THE IMPACT OF TIMBER HARVEST ON WILDLIFE DISTRIBUTION PATTERNS AND
POPULATION VITAL RATES:
DOES STRUCTURAL RETENTION AMELIORATE THE NEGATIVE EFFECTS OF
CLEARCUTTING?

By

Clint R.V. Otto

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Fisheries and Wildlife
Ecology, Evolutionary Biology, and Behavior

2012

ABSTRACT

THE IMPACT OF TIMBER HARVEST ON WILDLIFE DISTRIBUTION PATTERNS AND
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Anthropogenic habitat degradation is a primary threat to global biodiversity. The overarching

theme of my dissertation is one of conservation-based research for reducing the impacts of

anthropogenic disturbances, specifically timber harvesting, on forest wildlife. Although the

primary objective of my dissertation is to assess the effectiveness of structural retention (*i.e.,*

canopy green trees and coarse woody debris) for conserving wildlife in harvested forests, it also

provides valuable insight to other areas of ecology and wildlife management.   Throughout my

dissertation I highlight the need to use design- and model-based approaches for minimizing bias

associated with the limited detectability of wildlife. Doing so allowed me to achieve stronger

inference when determining how wildlife interacts with their environment. For my first two

chapters I use species occupancy models and multiple sampling techniques to estimate detection

probabilities of forest-floor wildlife. These chapters demonstrate the need to incorporate species

detectability when comparing the effectiveness of different trapping methodologies.

Furthermore, these studies highlight the utility of power analyses for exploring study design

tradeoffs for research and monitoring programs. I used results from these chapters to develop a

strong sampling design for Chapter 5. In Chapter 3 I lead a detailed investigation into the

performance of wildlife occupancy models when model assumptions were openly violated.

Analyses from Chapter 3 revealed general sensitivity of estimates from single-season occupancy

models to violations of closure. This chapter highlights the importance of addressing the

population "closure" assumption and the impact of non-random organism movements in wildlife occupancy studies. I provide multiple solutions for minimizing bias associated with non-random changes in occupancy within a field season. For my final two chapters I assess the effectiveness of structural retention for conserving wildlife in harvested forests. Both studies represent an empirical evaluation of the Michigan Department of Natural Resources (MDNR) structural retention guidelines in harvested aspen stands. Results from Chapters 4 and 5 suggest that broad-scale conservation goals for forest songbirds and terrestrial salamanders will not be accomplished by simply retaining structure within individual harvest units. Rather, successful conservation efforts for these species may also require conservation of late-successional forests as part of managed landscapes. Future management objectives in aspen forests should reflect the value of clearcutting to early-successional and generalist bird species while recognizing that green-tree and coarse woody debris (CWD) retention, as observed here, did little to promote site occupancy of interior forest bird and terrestrial salamanders. However, if the management goal is to reduce mortality of local salamander populations following timber harvest, then my research suggests that implementing structural retention prescriptions is a viable management option. Results from Chapter 5 demonstrate that organismal pattern (occupancy) and process (survival) can function independently in response to habitat change, and thus emphasizes the importance joint-evaluation of these state variables when evaluating mitigation techniques presumed beneficial to wildlife.

ACKNOWLEDGEMENTS

I would also like to thank my friends and family. Whether in Michigan or abroad, past or present, I appreciate your support. I could have never succeeded without you. In particular, I want to thank the Greenways, Grandma Marcia, Emily Johnston, Andy Flies, Dan Linden, and Leslie Curren for helping with care of my children whenever Tammy and I needed a hand. I thank Gerard and Kim Fuehrer (*i.e.,* Papa and Nana) for their support throughout my dissertation and for nurturing my children during a lengthy 2011 field season. To my parents Dick and Pat (*i.e.,* Bopu and Grandma): the value system in which you have instilled has served me well throughout life. Thank you for your love and guidance. I thank my daughters Coralyn and Aurelia (*i.e.,* the Bumps) for giving me a new life perspective: Your Mother and I look forward to a lifetime of adventure, love, and learning with you. I am forever indebted to the undying support and sacrifice of my wife and friend, Tammy Otto. Words will never fully describe the sense of gratitude that I feel to my Babes.

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INTRODUCTION

Ecologists employ a systematic and objective system of inquiry to infer relationships between organisms and their environment. Although they strive to achieve "strong inference" in their research (Platt 1964), judicious ecologists recognize that research results are seldom clean: stochasticity and process variability are phenomenon that must be acknowledged, if not openly embraced. This requires ecologists, willingly or otherwise, to venture into the worlds of quantitative modeling, probability theory, statistical inference, and hypothesis development. Ecologists must be strategic in the development of their *a priori* research hypotheses, represent those hypotheses by statistical models, and carefully design a study, or studies, that will allow them to assess the evidence for these hypotheses, given the observed data.

The overarching theme of my dissertation is one of conservation-based research for understanding the impacts of anthropogenic disturbances, specifically timber harvesting, on forest wildlife. To the best of my ability, I have adopted scientific approaches that have been advocated by Chamberlin (1965), Platt (1964), and Anderson (2008), among others. All five of my dissertation chapters involve observational wildlife data, and hence possesses some degree of observation sampling error. I view the data for my dissertation as generated from two distinct processes: biological and observational. The biological process is of interest to most ecologists and conservation biologists. Examples include the effect of habitat alteration on a particular species or annual changes in population growth rate. However, biological reality is often obfuscated by observational sampling error, such that the true state of the study system is difficult to observe. For most ecologists, sampling error represents statistical "noise", which needs to be accounted for, so that biological reality may be viewed more clearly.

Detectability is a fundamental, and yet often overlooked, issue when modeling species distribution patterns. For example, a species may be present at a study site and yet go undetected during routine sampling events. For most animals, natural selection has favored traits that allow the organisms to conceal themselves within their environment. Thus, it is of no surprise to most field-savvy naturalists that many wildlife species are difficult to detect. However, many ecologists have ignored the issue of detection and thus wide-spread confusion exists regarding what variable is actually being estimated in species distribution models (Yoccoz et al. 2001). This point can be summarized succinctly via the equation $E(C) = N \times p$, where $E(C)$ is the expected count of sites where species x was observed (*i.e.,* the field data), N is the true number of occupied sites (which is unknown to the researcher), and p is the probability of detecting species x, given it occurs at the site. After rearranging the above equation to $\widehat{N} = E(C)/\hat{p}$ it becomes clear that obtaining unbiased estimates of $\widehat{N}$, require inferences about $\hat{p}$. Thus, distribution models that do not account for imperfect detection actually estimate *apparent occurrence* or *effective detection probability*: the combination between true occurrence of species x and the probability of detecting species x, given it is present. A similar line of reasoning can be applied to estimating animal abundance or population vital rates (*i.e.,* survival, fecundity, movement).

Species distribution modeling is a common theme of my dissertation; hence, I felt it prudent to use both design- and model-based approaches to account for the limited detectability of my target wildlife species. Indeed, my first three dissertation chapters are dedicated to improving inferential power in wildlife research when the target species are difficult to detect. I used the results from Chapters 1-3 to develop a strong study design for assessing the effectiveness of structural retention for conserving wildlife in Michigan's harvested forests (Chapters 4 and 5).

For my first two chapters I used species occupancy models and multiple sampling techniques to estimate detection probabilities of small mammals, amphibians, and reptiles (*i.e.,* forest-floor wildlife). Specifically, I assessed the influence of survey method, seasonality, and precipitation on detection probability of forest-floor wildlife and explored study design tradeoffs using parameter estimates from my primary analyses and simulated data. These chapters highlight the importance of coupling design- and model-based approaches for reducing false absences, and highlight the utility of pilot data for designing wildlife research projects which yield strong inferences. I used results from these analyses to inform the sampling design for Chapter 5.

My third chapter involves a detailed investigation into performance of wildlife occupancy models when model assumptions are knowingly violated. In this study I investigated potential bias associated with two processes that violate the closure assumption (*i.e.,* no colonization or extinction) during a sampling season: 1) repeated destructive sampling events that result in either short- or long-term site avoidance by the target species and 2) sampling occurring over a time period during which non-random movements of the target species result in variable occupancy status. I used dynamic occupancy models to quantify the potential bias in occupancy estimation associated with these processes for a terrestrial salamander system. I generalized my findings by conducting a simulation to evaluate how violations of closure can bias occupancy estimates when organism availability declines within a field season. This chapter highlights the importance of addressing closure and non-random organism movements in wildlife occupancy studies. I provide multiple solutions for minimizing bias associated with non-random changes in occupancy and repeated sampling disturbances.

Chapters 4 and 5 represent the impetus for my dissertation research: Assessing the role of structural retention for conserving wildlife in harvested forests. Both studies represented an empirical evaluation of the Michigan Department of Natural Resources (MDNR) structural retention guidelines. In Chapter 4 I evaluated the effectiveness of green-tree retention for promoting site occupancy of interior forest, generalist, and early-successional songbirds in aspen stands that were 1 to 15 years post-harvest. I provide multiple management recommendations for the future use of structural retention in actively managed landscapes.

In Chapter 5 I used correlative and experimental evidence to evaluate how retention of vertical green trees (CANOPY) and coarse woody debris (CWD) influenced terrestrial salamander occupancy and survival in clearcut forests. First, I studied how patterns in salamander occupancy were related to retention of green trees and coarse woody debris within a managed, forested landscape (560,000ha). Second, I quantified how salamander survival was influenced by CANOPY and CWD within timber harvest areas. By focusing my study on the same species, forested areas, and time period I was able to evaluate if occupancy and survival measurements yielded similar inferences regarding amphibian response to structural retention. Thus, this study informs the current debate over which population parameters are most useful for assessing amphibian response to habitat degradation and highlights the importance of coupling broad-scaled distribution research with detailed demographic studies.

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CHAPTER 1

USING MULTIPLE METHODS TO ASSESS DETECTION PROBABILITIES OF FOREST-FLOOR WILDLIFE

Abstract

Many previous comparisons of multiple sampling methods have assumed that detection probabilities for each method are either constant or equal to one. I used 4 sampling methods to estimate detection probabilities for forest-floor dwelling amphibians, reptiles, and small mammals. I investigated associations between seasonality and precipitation on species detection and explored sample design tradeoffs for future studies. Although I captured 25 species, I could reliably detect (detection probability >0.15) only northern short-tailed shrews (*Blarina brevicauda*) and pygmy and masked shrews (*Sorex* spp.) using drift fences and red-backed salamanders (*Plethodon cinereus*) using visual encounter surveys (VES). The use of multiple sampling methods improved detection probabilities for only red-backed salamanders ($\hat{p}_{VES} = 0.32$, 95% CI: 0.24−0.38, $\hat{p}_{all\ methods} = 0.38$, 95% CI: 0.32−0.44). Parameter estimates indicated detection of both shrew species was positively related to increased precipitation. Detection probabilities for pygmy and masked shrews and red-backed salamanders were positively and negatively associated with date, respectively. My power analysis revealed that sampling during rain events increased the power of detecting a change in sorid occupancy by $\geq 40\%$ ($\alpha = 0.05$). My results demonstrate the need to incorporate species detectability when comparing the effectiveness of different trapping methodologies. Furthermore, my study highlights the utility of power analyses for exploring study design tradeoffs for research and monitoring programs.

1.1. Introduction

Failure to account for imperfect detection has been strongly criticized as a shortcoming of endangered species conservation, forest management, and wildlife monitoring (Yoccoz et al. 2001, MacKenzie et al. 2005, Kéry and Schmidt 2008, Kroll 2009). Indeed, detection of most forest-floor vertebrates, such as terrestrial amphibians, reptiles, and small mammals, is likely confounded by seasonality, weather, habitat, survey type, and effort. Detection probabilities of these taxa may be further confounded if only a small fraction of the population is available for sampling (i.e., fossorial behavior patterns; Bailey et al. 2004*a*). Hence, imperfect detection can lead to biased or erroneous conclusions about population and community parameters (Mazerolle et al. 2005, Jackson et al. 2006).

Several authors suggest using multiple survey methods to reduce or eliminate statistical noise caused by poor detection probability (e.g., Ryan et al. 2002, Garden et al. 2007, Ribeiro-Júnior et al. 2008, Hutchens and DePerno 2009). However, the assumption that multiple methods alleviate biases associated with poor detection is rarely tested. One negative aspect of employing multiple methods is the potential to collect redundant information if one method performs better than all others, adding to costs for time and materials (Mattfeldt and Grant 2007). Also, the use of multiple methods could lead to erroneous conclusions if all methods perform poorly. Past multi-method studies that accounted for imperfect detection have been limited to salamanders and meso- and large mammals (Bailey et al. 2004*b*, O'Connell et al. 2006, Mattfeldt

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and Grant 2007). I utilized detection data collected on plethodontid salamanders, reptiles, and small mammals (hereafter forest-floor wildlife) in northern Michigan, USA to estimate species detection probability and occupancy using multiple survey methods. My objectives were to 1) assess the influence of survey method, seasonality, and precipitation on detection probability of forest-floor wildlife and 2) explore future study design tradeoffs using parameter estimates from both my analysis and simulated population data. Specifically, I compared the ability of 3 competing study designs to detect a 50% change in the proportion of sites occupied by northern short-tailed shrews (*Blarina brevicauda*) and pygmy and masked shrews (*Sorex* spp.).

