.08	620.90	115.74	0.00	
				5	6	-305.30	623.65	118.49	0.00	
				3	5	-306.90	624.53	119.37	0.00	
				0	4	-309.92	628.32	123.16	0.00	
				2	5	-429.13	869.00	363.84	0.00	
				6	6	-650.61	1314.26	809.10	0.00	
23	21.02	61	11.02	2	5	-188.13	387.40	0.00	0.63	
				4	6	-188.04	389.69	2.29	0.20	
				6	6	-188.82	391.25	3.86	0.09	
				7	7	-188.07	392.34	4.95	0.05	
				1	5	-192.03	395.19	7.79	0.01	
				5	6	-191.35	396.32	8.92	0.01	
				3	5	-192.88	396.90	9.50	0.01	
				0	4	-201.94	412.63	25.23	0.00	

Table A8 (Continued)

Species	ID	Home time (hr)	Steps	Break time (hr)	Model	DF	LogLik	AICc	Delta AICc	Weight
Wood Thrush	24	21.15	71	8.27	1	5	-137.21	285.36	0.00	0.32
					2	5	-137.64	286.23	0.87	0.21
					3	5	-137.77	286.49	1.13	0.18
					4	6	-137.19	287.74	2.38	0.10
					5	6	-137.21	287.78	2.41	0.10
					6	6	-137.65	288.65	3.29	0.06
					7	7	-137.19	290.22	4.86	0.03
					0	4	-142.05	292.72	7.35	0.01
	25	21.65	107	11.27	6	6	-388.76	790.37	0.00	0.31
					7	7	-387.61	790.38	0.01	0.31
					4	6	-389.00	790.86	0.49	0.24
					2	5	-390.65	791.91	1.54	0.14
					3	5	-408.84	828.29	37.92	0.00
					1	5	-409.65	829.90	39.52	0.00
					5	6	-408.98	830.81	40.44	0.00
					0	4	-414.06	836.52	46.15	0.00
	26	22.22	52	5.15	4	6	-139.91	293.77	0.00	0.79
					7	7	-139.91	296.48	2.71	0.20
					2	5	-145.93	303.23	9.45	0.01
					6	6	-145.92	305.78	12.01	0.00
					1	5	-152.15	315.67	21.90	0.00
					3	5	-153.23	317.83	24.06	0.00
					5	6	-152.15	318.26	24.49	0.00
					0	4	-155.92	320.74	26.97	0.00
	27	23.92	34	7.35	4	6	-73.05	161.46	0.00	0.81
					7	7	-72.83	164.34	2.88	0.19
					1	5	-133.04	278.39	116.93	0.00
					3	5	-134.32	280.95	119.49	0.00
					5	6	-132.89	281.14	119.68	0.00
					0	4	-138.51	286.51	125.05	0.00
					6	6	-150.90	317.16	155.70	0.00
					2	5	-165.12	342.55	181.09	0.00
	28	35.28	166	10.35	4	6	-388.64	789.82	0.00	0.54
					7	7	-388.21	791.13	1.31	0.28
					2	5	-391.22	792.81	2.99	0.12
					6	6	-390.90	794.33	4.50	0.06
					1	5	-407.62	825.62	35.79	0.00
					5	6	-407.52	827.58	37.75	0.00
					3	5	-408.61	827.61	37.78	0.00
					0	4	-411.57	831.38	41.56	0.00
	29	40.82	41	20.08	1	5	-54.75	121.32	0.00	0.24
					2	5	-54.76	121.33	0.01	0.24
0					4	-56.45	122.08	0.76	0.16	
3					5	-55.42	122.66	1.34	0.12	
4					6	-54.16	122.94	1.62	0.11	
5					6	-54.75	124.13	2.81	0.06	
6					6	-54.76	124.15	2.82	0.06	
7					7	-54.16	125.93	4.61	0.02	

Table A8 (Continued)

Species	ID	Home time (hr)	Steps	Break time (hr)	Model	DF	LogLik	AICc	Delta AICc	Weight
Wood Thrush	30	43.93	184	30.08	4	6	-679.15	1370.78	0.00	0.52
					7	7	-678.15	1370.94	0.16	0.48
					2	5	-685.66	1381.67	10.89	0.00
					6	6	-684.65	1381.79	11.01	0.00
					1	5	-787.14	1584.63	213.85	0.00
					5	6	-787.20	1586.88	216.11	0.00
					3	5	-788.84	1588.02	217.24	0.00
					0	4	-797.03	1602.28	231.50	0.00
	31	45.83	51	20.48	7	7	-133.27	283.28	0.00	0.77
					4	6	-136.55	287.10	3.83	0.11
					6	6	-136.64	287.27	4.00	0.10
					2	5	-140.43	292.25	8.97	0.01
					1	5	-171.22	353.83	70.55	0.00
					3	5	-173.19	357.77	74.49	0.00
					5	6	-173.20	360.40	77.12	0.00
					0	4	-196.09	401.10	117.82	0.00
	32	69.17	254	44.98	7	7	-649.77	1314.01	0.00	0.65
					4	6	-651.46	1315.27	1.26	0.35
					6	6	-662.70	1337.74	23.73	0.00
					2	5	-666.37	1342.98	28.97	0.00
5					6	-762.61	1537.57	223.56	0.00	
1					5	-763.74	1537.72	223.72	0.00	
3					5	-766.83	1543.90	229.89	0.00	
0					4	-773.17	1554.51	240.50	0.00	
Ovenbird	33	4.57	65	3.22	4	6	-242.09	497.68	0.00	0.67
					7	7	-241.83	499.70	2.02	0.24
					2	5	-245.60	502.25	4.57	0.07
					6	6	-245.44	504.37	6.70	0.02
					1	5	-263.73	538.51	40.83	0.00
					3	5	-264.40	539.86	42.18	0.00
					5	6	-263.54	540.58	42.90	0.00
					0	4	-268.78	546.25	48.57	0.00
	34	11.75	72	5.12	2	5	-258.07	527.09	0.00	0.46
					4	6	-257.56	528.45	1.37	0.23
					6	6	-258.01	529.35	2.26	0.15
					7	7	-257.50	530.80	3.72	0.07
					1	5	-260.41	531.76	4.67	0.04
					3	5	-260.84	532.63	5.54	0.03
					5	6	-260.42	534.18	7.09	0.01
					0	4	-264.33	537.27	10.18	0.00
	35	20.60	84	11.07	4	6	-203.90	420.93	0.00	0.75
					7	7	-203.80	423.11	2.18	0.25
					2	5	-239.01	488.81	67.88	0.00
					6	6	-256.54	526.21	105.28	0.00
1					5	-279.48	569.75	148.82	0.00	
5					6	-283.25	579.62	158.70	0.00	
3					5	-286.18	583.14	162.22	0.00	
0					4	-287.55	583.62	162.69	0.00	

Table A8 (Continued)

Species	ID	Home time (hr)	Steps	Break time (hr)	Model	DF	LogLik	AICc	Delta AICc	Weight
Ovenbird	36	21.23	48	8.70	2	5	-119.18	249.86	0.00	0.46
					4	6	-118.59	251.33	1.47	0.22
					6	6	-119.18	252.51	2.65	0.12
					1	5	-121.17	253.84	3.98	0.06
					7	7	-118.59	254.12	4.26	0.05
					3	5	-121.48	254.46	4.60	0.05
					5	6	-121.17	256.49	6.63	0.02
					0	4	-124.16	257.30	7.44	0.01
	37	23.07	69	10.00	4	6	-190.06	393.52	0.00	0.78
					7	7	-190.06	396.02	2.50	0.22
					1	5	-243.69	498.37	104.86	0.00
					5	6	-243.74	500.87	107.36	0.00
					3	5	-245.62	502.21	108.70	0.00
					0	4	-249.39	507.43	113.92	0.00
					6	6	-272.90	559.20	165.68	0.00
					2	5	-276.24	563.46	169.95	0.00
	38	28.27	95	21.55	2	5	-248.22	507.12	0.00	0.55
					6	6	-248.04	509.07	1.95	0.21
					4	6	-248.19	509.36	2.24	0.18
					7	7	-248.01	511.34	4.22	0.07
					1	5	-259.52	529.74	22.62	0.00
					3	5	-259.57	529.83	22.71	0.00
					5	6	-259.56	532.09	24.97	0.00
					0	4	-263.95	536.36	29.24	0.00
	39	42.95	70	20.67	2	5	-207.30	425.57	0.00	0.50
					4	6	-206.73	426.84	1.27	0.27
					6	6	-207.30	427.97	2.40	0.15
					7	7	-206.73	429.33	3.76	0.08
					1	5	-212.59	436.14	10.57	0.00
					3	5	-212.91	436.79	11.22	0.00
					5	6	-212.60	438.58	13.01	0.00
					0	4	-215.64	439.92	14.35	0.00
	40	45.45	152	31.90	4	6	-533.14	1078.86	0.00	0.71
					7	7	-532.92	1080.62	1.75	0.29
					2	5	-542.11	1094.64	15.77	0.00
					6	6	-541.65	1095.89	17.02	0.00
1					5	-619.55	1249.53	170.66	0.00	
5					6	-619.44	1251.46	172.60	0.00	
3					5	-624.25	1258.91	180.05	0.00	
0					4	-628.13	1264.53	185.66	0.00	
41	45.52	57	21.62	2	5	-155.02	321.27	0.00	0.52	
				4	6	-154.85	323.45	2.18	0.17	
				6	6	-155.02	323.79	2.53	0.15	
				1	5	-157.30	325.83	4.56	0.05	
				7	7	-154.85	326.08	4.81	0.05	
				3	5	-157.51	326.24	4.97	0.04	
				5	6	-157.30	328.35	7.08	0.02	
				0	4	-162.13	333.05	11.78	0.00	

Table A8 (Continued)

Species	ID	Home time (hr)	Steps	Break time (hr)	Model	DF	LogLik	AICc	Delta AICc	Weight
Ovenbird	42	46.72	97	12.17	2	5	-295.99	602.65	0.00	0.51
					6	6	-295.76	604.48	1.83	0.21
					4	6	-295.78	604.51	1.86	0.20
					7	7	-295.58	606.45	3.79	0.08
					1	5	-305.90	622.47	19.82	0.00
					3	5	-305.96	622.59	19.93	0.00
					5	6	-305.90	624.75	22.09	0.00
					0	4	-309.08	626.61	23.96	0.00
	43	50.57	48	22.50	2	5	-107.29	226.07	0.00	0.26
					1	5	-107.34	226.19	0.11	0.25
					3	5	-107.39	226.28	0.21	0.24
					4	6	-107.11	228.37	2.30	0.08
					6	6	-107.20	228.56	2.49	0.08
					5	6	-107.31	228.77	2.69	0.07
					7	7	-107.05	231.05	4.98	0.02
					0	4	-112.51	234.00	7.93	0.00
	44	66.97	72	21.53	4	6	-204.81	422.94	0.00	0.53
					2	5	-206.81	424.55	1.61	0.24
					7	7	-204.75	425.30	2.36	0.16
					6	6	-206.72	426.78	3.83	0.08
					1	5	-238.68	488.29	65.34	0.00
					3	5	-239.49	489.92	66.97	0.00
					5	6	-238.63	490.60	67.65	0.00
					0	4	-242.56	493.73	70.79	0.00
	45	67.88	153	16.95	4	6	-468.68	949.95	0.00	0.49
					2	5	-470.40	951.21	1.26	0.26
					7	7	-468.67	952.13	2.18	0.16
					6	6	-470.39	953.36	3.41	0.09
					1	5	-478.60	967.61	17.66	0.00
					5	6	-478.58	969.74	19.80	0.00
3					5	-480.53	971.48	21.54	0.00	
0					4	-483.38	975.03	25.09	0.00	
46	70.30	105	51.00	4	6	-322.11	657.10	0.00	0.76	
				7	7	-322.11	659.41	2.30	0.24	
				2	5	-369.32	749.27	92.17	0.00	
				6	6	-368.81	750.50	93.40	0.00	
				1	5	-436.29	883.20	226.10	0.00	
				5	6	-436.29	885.46	228.35	0.00	
				3	5	-440.07	890.75	233.65	0.00	
				0	4	-444.01	896.42	239.32	0.00	
47	72.20	250	57.57	7	7	-606.30	1227.07	0.00	0.57	
				4	6	-608.06	1228.48	1.41	0.28	
				6	6	-609.22	1230.78	3.71	0.09	
				2	5	-610.82	1231.88	4.81	0.05	
				1	5	-895.95	1802.15	575.08	0.00	
				3	5	-896.36	1802.97	575.90	0.00	
				5	6	-895.75	1803.85	576.79	0.00	
				0	4	-901.35	1810.86	583.80	0.00	

**Table A9.** Full results from models fit in the first phase of path-level model building. For each response variable, we compared a null model with models that included a single additional covariate for body condition (CONDITION), captivity time (CAPTIVITY), or total river/stream length in the local landscape (RIPARIAN). A covariate for number of recorded steps (STEPS) was included in all models for straightness. We retained covariates for the second phase if their models were than 2 AICc units lower than the null model.

Species	Response	Model	DF	LogLik	AICc results			
					AICc	Delta AICc	Weight	
Wood Thrush	Total time	CONDITION	3	-35.13	77.11	0.00	0.38	
		NULL	2	-36.37	77.15	0.04	0.38	
		RIPARIAN	3	-36.30	79.45	2.34	0.12	
		CAPTIVITY	3	-36.31	79.47	2.36	0.12	
	Exploring time	NULL	2	-108.25	220.95	0.00	0.40	
		CONDITION	3	-107.20	221.32	0.37	0.33	
		CAPTIVITY	3	-107.98	222.88	1.93	0.15	
		RIPARIAN	3	-108.22	223.37	2.42	0.12	
	Homing time	CONDITION	3	-100.37	207.67	0.00	0.69	
		NULL	2	-102.95	210.34	2.67	0.18	
		RIPARIAN	3	-102.75	212.42	4.75	0.06	
		CAPTIVITY	3	-102.76	212.44	4.77	0.06	
	Total straightness	NULL	3	21.49	-36.11	0.00	0.53	
		CAPTIVITY	4	21.60	-33.72	2.39	0.16	
		CONDITION	4	21.58	-33.68	2.43	0.16	
		RIPARIAN	4	21.49	-33.50	2.61	0.14	
	Exploring straightness	NULL	3	20.75	-34.58	0.00	0.53	
		CAPTIVITY	4	21.07	-32.54	2.04	0.19	
		RIPARIAN	4	20.78	-31.96	2.62	0.14	
		CONDITION	4	20.76	-31.92	2.66	0.14	
	Homing straightness	NULL	3	13.82	-20.71	0.00	0.43	
		CAPTIVITY	4	14.73	-19.86	0.85	0.28	
		CONDITION	4	14.31	-19.02	1.69	0.18	
		RIPARIAN	4	13.84	-18.08	2.63	0.11	
	Ovenbird	Total time	CAPTIVITY	3	-10.99	30.17	0.00	0.96
			RIPARIAN	3	-14.97	38.13	7.96	0.02
			NULL	2	-16.87	38.74	8.57	0.01
			CONDITION	3	-16.30	40.78	10.61	0.00
		Exploring time	CAPTIVITY	3	-59.70	127.59	0.00	0.54
			NULL	2	-61.95	128.89	1.30	0.28
CONDITION			3	-61.22	130.62	3.03	0.12	
RIPARIAN			3	-61.84	131.86	4.27	0.06	
Homing time		CAPTIVITY	3	-58.79	125.76	0.00	0.36	
		RIPARIAN	3	-58.84	125.86	0.10	0.34	
		NULL	2	-60.74	126.47	0.71	0.25	
		CONDITION	3	-60.70	129.58	3.82	0.05	
Total straightness		NULL	3	13.49	-18.80	0.00	0.50	
		CAPTIVITY	4	15.05	-18.10	0.70	0.35	
		RIPARIAN	4	13.53	-15.06	3.74	0.08	
		CONDITION	4	13.49	-14.98	3.82	0.07	
Exploring straightness		NULL	3	8.89	-9.60	0.00	0.56	
		CAPTIVITY	4	9.51	-7.01	2.59	0.15	
		CONDITION	4	9.44	-6.88	2.72	0.14	
		RIPARIAN	4	9.39	-6.78	2.82	0.14	
Homing straightness		CAPTIVITY	4	8.46	-4.93	0.00	0.79	
		NULL	3	4.96	-1.74	3.19	0.16	
		CONDITION	4	5.16	1.69	6.62	0.03	
		RIPARIAN	4	4.97	2.06	6.99	0.02	



Table A9 (Continued)

Species	Response	Model	Parameter estimates (SE)				
			INTERCEPT	STEPS	CONDITION	CAPTIVITY	RIPARIAN
Wood Thrush	Total time	CONDITION	2.62 (0.13)	--	0.21 (0.13)	--	--
		NULL	2.62 (0.14)	--	--	--	--
		RIPARIAN	2.62 (0.14)	--	--	--	-0.05 (0.14)
		CAPTIVITY	2.62 (0.14)	--	--	-0.05 (0.14)	--
	Exploring time	NULL	9.24 (1.66)	--	--	--	--
		CONDITION	9.24 (1.63)	--	2.37 (1.66)	--	--
		CAPTIVITY	9.24 (1.67)	--	--	1.22 (1.7)	--
		RIPARIAN	9.24 (1.69)	--	--	--	-0.39 (1.71)
	Homing time	CONDITION	9.92 (1.3)	--	3.02 (1.32)	--	--
		NULL	9.92 (1.39)	--	--	--	--
		RIPARIAN	9.92 (1.4)	--	--	--	-0.87 (1.43)
		CAPTIVITY	9.92 (1.41)	--	--	0.85 (1.43)	--
	Total straightness	NULL	0.49 (0.02)	-0.12 (0.02)	--	--	--
		CAPTIVITY	0.49 (0.02)	-0.12 (0.02)	--	0.01 (0.02)	--
		CONDITION	0.49 (0.02)	-0.12 (0.02)	-0.01 (0.02)	--	--
		RIPARIAN	0.49 (0.02)	-0.12 (0.02)	--	--	0 (0.02)
	Exploring straightness	NULL	0.23 (0.02)	-0.07 (0.02)	--	--	--
		CAPTIVITY	0.23 (0.02)	-0.07 (0.02)	--	0.02 (0.02)	--
		RIPARIAN	0.23 (0.02)	-0.08 (0.02)	--	--	0.01 (0.02)
		CONDITION	0.23 (0.02)	-0.07 (0.02)	0 (0.02)	--	--
	Homing straightness	NULL	0.64 (0.03)	-0.12 (0.03)	--	--	--
		CAPTIVITY	0.64 (0.03)	-0.12 (0.03)	--	-0.04 (0.03)	--
		CONDITION	0.64 (0.03)	-0.11 (0.03)	-0.03 (0.03)	--	--
		RIPARIAN	0.64 (0.03)	-0.12 (0.03)	--	--	0.01 (0.03)
Ovenbird	Total time	CAPTIVITY	3.51 (0.14)	--	--	0.57 (0.14)	--
		RIPARIAN	3.51 (0.18)	--	--	--	-0.36 (0.19)
		NULL	3.51 (0.2)	--	--	--	--
		CONDITION	3.51 (0.2)	--	0.21 (0.21)	--	--
	Exploring time	CAPTIVITY	21.04 (3.59)	--	--	7.91 (3.72)	--
		NULL	21.04 (4.02)	--	--	--	--
		CONDITION	21.04 (3.97)	--	4.74 (4.11)	--	--
		RIPARIAN	21.04 (4.14)	--	--	--	-1.83 (4.29)
	Homing time	CAPTIVITY	20.17 (3.38)	--	--	6.86 (3.5)	--
		RIPARIAN	20.17 (3.39)	--	--	--	-6.79 (3.51)
		NULL	20.17 (3.71)	--	--	--	--
		CONDITION	20.17 (3.84)	--	-1 (3.97)	--	--
	Total straightness	NULL	0.36 (0.03)	-0.09 (0.03)	--	--	--
		CAPTIVITY	0.36 (0.03)	-0.09 (0.03)	--	-0.04 (0.03)	--
		RIPARIAN	0.36 (0.03)	-0.09 (0.03)	--	--	0.01 (0.03)
		CONDITION	0.36 (0.03)	-0.09 (0.03)	0 (0.03)	--	--
	Exploring straightness	NULL	0.22 (0.04)	-0.05 (0.04)	--	--	--
		CAPTIVITY	0.22 (0.04)	-0.05 (0.04)	--	0.04 (0.04)	--
		CONDITION	0.22 (0.04)	-0.05 (0.04)	0.04 (0.04)	--	--
		RIPARIAN	0.22 (0.04)	-0.05 (0.04)	--	--	-0.04 (0.04)
	Homing straightness	CAPTIVITY	0.51 (0.04)	-0.1 (0.04)	--	-0.11 (0.04)	--
		NULL	0.51 (0.05)	-0.11 (0.05)	--	--	--
		CONDITION	0.51 (0.05)	-0.12 (0.05)	-0.03 (0.05)	--	--
		RIPARIAN	0.51 (0.05)	-0.11 (0.06)	--	--	-0.01 (0.06)

**Table A10.** Full results from models fit in the second phase of path-level model building. In each model table, the baseline model was chosen in a previous step (Table A9) to determine whether effects of body condition (CONDITION) or captivity time (CAPTIVITY) should be included. For each response variable, this baseline model had greater support than models that built on it with covariates for forest cover (PROP.FOR) and number of patches (PATCHES) in the local landscape.

Species	Response	Model	Parameter estimates (SE)							AICc results		
			INTERCEPT	STEPS	CAPTIVITY	CONDITION	PATCHES	PROP.FOR	PATCHES* PROP.FOR	AICc	Delta AICc	Weight
Wood Thrush	Total time	NULL	2.62 (0.14)	--	--	--	--	--	--	77.15	0.00	0.45
		PATCHES * PROP.FOR	2.9 (0.18)	--	--	--	-0.11 (0.19)	-0.1 (0.19)	0.4 (0.18)	78.85	1.70	0.19
		PATCHES	2.62 (0.14)	--	--	--	-0.06 (0.14)	--	--	79.38	2.23	0.15
		PROP.FOR	2.62 (0.14)	--	--	--	--	-0.04 (0.14)	--	79.49	2.34	0.14
		PATCHES + PROP.FOR	2.62 (0.14)	--	--	--	-0.19 (0.2)	-0.18 (0.2)	--	81.12	3.97	0.06
	Exploring time	NULL	9.24 (1.66)	--	--	--	--	--	--	220.95	0.00	0.54
		PATCHES	9.24 (1.68)	--	--	--	-0.92 (1.71)	--	--	223.12	2.17	0.18
		PROP.FOR	9.24 (1.68)	--	--	--	--	-0.54 (1.71)	--	223.32	2.37	0.17
		PATCHES + PROP.FOR	9.24 (1.68)	--	--	--	-2.6 (2.42)	-2.38 (2.42)	--	224.74	3.79	0.08
		PATCHES * PROP.FOR	10.66 (2.37)	--	--	--	-2.18 (2.48)	-1.93 (2.48)	2.07 (2.44)	226.82	5.87	0.03
	Homing time	CONDITION	9.92 (1.3)	--	--	3.02 (1.32)	--	--	--	207.67	0.00	0.41
		PROP.FOR	9.92 (1.29)	--	--	3.01 (1.31)	--	1.59 (1.31)	--	208.74	1.07	0.24
		PATCHES	9.92 (1.29)	--	--	2.76 (1.33)	-1.59 (1.33)	--	--	208.79	1.12	0.23
		PATCHES + PROP.FOR	9.92 (1.31)	--	--	2.87 (1.36)	-0.89 (1.93)	0.96 (1.9)	--	211.40	3.73	0.06
		PATCHES * PROP.FOR	11.88 (1.81)	--	--	2.47 (1.36)	-0.45 (1.9)	1.49 (1.89)	2.86 (1.87)	211.87	4.20	0.05
	Total straightness	NULL	0.49 (0.02)	-0.12 (0.02)	--	--	--	--	--	-36.11	0.00	0.46
		PROP.FOR	0.49 (0.02)	-0.12 (0.02)	--	--	--	0.03 (0.02)	--	-34.77	1.34	0.24
		PATCHES	0.49 (0.02)	-0.12 (0.02)	--	--	-0.02 (0.02)	--	--	-34.37	1.74	0.19
		PATCHES + PROP.FOR	0.49 (0.02)	-0.12 (0.02)	--	--	-0.01 (0.03)	0.02 (0.04)	--	-31.97	4.14	0.06
		PATCHES * PROP.FOR	0.46 (0.03)	-0.11 (0.02)	--	--	-0.01 (0.03)	0.01 (0.03)	-0.05 (0.03)	-31.51	4.60	0.05
	Exploring straightness	NULL	0.23 (0.02)	-0.07 (0.02)	--	--	--	--	--	-34.58	0.00	0.60
		PATCHES	0.23 (0.02)	-0.08 (0.02)	--	--	-0.01 (0.02)	--	--	-32.10	2.48	0.17
		PROP.FOR	0.23 (0.02)	-0.07 (0.02)	--	--	--	0.01 (0.02)	--	-32.00	2.58	0.17
		PATCHES + PROP.FOR	0.23 (0.02)	-0.08 (0.03)	--	--	-0.01 (0.04)	0 (0.04)	--	-29.20	5.38	0.04
		PATCHES * PROP.FOR	0.21 (0.03)	-0.07 (0.03)	--	--	-0.02 (0.04)	-0.01 (0.04)	-0.03 (0.03)	-27.08	7.50	0.01
	Homing straightness	NULL	0.64 (0.03)	-0.12 (0.03)	--	--	--	--	--	-20.71	0.00	0.61
		PROP.FOR	0.64 (0.03)	-0.12 (0.03)	--	--	--	-0.01 (0.03)	--	-18.09	2.62	0.17
		PATCHES	0.64 (0.03)	-0.12 (0.03)	--	--	0 (0.03)	--	--	-18.04	2.67	0.16
		PATCHES + PROP.FOR	0.64 (0.03)	-0.12 (0.03)	--	--	0 (0.04)	-0.01 (0.04)	--	-15.20	5.51	0.04
		PATCHES * PROP.FOR	0.6 (0.04)	-0.11 (0.03)	--	--	-0.01 (0.04)	-0.02 (0.04)	-0.05 (0.04)	-13.67	7.04	0.02