1.2. Methods

1.2.1. Study Area

I conducted my study in the Cadillac-Traverse City area in the northwestern Lower Peninsula of Michigan, USA, in 2009. This area occurs in a glacial outwash-plain with porous sandy soils, intermixed with ice-contact zones and moraines (Barnes and Wagner 2004). My study took place on state-owned lands with a history of timber harvest that were managed for aspen (*Populus* sp.) production at the time of my study. I sampled 3 forest stands that were 5-8 yr postharvest and 15-28 ha in size. Within each stand the Michigan Department of Natural Resources and Environment (MDNR) implemented variable-retention harvest prescriptions (Bielecki et al. 2006), which call for retention of 3-10% of live tree basal area and retention of vertical snags and coarse woody debris (CWD) whenever possible. Retained canopy trees consisted of mixed oak (*Quercus* spp.), eastern white pine (*Pinus strobus*), red maple (*Acer rubrum*), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), and aspen, whereas dominate understory woody plants were aspen, red maple, blackberry (*Rubus* spp.), black cherry, downy serviceberry (*Amelanchier arborea*), witch-hazel (*Hamamelis virginiana*),

American beech, and hophornbeam (*Ostrya carpinifolia*). Prior to European settlement, this ecosystem was dominated by eastern white and jack pine (*Pinus banksiana*) and prone to fire disturbances (Barnes and Wagner 2004).

1.2.2. Site Selection

I used HAWTH'S TOOLS (Hawth's Tools, version 3.27, http://www.spatialecology.com/htools/, accessed 1 Feb 2009) in a Geographic Information System (ArcGIS 9.1) to overlay each stand with a sampling lattice, consisting of 60×60-m cells, to delineate potential study sites. I recognized that the characteristics of the surrounding landscape could introduce heterogeneity in wildlife occupancy (Prugh et al. 2008). Therefore, I eliminated all lattice cells whose borders intersected or encompassed an unharvested forest edge, active logging road or off-road recreational vehicle trail, or wetland appearing on 2005 National Agricultural Imagery Program imagery (Michigan Department of Information Technology 2009). I considered all remaining lattice cells as potential sampling locations and randomly selected 7 within each forest stand. My selection process produced 21 sampling sites, spaced ≥60 m apart. I chose 7 sites per stand to ensure I had adequate replication of sites at each stand while still allowing for sufficient site separation.

Within each 60×60-m site, I used 4 techniques to detect forest-floor wildlife: drift fence arrays, pitfall arrays, coverboard arrays, and visual encounter surveys (VES). I systematically arranged the various detection methods with a drift fence at the center, a coverboard or pitfall array placed equidistant from the drift fence array in the 4 corners of the site, and paired VES transects at the north and south ends (Figure 1.1). I positioned Y-shaped drift fences along an east-west axis (Figure 1.1). Each segment of the fence was 5 m long. I constructed fences of silt fencing (45 cm tall) and buried them 15 cm in the ground with one 19-L bucket buried at each

end (Figure 1.1). I buried another bucket where the 3 wings converged. I placed a pair of 1-m double-ended funnel traps flush with the ground along each drift fence wing (Figure 1.1). Funnel traps had 20-cm and 5-cm outer and inner openings, respectively (Corn 1994).

For each pitfall array, I buried 4 19-L buckets in the shape of a diamond and spaced them approximately 1 m apart (Figure 1.1). I drilled holes in the bottoms of the buckets to facilitate water drainage and placed a piece of carpet in each bucket to provide shading. A coverboard array (Fellers and Drost 1994, Marsh and Goicochea 2003) consisted of 2 1.5 × 0.75-m plywood boards laid flush with the ground, spaced 1 m apart (Figure 1.1). The VES (Crump and Scott 1994) consisted of a 20-m transect set at 20 m from the north and south ends of the drift fence array (Figure 1.1). For each VES, one observer searched for wildlife under CWD >4 cm diameter, >15 cm long, and within 1 m of the transect centerline. Wildlife observers were rotated among transects to minimize observer bias in detection (i.e., no observer surveyed the same transect twice in a row).   I positioned pitfall and coverboard arrays and VES 10 m from the edge of a site's boundary (Figure 1.1).

I sampled sites from 5 May 2009–2 July 2009. I adopted a rotating sampling design where I sampled all sites within one forest stand twice in a 24-hr period (i.e., 2 visits). I opened traps 24 hr prior to the first visit and closed them after the second visit. I then commenced sampling at another forest stand and visited all sites at this stand twice. I rotated sampling effort between 3 stands until all sites had 12 visits. I ensured that primary sampling events were 7-10 days apart (i.e., visits 1-2, 3-4, 5-6, ect. were each 7-10 days apart). During each visit, I collected species detection information for all methods and released organisms >5 m from the point of capture for drift fence arrays and pitfalls. I identified all organisms to species with the exception of pygmy (*S. hoyi*) and masked shrews (*S. cinereus*), which I could only identify to

genus. My sampling and handling protocols were approved by the Michigan State University Animal Care and Use Committee (Animal Use Form no. 07/08-118-00).

At each forest stand, I used 4 rain gauges to determine average precipitation within a 24-hr period prior to each sampling visit. I also recorded the Julian date of each visit. For VES transects, I quantified the number of cover objects rolled during each visit and the survey duration.

1.2.3. Model Generation

I used single-season models to estimate species occupancy and detection probabilities at a site (MacKenzie et al. 2002). The single-season model allowed for estimation of occupancy for species whose detection probability was <1. For all analyses, I held species occupancy probability constant ($\psi(.)$), which assumes that habitat heterogeneity does not have an appreciable effect on species occurrence at a site. This assumption was robust for the 3 species I detected effectively (i.e., only northern short-tailed shrews, pygmy and masked shrews, and red-backed salamanders had $\hat{p} \geq 0.15$; see Results). Site occupancy probabilities were ≥ 0.75 for all 3 species, suggesting they were relatively ubiquitous across my study sites. Therefore, the influence of habitat covariates on the probability of site occupancy would likely be minor.

I pooled detection data for all methods and constructing a model for each species that assumed constant occupancy and detection probabilities. This model estimated the probability of detecting species *x* with ≥ 1 survey method during one visit, given the species was present at the site. I used this analysis to determine which species I would remove from subsequent analyses, as reliable estimates of occupancy cannot be calculated for species with very low detection probabilities (i.e., $\hat{p} \leq 0.15$). I predicted detection probability of pond-breeding amphibians would be ≤ 0.15 because my study sites were not near wetlands. However, I included pond-

breeding amphibians in my initial analysis because other multi-method studies have captured

pond-breeding amphibians in terrestrial habitat (Ryan et al. 2002, Roloff et al. 2010).

Furthermore, use of terrestrial habitat by pond-breeding amphibians has been increasingly

documented (Semlitsch and Bodie 2003, Rittenhouse and Semlitsch 2007, Rittenhouse et al.

2009). I felt it was reasonable for most small mammal, squamate, and plethodontid species to

have $\hat{p} > 0.15$ for this initial analysis.

For species with $\hat{p} > 0.15$, I analyzed data from each survey method independently, to

evaluate how different survey methods may influence bias and precision of detection and

occupancy estimates. I predicted that coverboard arrays would perform well for sampling

plethodontids and squamates (Monti et al. 2000, Marsh and Goicochea 2003, Bailey et al.

2004b). I recognized that microclimate conditions developing underneath coverboards would

dictate species utilization: whereas desiccation-prone species are less likely to occur under a

coverboard if the habitat remains dry, this circumstance would be ideal for squamates. I

predicted VES would provide high detection probabilities for sedentary species such as

plethodontids but not for more mobile organisms such as squamates and small mammals (Smith

and Petranka 2000). I expected drift-fences would perform well in detecting more mobile

organisms, as well as plethodontids during rain events (Ryan et al. 2002). I considered pitfall

traps as a cheaper (both in installation time and money) alternative to drift fences and predicted

they would be effective for detecting small mammals, terrestrial salamanders, and small

squamates (Butts and McComb 2002, McDade and Maguire 2005, Garden et al. 2007). I

eliminated method-specific models with $\hat{p} \leq 0.15$ for individual species from subsequent

analyses (see O'Connell et al. 2006).

For all remaining species, I constructed method-specific models that allowed detection probability to vary as a function of Julian date and precipitation within a 24-hr period. I explored potential correlation between Julian date and 24-hr precipitation using Pearson's product moment correlation (Sokal and Rohlf 1981). I predicted that Julian date would positively associate with detection probability of squamates, negatively associate with plethodontid detectability, and exhibit no association with shrew detectability (Gibbons and Semlitsch 1987, Kurta 1995, Petranka 1998:342, Ford et al. 2002). I predicted that rain events would increase the probability of detecting plethodontid salamanders and shrews due to their increased surface activity during wet weather (Petranka 1998:342, Umetsu et al. 2006). I constructed linear and quadratic terms for each covariate, and constructed additive models that included precipitation and Julian date together, yielding 8 potential a priori models for each species and method.

I also conducted an exploratory analysis to see if red-backed salamander detection was negatively associated with observers repeatedly performing VESs. During my study, I noticed that repeated handling of CWD along VES transects resulted in fragmentation of those objects during later visits (t_i). Therefore, I used the change in cover object number as a surrogate for observer-induced disturbance and modeled its influence on salamander detection probability. I used the number of cover objects tallied during the first visit as my baseline (t_0) and calculated

the difference in cover objects at t_i and t_0 as my measure of observer-induced disturbance. This calculation provided an estimate of cover object fragmentation during each visit and for each site. I developed one model with this variable as a detection covariate and compared it to my a priori model set.

I generated parameter estimates via maximum likelihood estimation using Program

PRESENCE (PRESENCE, version 2.3, http://www.mbr-pwrc.usgs.gov/software/presence.html,

accessed 1 May 2009). I used Akaike's Information Criterion, adjusted for small sample size

(AIC_c), and model weights to rank models (Burnham and Anderson 2002). I used model

averaging and unconditional variance estimation when multiple models received support in the

analysis (i.e., $\Delta AIC_c \leq 10.0$, Burnham and Anderson 2002). To account for potential

overdispersion in model selection, I used Pearson's chi-square as a goodness-of-fit test for the

global model of each species (MacKenzie and Bailey 2004). I used a parametric bootstrap

procedure with 10,000 iterations to estimate the overdispersion parameter ($\hat{c}$). I used Quasi

Akaike's Information Criterion ($QAIC_c$; Burnham and Anderson 2002) for model selection and

inflated the standard error of the parameter estimates by $\sqrt{\hat{c}}$ if there was evidence that the global

model fit the data poorly (i.e*., $\hat{c}$ >1*; MacKenzie et al. 2006). I reported 95% confidence intervals

for all parameter estimates, unless otherwise stated.

1.2.4. Exploring Future Sampling Designs

I used parameter estimates generated from my top ranking drift fence model to explore how

sampling effort can be allocated in future studies to maximize power for detecting a 50%

decrease in the proportion of sites occupied by northern short-tailed shrews and pygmy and

masked shrews. I developed 3 potential study designs that included 2 groups of 25 sites with 4

replicate visits. For the first design, I used detection estimates for each species during non-rain

events (i.e., 0 mm precipitation within the past 24 hr). The first design represented a situation

where researchers sample for sorids without targeting rain events. For the final 2 designs, I used

detection estimates from sampling visits with 5 mm and 10 mm of precipitation, respectively.

The final 2 designs represented situations where researchers are able to focus their sampling effort during periods of rain. I used the estimate of occupancy from the top ranking model as my baseline for the first group of 25 sites and multiplied this value by 50% for my estimate of occupancy for the second group.

I used Program GENPRES (GENPRES, http://www.mbr-pwrc.usgs.gov/software/presence.html, accessed 1 May 2009) to simulate detection history data using the parameter estimates described above. I constructed competing models in Program MARK (MARK, version 5.1, http://www.cnr.colostate.edu/~gwhite/mark/mark.htm, accessed 1 Aug 2009) using the simulated data. I compared a null model ($H_0 = \psi(.), p(.)$) that assumed occupancy was constant between the 2 groups to an alternative model ($H_a = \psi(group), p(.)$) that allowed occupancy to vary between groups. In all cases, I considered H_a the true model, as I used this model to generate the data. I compared the null and alternative models using a likelihood ratio test (LRT) in MARK and approximated power using the chi-square statistic from the LRT output (Burnham et al. 1987, Bailey et al. 2007). This analysis allowed us to approximate the power of a proposed sampling design for detecting a simulated change in species occupancy.

1.3. Results

I detected 659 organisms representing 9, 9, and 7 species of small mammals, amphibians, and reptiles, respectively (Table 1). Drift fence arrays detected the most species (22), followed by pitfall traps (11), VES (10), and coverboards (7; Table 1). Estimated detection probabilities varied between 0.01−0.38 when I combined capture data for all methods (Table 2). Red-backed salamander, northern short-tailed shrew, and pygmy and masked shrews were the only species

with $\hat{p} \geq 0.15$. The method-specific analysis revealed that pitfall traps and coverboards alone could not reliably detect any species ($\hat{p} < 0.15$), whereas VES were sufficient for detecting only red-backed salamanders ($\hat{p} = 0.32$, 95% CI: 0.26 - 0.38; Table 2). Detection probabilities for drift fence arrays were <0.15 for all species except pygmy and masked shrews ($\hat{p} = 0.24$, 95% CI: 0.18 - 0.30). However, I also included northern short-tailed shrews for further analysis because of a borderline detection probability ($\hat{p} = 0.14$, 95% CI: 0.08 - 0.20) when using drift fences.