Table A10 (Continued)

Species	Response	Model	Parameter estimates (SE)							AICc results		
			INTERCEPT	STEPS	CAPTIVITY	CONDITION	PATCHES	PROP.FOR	PATCHES* PROP.FOR	AICc	Delta AICc	Weight
Ovenbird	Total time	CAPTIVITY	3.51 (0.14)	--	0.57 (0.14)	--	--	--	--	30.17	0.00	0.58
		PATCHES + PROP.FOR	3.51 (0.13)	--	0.6 (0.14)	--	-0.37 (0.19)	-0.4 (0.19)	--	32.92	2.75	0.15
		PROP.FOR	3.51 (0.14)	--	0.62 (0.16)	--	--	-0.14 (0.16)	--	32.95	2.78	0.15
		PATCHES	3.51 (0.14)	--	0.54 (0.16)	--	-0.11 (0.16)	--	--	33.42	3.25	0.11
		PATCHES * PROP.FOR	3.4 (0.21)	--	0.64 (0.16)	--	-0.45 (0.23)	-0.49 (0.24)	-0.16 (0.25)	38.17	8.00	0.01
	Exploring time	NULL	21.04 (4.02)	--	--	--	--	--	--	128.89	0.00	0.56
		PATCHES	21.04 (3.98)	--	--	--	-4.71 (4.12)	--	--	130.63	1.74	0.23
		PROP.FOR	21.04 (4.17)	--	--	--	--	0.57 (4.31)	--	132.05	3.16	0.12
		PATCHES + PROP.FOR	21.04 (3.99)	--	--	--	-8.76 (5.89)	-5.68 (5.89)	--	133.33	4.44	0.06
		PATCHES * PROP.FOR	28.29 (5.86)	--	--	--	-3.07 (6.57)	-0.52 (6.39)	10.9 (6.77)	134.82	5.93	0.03
	Homing time	NULL	20.17 (3.71)	--	--	--	--	--	--	126.47	0.00	0.69
		PATCHES	20.17 (3.84)	--	--	--	-0.72 (3.98)	--	--	129.62	3.15	0.14
		PROP.FOR	20.17 (3.85)	--	--	--	--	-0.25 (3.98)	--	129.65	3.18	0.14
		PATCHES + PROP.FOR	20.17 (3.99)	--	--	--	-1.81 (5.89)	-1.54 (5.89)	--	133.35	6.88	0.02
		PATCHES * PROP.FOR	18.64 (6.49)	--	--	--	-3.01 (7.27)	-2.62 (7.08)	-2.29 (7.5)	137.89	11.42	0.00
	Total straightness	NULL	0.36 (0.03)	-0.09 (0.03)	--	--	--	--	--	-18.80	0.00	0.76
		PATCHES	0.36 (0.03)	-0.09 (0.03)	--	--	-0.01 (0.03)	--	--	-15.02	3.78	0.11
		PROP.FOR	0.36 (0.03)	-0.09 (0.03)	--	--	--	0 (0.03)	--	-15.01	3.79	0.11
		PATCHES + PROP.FOR	0.36 (0.03)	-0.09 (0.03)	--	--	0 (0.05)	0 (0.05)	--	-10.36	8.44	0.01
		PATCHES * PROP.FOR	0.32 (0.05)	-0.08 (0.04)	--	--	-0.03 (0.05)	-0.02 (0.05)	-0.06 (0.06)	-5.88	12.92	0.00
	Exploring straightness	NULL	0.22 (0.04)	-0.05 (0.04)	--	--	--	--	--	-9.60	0.00	0.65
		PROP.FOR	0.22 (0.04)	-0.04 (0.04)	--	--	--	0.04 (0.04)	--	-6.87	2.73	0.17
		PATCHES	0.22 (0.04)	-0.06 (0.04)	--	--	-0.04 (0.04)	--	--	-6.81	2.79	0.16
		PATCHES + PROP.FOR	0.22 (0.04)	-0.05 (0.04)	--	--	-0.02 (0.06)	0.02 (0.06)	--	-2.32	7.28	0.02
		PATCHES * PROP.FOR	0.18 (0.07)	-0.04 (0.05)	--	--	-0.04 (0.07)	0 (0.07)	-0.05 (0.08)	2.86	12.46	0.00
	Homing straightness	CAPTIVITY	0.51 (0.04)	-0.1 (0.04)	-0.11 (0.04)	--	--	--	--	-4.93	0.00	0.81
		PATCHES	0.51 (0.04)	-0.11 (0.04)	-0.1 (0.04)	--	0.03 (0.05)	--	--	-0.76	4.17	0.10
		PROP.FOR	0.51 (0.04)	-0.1 (0.04)	-0.12 (0.05)	--	--	0.01 (0.05)	--	-0.36	4.57	0.08
		PATCHES + PROP.FOR	0.51 (0.04)	-0.11 (0.04)	-0.11 (0.05)	--	0.06 (0.06)	0.06 (0.06)	--	3.86	8.79	0.01
		PATCHES * PROP.FOR	0.5 (0.07)	-0.11 (0.05)	-0.11 (0.05)	--	0.06 (0.08)	0.05 (0.08)	-0.02 (0.09)	11.28	16.21	0.00

**Table A11.** Full results from all mixed conditional logistic regression models fit to step level data for translocated Wood Thrush and Ovenbirds. Variables included in models were distance from the step endpoint to the capture site (CAPDIST) or stream (RIPDIST), forest cover within 50 m of the start point (FOR50), number of gaps (GAPS), total gap distance (GAPDIST), proportion of the step in forest (FOR%), and an indicator variable for behavioral mode (BEHAV) equal to one if the step occurred during exploring. All regression coefficients were treated as random to account for correlation among steps taken by the same individual birds. Thus, we report the estimated mean and standard deviation for each parameter, and 95% confidence intervals.

Species	Model	DF	LogLik	AICc	Delta AICc	Weight	Variable	Mean			SD		
								Est	LCL	UCL	EST	LCL	UCL
Wood Thrush	1	7	-2235.47	4485.09	0.00	0.46	CAPDIST	-2.10	-2.66	-1.53	0.78	0.16	1.40
							CAPDIST*BEHAV	0.07	-1.45	1.58	2.55	1.17	3.94
							GAPS	-0.23	-0.39	-0.08	0.21	0.04	0.37
	2	9	-2234.58	4487.41	2.32	0.14	CAPDIST	-2.20	-2.84	-1.55	0.99	0.31	1.66
							CAPDIST*BEHAV	0.44	-1.06	1.94	2.58	4.05	1.10
							GAPS	-0.29	-0.48	-0.10	0.23	0.06	0.41
							GAPS*FOR50	-0.04	-0.13	0.05	0.04	0.15	0.23
	3	7	-2236.71	4487.57	2.48	0.13	CAPDIST	-2.39	-3.09	-1.68	1.13	1.88	0.37
							CAPDIST*BEHAV	0.39	-1.14	1.93	2.61	0.94	4.27
							GAPDIST	-0.25	-0.42	-0.07	0.08	0.39	0.23
	4	9	-2235.21	4488.67	3.58	0.08	CAPDIST	-2.06	-2.63	-1.50	0.76	0.14	1.38
							CAPDIST*BEHAV	0.03	-1.51	1.56	2.60	1.21	3.99
							GAPS	-0.22	-0.38	-0.06	0.21	0.05	0.38
							GAPS*BEHAV	-0.13	-0.49	0.23	0.00	0.52	0.53
	5	9	-2235.59	4489.43	4.33	0.05	CAPDIST	-2.09	-2.67	-1.50	0.86	0.24	1.49
							CAPDIST*BEHAV	0.13	-1.39	1.64	2.52	0.97	4.06
							FOR%	0.32	0.12	0.51	0.12	0.10	0.35
							FOR%*FOR50	0.08	-0.01	0.16	0.05	0.05	0.15
	6	11	-2233.96	4490.27	5.18	0.03	CAPDIST	-2.18	-2.81	-1.55	0.99	0.34	1.63
							CAPDIST*BEHAV	0.45	-1.08	1.99	2.67	4.23	1.12
							GAPS	-0.27	-0.47	-0.08	0.24	0.07	0.41
							GAPS*BEHAV	-0.15	-0.54	0.24	0.05	0.59	0.49
							GAPS*FOR50	-0.04	-0.13	0.05	0.07	0.04	0.17
	7	9	-2236.11	4490.47	5.37	0.03	CAPDIST	-2.34	-3.03	-1.66	1.10	0.31	1.90
CAPDIST*BEHAV							0.48	-1.41	2.36	2.48	4.14	0.82	
GAPDIST							-0.29	-0.72	0.14	0.11	0.67	0.89	
GAPDIST*FOR50							-0.04	-0.16	0.08	0.01	0.18	0.15	
8	9	-2236.18	4490.59	5.50	0.03	CAPDIST	-2.26	-2.90	-1.62	0.92	0.27	1.57	
						CAPDIST*BEHAV	0.18	-1.37	1.73	2.57	1.08	4.07	
						GAPDIST	-0.21	-0.37	-0.04	0.04	0.59	0.67	
						GAPDIST*BEHAV	-0.43	-1.42	0.57	0.30	1.65	1.06	

Table A11 (Continued)

Species	Model	DF	LogLik	AICc	Delta AICc	Weight	Variable	Mean			SD		
								Est	LCL	UCL	EST	LCL	UCL
Wood Thrush	9	7	-2239.14	4492.43	7.34	0.01	CAPDIST	-2.01	-2.59	-1.43	0.87	1.54	0.21
							CAPDIST*BEHAV	0.08	-1.42	1.57	2.71	1.05	4.36
							FOR%	0.20	0.04	0.37	0.19	0.02	0.36
	10	11	-2235.47	4493.29	8.20	0.01	CAPDIST	-2.07	-2.65	-1.48	0.84	0.19	1.48
							CAPDIST*BEHAV	0.07	-1.46	1.60	2.48	0.99	3.97
							FOR%	0.30	0.10	0.50	0.13	0.08	0.34
							FOR%*BEHAV	0.08	-0.22	0.38	0.00	0.43	0.44
	FOR%*FOR50	0.07	-0.02	0.16	0.04	0.14	0.05						
	11	11	-2235.47	4493.29	8.20	0.01	CAPDIST	-2.38	-3.09	-1.66	1.12	1.85	0.40
							CAPDIST*BEHAV	0.54	-1.12	2.20	2.66	0.91	4.41
							GAPDIST	-0.36	-0.74	0.02	0.22	0.62	0.18
							GAPDIST*BEHAV	-0.34	-1.24	0.56	0.22	1.20	0.75
	GAPDIST*FOR50	-0.04	-0.15	0.07	0.06	0.10	0.23						
	12	13	-2233.86	4494.22	9.13	0.00	CAPDIST	-2.17	-2.80	-1.55	0.98	0.33	1.62
							CAPDIST*BEHAV	0.44	-1.09	1.98	2.66	4.22	1.09
							GAPS	-0.27	-0.46	-0.07	0.24	0.07	0.41
							GAPS*BEHAV	-0.22	-0.73	0.29	0.05	0.61	0.51
							GAPS*FOR50	-0.04	-0.13	0.05	0.06	0.06	0.18
	GAPS*BEHAV*FOR50	-0.06	-0.37	0.25	0.01	0.21	0.23						
	13	13	-2234.63	4495.74	10.65	0.00	CAPDIST	-2.26	-2.93	-1.60	0.95	0.19	1.70
							CAPDIST*BEHAV	0.13	-1.38	1.65	2.55	1.05	4.04
							GAPDIST	-0.30	-0.59	-0.02	0.15	0.15	0.45
							GAPDIST*BEHAV	-1.01	-2.50	0.49	0.02	1.10	1.07
							GAPDIST*FOR50	-0.05	-0.14	0.05	0.03	0.18	0.13
	GAPDIST*BEHAV*FOR50	-0.35	-0.93	0.22	0.01	0.36	0.39						
	14	13	-2234.79	4496.06	10.97	0.00	CAPDIST	-2.12	-2.74	-1.50	0.95	0.32	1.58
							CAPDIST*BEHAV	0.15	-1.35	1.64	2.70	4.27	1.13
							FOR%	0.29	0.08	0.49	0.13	0.08	0.34
							FOR%*BEHAV	0.27	-0.30	0.85	0.02	0.38	0.41
							FOR%*FOR50	0.06	-0.04	0.16	0.05	0.14	0.05
	FOR%*BEHAV*FOR50	0.10	-0.14	0.35	0.01	0.13	0.15						
	15	9	-2238.97	4496.18	11.09	0.00	CAPDIST	-2.00	-2.58	-1.42	0.87	1.53	0.21
							CAPDIST*BEHAV	0.05	-1.46	1.56	2.72	1.08	4.36
							FOR%	0.19	0.02	0.36	0.19	0.02	0.35
							FOR%*BEHAV	0.10	-0.24	0.43	0.05	0.35	0.46
	16	5	-2244.45	4498.97	13.88	0.00	CAPDIST	-1.86	-2.37	-1.34	0.73	0.18	1.28
							CAPDIST*BEHAV	-0.06	-1.51	1.40	2.39	1.02	3.77



Table A11 (Continued)

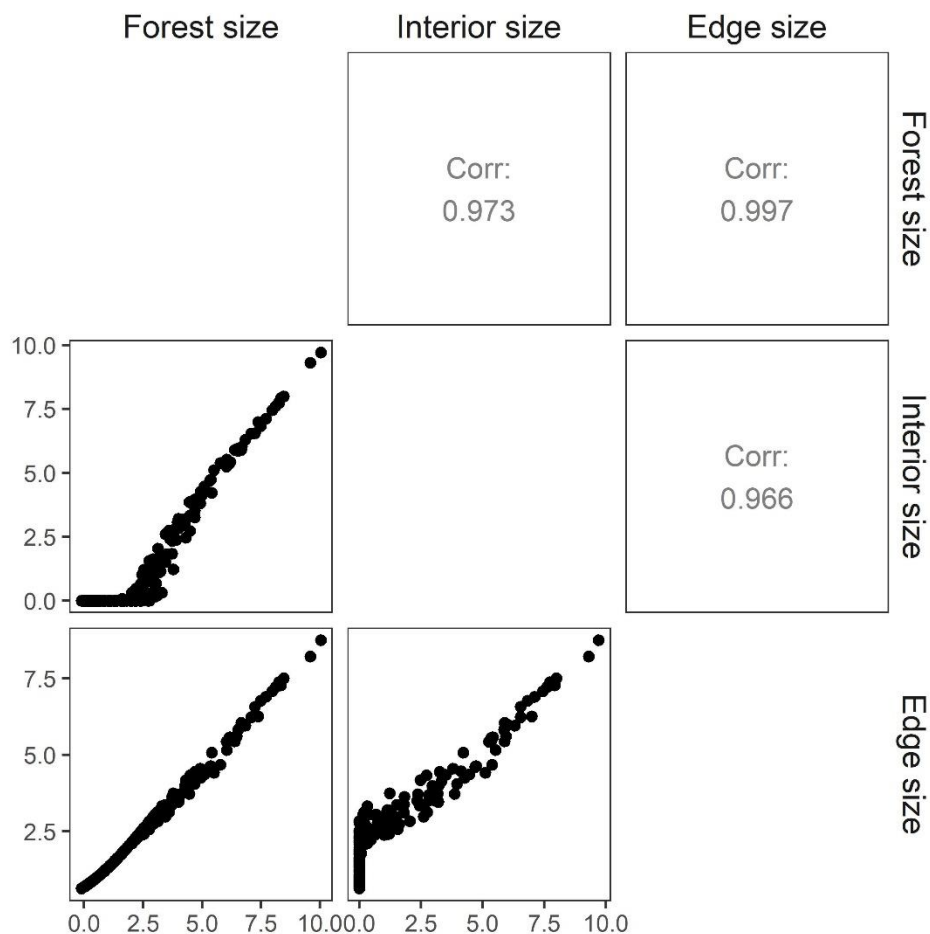
Species	Model	DF	LogLik	AICc	Delta AICc	Weight	Variable	Mean			SD		
								Est	LCL	UCL	EST	LCL	UCL
Ovenbird	7	11	-1596.92	3216.34	9.18	0.01	CAPDIST	-4.46	-5.46	-3.45	0.74	0.43	1.91
							CAPDIST*BEHAV	2.37	0.84	3.90	0.32	2.81	2.18
							RIPDIST	-0.13	-0.39	0.13	0.42	0.16	0.68
							FOR%	0.48	0.13	0.83	0.00	0.24	0.24
							FOR%*FOR50	0.02	-0.10	0.14	0.00	0.07	0.07
	8	15	-1592.73	3216.37	9.21	0.01	CAPDIST	-5.01	-6.38	-3.64	0.88	0.66	2.42
							CAPDIST*BEHAV	2.88	1.16	4.60	0.21	2.09	1.68
							RIPDIST	-0.13	-0.38	0.12	0.45	0.17	0.73
							GAPS	-0.43	-0.78	-0.07	0.12	0.21	0.44
							GAPS*BEHAV	-0.01	-0.88	0.86	0.12	2.24	2.48
							GAPS*FOR50	0.05	-0.10	0.19	0.02	0.13	0.09
	GAPS*BEHAV*FOR50	-0.10	-0.88	0.69	0.31	1.35	0.72						
	9	9	-1599.82	3217.98	10.82	0.00	CAPDIST	-4.91	-6.13	-3.70	1.03	0.00	2.05
							CAPDIST*BEHAV	2.74	1.16	4.33	0.31	2.01	1.40
							RIPDIST	-0.13	-0.37	0.11	0.45	0.17	0.74
							GAPDIST	-0.55	-1.06	-0.05	0.31	0.17	0.79
	10	13	-1596.59	3219.87	12.70	0.00	CAPDIST	-4.52	-5.58	-3.45	0.77	0.46	2.00
							CAPDIST*BEHAV	2.49	0.90	4.07	0.35	2.56	1.87
							RIPDIST	-0.13	-0.39	0.14	0.43	0.15	0.70
							FOR%	0.56	0.15	0.97	0.00	0.27	0.26
							FOR%*BEHAV	-0.16	-0.57	0.25	0.07	1.14	0.99
							FOR%*FOR50	0.02	-0.10	0.15	0.00	0.06	0.06
	11	11	-1598.88	3220.25	13.08	0.00	CAPDIST	-4.78	-5.94	-3.61	1.34	0.20	2.49
							CAPDIST*BEHAV	2.63	1.00	4.27	0.58	1.72	2.87
							RIPDIST	-0.11	-0.38	0.16	0.43	0.14	0.73
							GAPDIST	-0.61	-1.11	-0.11	0.58	0.07	1.22
							GAPDIST*BEHAV	-0.34	-1.68	0.99	0.78	2.07	0.50
	12	11	-1599.69	3221.87	14.71	0.00	CAPDIST	-4.94	-6.16	-3.73	1.14	2.35	0.07
							CAPDIST*BEHAV	2.86	1.25	4.48	0.47	2.75	1.81
							RIPDIST	-0.19	-0.44	0.07	0.40	0.16	0.63
							GAPDIST	-0.50	-0.95	-0.05	0.15	0.13	0.43
							GAPDIST*FOR50	-0.01	-0.14	0.11	0.05	0.04	0.14
	13	15	-1595.75	3222.40	15.24	0.00	CAPDIST	-4.89	-6.04	-3.75	1.56	2.75	0.36
							CAPDIST*BEHAV	2.91	1.28	4.54	0.42	2.39	1.54
							RIPDIST	-0.16	-0.40	0.08	0.41	0.18	0.64
							GAPDIST	-0.56	-1.02	-0.10	0.34	0.65	0.03
GAPDIST*BEHAV							-0.52	-1.92	0.87	0.21	0.92	1.33	
GAPDIST*FOR50							0.07	-0.10	0.24	0.16	0.04	0.29	
GAPDIST*BEHAV*FOR50							-0.01	-0.68	0.66	0.41	0.09	0.91	

Table A11 (Continued)

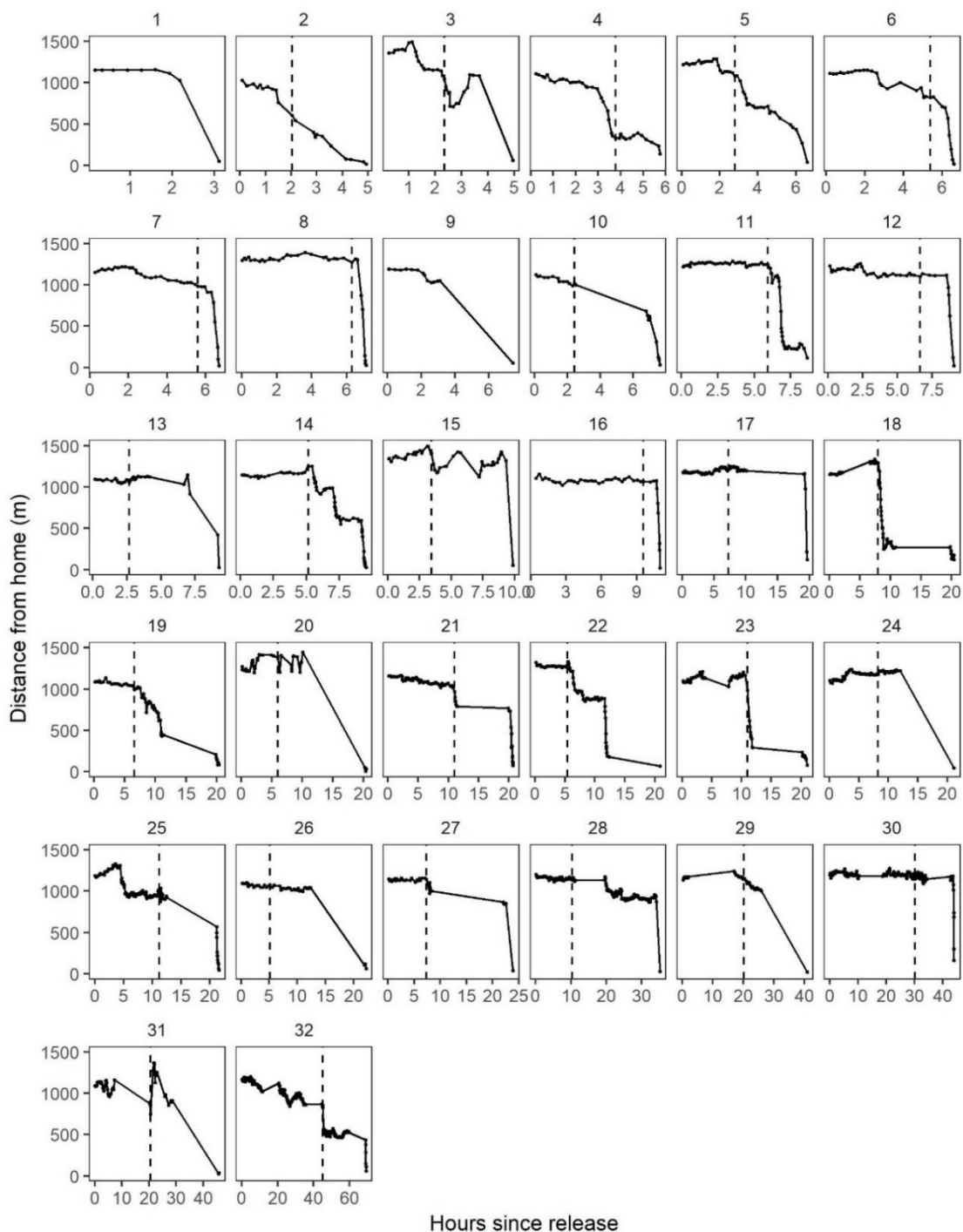
Species	Model	DF	LogLik	AICc	Delta AICc	Weight	Variable	Mean			SD		
								Est	LCL	UCL	EST	LCL	UCL
Ovenbird	14	15	-1596.21	3223.33	16.17	0.00	CAPDIST	-4.49	-5.51	-3.48	0.81	1.97	0.35
							CAPDIST*BEHAV	2.49	0.90	4.08	0.49	2.44	1.47
							RIPDIST	-0.15	-0.41	0.12	0.41	0.16	0.66
							FOR%	0.55	0.11	1.00	0.02	0.35	0.30
							FOR%*BEHAV	-0.08	-0.92	0.76	0.13	0.73	0.47
							FOR%*FOR50	0.02	-0.13	0.17	0.02	0.12	0.07
							FOR%*BEHAV*FOR50	0.01	-0.34	0.36	0.07	0.23	0.09
	15	13	-1598.65	3223.98	16.82	0.00	CAPDIST	-4.82	-5.96	-3.67	1.17	2.85	0.50
							CAPDIST*BEHAV	2.70	1.00	4.41	0.49	2.39	1.40
							RIPDIST	-0.17	-0.43	0.09	0.42	0.15	0.69
							GAPDIST	-0.48	-0.94	-0.02	0.16	0.11	0.43
							GAPDIST*BEHAV	-0.39	-1.34	0.56	0.58	0.24	1.41
							GAPDIST*FOR50	-0.01	-0.19	0.16	0.09	0.05	0.23
	16	7	-1613.19	3240.59	33.42	0.00	CAPDIST	-3.81	-4.64	-2.97	0.26	3.04	2.52
							CAPDIST*BEHAV	2.02	0.57	3.47	0.27	3.16	2.63
							RIPDIST	-0.12	-0.38	0.14	0.38	0.14	0.62
	17	9	-1613.14	3244.61	37.45	0.00	CAPDIST	-3.84	-4.72	-2.96	0.38	1.17	1.93
							CAPDIST*BEHAV	2.05	0.62	3.49	0.25	2.93	2.44
							RIPDIST	-0.11	-0.39	0.17	0.39	0.15	0.64
							RIPDIST*BEHAV	-0.02	-0.35	0.32	0.01	0.45	0.44
	18	5	-1617.49	3245.09	37.93	0.00	CAPDIST	-3.52	-4.42	-2.63	0.79	0.33	1.92
							CAPDIST*BEHAV	1.70	0.30	3.09	0.04	4.52	4.44