Julian date and 24-hr precipitation were not correlated ($n = 36$, $r = 0.05$, 95% CI: −0.28 - 0.37), which allowed us to treat them as independent detection covariates. Models containing the 24-hr precipitation covariate received substantial support for both shrew species detected with drift fences (Table 3). As predicted, precipitation was positively related to detection of both sorid species (Figure 1.2). Models that included a quadratic precipitation term received >95% and 70% of the total model weight for northern short-tailed shrews and pygmy shrews, respectively. Detection probabilities for both of these species were lower during dry periods and heavy rain events (Figure 1.2). Detection probability increased as the season progressed for pygmy and masked shrews ($\hat{\bar{\beta}}_{Julian} = 1.04$, 95% CI: 0.54 - 1.54; Figure 1.3a). Furthermore, some support existed for models containing the quadratic form of Julian date, which suggested pygmy and masked shrew detection decreased during the later part of my study ($\hat{\bar{\beta}}_{Julian}^{2} = -0.02$, 95% CI: −0.01 - −0.03; Figure 1.3a). I found less support for models containing Julian date on northern short-tailed shrew detection ($\Delta AIC_c = 3.1$; Table 3).

I found evidence of poor model fit for red-backed salamanders (χ^2 = 223.3, P = 0.02).

Therefore, I used QAIC$_c$ for model selection and inflated the standard error of the parameter

estimates by $\sqrt{\hat{c}}$ = 1.88. Top model weights indicated that Julian date was associated with red-

backed salamander detection (Table 3) with detection probability decreasing as the season

progressed (Figure 1.3b). However, there was also support for the constant detection model

(ΔQAIC$_c$ = 1.97, w_i = 0.20) and model-averaging results revealed the 95% confidence interval

for the Julian date beta estimate approached zero ($\hat{\bar{\beta}}_{Julian}$ = −0.63, 95% CI: −0.02 - −1.24).

Counter to my prediction, models containing precipitation showed little support for being

associated with salamander detection. My exploratory analysis revealed that the model

containing the change in the number of cover objects covariate, my surrogate for habitat

disturbance, ranked higher than all other models in my candidate set and received 57% of the

total model weight. As predicted, salamander detection probability was negatively associated

with the number of fragmented cover objects along a transect ($\hat{\bar{\beta}}_{cover}$ = −0.49, 95% CI: −0.15 -

−0.83). The next highest ranking model included Julian date (ΔQAIC$_c$ = 1.77 w_i = 0.23).

My simulation revealed variation in the ability of the 3 proposed study designs to detect a

50% change in occupancy of northern short-tailed shrews and pygmy and masked shrews (Table

4). For both species, designs that focused sampling effort during rain events yielded the highest

approximated power. Sampling during non-rain events provided moderate power for detecting a

change in pygmy and masked shrew occupancy (40%, α = 0.05) but virtually no power for

detecting a change in northern short-tailed shrew occupancy (5%, α = 0.05). Although estimated

detection probabilities for northern short-tailed shrews varied during events with 5 mm or 10 mm

of precipitation (Figure 1.2a), it did not appear to influence approximated power of the 2 study designs (61% and 63%, respectively, $\alpha = 0.05$).

1.4. Discussion

My study corroborates a growing body of literature highlighting the importance of accounting for imperfect detection in wildlife studies (e.g., O'Connell et al. 2006, Mazerolle et al. 2007, Kéry and Schmidt 2008, Kroll 2009). Some researchers advocate use of multiple sampling techniques to help ameliorate the effects of variable detection (e.g., Garden et al. 2007, Ribeiro-Júnior et al. 2008, Hutchens and DePerno 2009). However, using multiple methods alone does not address the problem of imperfect detection when all methods perform poorly or if one method influences another when multiple methods are used simultaneously (Nichols et al. 2008). With the exception of red-backed salamanders, multiple detection methods did not improve detection probabilities for any species. In most wildlife studies, implementation of multiple methods may be constrained by limited sampling effort and higher equipment costs (Garden et al. 2007, Ribeiro-Júnior et al. 2008). My results suggest that implementing one detection method based on the behavior and ecology of the target species and accounting for imperfect detection through estimation may be more cost-effective than implementing multiple methods.

I was unable to reliably detect any of the 7 species I observed using coverboards, which was counter to my prediction, given coverboards are extensively utilized to detect herpetofauna species, especially terrestrial salamanders and squamates (e.g., Monti et al. 2000, Ryan et al. 2002, Marsh and Goicochea 2003, Bailey et al. 2004*b*). Monti et al. (2000) suggested that coverboards should age for ≥ 1 yr to allow the ideal microclimate to develop underneath and also allow time for organisms to encounter the artificial refugia. Indeed, the microclimate under many of my coverboards remained dry, which likely hindered their ability to provide refuge for

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salamanders but not for squamates. Strangely, the aging period of my coverboards was similar to that of other studies that successfully used this method to capture these organisms (e.g., Hyde and Simons 2001, Ryan et al. 2002, Marsh and Goicochea 2003). Bailey et al. (2004b) found coverboards provided >0.15 detection probabilities for 6 out of 7 terrestrial salamander species. However, coverboards used by Bailey et al. (2004*b*) were aged 2-4 yr prior to sampling (L. L. Bailey, Colorado State University, personal communication), which may explain discrepancies between detection estimates in Bailey et al. (2004*b*) and my study.

Similar to my results for coverboards, I could not reliably detect any of the 11 species I captured using pitfall traps. Pitfall traps have been used to sample a variety of forest-floor wildlife (Butts and McComb 2002, McDade and Maguire 2005, Garden et al. 2007). To my knowledge, no other study has questioned the assumption of perfect detection probability at the species level when using pitfall traps.

Of the 22 species I captured using drift fences, only northern short-tailed shrews and pygmy and masked shrews had detection probabilities ≥0.15. Detection probabilities for those species were positively associated with precipitation events, a phenomenon documented for some shrew species (Brannon 2002, Umetsu et al. 2006) but not others (Laakkonen et al. 2003, Whittaker and Feldhamer 2005). I was 3 times more likely to detect pygmy and masked shrews and 30 times more likely to detect northern short-tailed shrews when sampling on days with 10 mm of precipitation within a 24-hr period compared to days without rain (Figure 1.2). Counter to my prediction, the top pygmy and masked shrew model also included Julian date as a covariate, with detection probability increasing as the season progressed. Although pygmy and masked shrews are known to be active year-round, they may also increase foraging activity as more insect prey become available during the early summer (Kurta 1995).

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Although I detected 10 species using VES, only red-backed salamanders had a constant detection probability >0.15. I found evidence that my global model for red-backed salamanders fit the data poorly; therefore I exercised caution when interpreting covariate effects. I found some support for a negative association between seasonality and salamander detection probability, which could result from reduced surface activity during summer (Petranka 1998 and references therein). Alternatively, the observed decrease in detection probability could result from disturbances associated with repeated transect visitation. My exploratory analysis revealed a decrease in salamander detection probability at sites where the number of cover objects increased over time, which may be attributed to an increased fragmentation of CWD caused by repeated observer handling. The notion that invasive sampling techniques, such as VES, can influence population parameters through repeated habitat disturbances has been proposed but not empirically tested (Bailey et al. 2004*b*). More research is needed to determine how salamander occupancy and detection probabilities may be impacted by seasonality and observer-induced disturbances. Based on current information, I suggest sampling effort be allocated in May-June for environments similar to what I sampled in northern Michigan and the number of replicate surveys should be ≤4 to minimize site disturbance.

I acknowledge a potential lack of method independence resulting from animals captured in drift fences and pitfall traps not being available for detection by my other methods during a daily sampling event. Violation of the independence assumption would result in underestimated detection probability for any method where a species was unavailable. Although I did not explicitly test for trap independence, I think the probability of violating this assumption was acceptably low for my study species because they exhibit high local abundances and low daily movement rates relative to the distance between my sampling methods (Heatwole 1962,

Kleeberger and Werner 1982, Kurta 1995, Getz and McGuire 2008). Furthermore, I reliably detected only 3 species when I combined detection data for all methods, suggesting that potential method dependence did not influence my overall conclusions. Nichols et al. (2008) recommended a multi-method occupancy model, which accounts for a lack of independence between methods. However, low detection estimates for most methods in my study precluded its use. To my knowledge, only O'Connell et al. (2006) and Nichols et al. (2008) have acknowledged method dependence in multi-method studies. However, I am not aware of any research that has quantified this potential source of bias.

One benefit of using occupancy modeling is the availability of simulation methods for assessing the statistical power of proposed study designs (Bailey et al. 2007, Mattfeldt et al. 2009). My simulation study revealed that not all sampling designs were equal in their ability to detect a change in sorid occupancy. Although my simulation study was based on overly simplistic sampling designs, it does highlight how researchers can use pilot data to improve sampling efficiency. In this case, rather than using pitfall traps and drift fences for detecting sorid species during random days throughout a season, a more efficient design would include a focused sampling effort during rain events using only drift fences. When pilot data are not available, researchers can still explore design trade-offs using parameter estimates from other studies or best professional judgment (MacKenzie and Royle 2005, Bailey et al. 2007).

1.4.1. Management Implications

My results do not support the assumption from past multi-method studies that using multiple sampling techniques will ameliorate the effects of poor detection. As a result, I recommend that studies and monitoring efforts use pilot data to estimate detection probabilities of targeted species using multiple methods and use this information as a basis for selecting a primary

sampling method for future studies. As part of this process, I recommend that managers and researchers explore sampling design tradeoffs to ensure the proposed design has sufficient power for detecting real population trends. Pilot data can be used to investigate study designs tradeoffs for detecting changes in species occupancy and improve the allocation of sampling resources for monitoring and managing populations of concern.

1.5. Acknowledgments

Table 1.1. Small mammals, amphibians, and reptiles detected using drift fence arrays, pitfall traps, visual encounter surveys (VES), and coverboards at 21 sites during 36 trap days in northern Michigan, USA, 2009.

Species	Scientific name	Drift fence	Pitfall	VES	Coverboard
Mammals					
Eastern chipmunk	*Tamias striatus*	x			
Meadow vole	*Microtus*	x			
Northern short-tailed shrew[a]	*Blarina brevicauda*	x	x		x
Peromyscus sp.	*Peromyscus* sp.	x	x		x
Pygmy and masked shrew[a]	*Sorex* spp.	x	x	x	x
Southern bog lemming	*Synaptomys cooperi*	x	x		
Southern red-backed vole	*Clethrionomys gapperi*	x	x		
Star-nosed mole	*Condylura cristata*	x			
Woodland vole	*Microtus pinetorum*	x	x		
Amphibians					
American toad	*Anaxyrus americanus*	x			
Eastern gray treefrog	*Hyla versicolor*		x		
Green frog	*Lithobates clamitans*	x			
Northern leopard frog	*Lithobates pipiens*	x			
Red-backed salamander[a]	*Plethodon cinereus*	x	x	x	x
Red-spotted newt	*Notophthalmus*	x		x	
Spotted salamander	*Ambystoma maculatum*	x		x	

Table 1.1 (cont'd)

Species	Scientific name	Drift fence	Pitfall	VES	Coverboard
Spring peeper	*Pseudacris crucifer*	x	x	x	
Wood frog	*Lithobates sylvaticus*	x	x	x	
Reptiles					
Brown snake	*Storeria dekayi*	x		x	
Eastern garter snake	*Thamnophis sirtalis*	x		x	x
Five-lined skink	*Plestiodon faciatus*	x	x		x
Hog-nosed snake	*Heterodon platirhinos*			x	
Red-bellied snake	*Storeria*	x			x
Ring-necked snake	*Diadophis punctatus*	x			
Smooth green snake	*Liochlorophis vernalis*			x	
No. of species		22	11	10	7

[a] Species that surpassed the minimum detection threshold of 0.15 when modeled using site-occupancy estimation and which we considered for further analysis.

Table 1.2. Parameter estimates for occupancy ($\hat{\psi}$) and detection probabilities ($\hat{p}$) for red-backed salamanders (RBSA), northern short-tailed shrews (NSTS), and pygmy and masked shrews (*Sorex* spp.) detected by all methods combined, visual encounter surveys (VES), pitfall traps, drift fences, and cover boards (not shown[a]) at 21 sites and 36 trap days in northern Michigan, USA, 2009. We estimated all parameters from a model assuming constant occupancy and detection probabilities ($\psi(.)$, $p(.)$). ψ_{obs} = the proportion of sites where a species was known to occur (i.e., naïve estimate).

Species	All methods combined					VES transect				
	$\hat{p}$	SE $\hat{p}$	ψ_{obs}	$\hat{\psi}$	SE $\hat{\psi}$	$\hat{p}$	SE $\hat{p}$	ψ_{obs}	$\hat{\psi}$	SE $\hat{\psi}$
RBSA	0.38	0.03	1.00	1.00	0.00	0.32	0.03	0.86	0.86	0.08
NSTS	0.15	0.03	0.76	0.91	0.13					
Sorex spp.	0.29	0.03	1.00	1.00	0.00					

Table 1.2 (cont'd)

Species	Pitfall traps					Drift fence				
	$\hat{p}$	SE $\hat{p}$	ψ_{obs}	$\hat{\psi}$	SE $\hat{\psi}$	$\hat{p}$	SE $\hat{p}$	ψ_{obs}	$\hat{\psi}$	SE $\hat{\psi}$
RBSA	0.03	0.03	0.24	0.70	0.61	0.12	0.52	0.81	Na[b]	Na[b]
NSTS	0.04	0.14	0.48	Na[b]	Na[b]	0.14	0.03	0.62	0.74	0.14
Sorex spp.	0.12	0.02	0.86	Na[b]	Na[b]	0.24	0.03	0.95	0.99	0.05

[a] We omitted parameter estimates for cover boards (all species) and VES (all species except red-backed salamander) because all detection probabilities were <0.15.