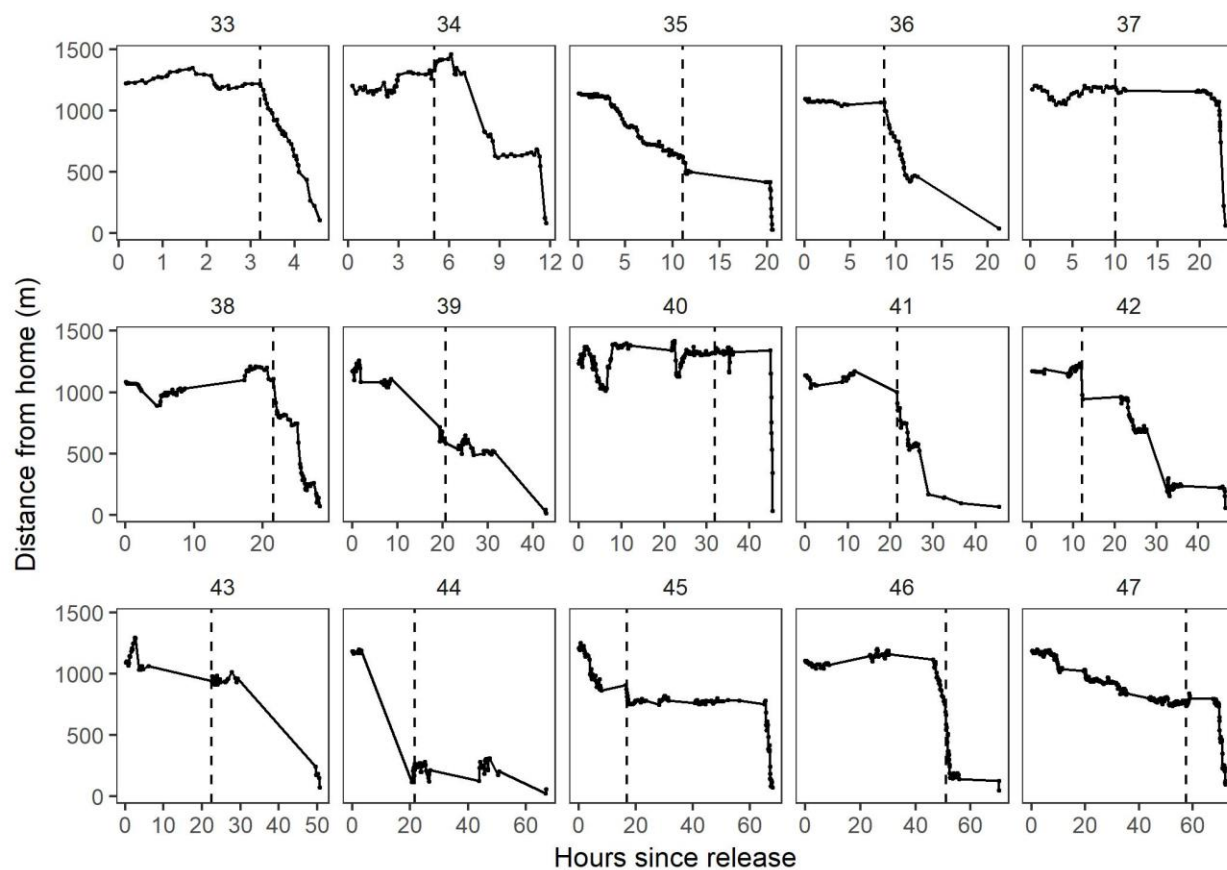




**Figure A2.** A comparison of three measures of patch size for the 202 forest patches we sampled. We calculated interior patch size by excluding all parts of the patch within 100 m of a forest edge. Edge patch size is the difference between forest patch size and interior patch size. Here we show the relationship between these metrics for our 490 point count stations. Because all of these measures of patch size are highly correlated, replacing forest patch size with either interior or edge patch size resulted in very similar parameter estimates for patch size effects. Because some interior patch sizes were zero, we transformed all values by adding 1 and then taking the natural logarithm.



**Figure A3.** Plots showing distance from home as a function of time for the 32 translocated Wood Thrush that homed successfully. Dots represent recorded GPS points. Vertical dashed lines indicate the behavioral change point (Table A8). Birds tended to move towards home quickly and directly after switching from exploring behavior (left of dashed line) to homing (right of dashed line). Birds are numbered in order from quickest to home (1) to slowest (32).



**Figure A4.** Plots showing distance from home as a function of time for the 15 translocated Ovenbirds that homed successfully. Dots represent recorded GPS points. Vertical dashed lines indicate the behavioral change point (Table A8). Birds tended to move towards home quickly and directly after switching from exploring behavior (left of dashed line) to homing (right of dashed line). Birds are numbered in order from quickest to home (33) to slowest (47).

## APPENDIX B: R CODE USED FOR SIMULATION AND ANALYSIS OF OCCUPANCY AND USE SAMPLING DATA

```

#Remove all objects from the workspace
rm(list=ls())

#Load required packages
library(unmarked)
library(gdata)

#####
##
#This function simulates and analyzes presence/absence datasets as described in our
#manuscript. All datasets generated mimic those collected using Pollock's robust
sampling
#design (Pollock 1982), where 3 secondary sampling periods are nested
#within each of 3 primary sampling periods. By default, the function creates
#1000 datasets containing 500 sites each, but these values can be specified.

#Other parameters that can be specified include:
  #psi0 - the initial probability of site use
  #eps0 - the probability a used site becomes unused during a subsequent primary
period
  #Pa - the probability at least one individual using the site was available for
sampling
  #Pd = the probability at least one available individual is detected

#Note that gamma0 is the probability an unused site becomes used during a subsequent
primary period,
#and that gamma0 is calculated such that the expected value of psi0 remains constant
across all primary periods

#Additionally, when the user specifies sampling="USE", datasets are generated
#such that availability for detection is independent on each of the 9 sampling
#occasions, representing a sampling scheme where probability of
#site use is estimated within primary sampling periods.

#When the user specifies sampling="OCCUPANCY", availability for detection
#only changes between primary periods, representing a sampling scheme where
#instantaneous occupancy rates are estimated within primary sampling periods

#For each simulated dataset, we then fit both a static (Mackenzie et al. 2002)
#and dynamic (Mackenzie et al. 2003) occupancy model, evaluate the proportion
#of the time the dynamic (open) model is selected over the static (closed) model,
#and calculate the mean, variance, and bias of parameter estimates generated
#from both models.
#####
##
pres.abs.sim = function(psi0=NULL, eps0=NULL, Pa=NULL, Pd=NULL, sampling=NULL,
nsites=500, nsim=1000){

  #Calculate colonization rate such that probability of site use remains
  #constant across all primary periods
  gamma0 = (psi0*eps0)/(1-psi0)

  #Create dataframe for storing results of simulations
  data.summ=data.frame(matrix(NA, nrow=nsim, ncol=14))
  colnames(data.summ) = c("psi0", "gamma0", "eps0", "Pa", "Pd", "closed.psi",
"closed.p", "open.psi", "open.p", "open.col", "open.ext", "tstat", "delta", "LRT")

  for(j in 1:nsim){
    if(sampling=="USE"){ #Simulations generated when sampling=="USE"
      a = matrix(NA, nrow=nsites, ncol=9) #Create availability matrix
      y = matrix(NA, nrow=nsites, ncol=9) #Create observation matrix
      z = matrix(NA, nrow=nsites, ncol=9) #Create use matrix
      z[,1] = rbinom(n=nsites, size=1, prob=psi0) #Simulate initial site use, which
remains constant for 3 sampling periods
    }
  }
}

```

```

    z[,2] = z[,3] = z[,1]
    z[,4] = rbinom(n=nsites, size=1, prob=z[,1]*(1-eps0)) + rbinom(n=nsites, size=1,
prob=((z[,1]-1)^2)*gamma0) #Simulate changes in site use between first and second
primary periods.
    z[,5] = z[,6] = z[,4]
    z[,7] = rbinom(n=nsites, size=1, prob=z[,4]*(1-eps0)) + rbinom(n=nsites, size=1,
prob=((z[,4]-1)^2)*gamma0) #Simulate changes in site use between second and third
primary periods.
    z[,8] = z[,9] = z[,7]

    for(i in 1:9){#Simulate availability given use independently for each sampling
occasion
      a[,i] = rbinom(n=nsites, size=1, prob=z[,i]*Pa)
    }
    for(i in 1:9){#Simulate detection given availability
      y[,i] = rbinom(n=nsites, size=1, prob=a[,i]*Pd)
    }
  }

  if(sampling=="OCCUPANCY"){ #Simulations generated when sampling=="OCCUPANCY"
    a = matrix(NA, nrow=nsites, ncol=9) #Create availability matrix
    y = matrix(NA, nrow=nsites, ncol=9) #Create observation matrix
    z = matrix(NA, nrow=nsites, ncol=9) #Create use matrix
    z[,1] = rbinom(n=nsites, size=1, prob=psi0) #Simulate initial site use, which
remains constant for 3 sampling periods
    z[,2] = z[,3] = z[,1]
    z[,4] = rbinom(n=nsites, size=1, prob=z[,1]*(1-eps0)) + rbinom(n=nsites, size=1,
prob=((z[,1]-1)^2)*gamma0)#Simulate changes in site use between first and second
primary periods.
    z[,5] = z[,6] = z[,4]
    z[,7] = rbinom(n=nsites, size=1, prob=z[,4]*(1-eps0)) + rbinom(n=nsites, size=1,
prob=((z[,4]-1)^2)*gamma0)#Simulate changes in site use between second and third
primary periods.
    z[,8] = z[,9] = z[,7]

    for(i in c(1,4,7)){#Simulate availability given use such that availability can
change only between primary periods
      a[,i] = rbinom(n=nsites, size=1, prob=z[,i]*Pa)
    }
    a[,2] = a[,3] = a[,1]
    a[,5] = a[,6] = a[,4]
    a[,8] = a[,9] = a[,7]
    for(i in 1:9){#Simulate detection given availability
      y[,i] = rbinom(n=nsites, size=1, prob=a[,i]*Pd)
    }
  }

  #Construct unmarked dataframes for fitting closed and open occupancy models
  closed = unmarkedFrameOccu(y=y)
  open = unmarkedMultFrame(y=y, numPrimary=3)

  #Fit closed and open occupancy models
  try({closed.test = occu(~1~1, closed)}, silent=T)
  try({open.test = colext(~1,~1,~1,~1, open)}, silent=T)

  #Provide starting values for parameters, only if necessary
  if(exists("closed.test")==F){
    try({closed.test = occu(~1~1, closed, starts=c(qlogis(psi0), qlogis(Pa*Pd))))}
  }
  if(exists("open.test")==F){
    try({open.test = colext(~1,~1,~1,~1, open, starts=c(qlogis(psi0), 0, 0,
qlogis(Pa*Pd))})}
  }
}

#Save parameter estimates from closed and open occupancy models
try({data.summ$open.col[j] = plogis(coef(open.test)[2])}, silent=T)
try({data.summ$open.ext[j] = plogis(coef(open.test)[3])}, silent=T)
try({data.summ$open.psi[j] = plogis(coef(open.test)[1])}, silent=T)
try({data.summ$open.p[j] = plogis(coef(open.test)[4])}, silent=T)

```

```

try({data.summ$closed.psi[j] = plogis(coef(closed.test)[1])}, silent=T)
try({data.summ$closed.p[j] = plogis(coef(closed.test)[2])}, silent=T)

#Calculate likelihood ratio test statistic
try({data.summ$tstat[j] = LRT(closed.test, open.test)[1,1]}, silent=T)

#Find delta value required to appropriately calculate chi-square
#mixing proportions for comparison with the test statistic (Self & Liang 1987)
try({I1 = open.test@opt$hessian[2:3,2:3]}, silent=T)
try({I2 = open.test@opt$hessian[2:3,c(1,4)]}, silent=T)
try({I3 = solve(open.test@opt$hessian[c(1,4),c(1,4)])}, silent=T)
try({I4 = open.test@opt$hessian[c(1,4),2:3]}, silent=T)
try({sub.hessian = I1-I2%*%I3%*%I4}, silent=T)

#Delta is set at 0.5 when it cannot be appropriately calculated, as this
#minimizes the probability of rejecting H0.
try({data.summ$delta[j] =
min(acos(sub.hessian[1,2]/sqrt(sub.hessian[1,1]*sub.hessian[2,2]))/(2*pi), 0.5,
na.rm=T)}, silent=T)

#Calculate p-value
try({data.summ$LRT[j] = (0.5-data.summ$delta[j])*0 + 0.5*(1-
pchisq(data.summ$tstat[j],1)) + data.summ$delta[j]*(1-pchisq(data.summ$tstat[j], 2))},
silent=T)

#Identify non-invertible Hessian matrices
try({data.summ$invert.closed.hess[j] =
ifelse(min(diag(closed.test@opt$hessian))<0, 0, 1)}, silent=T)
try({data.summ$invert.open.hess[j] = ifelse(min(diag(open.test@opt$hessian))<0, 0,
1)}, silent=T)

  rm(closed, open, closed.test, open.test, sub.hessian, I1, I2, I3, I4)
}

#Record simulation parameters
data.summ$psi0 = psi0
data.summ$gamma0 = gamma0
data.summ$eps0 = eps0
data.summ$Pa = Pa
data.summ$Pd = Pd
data.summ$sampling = sampling

data.summ$open.selected = ifelse(data.summ$LRT < 0.05, 1, 0)

#Eliminate parameter estimates from models with non-invertible Hessian matrices
data.summ$closed.psi = ifelse(data.summ$invert.closed.hess==0, NA,
data.summ$closed.psi)
data.summ$closed.p = ifelse(data.summ$invert.closed.hess==0, NA, data.summ$closed.p)
data.summ$open.psi = ifelse(data.summ$invert.open.hess==0, NA, data.summ$open.psi)
data.summ$open.p = ifelse(data.summ$invert.open.hess==0, NA, data.summ$open.p)
data.summ$open.col = ifelse(data.summ$invert.open.hess==0, NA, data.summ$open.col)
data.summ$open.ext = ifelse(data.summ$invert.open.hess==0, NA, data.summ$open.ext)

#Calculate bias in colonization and extinction rates
data.summ$col.bias = data.summ$open.col - data.summ$gamma0
data.summ$ext.bias = data.summ$open.ext - data.summ$eps0

#Summarize data from all simulations
tmp = aggregate(cbind(closed.psi, closed.p, open.psi, open.p, open.col, open.ext,
col.bias, ext.bias)~sampling+psi0+Pa+Pd+gamma0+eps0, data=data.summ, FUN="mean")
colnames(tmp) = c("sampling", "psi0", "Pa", "Pd", "gamma0", "eps0",
"closed.psi.mean", "closed.p.mean", "open.psi.mean", "open.p.mean", "open.col.mean",
"open.ext.mean", "col.bias", "ext.bias")
tmp2 = aggregate(cbind(closed.psi, closed.p, open.psi, open.p, open.col,
open.ext)~sampling+psi0+Pa+Pd+gamma0+eps0, data=data.summ, FUN="var")
colnames(tmp2) = c("sampling", "psi0", "Pa", "Pd", "gamma0", "eps0",
"closed.psi.var", "closed.p.var", "open.psi.var", "open.p.var", "open.col.var",
"open.ext.var")

```

```
results = merge(tmp, tmp2, by=c("sampling", "psi0", "Pa", "Pd", "gamma0", "eps0"))
results$perc.open = 100*(sum(data.summ$open.selected,
na.rm=T)/sum(!is.na(data.summ$open.selected)))
  return(results)
}

#Note that simulating and analyzing 1000 presence/absence datasets with a
#given set of parameters took approximately 30 minutes.
example1 = pres.abs.sim(psi0=0.7, eps0=0, Pa=0.5, Pd=0.5, sampling="USE", nsites=500,
nsim=100)
example2 = pres.abs.sim(psi0=0.7, eps0=0, Pa=0.5, Pd=0.5, sampling="OCCUPANCY",
nsites=500, nsim=100)
```



## **APPENDIX C: A DYNAMIC, MULTI-SCALE OCCUPANCY MODEL FOR ESTIMATING BOTH TEMPORARY EMIGRATION AND DYNAMIC DISTRIBUTION RATES FROM REPEATED PRESENCE-ABSENCE SURVEYS**

### **Sampling Situation**

Consider a situation in which there are  $N$  spatially discrete sampling sites. Site use may change over time as a function of distribution dynamics (hereafter *dynamics*), defined as distributional shifts resulting from dispersal or other demographic processes that lead to unused sites becoming used, or vice versa. Additionally, instantaneous occupancy may change as a function of either dynamics or temporary emigration. There must be intervals within the study during which it is reasonable to assume that the occupancy state of the site is closed to both temporary emigration and dynamics. Further, there must be intervals during which it is reasonable to assume that occupancy changes in a non-Markovian way due to temporary emigration, but site use is closed to changes resulting from dynamics. That is, temporary changes in occupancy occur over finer time scales than changes in site use.

The sampling scheme can be seen as an extension of Pollock's robust sampling design (Pollock 1982) that includes tertiary sampling periods. Sampling consists of  $P$  primary sampling periods between which site use can change as a function of dynamics (*e.g.* consecutive breeding seasons, or even consecutive weeks for short-lived species). Within each primary period, there are  $S$  secondary sampling periods, between which temporary emigration may occur, but not dynamics. These secondary periods are spaced in time such that the probability one or more individuals are available for sampling is independent during each secondary period. Finally, within each secondary period there are  $T$  tertiary sampling periods between which the occupancy state of the site does not change. MacKenzie & Royle (2005) provide useful suggestions for spacing repeated samples to ensure complete site closure, which may include using multiple

observers or detection methods simultaneously. This results in a study in which there are  $P*S*T$  samples of presence/absence of the species at each site.

During each sampling occasion, the researcher uses an appropriate sampling method, and the species is detected (1) or not (0). We assume that the species is not falsely detected when completely absent from the site, and consider each detection within a secondary sampling period an independent observation. A non-detection event may occur either because 1) the species does not use the site, 2) it uses the site but has temporarily emigrated, or 3) it uses the site and was available for sampling, but was not detected by the observation method. For each site, the resulting detection history  $\mathbf{Y}_i$  will be a vector of 0s and 1s of length  $P*S*T$ . Under this sampling scenario, we can use likelihood theory to estimate the initial probability of site use ( $\psi_0$ ), probability of availability given use ( $p_a$ ), the probability of detection given availability ( $p_d$ ), the probability of a death or emigration event ( $\epsilon_0$ ), and the probability of a birth or immigration event ( $\gamma_0$ ).

### Statistical Model and Likelihood

We define  $\Pr(\mathbf{Y}_i)$  as the probability of the observed detection history at site  $i$ . Let  $y_{ijkl} = 1$  if the species is detected at site  $i$  in tertiary period  $l$  of secondary period  $k$ , in primary period  $j$ , and 0 otherwise. Further, let  $y_{ijk.} = 1$  if the species is detected during any tertiary period at site  $i$  in secondary period  $k$  of primary period  $j$ . Lastly, let  $y_{ij..} = 1$  if the species is detected during any sampling occasion at site  $i$  in primary period  $j$ .

It is easiest to express  $\Pr(\mathbf{Y}_i)$  using matrix notation. Let  $\boldsymbol{\psi}_i$  be a  $1 \times 2$  matrix

$$\boldsymbol{\psi}_{0,i1} = [\psi_{0,i1} \quad (1 - \psi_{0,i1})I(y_{i1..} = 0)]$$

Here we use the indicator function  $I()$  to specify that the site cannot be unused in primary period 1 if it was detected at least once during that primary period. Further, we define  $\phi_{ij}$  as a  $2 \times 2$  matrix of use transition probabilities between primary periods

$$\phi_{ij} = \begin{bmatrix} (1 - \varepsilon_{0,ij}) & \varepsilon_{0,ij}I(y_{ij..} = 0) \\ \gamma_{0,ij}I(y_{ij-1..} = 0) & (1 - \gamma_{0,ij})I(y_{ij-1..} = y_{ij..} = 0) \end{bmatrix}$$

where the probability a site becomes unused (death/emigration) between primary periods  $j-1$  and  $j$  ( $\varepsilon_{0,ij}$ ) is 0 if it was ever detected in primary period  $j$ , and the probability a site becomes used (birth/immigration event,  $\gamma_{0,ij}$ ) is 0 if it was ever detected in primary period  $j-1$ . Similarly, the probability a site is not colonized ( $1-\gamma_{0,ij}$ ) is 0 if the species was either detected in either of the primary periods  $j-1$  or  $j$ .

Within a primary period, we define  $\mathbf{pa}_{ijk}$  for each secondary period as a  $2 \times 3$  availability matrix

$$\mathbf{pa}_{ijk} = \begin{bmatrix} pa_{ijk} & (1 - pa_{ijk})I(y_{ijk.} = 0) & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

where again, the probability an individual is unavailable (*i.e.*, the site is not occupied) is 0 if it was detected at least once during that secondary period. We then define  $\mathbf{pd}_{ijk}$  as a  $3 \times 2$  detection matrix

$$\mathbf{pd}_{ijk} = \begin{bmatrix} \prod_{l=1}^T (pd_{ijkl})^{y_{ijkl}} (1 - pd_{ijkl})^{1-y_{ijkl}} & 0 \\ 1 & 0 \\ 0 & 1 \end{bmatrix}$$

If we allow  $\mathbf{D}_{ij}$  to be a  $2 \times 2$  overall detection matrix such that

$$\mathbf{D}_{ij} = \prod_{k=1}^S \mathbf{pa}_{ijk} \mathbf{pd}_{ijk}$$

then the probability of the detection history  $\mathbf{Y}_i$  at any given site is

$$\Pr(\mathbf{Y}_i) = \left( \boldsymbol{\psi}_{0,i1} \mathbf{D}_{i1} \prod_{j=2}^P \boldsymbol{\phi}_{ij} \mathbf{D}_{ij} \right) \begin{bmatrix} 1 \\ 1 \end{bmatrix}$$

and

$$L(\boldsymbol{\psi}, pa, pd, \boldsymbol{\varepsilon}, \boldsymbol{\gamma} | \mathbf{Y}_1, \mathbf{Y}_2, \dots, \mathbf{Y}_N) = \prod_{i=1}^N \Pr(\mathbf{Y}_i)$$

We can use this equation to generate estimates of  $\psi_0$ ,  $pa$ ,  $pd$ ,  $\varepsilon_0$ , and  $\gamma_0$  by finding the values that maximize this likelihood given the observed detection histories. While the model directly estimates probability of site use in the first primary period, probability of use in subsequent primary periods can be calculated as

$$\psi_{0,ij} = \psi_{0,ij-1}(1 - \varepsilon_{0,ij}) + (1 - \psi_{0,ij-1})\gamma_{0,ij}$$

Further, the probability of occupancy at any given moment may be calculated as

$$\psi_{ijk} = \psi_{0,ij} pa_{ijk}$$

and the temporary emigration rate as

$$TE_{ijk} = (1 - pa_{ijk})$$

### Model Extensions

It is easy to envision a situation in which the researcher might be interested in the effects of covariates on the model parameters. For instance, the researcher may be interested in understanding the effects of habitat features on site occupancy, use, or dynamic rates, or the effects of survey covariates on detection probability. The model can be extended to account for

covariate effects on any parameter using the logistic model. For any parameter of interest  $\theta$ , with a matrix of covariate information  $\mathbf{X}$ , and logistic regression coefficients to be estimated  $\boldsymbol{\beta}$ ,

$$\theta = \frac{\exp(\mathbf{X}\boldsymbol{\beta})}{1 + \exp(\mathbf{X}\boldsymbol{\beta})}$$

### **Simulation Study**

We simulated and analyzed datasets based on the sampling situation described above to evaluate the model's performance under different scenarios. We used values of  $N = 200$  or  $50$ ,  $\psi_0 = 0.3$  or  $0.7$ ,  $p_a = 0.5$  or  $0.8$ ,  $p_d = 0.5$  or  $0.8$ , and  $\varepsilon_0 = 0.2$  or  $0.4$ . In all simulations  $\gamma_0$  was calculated so the expected occupancy rate remained constant. All simulations included 3 primary, 3 secondary, and 3 tertiary sampling periods. We thus considered 32 scenarios, each repeated 1000 times. In each scenario we compared parameter estimates from the fitted models with the values used to generate the data. We subtracted the simulation parameter from each estimate and averaged these values over all 1000 datasets to estimate bias. Variance was calculated among the estimates themselves, and mean squared error (MSE) as the sum of the variance and the squared bias. Full data simulation and analysis code is provided below.