[b] Na: unrealistic parameter estimate because of low detection probability ($\hat{p} < 0.05$) or unsuccessful computation of the variance–covariance matrix for the given method.

Table 1.3. Ranking of candidate detection models for 3 wildlife species at 21 sites in northern Michigan, USA, 2009. Covariates include Julian date and 24-hr precipitation for each visit. A squared symbol represents the quadratic term for the respective covariate. I generated models using detection data from drift fences for northern short-tailed shrews and pygmy and masked shrews and visual encounter surveys for red-backed salamanders. All other method-species combinations yielded insufficient detection probabilities ($\hat{p} \leq 0.15$, see Results) for inclusion in this analysis. I report the complete model set for red-backed salamanders, but I report only models accounting for 0.90 of the total Akaike weight (w_i) for the shrew species.

Table 1.3. (cont'd)

Species	Model	AIC_c[a]	ΔAIC_c[a]	w_i[a]	K[a]
Northern short-tailed shrew	Precipitation + precipitation^2	122.4	0.0	0.80	4
	Precipitation + precipitation^2 + Julian date	125.5	3.1	0.17	5
Pygmy and masked shrew	Precipitation + precipitation^2 + Julian date	234.3	0.0	0.64	5
	Precipitation + Julian date + Julian date^2	236.5	2.2	0.21	5
	Julian date	238.4	4.1	0.08	3
Red-backed salamander	Julian date	83.4[b]	0.0	0.54	3
	Null model	85.4[b]	2.0	0.20	2
	Julian Date + Julian date^2	86.5[b]	3.1	0.12	4
	Precipitation	87.9[b]	4.5	0.06	3
	Precipitation + precipitation^2	89.3[b]	5.9	0.03	4
	Precipitation + Julian date + Julian date^2	89.6[b]	6.2	0.02	5
	Precipitation + precipitation^2 + Julian date	89.6[b]	6.2	0.02	5
	Precipitation + precipitation^2 + Julian date + Julian date^2	93.6[b]	10.2	0.00	6

Table 1.3. (cont'd)

[a] AIC_c = Akaike's Information Criterion adjusted for small sample size; ΔAIC_c = difference from the best model: K = no. of

parameters.

[b] Evidence of poor model fit occurred for red-backed salamanders, therefore we used the quasi-likelihood version of AIC_c, $QAIC_c$ for

model ranking.

Table 1.4. Statistical power approximations for detecting a simulated change in northern short-tailed shrew and pygmy and masked shrew occupancy using 3 alternative sampling scenarios. For all scenarios I simulated detection history data for 2 groups of 25 sites that we visited 4 times in a season. I used the parameter estimates from the highest ranking model for drift fences (Table 3) to represent site occupancy probability for the first group of 25 sites ($\hat{\psi}_{G1}$) and for species detection probability ($\hat{p}$). To simulate a decline in species occupancy, I set the occupancy probability for the second group of sites ($\hat{\psi}_{G2}$) to 50% of $\hat{\psi}_{G1}$. Each scenario represents a situation where researchers target sampling effort during days within 24 hr of moderate (10 mm), light (5 mm), or no rainfall (0 mm).

Table 1.4. (cont'd)

Sampling scenario	Parameters for simulation			Power approximation (H_a vs. H_0)[a]			
	$\hat{\psi}_{G1}$ (n = 25)	$\hat{\psi}_{G2}$ (n = 25)	$\hat{p}$	χ^2	df	Power ($\alpha = 0.05$)[a]	Power ($\alpha = 0.01$)[a]
Northern short-tailed shrew							
10mm rainfall	0.64	0.32	0.89	5.2	1	63%	38%
5mm rainfall	0.64	0.32	0.61	5.0	1	61%	37%
No rainfall	0.64	0.32	0.03	0.0	1	5%	5%
Sorex spp.							
10mm rainfall	0.99	0.49	0.44	12.4	1	94%	82%
5mm rainfall	0.99	0.49	0.31	7.9	1	80%	59%
No rainfall	0.99	0.49	0.14	2.9	1	40%	19%

[a] Approximated power is the chance that the false null hypothesis (H_0 = no difference in the occupancy probability of $\hat{\psi}_{G1}$ and $\hat{\psi}_{G2}$ is correctly rejected.

Figure 1.1. Schematic for a randomly selected 60 × 60-m site with 4 sampling methods to detect (species) in northern Michigan, USA, 2009. Background image represents a sampling lattice with 9 potential sampling sites and shaded areas denote retained canopy green-trees. Symbols represent an array of 4 19-L buckets (circles), 2 1.5 × 0.75-m plywood cover boards (squares), a 20-m visual encounter survey (line), or a drift fence with 5-m wings (sideways "Y"). Each drift fence had paired funnel traps (thin lines) and a bucket at each end and one in the center (circle). I spaced all sampling methods >10 m apart and >10 m from the site boundary.
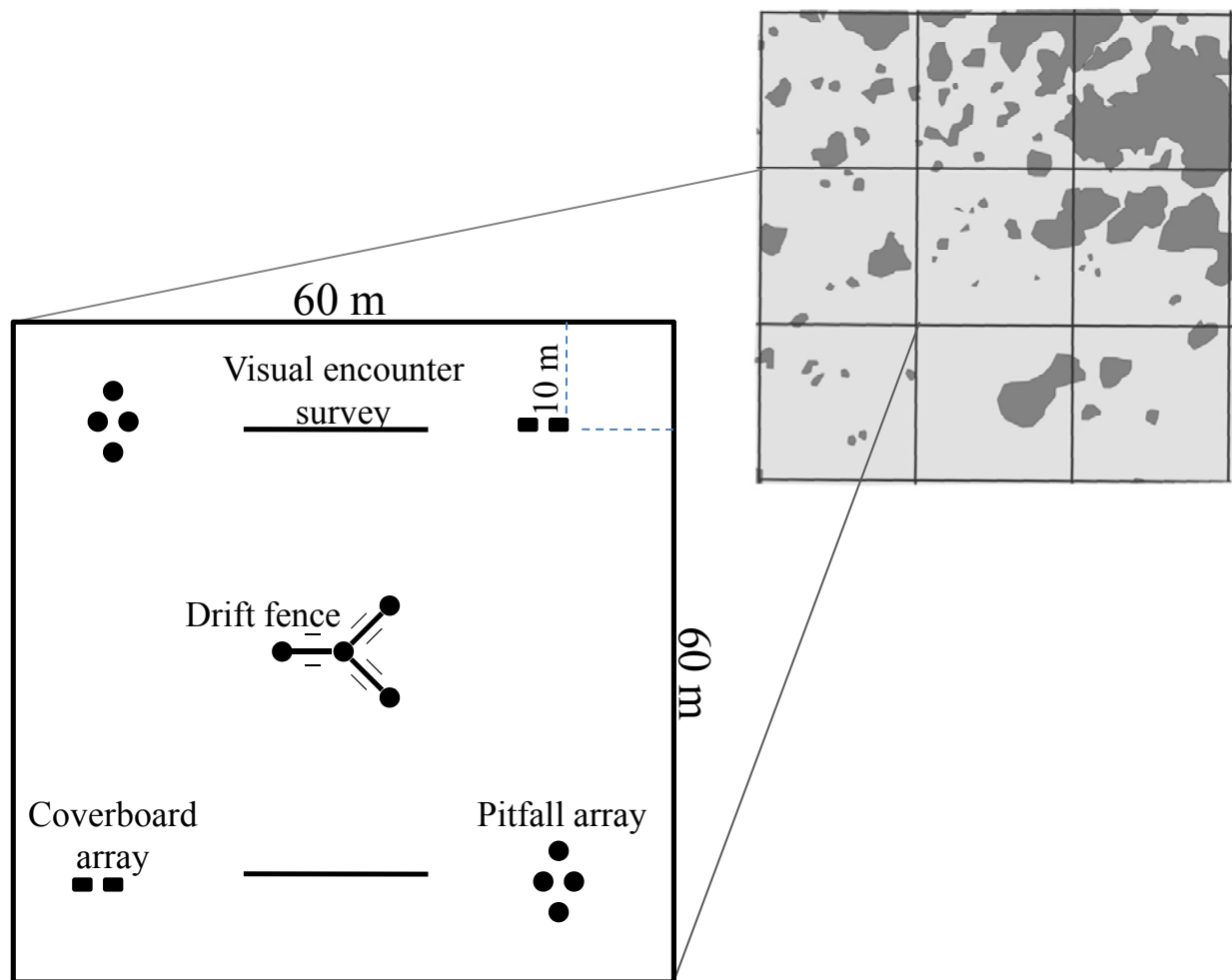
Figure 1.2. Estimated detection probability as a function of precipitation within a 24-hr period prior to sampling for (A) northern short-tailed shrews and (B) pygmy and masked shrews in northern Michigan, USA, 2009. I calculated detection probabilities using model averaged estimates based on the most supported models.

A
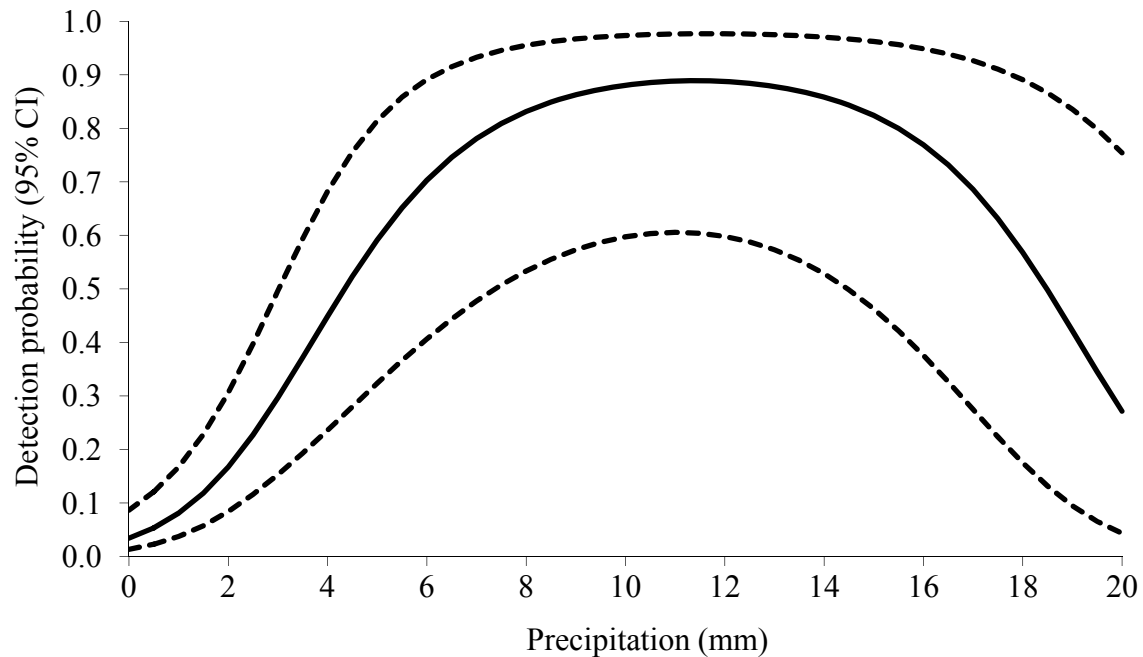
B
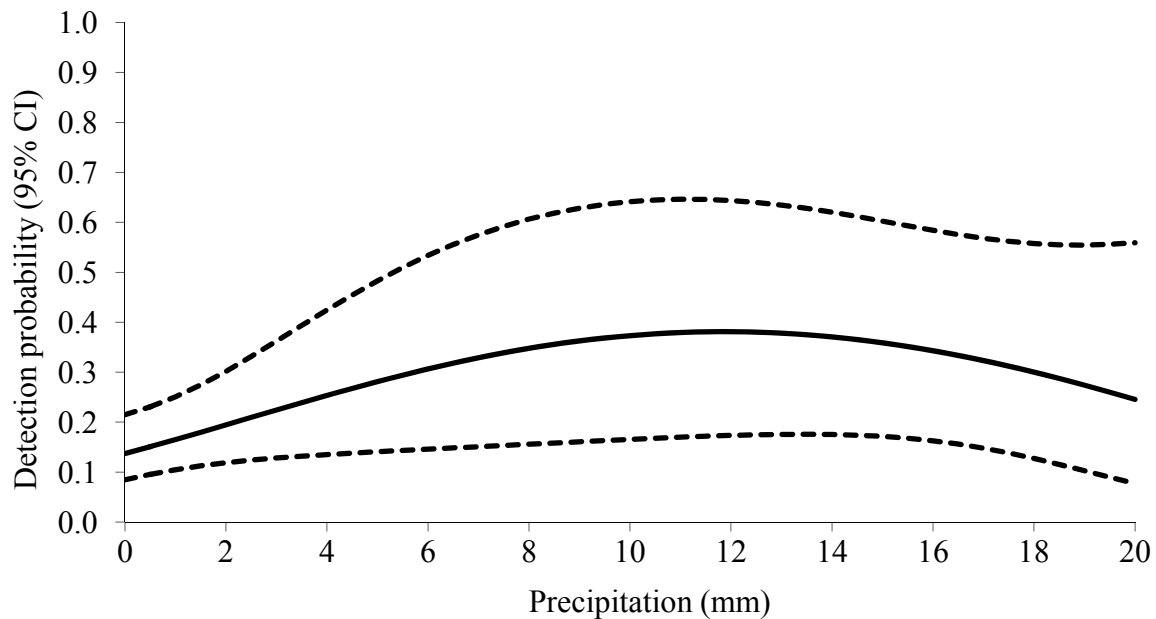
Figure 1.3. Estimated detection probability as a function of sampling date for (A) pygmy and masked shrews and (B) red-backed salamanders in northern Michigan, USA, 2009. I calculated detection probabilities using model averaged estimates based on the most supported models.
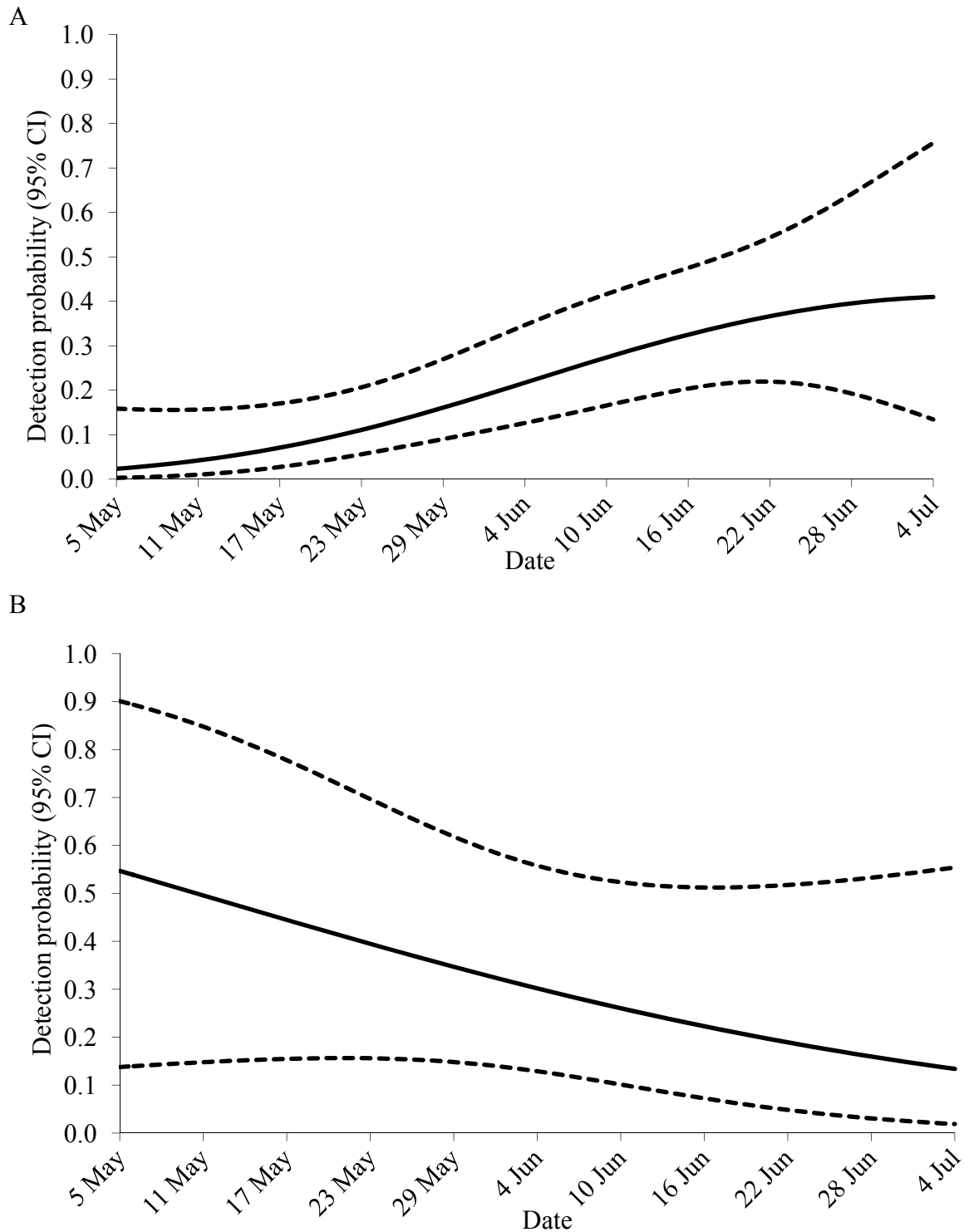
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CHAPTER 2

COMPARING COVER OBJECT AND LEAF LITTER SURVEYS FOR DETECTING RED-BACKED SALAMANDERS, *PLETHODON CINEREUS*

Abstract

Sampling methods that can be efficiently implemented while minimizing bias are central for achieving strong statistical power in field studies. I estimated site occupancy and detection probabilities for Red-backed Salamanders, *Plethodon cinereus,* using natural cover object (NCO) and leaf litter surveys, and tested the power of these methods to detect occupancy differences in simulated data. Both NCO and leaf litter surveys performed well in their ability to detect *P. cinereus* ($\hat{p} = 0.59 \pm 0.07$ ($\pm 1SE$); 0.49 ± 0.08, respectively) and produced similar site occupancy estimates ($\hat{\psi} = 0.75 \pm 0.09$; 0.77 ± 0.11, respectively); however, leaf litter searches took 3 times longer to complete. My simulation study revealed the time required to complete leaf litter surveys limited the number of sampling sites, which reduced statistical power for detecting a 25% change in salamander occupancy between two groups of sites. Natural cover object searches provided greater power for detecting a similar change in occupancy, largely because of high sampling size. Although reliable salamander detection data can be collected quickly using NCO surveys, I discuss situations where this technique may not be appropriate. My study highlights the importance of accounting for imperfect detection probability when conducting visual encounter surveys for terrestrial plethodontids.

2.1 Introduction

Terrestrial salamanders of the genus *Plethodon* are important components of forest ecosystems in eastern North America through their contribution to forest biomass and as potential indicators of environmental change (Burton and Likens, 1975; Welsh and Droege, 2001; Welsh and Hodgson, 2008). As a result, this genus has been utilized in many ecological and forest management studies (Petranka et al., 1993; Ash, 1997; Davic and Welsh, 2004; Bailey et al. 2004a). Visual encounter surveys (VES) are commonly used for sampling terrestrial plethodontids because they are relatively easy to conduct and produce high detection probabilities and capture rates (Bailey et al., 2004a; Williams and Berkson, 2004; Strain et al., 2009). Most VES focus on detecting plethodontids under natural cover objects (NCO: woody debris, logs, rocks). When making inference, researchers assume the number of salamanders detected under these objects is positively correlated with true population size. However, research has shown that a substantial proportion of salamanders occur in the leaf litter or underground and therefore are unavailable for sampling under NCOs (Petranka, 1998:341-342). This suggests the use of NCO surveys alone could lead to biased population metrics if researchers do not account for imperfect detection probability or employ more rigorous sampling methods.

Strain et al. (2009) compared NCO and leaf litter surveys using stream salamander counts and species richness as their metric of inference. They found that NCO surveys were generally more cost effective than leaf litter searches, though their analysis did not account for imperfect detection. Leaf litter searches have the potential to yield more accurate population information but require more time to complete. If only a small number of sites can be visited in a field season, inferential power may be limited. Comparing detection estimates and statistical power of these two methods would provide valuable information to researchers developing long-term monitoring programs or forest management studies (Field et al., 2005).

I compared the effectiveness of NCO and leaf litter searches by estimating occupancy and detection probability parameters for Red-backed Salamanders (*Plethodon cinereus*) occurring in harvested forests. Because a substantial proportion of salamanders may reside in the leaf litter (Petranka, 1998:341-342; Bailey et al., 2004b), I predicted that NCO surveys would yield lower detection probabilities and hence overestimate salamander occupancy with reduced precision. Furthermore, I predicted an analysis that combines NCO and leaf litter searches would yield the most precise estimates of detection and occupancy. I tested whether survey duration and the number of search NCOs influenced *P. cinereus* detection probability. Last, I conducted a simulation to test the statistical power of each sampling method for detecting a 25% difference in salamander occupancy between 2 site types.

2.2. Methods

2.2.1. Site Selection

My study occurred in the northwestern Lower Peninsula of Michigan, USA, in 2009. I sampled 6, stand-owned, forest stands that are currently managed for aspen production (*Populus* sp.). The dominant tree species on these stands include quaking (*Populus tremuloides*) and big-tooth aspen (*P. grandidentata*) interspersed with eastern white pine (*Pinus strobus*), red maple (*Acer rubrum*) and mixed oak (*Quecus* sp.). Within each stand, I randomly selected 5 sites, yielding a total of 30 sites, where I searched for salamanders. To minimize the influence of habitat heterogeneity on salamander occupancy I did not selects sites that were within 30m of a forest stand boundary, active logging road, off-road recreational vehicle trail or isolated wetland. Each site consisted of a clearly demarcated 10 x 10m square. I divided each square into three 3.3 x 10m sub-plots where a single observer would perform NCO and leaf litter searches to detect *P. cinereus*.

2.2.2. Salamander Searches

Observers began searches at one end of the sub-plot and worked lengthwise to the opposite end. For the initial survey an observer walked through each sub-plot and searched for *P. cinereus* under and within visible NCOs that were >4 cm in diameter. Rotting logs that readily broke apart were thoroughly searched. During this survey all NCOs were removed from the sub-plot before starting leaf litter searches. To minimize pseudo-replication, observers also removed all detected salamanders from the sub-plot immediately after capture. Each observer recorded the number of searched NCOs and survey duration. After finishing the NCO survey within their assigned sub-plot the same observer performed a systematic search through all detritus, including leaf litter, coarse organic matter, and NCOs that were missed during the first survey. As before, all salamanders were removed after capture and search time and the number of newly discovered NCOs were recorded.

2.2.3. Statistical Analyses

I used single-season occupancy models (MacKenzie et al., 2002) and the program PRESENCE (version 2; James E. Hines, Patuxent Wildlife Research Center, Laurel, MD) to estimate occupancy and detection probability parameters for *P. cinereus*. I generated a detection history at each site by treating the three sub-plots as spatial subunits (MacKenzie et al., 2006:161-162; Kendall and White, 2009). I initially combined detection information for NCO and leaf litter surveys as a single sampling event ('combined' dataset) for each site. These data represent the likelihood that *P. cinereus* was detected using either a NCO or leaf litter survey at one or more sub-plots, given its presence at a site. Because this dataset includes detection information from both methods, it should yield the most accurate estimate of the true occupancy state at a site and the highest detection probability.

For my next analysis I created unique datasets for the NCO and leaf litter searches and analyzed each separately ('single-method' datasets). This represents a situation where only one method was used at a site, hence the potential for bias in site occupancy estimation was higher. Comparing site occupancy estimates between the 'single-method' and 'combined' datasets allowed me to investigate occupancy biases associated with each method, as well as differences in method-specific detection probability (Bailey et al., 2004a; Mattfeldt and Grant, 2007). Occupancy estimates with non-overlapping confidence intervals generated from these two analyses would suggest a bias associated with one of the sampling methods.

I also developed a set of *a priori* models to better understand how *P. cinereus* detection was influenced by survey effort. I modeled detection probability as a function of two covariates: the number of NCOs searched (COVER) and survey duration (TIME), while holding occupancy constant across all sites. I tested for correlation between COVER and TIME for both survey methods using Pearson's product moment correlation (Sokal and Rohlf 1981). I did not record covariate information at 2 and 3 sites for the NCO and leaf litter surveys, respectively. For these sites, I entered the covariates as missing values in program PRESENCE. I standardized all covariates prior to analysis.

Akaike's Information Criterion, adjusted for small sample size (AIC_c), and model weights were used to rank models in order of parsimony (Burnham and Anderson, 2002). For the NCO dataset I predicted that the COVER model would receive the strongest support, with detection positively associated with number of NCOs. For the leaf litter dataset I predicted that the TIME model would receive the strongest support, with salamander detection increasing with survey duration. I assumed the probability of detecting *P. cinereus* during a leaf litter search was independent of salamanders removed during the NCO searches. To test this I constructed a

model where salamander detection probability during a leaf litter survey was allowed to vary as a function of whether at least one *P. cinereus* was removed from the sub-plot during the initial NCO survey (REMOVAL). A negative beta parameter for the REMOVAL covariate would suggest that salamander detection probability during a leaf litter survey was lower at sub-plots where salamanders were removed during the initial NCO survey. This would provide evidence for a lack of method independence.

I also created a single dataset where detection information was included separately for each sampling method ('multi-method'), yielding a total of 6 sampling replicates (3 sub-plots x 2 sampling methods) for each site. I constructed two models where detection was either held constant (NULL) or allowed to vary by sampling method (METHOD). Support for the model including the METHOD covariate would suggest survey methods differ in their ability to detect *P. cinereus.*

2.2.4. Power Approximation

I conducted a simulation analysis to investigate how use of these two methods would affect statistical power of future study designs, with the understanding that sample size in field studies is often limited by time availability and project funding. My goal was to determine how survey method affected my ability to detect a 25% change in the proportion of sites occupied by *P. cinereus.* I utilized field data to estimate the maximum number of 10 x 10m sites that could realistically be surveyed in a 2-month field season using either method ($\hat{n} = 180$ for NCO and 60 for leaf litter surveys). I then simulated salamander detection data for two groups of sites in the program GENPRES (James E. Hines, Patuxent Wildlife Research Center, Laurel, MD) using occupancy and detection probability estimates from my previous analysis (Table 1). I assigned the first group of sites a 0.78 occupancy probability (see Table 1) and calculated a 25% decrease

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in occupancy for the second group ($\hat{\psi}_2 = 0.59$). The estimated number of sampling sites was split evenly between each group. Using the Program MARK (White and Burnham, 1999), I compared a null model (H_0) that assumed occupancy was constant between the 2 groups to an alternative model (H_a) that allowed occupancy to vary between groups. I considered H_a as the true model, as my simulated data were generated using a separate occupancy estimate for the two groups. I compared both models using a likelihood ratio test (LRT) in MARK (White and Burnham, 1999) and approximated power (Burnham et al., 1987:214-217; Bailey et al., 2007) using the chi-square statistic from the LRT output.