### **Simulation Results**

This dynamic, multi-scale occupancy model performed very well under our limited range of simulation conditions (Table C1). Both the bias and variance of all parameters tended to be larger when sample sizes were smaller ( $N = 50$ ), particularly for the dynamic parameters ( $\gamma_0$  and  $\varepsilon_0$ ). Nonetheless, these results indicate that this model may be useful for researchers interested in quantifying rates of both dynamics and temporary emigration simultaneously.



## R Code for Simulation and Analysis of Dynamic, Multi-Scale Occupancy Models

```
#####
##
#This function simulates and analyzes presence/absence datasets as described in
#Appendix C. All datasets generated mimic those collected using an extended
#version of Pollock's robust sampling design (Pollock 1982) that includes tertiary
#3 tertiary sampling periods nested within each of 3 secondary sampling periods
#nested within each of 3 primary sampling periods. The function allows the user
#to specify

#psi0 = probability of initial site use
#Pa = the probability that at least one individual using the site is available for
detection
#Pd = the probability at least one available individual is detected
#eps0 = the probability a used site becomes unused during a subsequent primary period
#nsites = the number of sampled sites
#nsim = the number of datasets to simulate and analyze

#Note that gamma0 is the probability an unused site becomes used during a subsequent
#primary period and that gamma0 is calculated such that the expected value of psi0
remains
#constant during all primary periods.

#The function returns parameter estimates for psi0, pa, pd, eps0, and gamma0
#on the logit scale. Use plogis() to view the estimates on the original
#probability scale
#####
##

Dyn.MS.Occ.Sim =function(psi0=NULL, Pa=NULL, Pd=NULL, eps0=NULL, nsites=NULL,
nsim=NULL){
  gamma0 = (psi0*eps0)/(1-psi0)

  #Create table for results
  results = data.frame(matrix(nrow=nsim, ncol=5))
  colnames(results) = c("psi0", "pa", "pd", "eps0", "gamma0")

  #Simulate detection history
  for(a in 1:nsim){
    z = matrix(NA, nrow=nsites, ncol=3)
    z[,1] = rbinom(n=nsites, size=1, prob=psi0)
    z[,2] = rbinom(n=nsites, size=1, prob=z[,1]*(1-eps0)) + rbinom(n=nsites, size=1,
prob=((z[,1]-1)^2)*gamma0)
    z[,3] = rbinom(n=nsites, size=1, prob=z[,2]*(1-eps0)) + rbinom(n=nsites, size=1,
prob=((z[,2]-1)^2)*gamma0)

    y = matrix(NA, nrow=nsites, ncol=9)
    for(i in 1:3){y[,i] = rbinom(n=nsites, size=1, prob=z[,1]*Pa)}
    for(i in 4:6){y[,i] = rbinom(n=nsites, size=1, prob=z[,2]*Pa)}
    for(i in 7:9){y[,i] = rbinom(n=nsites, size=1, prob=z[,3]*Pa)}

    data = matrix(NA, nrow=nsites, ncol=27)
    for(i in 1:3){data[,i] = rbinom(n=nsites, size=1, prob=y[,1]*Pd)}
    for(i in 4:6){data[,i] = rbinom(n=nsites, size=1, prob=y[,2]*Pd)}
    for(i in 7:9){data[,i] = rbinom(n=nsites, size=1, prob=y[,3]*Pd)}
    for(i in 10:12){data[,i] = rbinom(n=nsites, size=1, prob=y[,4]*Pd)}
    for(i in 13:15){data[,i] = rbinom(n=nsites, size=1, prob=y[,5]*Pd)}
    for(i in 16:18){data[,i] = rbinom(n=nsites, size=1, prob=y[,6]*Pd)}
    for(i in 19:21){data[,i] = rbinom(n=nsites, size=1, prob=y[,7]*Pd)}
    for(i in 22:24){data[,i] = rbinom(n=nsites, size=1, prob=y[,8]*Pd)}
    for(i in 25:27){data[,i] = rbinom(n=nsites, size=1, prob=y[,9]*Pd)}

    #Identify sites where species was detected at least once during
    #each primary period
    Y.. = cbind(apply(data[,1:9], 1, max), apply(data[,10:18], 1, max),
      apply(data[,19:27], 1, max))
  }
}
```

```

#Identify sites where species was detected at least once during
#each secondary period
Y. = cbind(apply(data[,1:3], 1, max), apply(data[,4:6], 1, max),
          apply(data[,7:9], 1, max), apply(data[,10:12], 1, max),
          apply(data[,13:15], 1, max), apply(data[,16:18], 1, max),
          apply(data[,19:21], 1, max), apply(data[,22:24], 1, max),
          apply(data[,25:27], 1, max))

i = nsites; j = 3; k = 3; l = 3

#Likelihood
nll = function(params){
  psi = plogis(params[1])
  pa = plogis(params[2])
  pd = plogis(params[3])
  eps0 = plogis(params[4])
  gamma0 = plogis(params[5])

  occ = matrix(NA, nrow=i, ncol=2)
  occ[,1] = psi
  occ[,2] = ifelse(Y..[,1]==1, 0, 1-psi)

  av = array(NA, c(2,3,k,j,i))
  av[2,,,,] = c(0,0,1)
  av[1,c(1,3),,,] = c(pa, 0)
  for(m in 1:i){
    av[1,2,1,1,m] = ifelse(Y.[m,1]==1, 0, 1-pa)
    av[1,2,2,1,m] = ifelse(Y.[m,2]==1, 0, 1-pa)
    av[1,2,3,1,m] = ifelse(Y.[m,3]==1, 0, 1-pa)
    av[1,2,1,2,m] = ifelse(Y.[m,4]==1, 0, 1-pa)
    av[1,2,2,2,m] = ifelse(Y.[m,5]==1, 0, 1-pa)
    av[1,2,3,2,m] = ifelse(Y.[m,6]==1, 0, 1-pa)
    av[1,2,1,3,m] = ifelse(Y.[m,7]==1, 0, 1-pa)
    av[1,2,2,3,m] = ifelse(Y.[m,8]==1, 0, 1-pa)
    av[1,2,3,3,m] = ifelse(Y.[m,9]==1, 0, 1-pa)
  }

  det = array(NA, c(3,2,k,j,i))
  det[2,,,,] = c(0,0,1)
  det[2:3,1,,,] = c(1,0)
  for(m in 1:i){
    det[1,1,1,1,m] = (data[m,1]*pd+(1-data[m,1])*(1-pd))*(data[m,2]*pd+(1-
data[m,2])*(1-pd))*(data[m,3]*pd+(1-data[m,3])*(1-pd))
    det[1,1,2,1,m] = (data[m,4]*pd+(1-data[m,4])*(1-pd))*(data[m,5]*pd+(1-
data[m,5])*(1-pd))*(data[m,6]*pd+(1-data[m,6])*(1-pd))
    det[1,1,3,1,m] = (data[m,7]*pd+(1-data[m,7])*(1-pd))*(data[m,8]*pd+(1-
data[m,8])*(1-pd))*(data[m,9]*pd+(1-data[m,9])*(1-pd))
    det[1,1,1,2,m] = (data[m,10]*pd+(1-data[m,10])*(1-pd))*(data[m,11]*pd+(1-
data[m,11])*(1-pd))*(data[m,12]*pd+(1-data[m,12])*(1-pd))
    det[1,1,2,2,m] = (data[m,13]*pd+(1-data[m,13])*(1-pd))*(data[m,14]*pd+(1-
data[m,14])*(1-pd))*(data[m,15]*pd+(1-data[m,15])*(1-pd))
    det[1,1,3,2,m] = (data[m,16]*pd+(1-data[m,16])*(1-pd))*(data[m,17]*pd+(1-
data[m,17])*(1-pd))*(data[m,18]*pd+(1-data[m,18])*(1-pd))
    det[1,1,1,3,m] = (data[m,19]*pd+(1-data[m,19])*(1-pd))*(data[m,20]*pd+(1-
data[m,20])*(1-pd))*(data[m,21]*pd+(1-data[m,21])*(1-pd))
    det[1,1,2,3,m] = (data[m,22]*pd+(1-data[m,22])*(1-pd))*(data[m,23]*pd+(1-
data[m,23])*(1-pd))*(data[m,24]*pd+(1-data[m,24])*(1-pd))
    det[1,1,3,3,m] = (data[m,25]*pd+(1-data[m,25])*(1-pd))*(data[m,26]*pd+(1-
data[m,26])*(1-pd))*(data[m,27]*pd+(1-data[m,27])*(1-pd))
  }

  trans = array(NA, c(2,2,j-1,i))
  trans[1,1,,] = 1-eps0
  for(m in 1:i){
    trans[1,2,1,m] = ifelse(Y..[m,2]==1, 0, eps0)
    trans[1,2,2,m] = ifelse(Y..[m,3]==1, 0, eps0)
    trans[2,1,1,m] = ifelse(Y..[m,1]==1, 0, gamma0)
    trans[2,1,2,m] = ifelse(Y..[m,2]==1, 0, gamma0)
    trans[2,2,1,m] = ifelse(Y..[m,1]==1 | Y..[m,2]==1, 0, 1-gamma0)
  }
}

```



```

    trans[2,2,2,m] = ifelse(Y..[m,2]==1 | Y..[m,3]==1, 0, 1-gamma0)
  }
  tmp = rep(NA, nsites)
  for(m in 1:nsites){
    tmp[m] =
occ[m,]%%av[, ,1,1,m]%%det[, ,1,1,m]%%av[, ,2,1,m]%%det[, ,2,1,m]%%av[, ,3,1,m]%%det[
, ,3,1,m]%%
trans[, ,1,m]%%av[, ,1,2,m]%%det[, ,1,2,m]%%av[, ,2,2,m]%%det[, ,2,2,m]%%av[, ,3,2,m]%%
%det[, ,3,2,m]%%
trans[, ,2,m]%%av[, ,1,3,m]%%det[, ,1,3,m]%%av[, ,2,3,m]%%det[, ,2,3,m]%%av[, ,3,3,m]%%
%det[, ,3,3,m]%%c(1,1)
  }
  -sum(log(tmp))
}

#Maximize the likelihood and record the results
try({test = optim(c(0,0,0,0,0), nll, method="BFGS")}, silent=T)
try({results[a,] = test$par}, silent=T)

  rm(test)
}
return(list(results))
}

example1 = Dyn.MS.Occ.Sim(psi0=0.3, Pa=0.5, Pd=0.5, eps0=0.2, nsites=50, nsim=10)

```

## APPENDIX D: COMMUNITY OCCUPANCY MODEL SPECIFICATION

Below we present R code for importing three data files (BirdCounts.csv, HabitatVars.csv, and SurveyVars.csv), and formatting those data for analysis in our community occupancy model. We then provide the full specification of the hierarchical model, and associated R code for running the model in JAGS (Plummer 2003) using the R package jagsUI v 1.4.2 (Kellner 2016). Though we also fit a model that included an interaction term between forest patch size and forest amount, the model presented excludes this term, because it was non-significant for 98% of species examined.

In order to assess model fit, we used a Bayesian p-value approach (Gelman et al. 1996, Zipkin et al. 2009, Kéry and Royle 2016). At each iteration of the MCMC chain, we calculated a discrepancy statistic ( $D$ ) as the sum of the squared differences between each observed data point ( $y_{i,j,k,l,m}$ , below), and its expected value ( $E_{i,j,k,l,m}$ ) under the fitted model. We then simulated a unique dataset based on the fitted model ( $y_{sim}$ ) and calculated the same discrepancy statistic ( $D_{sim}$ ) for this dataset as well. Thus, the posterior distribution of  $D_{sim}$  provides a reference distribution against which to compare  $D$ . We calculated our p-value as the proportion of the time (out of 6000 retained MCMC iterations)  $D$  was larger than  $D_{sim}$ .