2.3. Results

Natural cover object and leaf litter surveys took an average of 16.3 ± 0.9(SE) and 42.6 ± 1.6 minutes to complete at each sub-plot, respectively. I searched through an average of 21.1 ± 1.2 and 10.9 ± 1.2 NCOs during the NCO and leaf litter surveys, respectively. Natural cover object searches yielded slightly higher detection estimates than leaf litter searches; however, both methods had overlapping 95% confidence intervals (95% CI; Table 1). For all analyses naïve occupancy (proportion of sites known to be occupied, without accounting for imperfect detection) was smaller than occupancy estimates adjusted for imperfect detection (Table 1). Site occupancy estimates from the 'single-method' and 'combined' datasets had overlapping 95% CI, suggesting low bias in occupancy estimation for either method (Table 1).

Modeling results were counter to my *a priori* predictions for both method-specific analyses. For the NCO analysis, the detection model containing the COVER covariate received virtually no support when compared to the model including the TIME covariate (Table 2). The positive beta parameter estimate for TIME indicated that salamander detection probability increased with survey duration ($\hat{\beta}_{Time} = 1.46 \pm 0.42$; Figure 2.1). For the leaf litter analysis, the

model containing COVER received the strongest support, with salamander detection probability decreasing as the number of searched NCOs increased ($\hat{\beta}_{Cover} = -0.77 \pm 0.39$; Figure 2.2). I found little support for the amount of search time influencing salamander detection probability during leaf litter surveys ($\Delta AIC_c = 6.56$, $w_i = 0.04$; Table 2). I found no evidence that removal of salamanders during the NCO searches negatively impacted my ability to detect salamanders during the leaf litter searches ($\Delta AIC_c = 17.06$, $w_i = 0.00$). The beta parameter for the REMOVAL covariate was positive, suggesting I was more likely to detect *P. cinereus* during a leaf litter survey if I removed at least one salamander during the NCO survey ($\hat{\beta}_{Removal} = 0.80 \pm 0.56$). COVER and TIME were weakly correlated for the NCO surveys ($r = 0.31$, $t_{82} = 2.96$, $P = 0.004$), but not for leaf litter surveys ($r = -0.06$, $t_{79} = 0.05$, $P = 0.61$).

Ranking for the 'multi-method' analysis indicated model selection uncertainty between the NULL and METHOD detection models (Table 2). Although NULL was my top supported model, the second best model, METHOD, received 32% of the total model weight and was <2 AIC_c from the top model (Table 2). However, estimated detection probabilities for both sampling methods in the METHOD model overlapped considerably (95% $CI_{NCO} = 0.45\text{-}0.69$, and 95% $CI_{Leaf\ litter} = 0.37\text{-}0.61$). This finding, combined with results from the individual NCO and leaf litter survey analyses, suggest NCO and leaf litter searches yielded comparable occupancy and detection estimates for *P. cinereus*.

There was substantial variation in the ability of either sampling method to detect a 25% change in salamander site occupancy (Table 3). Approximated power values for NCO and leaf litter surveys were 76% and 5%, respectively ($\alpha = 0.05$).

2.4. Discussion

My results show that NCO searches are a more cost-effective method than leaf litter searches for detecting *P. cinereus* in harvested aspen stands. Counter to my prediction, the use of two sampling methods only slightly improved the precision of occupancy estimates for *P. cinereus*. Both methods performed well in their ability to detect *P. cinereus*; however, my field crew and I could conduct ≈3 NCO surveys in the time required to complete one leaf litter survey. Hence, leaf litter searches merely provided redundant detection information at a substantial time cost. Because most herpetological field studies operate on a finite time budget and limited sampling size, it is important to understand how sampling method(s) may affect statistical power, and ultimately scientific inference (Smith and Petranka, 2000; Bailey et al., 2007). My simulation study revealed that leaf litter searches yielded surprisingly low power for detecting a 25% change in salamander occupancy between two groups of sites, largely because of low sample size. Hence, even though leaf litter searches may generate reliable occupancy and detection estimates, the time required to conduct them limited the number of sites that could be visited during a simulated field season, which increased my probability of making a Type II Error (Sokal and Rolf, 1981:159-169). The higher approximated power for NCO surveys was because of the large number of sampling sites that could be visited, while still providing relatively high *P. cinereus* detection probabilities.

Counter to my prediction, I found little support for the model testing the influence of the number of searched cover objects on detecting *P. cinereus* during NCO surveys. Coarse woody debris provides ideal micro-habitat conditions for *P. cinereus* and is an important structural component for recovering salamander populations in harvested forests (*e.g.,* McKenny et al., 2006, Owens et al., 2008). Therefore, I predicted that searching more cover objects should yield

a higher probability of detection. Rather, model selection statistics revealed strongest support for the NCO survey model that included survey duration on salamander detection. For my study the number of searched NCOs ranged from 15 to 112, which may be above the minimum number of cover objects required to affect detection probability. Furthermore, large, well-decayed logs required considerable time to search through, but only counted as single NCO in my analysis. This potentially explains why my TIME model received more support than COVER. Future analyses should explore how NCO size and decay-class influences salamander detection.

Counter to my predictions, the leaf litter analysis revealed *P. cinereus* detection was negatively correlated with the number of searched NCOs. Some of my sites contained 1 to 2m^2 piles of woody debris fragments (i.e., slash piles), which may explain the high number of NCOs found during the leaf litter surveys at these sites. These slash piles were difficult to search through and likely hindered my ability to detect salamanders. I found little support for the model containing survey duration on salamander detection probability during the leaf litter surveys. At this time it is not clear why spending additional search time may improve *P. cinereus* detection during NCO surveys, but not during leaf litter surveys.

My generated parameter estimates are specific to the methodologies I used and are subject to change depending on sampling protocol or study organism. For example, in my study observers conducting NCO searches thoroughly dismantled all rotting logs, which likely resulted in higher detection probabilities than if observers rolled them over. Dismantling logs may not be appropriate for other studies where sites need to be revisited or when dealing with species of conservation concern (e.g., Flint and Harris, 2005; O'Donnell et al., 2009). The invasiveness of NCO searches in previous terrestrial salamander studies varies from totally dismantling cover objects (O'Donnell et al., 2009; Kluber et al., 2008; this study) to merely turning them over

(Bailey et al., 2004a; McKenny et al., 2006; Strain et al., 2009). At this time it is unclear how the rigor of NCO searches may impact salamander population or detection estimates. Furthermore, my results show that some *P. cinereus* reside in the leaf litter, hence conducting only NCO surveys may lead to an incorrect characterization of site occupancy at sites lacking NCOs. This is an important point of consideration for research conducted in areas with low numbers of NCOs.

Time investment and statistical power are two factors that researchers must consider when selecting a method(s) for herpetological research (Smith and Petranka, 2000; Mattfeldt et al., 2009; Strain et al., 2009). I found NCO surveys were a more cost-effective method than leaf litter searches for estimating *P. cinereus* site occupancy and detection probabilities and, as a consequence, yielded greater statistical power. For both of my methods, detection probability was consistently <1, which highlights the importance of accounting for imperfect detection. Whether using the proportion of sites occupied or abundance as the state variable, herpetologists should consider how imperfect detection probability may bias results (Mazerolle et al., 2007). Furthermore, models developed by MacKenzie et al. (2006) and Nichols et al. (2008) provide a flexible framework for addressing potential biases associated with sampling methodology.

2.5. Acknowledgements

sampling and handling protocol used in this study were approved by the Michigan State

University Animal Care and Use Committee (AUF# 07/08-118-00).

Table 2.1. Parameter estimates for occupancy ($\hat{\psi}$) and detection probabilities ($\hat{p}$) for Red-backed Salamanders using natural cover object (NCO) and leaf litter surveys at 30 sites in northern Michigan, 2009 (95% confidence interval in parentheses). ψ(obs) is the proportion of sites occupied without accounting for imperfect detection. All parameters were estimated from a model assuming constant occupancy and detection probabilities.

Survey method	$\hat{p}$	ψ(obs)	$\hat{\psi}$
NCO survey	0.59 (0.45-0.72)	0.70	0.75 (0.53-0.89)
Leaf litter survey	0.49 (0.34-0.65)	0.67	0.77 (0.48-0.91)
Combined methods	0.77 (0.65-0.86)	0.77	0.78 (0.59-0.89)

Table 2.2. Ranking of candidate models for Red-backed Salamanders detected using natural

cover object (NCO) and leaf litter surveys at 30 sites in northern Michigan, 2009. Detection

covariates include the number of searched NCOs (COVER), survey duration (TIME) and survey

type (METHOD). The NULL model assumes detection probability was constant across all sub-

plots. 'Multi-method' includes data from both surveys types. For all models, occupancy was

held constant between sites. Weight (w_i) and K represent the probability that model i is the best

in the candidate set and number of estimated parameters, respectively. Logit-link parameter

estimates are provided for the detection portion of each model ($\hat{\beta}_0$ = detection intercept estimate,

$\hat{\beta}_1$ = detection covariate estimate).

Table 2.2. (cont'd)

Model	AIC_c	ΔAIC_c	w_i	K	$\hat{\beta}_0$ (SE)	$\hat{\beta}_1$ (SE)
NCO surveys						
TIME	98.26	0.00	1.00	3	0.13 (0.36)	1.46 (0.42)
COVER	112.84	14.58	0.00	3	0.41 (0.32)	0.33 (0.31)
NULL	121.32	23.06	0.00	2	0.37 (0.30)	-
Leaf litter surveys						
COVER	104.14	0.00	0.96	3	−0.60 (0.42)	−0.77 (0.39)
TIME	110.73	6.59	0.04	3	−0.51 (0.39)	0.61 (0.29)
NULL	120.46	16.32	0.00	2	−0.03 (0.32)	-
Multi-method						
NULL	227.15	0.00	0.67	2	0.12 (0.18)	-
METHOD	228.59	1.44	0.33	3	−0.05 (0.24)	0.35 (0.34)

Table 2.3. Parameter estimates used to simulate a 25% change in salamander occupancy probability and power approximations (Burnham et al., 1987:214-217; Bailey et al., 2007) for detecting the simulated change between two groups of sites using natural cover object (NCO) or leaf litter surveys. Occupancy ($\hat{\psi}$) and detection probability ($\hat{p}$) estimates were generated from Table 1, while the maximum sample size ($\hat{n}$) was estimated from my field data. Approximated power is the chance that the false null hypothesis (*i.e.,* no difference in the occupancy probability of ψ_{g1} and ψ_{g2}) was correctly rejected.

| | Parameters used for simulation | | | | Power approximation (H_a vs H_0) | | | |
Sampling method	$\hat{\psi}_{g1}$	$\hat{\psi}_{g2}$	$\hat{p}$	$\hat{n}$	χ^2	df	Power ($\alpha = 0.05$)	Power ($\alpha = 0.01$)
NCO survey	0.78	0.59	0.59	180	6.2	1	70%	47%
Leaf litter survey	0.78	0.59	0.49	60	0.0	1	5%	1%