### R and JAGS Code

```
#Load jagsUI package
library(jagsUI)

#Import data and create a unique line for each combination of year, patch, point,
#survey, and species

birds = read.csv("BirdCounts.csv")
habitat = read.csv("HabitatVars.csv")
data = merge(birds, habitat, by=c("num.patch", "num.point", "year", "num.year"))
tmp1 = expand.grid("num.year"=unique(data$num.year),
  "num.patch"=unique(data$num.patch), "num.point" = unique(data$num.point),
  "surveyorder"=unique(data$surveyorder), "num.species"=unique(data$num.species))
```

```

data = merge(tmp1, data, by=c("num.year", "num.patch", "num.point", "surveyorder",
  "num.species"), all=T)

#Create arrays for edge distance, patch size, and habitat amount.
tmp1 = unique(data[, c("num.patch", "num.point", "edge.dist", "amount.prop",
  "Area_ha")])
tmp1$amount.prop = scale(tmp1$amount.prop, center=T, scale=T)
tmp1$edge.dist = scale(tmp1$edge.dist, center=T, scale=T)
tmp1$Area_ha = scale(log(tmp1$Area_ha), center=T, scale=T)
tmp1 = tmp1[order(tmp1$num.point, tmp1$num.patch),]
edge = array(tmp1$edge.dist, c(202, 10))
amount = array(tmp1$amount.prop, c(202, 10))
size = array(tmp1$Area_ha, c(202, 10))

#Conduct principal components analysis on local vegetation variables, and create
#arrays for PC1, PC2, PC3, and tree basal area
tmp1 = unique(data[which(!is.na(data$shrubtotal)),c("num.patch", "num.point",
  "num.year", "shrubtotal", "tottrees", "canopy_vvt", "leafmean", "vfd5m")])
tmp1$shrubtotal = scale(tmp1$shrubtotal, center=T, scale=T)
tmp1$tottrees = scale(tmp1$tottrees, center=T, scale=T)
tmp1$canopy_vvt = scale(tmp1$canopy_vvt, center=T, scale=T)
tmp1$vfd5m = scale(tmp1$vfd5m, center=T, scale=T)
tmp1$leafmean = scale(tmp1$leafmean, center=T, scale=T)

tmp2 = prcomp(~tottrees+shrubtotal+canopy_vvt+vfd5m+leafmean, data=tmp1)
tmp1 = cbind(tmp1, tmp2$x)

tmp2 = expand.grid("num.year"=c(1:3), "num.point"=c(1:10), "num.patch"=c(1:202))
tmp1 = merge(tmp1, tmp2, by=c("num.year", "num.point", "num.patch"), all=T)
tmp1 = tmp1[order(tmp1$num.year, tmp1$num.point, tmp1$num.patch),]

pc1 = array(tmp1$PC1, c(202, 10, 3))
pc2 = array(tmp1$PC2, c(202, 10, 3))
pc3 = array(tmp1$PC3, c(202, 10, 3))
trees = array(tmp1$tottrees, c(202, 10, 3))

#Create array for response variable
data$count = ifelse(data$count > 0, 1, 0)
data = data[order(data$surveyorder, data$num.year, data$num.point, data$num.patch,
  data$num.species),]
y = array(data$count, c(52,202,10,3,3))

#Create vector for number of sampling sites (points) in each patch
tmp1 = data[which(!is.na(data$count) & data$num.year==1),]
tmp1 = aggregate(num.point ~ num.patch, data=tmp1, FUN="max")
tmp1 = tmp1[order(tmp1$num.patch),]
nsites = tmp1$num.point

#Create vector for group membership of each species
tmp1 = unique(data[-which(is.na(data$num.group)),c("num.species", "num.group")])
tmp1 = tmp1[order(tmp1$num.species),]
group = tmp1$num.group

#Read in Julian dates and create array
tmp = read.csv("SurveyVars.csv")
tmp$julian = scale(tmp$julian, center=T, scale=T)
tmp2 = expand.grid("num.year"=unique(tmp$num.year), "num.patch"=unique(tmp$num.patch),
  "num.point" = unique(tmp$num.point), "surveyorder"=unique(tmp$surveyorder))
tmp = merge(tmp, tmp2, by=c("num.year", "num.patch", "num.point", "surveyorder"),
  all=T)
tmp = tmp[order(tmp$surveyorder, tmp$num.year, tmp$num.point, tmp$num.patch),]
julian = array(tmp$julian, c(202, 10, 3, 3))

#Model specification
sink("Model.txt")
cat("model{

  mu.alpha0 ~ dnorm(0, 0.001)
  sigma.alpha0 ~ dunif(0, 5)

```

```

tau.alpha0 <- 1/(sigma.alpha0*sigma.alpha0)

mu.alpha1 ~ dnorm(0, 0.001)
sigma.alpha1 ~ dunif(0, 5)
tau.alpha1 <- 1/(sigma.alpha1*sigma.alpha1)

mu.alpha2 ~ dnorm(0, 0.001)
sigma.alpha2 ~ dunif(0, 5)
tau.alpha2 <- 1/(sigma.alpha2*sigma.alpha2)

for(h in 1:ngroups){
  sigma.patch[h] ~ dunif(0, 5)
  tau.patch[h] <- 1/(sigma.patch[h]*sigma.patch[h])

  mu.beta0[h] ~ dnorm(0, 0.001)
  sigma.beta0[h] ~ dunif(0, 5)
  tau.beta0[h] <- 1/(sigma.beta0[h]*sigma.beta0[h])

  mu.beta1[h] ~ dnorm(0, 0.001)
  sigma.beta1[h] ~ dunif(0, 5)
  tau.beta1[h] <- 1/(sigma.beta1[h]*sigma.beta1[h])

  mu.beta2[h] ~ dnorm(0, 0.001)
  sigma.beta2[h] ~ dunif(0, 5)
  tau.beta2[h] <- 1/(sigma.beta2[h]*sigma.beta2[h])

  mu.beta3[h] ~ dnorm(0, 0.001)
  sigma.beta3[h] ~ dunif(0, 5)
  tau.beta3[h] <- 1/(sigma.beta3[h]*sigma.beta3[h])

  mu.beta4[h] ~ dnorm(0, 0.001)
  sigma.beta4[h] ~ dunif(0, 5)
  tau.beta4[h] <- 1/(sigma.beta4[h]*sigma.beta4[h])

  mu.beta5[h] ~ dnorm(0, 0.001)
  sigma.beta5[h] ~ dunif(0, 5)
  tau.beta5[h] <- 1/(sigma.beta5[h]*sigma.beta5[h])

  mu.beta6[h] ~ dnorm(0, 0.001)
  sigma.beta6[h] ~ dunif(0, 5)
  tau.beta6[h] <- 1/(sigma.beta6[h]*sigma.beta6[h])

  mu.gamma0[h] ~ dnorm(0, 0.001)
  sigma.gamma0[h] ~ dunif(0, 5)
  tau.gamma0[h] <- 1/(sigma.gamma0[h]*sigma.gamma0[h])

  mu.gamma1[h] ~ dnorm(0, 0.001)
  sigma.gamma1[h] ~ dunif(0, 5)
  tau.gamma1[h] <- 1/(sigma.gamma1[h]*sigma.gamma1[h])

  for(j in 1:npatch){
    for(l in 1:nyears){
      beta0.patch[h,j,l] ~ dnorm(0, tau.patch[h])
    }
  }
}

for(i in 1:nspecies){
  alpha0[i] ~ dnorm(mu.alpha0, tau.alpha0)
  alpha1[i] ~ dnorm(mu.alpha1, tau.alpha1)
  alpha2[i] ~ dnorm(mu.alpha2, tau.alpha2)
  beta0[i] ~ dnorm(mu.beta0[group[i]], tau.beta0[group[i]])
  beta1[i] ~ dnorm(mu.beta1[group[i]], tau.beta1[group[i]])
  beta2[i] ~ dnorm(mu.beta2[group[i]], tau.beta2[group[i]])
  beta3[i] ~ dnorm(mu.beta3[group[i]], tau.beta3[group[i]])
  beta4[i] ~ dnorm(mu.beta4[group[i]], tau.beta4[group[i]])
  beta5[i] ~ dnorm(mu.beta5[group[i]], tau.beta5[group[i]])
  beta6[i] ~ dnorm(mu.beta6[group[i]], tau.beta6[group[i]])
}

```

```

gamma0[i] ~ dnorm(mu.gamma0[group[i]], tau.gamma0[group[i]])
gamma1[i] ~ dnorm(mu.gamma1[group[i]], tau.gamma1[group[i]])

for(j in 1:npatch){
  for(k in 1:nsites[j]){
    Z[i,j,k,1] ~ dbern(psi[i,j,k,1])
    logit(psi[i,j,k,1]) <- beta0[i] + beta0.patch[group[i], j, 1] +
      beta1[i]*pc1[j,k,1] + beta2[i]*pc2[j,k,1] +
      beta3[i]*pc3[j,k,1] + beta4[i]*edge[j,k] + beta5[i]*size[j,k] +
      beta6[i]*amount[j,k]

    for(l in 2:nyears){
      Z[i,j,k,l] ~ dbern(psi[i,j,k,l])
      logit(psi[i,j,k,l]) <- gamma0[i] + gamma1[i]*Z[i,j,k,l-1] +
        beta0.patch[group[i], j, l] +
        beta1[i]*pc1[j,k,l] + beta2[i]*pc2[j,k,l] + beta3[i]*pc3[j,k,l] +
        beta4[i]*edge[j,k] + beta5[i]*size[j,k] + beta6[i]*amount[j,k]
    }

    for(l in 1:nyears){

      for(m in 1:nsurveys){
        logit(p[i,j,k,l,m]) <- alpha0[i] + alpha1[i]*julian[j,k,l,m] +
          alpha2[i]*trees[j,k,l]
        y[i,j,k,l,m] ~ dbern(Z[i,j,k,l]*p[i,j,k,l,m])

        ysim[i,j,k,l,m] ~ dbern(Z[i,j,k,l]*p[i,j,k,l,m])
        E[i,j,k,l,m] <- Z[i,j,k,l]*p[i,j,k,l,m]

        D[i,j,k,l,m] <- pow(y[i,j,k,l,m]-E[i,j,k,l,m],2)
        Dsim[i,j,k,l,m] <- pow(ysim[i,j,k,l,m]-E[i,j,k,l,m],2)
      }
      D.1[i,j,k,l] <- sum(D[i,j,k,l,1:nsurveys])
      Dsim.1[i,j,k,l] <- sum(Dsim[i,j,k,l,1:nsurveys])
    }
    D.2[i,j,k] <- sum(D.1[i,j,k,1:nyears])
    Dsim.2[i,j,k] <- sum(Dsim.1[i,j,k,1:nyears])
  }
  D.3[i,j] <- sum(D.2[i,j,1:nsites[j]])
  Dsim.3[i,j] <- sum(Dsim.2[i,j,1:nsites[j]])
}
D.4[i] <- sum(D.3[i,1:npatch])
Dsim.4[i] <- sum(Dsim.3[i,1:npatch])
}
fit.data <- sum(D.4[1:nspecies])
fit.sim <- sum(Dsim.4[1:nspecies])
bpv <- fit.data - fit.sim
}"; fill=T)
sink()

#Specify model values
win.data = list(y=y, nsites=nsites, nsurveys=3, nyears=3, npatch=202, nspecies=52,
  ngroups=3, group=group,size=size, amount=amount, edge=edge, pc1=pc1, pc2=pc2,
  pc3=pc3, julian=julian, trees=trees)

#Initial values for Z
Zst = aggregate(count~num.year+num.point+num.patch+num.species, data=data, FUN="max")
tmp1 = expand.grid("num.year"= c(1:3), "num.point" = c(1:10), "num.patch" = c(1:202),
  "num.species"=c(1:52))
Zst = merge(Zst, tmp1, by=c("num.year", "num.point", "num.patch", "num.species"),
  all=T)
Zst = Zst[order(Zst$num.year, Zst$num.point, Zst$num.patch, Zst$num.species),]
Zst = array(Zst$count, c(52, 202, 10, 3))

#Specify the remainder of the initial values
inits=function()list(Z=Zst, mu.alpha0=rnorm(1), sigma.alpha0=runif(1),
  mu.alpha1=rnorm(1), sigma.alpha1=runif(1), mu.alpha2=rnorm(1),
  sigma.alpha2=runif(1), mu.beta0=rnorm(3), sigma.beta0=runif(3), mu.beta1=rnorm(3),

```

```

sigma.beta1=runif(3), mu.beta2=rnorm(3), sigma.beta2=runif(3), mu.beta3=rnorm(3),
sigma.beta3=runif(3), mu.beta4=rnorm(3), sigma.beta4=runif(3), mu.beta5=rnorm(3),
sigma.beta5=runif(3), mu.beta6=rnorm(3), sigma.beta6=runif(3), mu.gamma0=rnorm(3),
sigma.gamma0=runif(3), mu.gamma1=rnorm(3), sigma.gamma1=runif(3),
sigma.patch=runif(3))

#Identify parameters to track
params=c("alpha0", "mu.alpha0", "sigma.alpha0", "alpha1", "mu.alpha1", "sigma.alpha1",
"alpha2", "mu.alpha2", "sigma.alpha2", "beta0", "mu.beta0", "sigma.beta0",
"gamma0", "mu.gamma0", "sigma.gamma0", "gamma1", "mu.gamma1", "sigma.gamma1",
"beta1", "mu.beta1", "sigma.beta1", "beta2", "mu.beta2", "sigma.beta2", "beta3",
"mu.beta3", "sigma.beta3", "beta4", "mu.beta4", "sigma.beta4", "beta5",
"mu.beta5", "sigma.beta5", "beta6", "mu.beta6", "sigma.beta6", "sigma.patch",
"fit.data", "fit.sim", "bpv")

#Chains, iterations, burnin, and thinning
nc=3; ni=400000; nb=200000; nt=100

#Submit model to JAGS. Remove "parallel=T" argument for non-parallel processing
out = jags(win.data, inits, params, "Model.txt", n.chains=nc, n.thin=nt, n.iter=ni,
n.burnin=nb, parallel=T)

```