Figure 2.1. Estimated detection probability for Red-backed salamanders modeled as a function
of survey duration during natural cover object surveys in northern Michigan, USA, 2009.
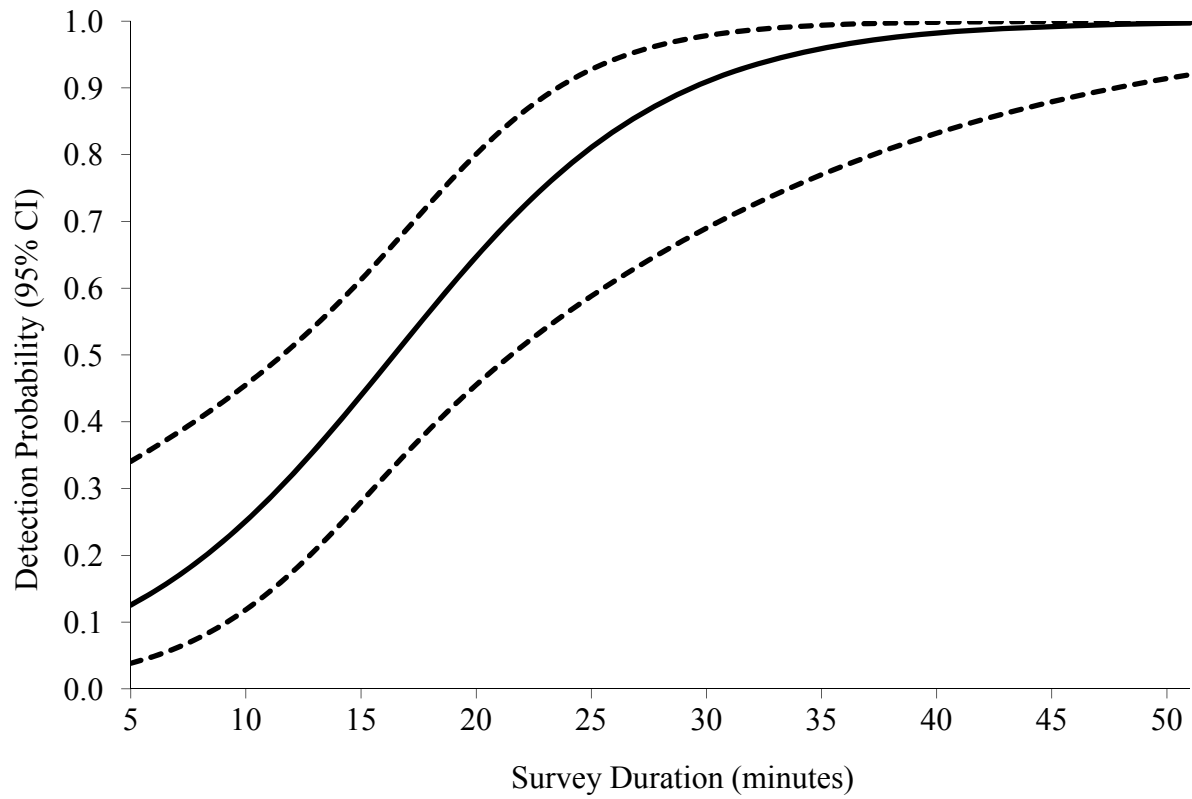
Figure 2.2. Estimated detection probability for Red-backed Salamanders modeled as a function of the number of cover objects that were searched through during leaf litter surveys in northern Michigan, USA, 2009.
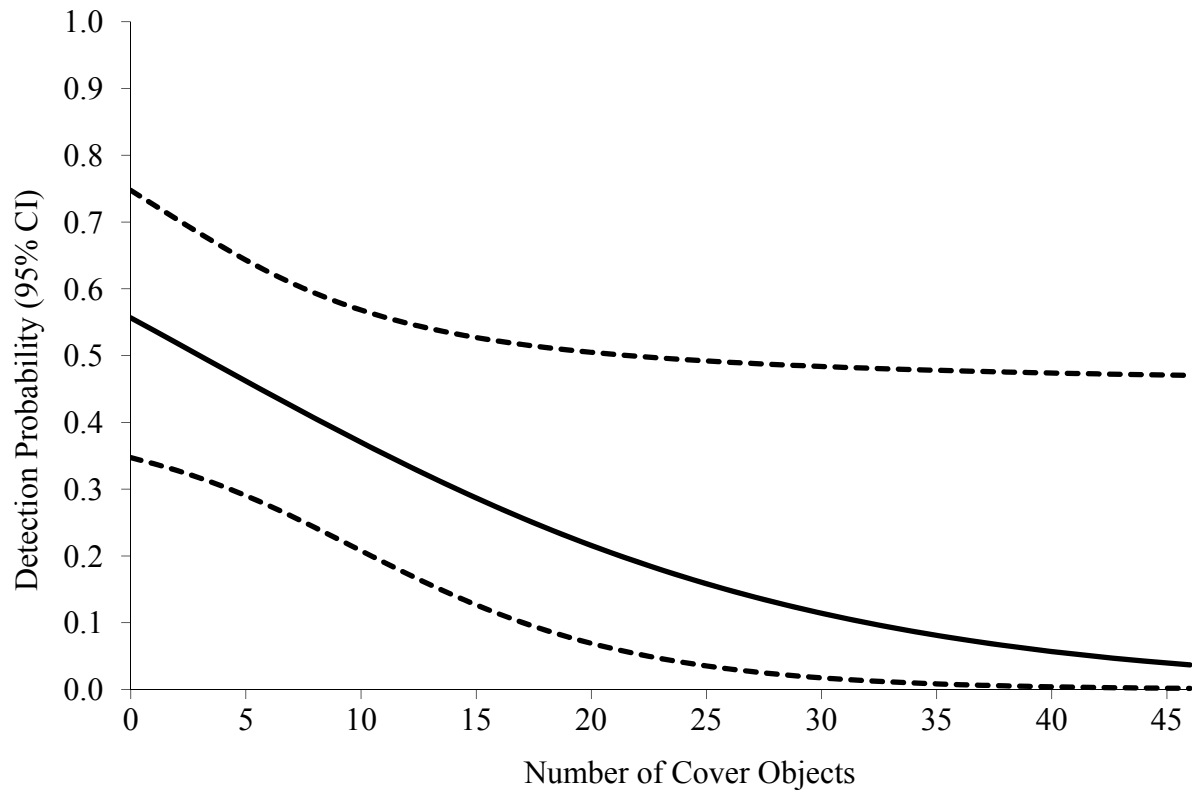
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CHAPTER 3

IMPROVING OCCUPANCY ESTIMATION WHEN SAMPLING DISTURBANCES AND ANIMAL MOVEMENTS VIOLATE THE CLOSURE ASSUMPTION

Abstract

Site occupancy models that account for species imperfect detection are increasingly utilized in ecological research and wildlife monitoring. Occupancy models require replicate surveys to estimate detection probability over a time period where the occupancy status at sampled sites is assumed closed (*i.e.,* no changes in occupancy due to local extinction or colonization). Unlike mark-recapture models, few studies have examined how violations of closure can bias occupancy estimates. My study design allowed me to differentiate among two processes that violate the closure assumption during a survey season: 1) repeated destructive sampling events that result in either short- or long-term site avoidance by the target species and 2) sampling occurring over a time period during which non-random movements of the target species result in variable occupancy status. I used dynamic occupancy models to quantify the potential bias in occupancy estimation associated with these processes for a terrestrial salamander system. I sampled 126 transects repeatedly within a single field season using invasive sampling techniques and constructed 17 candidate models that portrayed different sources of variation in occupancy, extinction, and detection probabilities. Model ranking indicated that both repeated sampling and non-random movement of organisms were evident in my system. I observed a chronic decrease in occupancy associated with cumulative sampling and non-random salamander movements over the entire field season. I also observed a strong but temporary disturbance effect on salamander detection probability associated with repeated sampling within a 24-hr. period. I generalized my findings by conducting a simulation to evaluate how violations of closure can bias occupancy

estimates when organism availability declines within a field season (*i.e.,* when local extinction

occurs within the season). My simulation study revealed general sensitivity of estimates from

single-season occupancy models to violations of closure, with the strength and direction of bias

varying between scenarios. Bias was minimal when extinction probability or the number of

sample occasions was relatively low. My research highlights the importance of addressing

closure in occupancy studies and I provide multiple solutions, using both design- and model-

based frameworks, for minimizing bias associated with non-random changes in occupancy and

repeated sampling disturbances.

Keywords: amphibian, detection probability, dynamic occupancy, extinction, multi-season,

Plethodon cinereus, salamander, sampling bias, simulation.

Status: This manuscript has successfully made it through the first round of reviews in Ecography.

Revisions are ongoing.

3.1 Introduction

Site occupancy models that account for species imperfect detection are increasingly utilized in

ecological research and conservation planning (Marsh and Trenham 2008). For example,

occupancy models have been used to assess the effects of anthropogenic disturbances on species

distributions (Ferraz et al. 2007, Kroll et al. 2008, Zuckerberg et al. 2011), determine the efficacy

of wildlife monitoring programs (Mattfeldt et al. 2009, Collier et al. 2010, Weller 2008), and

investigate species habitat selection (Seamans and Gutierrez 2007). Occupancy models are

generally preferred over traditional logistic regression or incidence function models because of

their ability to account for false-absences caused by imperfect species detection (Mazerolle et al.

2005, MacKenzie et al. 2006). Although a number of occupancy models have been developed to

account for imperfect detection (*e.g.,* Giessler and Fuller 1987, MacKenzie et al. 2002, Nichols

and Karanth 2002, Tyre et al. 2003), the model developed by MacKenzie et al. (2002) has been the most readily adopted and numerous extensions of this model are available for use (reviewed in MacKenzie et al. 2006, Nichols et al. 2008, Martin et al. 2010).

To account for false absences, the MacKenzie et al. (2002) occupancy model uses detection and non-detection data collected during multiple site surveys to estimate species detection probability. These repeated surveys are typically performed within a time period where sites are assumed to be closed to changes in occupancy (*i.e.,* 'closure' implies no local extinction or colonization; MacKenzie et al. 2002). If the species is detected during a survey within a period where closure is assumed, the site is considered occupied. Hence, surveys at occupied sites that did not result in positive detection within a closed period can only be caused by imperfect detection (*i.e.,* false-absences, false-zeros). Failure to detect the target species at a site within a closed period could result from true species absence or the species was present, but undetected during all sampling events.

Investigators must use knowledge of the species biology to inform the study design with respect to the closure assumption (MacKenzie et al. 2006:104-106). In this regard occupancy studies share a similar sampling framework with mark-recapture research, which require repeated samples to estimate detectability of individual organisms within a closed period (Williams et al. 2002). Unlike mark-recapture research, however, relatively little is known about how violations of the 'closure assumption' can bias occupancy or detection estimates (but see Rota et al. 2009). Here I evaluate how the physical act of repeated sampling and seasonal changes in occupancy status result in bias if closure is assumed within a field season.

The physical act of sampling may bias occupancy or detection estimates if destructive techniques are used or if sampling alters the behavior of the target species during subsequent

sampling events. Altered organism behavior as a consequence of sampling is typically referred to as a 'trap-response' in mark-recapture literature and multiple models have been developed to account for its potential bias (Zippin 1956, Otis et al. 1978). However, bias resulting from a 'trap-shy' response has not been tested in occupancy research. Furthermore, it is unknown to what degree invasive sampling techniques, which are often utilized for sampling cryptic species such as amphibians, reptiles and birds, can bias occupancy and detection estimates if not properly accounted for (Marsh and Goicochea 2003, Pike et al. 2010, Manning and Kaler 2011). Here, sampling can be viewed as an anthropogenic disturbance where the organism's habitat or behavior is altered as a byproduct of investigators gathering species detection information. Examples of commonly used invasive sampling techniques include natural (*i.e.,* rocks, logs, leaf-litter) or artificial (*i.e.,* wooden boards, sheet metal) cover object surveys for herpetofauna (reviewed in Dodd 2010) and intensive monitoring at avian nest sites or territories (Bolduc and Guillemette 2003, Manning and Kaler 2011).

Occupancy studies are often conducted over time periods (*e.g.,* weeks, months) where it may be inappropriate to assume closure for some species. For example, sampling often occurs during the breeding season for many species (*e.g.,* pond-breeding amphibians, migratory birds, spawning fish). If the species synchronously arrives to all sites and sampling events correspond to this time period, then the closure assumption is likely met. However if organism arrival or departure is asynchronous, or if sampling events do not correspond to the time period when occupancy is static, the resulting non-random process of species availability may cause bias in occupancy estimates obtained via single-season occupancy models (MacKenzie et al. 2002, MacKenzie et al. 2006). Thus, identifying the appropriate time-scale for assuming closure requires investigators to incorporate knowledge of species phenology and movement ecology

into the sampling design (MacKenzie et al. 2006). Unfortunately, planning for field studies is often based on convenient calendar dates (*e.g.,* single month, field season, or year) rather than the ecology of the target organism (Rota et al. 2009). Past research has highlighted the importance of accounting for violations of closure in mark-recapture research (*e.g.,* Schwarz and Stobo, 1997, Kendall 1999, Kendall and Bjorkland 2001); however, I am aware of only one study that investigated occupancy bias resulting from violations of closure within a single field season. Rota et al. (2009) found substantial bias in songbird occupancy estimates when failing to account for violations of closure over sampling periods that are typical of ornithological research (*i.e.,* spring and summer within a single year).

I used a sampling design that allowed me to evaluate potential changes in site occupancy for a terrestrial salamander during a time period what would normally be considered a single sampling season (*i.e.,* data analyzed using a single-season model; MacKenzie et al. 2002). Specifically, I determined if repeated sampling events caused a chronic decrease in red-backed salamander (*Plethodon cinereus*) occupancy during the sampling season, or if sampling only caused a temporary reduction in availability of salamanders that persisted for a short time following a sampling event. I also investigated whether species occurrence changed within the season due to natural processes, like seasonal movement, and its influence on occupancy estimates obtained from single-season models. I generalized my findings by conducting a simulation study to evaluate the sensitivity of occupancy estimates to general violations of closure when failing to account for local extinction occurring within a season. I use my results to develop design- and model-based recommendations for minimizing bias caused by animal movements or sampling disturbances.

3.2 Methods

3.2.1 Study Area

I conducted my study in the Cadillac-Traverse City area in the northwestern Lower Peninsula of Michigan, USA, in 2009. This area is characterized as a glacial outwash plain with porous, sandy soils (Albert 1995). Temperate coniferous forests dominated this landscape prior to European settlement, but have since been replaced by hardwoods. My study occurred on state-owned forest lands that are currently managed for aspen (*Populus* sp.) production and have a history of timber harvest. I sampled three forest stands that were 5-8 years post-harvest and 15-28 ha in size. Dominate understory woody plants were aspen, red maple (*Acer rubrum*), and blackberry (*Rubus* spp.).

3.2.2. Site Selection

I used a two-step approach to select sample sites (*i.e.,* transects). First, I used HAWTH'S TOOLS (Hawth's Tools, version 3.27, http://www.spatialecology.com/htools/, accessed 1 Feb 2009) in a Geographic Information System (ArcGIS 9.1; Environmental Systems Research Institute, Redlands, CA) to overlay each aspen stand with a sampling lattice comprised of 60 x 60 m cells (Figure 3.1). I minimized potential heterogeneity in salamander occupancy from local landscape factors by eliminating all lattice cells whose borders intersected or encompassed an unharvested forest edge, active logging road, off-road recreational vehicle trail, or wetland appearing on 2005 National Agricultural Imagery Program imagery (Michigan Department of Information Technology 2007). I considered all remaining lattice cells as potential sampling locations and randomly selected seven within three aspen stands (*i.e.,* 21 total cells). All selected cells were spaced ≥60 m apart. I assumed that habitat conditions known to affect red-backed salamander occurrence were relatively constant within each 60 x 60m cell (*e.g.,* amount and type of forest, elevation) with the exception of the number of natural cover objects (NCO) along each

transect. I felt this assumption was reasonable because each forest stand was clearcut 5-7 years ago, possessed similar vegetation characteristics, and had little topographic relief.

Second, I systematically placed six, 20 x 2m natural cover object (NCO) transects within each 60 x 60m cell (Figure 3.1). Each transect was assigned to one of three transect "groups", which dictated when salamander sampling would be initiated: early May (Group 1), mid-June (Group 2), or late July (Group 3). Terrestrial salamanders, almost exclusively red-backed salamanders, are active and available during this period (Petranka 1998, Otto and Roloff 2011), and thus, investigators would normally assume closure. Group 1 transects were oriented east to west, at the north and south ends of each cell. Group 2 transects were oriented north to south, at the east and west ends of each 60 x 60 m cell. I randomly selected, without replacement, which cardinal direction the two transects in Group 3 faced. I positioned all transects in the third group 5 m from, and running parallel to, transects Groups 1 or 2 (Figure 3.1). This design provided three groups of 42 independent transects (n = 126 transects). Grouping transects in this fashion allowed me to determine if salamander occupancy was influenced by repeated sampling disturbances or if occupancy varied across time within a single field season due to organism non-random movements. Each transect represented an independent site in my analyses.

I sampled all transects within an aspen stand twice in a 24-hr period (*i.e.,* two surveys), allowing me to use a dynamic occupancy model to formally test the closure assumption over a time period that closure would normally be assumed. Under this approach, the two surveys within 24-hr constituted a "single-season" (hereafter "primary period": MacKenzie et al. 2003). For each survey, one observer searched for red-backed salamanders under cover objects >4 cm diameter, >15 cm long, and within 1 m of the transect centerline. I ensured that the same observer did not survey the same transect twice in a single primary period. Observers recorded

70

the number of cover objects they searched and released all salamanders at the point of capture.

Observers replaced all intact cover objects to their original point of origin and reconstructed

fragmented cover objects to the best of their ability. After conducting two surveys within 24

hrs., observers revisited each transect 7-10 days later and continued sampling in this fashion until

transect Groups 1 and 2 were surveyed 14 and 12 times, respectively (*i.e.,* 7 and 6 primary

periods). I surveyed Group 3 transects, four times (*i.e.,* 2 primary periods). My sampling and

handling protocols were approved by the Michigan State University Animal Care and Use

Committee (Animal Use Form no. 07/08-118-00).

3.2.3. Model Development and Analysis

I generated detection histories of red-backed salamanders for each transect. I coded detection

histories so that each primary period represented the same calendar days for all transect groups.

For example, detection histories for transects in each of the respective groups could include:

Group1-Transect1   10 11 10 00 00 00 00 -- --,

Group1-Transect2   11 10 00 11 10 01 00 -- --,

Group2-Transect3   -- -- -- 11 01 00 00 00 01,

Group2-Transect4   -- -- -- 00 01 11 00 00 00,

Group3-Transect5   -- -- -- -- -- -- -- 01 00,

Group3-Transect6   -- -- -- -- -- -- -- 11 10,

where "1" represents a positive detection of at least one red-backed salamander during a single

survey, "0" represents non-detection, and "-" represents a missing value, indicating that the

transect was not surveyed. At Group1-Transect1, an observer detected $\geq$1 red-backed

salamander during the first survey of the first primary period, but failed to detect a salamander

during the second survey. During the second primary period (*i.e.,* 7-10 days later), $\geq$1

salamanders were detected during both surveys. During the third primary period the species was detected during the first survey, but not the second. Observers did not detect salamanders during the fourth, fifth, sixth, or seventh primary periods and the transect was not sampled during the final two primary periods (*i.e.,* not surveyed in July). Non-detections of salamanders during primary periods 4-7 could arise from (1) failure of the observer to detect red-backed salamanders when the transect (site) was occupied (*i.e.,* false negative, false zero) or (2) localized extinction that resulted in the site becoming unoccupied, which would violate the closure assumption if it was applied to the entire sampling season.

MacKenzie et al. (2003) developed 3 parameterizations for the dynamic occupancy model. I used the parameterization that allows direct estimation of time-specific occupancy and extinction probabilities ($\psi(t)$, $\varepsilon(t)$) to test 3 hypotheses regarding possible changes in salamander occupancy and extinction probability over time. These hypotheses are common to any species that is seasonally available or may be influenced by the sampling process. First, I considered a hypothesis where occupancy (ψ) remained static over time, but varied as a function of the number of cover objects along a transect (ψ(Cover), and no site extinction ($\varepsilon(=0)$) occurred throughout the duration of my study (see below for a description of COVER). Support for this hypothesis would suggest the closure assumption was not violated thereby permitting use of a single-season model to fit data from the entire sampling season (MacKenzie et al. 2002); ψ(Cover),$\varepsilon(=0)$). I considered this my null hypothesis for comparison to dynamic occupancy hypotheses that included the processes causing changes in occupancy and extinction probabilities within the sampling season.

I hypothesized that changes in occupancy within my sampling season could result from the displacement of individuals (cumulative sampling hypothesis) caused by the cumulative

effects of repeated sampling or from natural processes of salamanders moving underground during warmer, drier months (seasonal movement hypothesis). I represented my cumulative sampling hypothesis by including a DISTURBANCE parameter that reflected the total number of times a transect was surveyed prior to primary period i (*e.g.,* for a model with a ψ(Disturbance), ε(Disturbance) structure, occupancy probability at time i is modeled as logit(ψ_i) = β_0+ β_1(Number of surveys prior to i), and extinction as logit(ε_i) = β_2+ β_3(Number of surveys prior to i)). A competing hypothesis is that the seasonal availability of salamanders under cover objects may naturally decrease over summer, leading to local extinction and decreasing occupancy estimates during later primary periods (seasonal movement hypothesis). Support for this hypothesis is based on observations of directional salamander movement from underneath cover objects to the leaf-litter and subterranean refugia to escape desiccation as summer progresses (Taub 1961, Heatwole 1962). To represent this hypothesis, I developed a TREND model structure to allow occupancy and extinction to vary linearly across time (*e.g.,* for a model with a ψ(Trend), ε(Trend) structure, logit(ψ_i) = β_0+ β_1(i-1), logit(ε_i) = β_2+ β_3(i-1)). I hypothesized that DISTRURBANCE and TREND could operate independently, or as additive effects on both occupancy and extinction probabilities (*e.g.,* ψ(Disturbance+Trend), ε(Disturbance+Trend)).

In addition to my three primary hypotheses, I also believed that occupancy would be higher for transects with a greater number of cover objects because of the increased availability of refugia (McKenny et al. 2006). I modeled cover objects as a continuous covariate; however, these models had poor convergence, likely due to a heavily right-skewed distribution of cover object numbers. Therefore, I classified transects as having either high (>20 cover objects) or low

(≤20 cover objects) levels of cover and included COVER as a categorical covariate on occupancy and extinction (*e.g.,* ψ(Cover), ε(Cover)). Ranking of my top-five models did not change when using COVER as a categorical versus continuous covariate. I used cover object tallies from my first four surveys to quantify COVER for each site because repeated disturbances resulted in fragmented cover objects, thereby inflating my counts.

I explored whether salamanders were temporarily affected by NCO disturbances by fitting models where: (1) detection probabilities were set equal between the first and second surveys within a primary period (*i.e.,* within the same 24 hours; p(.)) and (2) detection probabilities varied between the two surveys, anticipating lower detection probability during the second survey (p($1^{st}\_2^{nd}$)). For these models I assumed that detection probability was constant among primary periods (*i.e.,* p(.,.) and p(.,$1^{st}\_2^{nd}$). Although my current study design does not allow me to infer a mechanism, it is reasonable to suspect that sampling temporarily disrupts the microhabitat beneath cover objects, resulting in salamanders avoiding these areas, or temporarily emigrating, during the second survey within each primary period (Kendall 1999). I considered this a site-effect that would occur regardless of whether red-backed salamanders were actually detected during the first survey, given they were present within the primary period.

Incorporating the hypotheses described above I developed a candidate model set consisting of 17 models (Table 1). First, I fit three models consistent with the closure assumption for the entire sampling season: 1) ψ(Cover), ε(=0), p(.,.), 2) ψ(Cover), ε(=0), p(.,$1^{st}\_2^{nd}$) and 3) ψ(Cover), ε(=0), p(t). These models assume static occupancy for the entire sampling season, but allow variation among high and low cover transects. The first closed model assumed detection probability is constant throughout the sampling season, the second model allows detection

probability to vary between surveys conducted with 24 hours, the third model allows detection to

vary for every survey occasion. Next, I fit models that relaxed the closure assumption and

allowed occupancy and extinction probability to vary within my sampling season as a function of

TREND, DISTURBANCE or COVER and the associated additive combinations of these

covariates. I believed that if these covariates were influential in my salamander system that

occupancy and extinction probability would both be affected. For each occupancy and extinction

structure I fit models where detection probability was constant (p(.,.)) or varied between the first

and second surveys within a primary period (p(.,1st_2nd)) .

I analyzed my data using Program MARK (MARK, version 5.1,

http://www.cnr.colostate.edu/~gwhite/mark/mark.htm, accessed 07 July 2010) and used Akaike's

Information Criterion, adjusted for small sample size (AIC$_c$), to rank models (Burnham and

Anderson 2002). I used cumulative AIC weights (w_+) and evaluation of 95% confidence

intervals to determine relative importance of covariates and model parameters. I report model

averaged estimates and unconditional 95% confidence intervals for all real parameters. Relative

bias in occupancy estimates was calculated as ($\hat{\psi}_{closed} - \hat{\psi}_{int}$)/ $\hat{\psi}_{int}$) where $\hat{\psi}_{closed}$ is

estimated occupancy probability for my AIC 'best' model that assumes closure and $\hat{\psi}_{int}$ is the

estimated probability for my 'best' dynamic model during primary period 1 (Bailey et al. 2007).

3.2.4. Simulation Study

To generalize my field study findings, I evaluated the sensitivity of single-season occupancy

models to violations of the closure assumption by quantifying bias for scenarios where local

extinction occurs within a primary period. Here, I envision a general sampling situation where

occupancy of the species of interest declines throughout the sampling season, however, the

investigator wrongfully assumes the system is closed and uses a single-season occupancy model

for data analysis. I used a dynamic occupancy framework to generate expected values and then

fit the data using a single-season occupancy model. This approach allowed me to assess bias

when multi-season data, which violate the closure assumption, were fit to single-season

occupancy models (see Bailey et al. 2007 for more details and associated software). I considered

cases with either high or low initial occupancy probabilities ψ_{int} (= 0.7, 0.4) and moderate or

low detection probabilities (p(.) = 0.4, 0.2). For each combination of ψ_{int} and p I allowed

extinction probability (ε) to vary between 0.0 and 1.0 between each primary period, which

consisted of two independent surveys. Although the focus of my simulation was on extinction, I

also considered two colonization probabilities that reflect my study system and may be realistic

for biological systems experiencing a chronic decrease in occupancy over time (γ = 0.0, 0.05).

For all simulations I considered designs with two or four primary periods (S) and two

surveys (x) within each primary period for N = 150 sites. Here, occupancy state is allowed to

change via local extinction and colonization between primary periods only. These simulations

mimic traditional sampling designs with a single observer for each site survey, similar to my

salamander data, where the total number of independent surveys (T) is equal to $S \times x$. I used a

dynamic occupancy structure ($\psi(.)_{int}$, $\gamma(.),\varepsilon(.),p(.)$; MacKenzie et al. 2003), and known

parameter values for ψ_{int}, γ, ε, p, S, and N, to generate expected values for all possible

detection histories in Program GENPRES (Bailey et al. 2007, GENPRES, version 3.0,

http://www.mbr-pwrc.usgs.gov/software/presence.html, accessed 29 March 2011). I analyzed

these expected values data to approximate bias and precision via an analytic-numeric approach

(Burnham et al. 1987) using a closed occupancy model where T was equal to $x \times S$. I fit two

single-season models to each set of expected values, one model where detection probability was

held constant $(\psi(.), p(.))$ and a second model that allowed detection probability to vary across all surveys $(\psi(.), p_t)$. The second model was included because MacKenzie et al. (2006, p. 104-106) suggested that a time-dependent model may reduce bias caused by violations of closure. I calculated relative bias as $(E(\hat{\psi}) - \psi_{int})/\psi_{int})$ where $E(\hat{\psi})$ is the estimated occupancy probability from my closed models fit to each expected value data set and ψ_{int} is the 'true' initial occupancy value used to generate these data.

3.3. Results

3.3.1. Salamander Field Study

The closure assumption over my sampling season was clearly not supported by the field data; the three models with constant occupancy and no extinction probability (*i.e.,* closed models) received no weight and AIC values were ≥ 29 units greater than my best models. Occupancy bias for my best static model (ψ(Cover), ε(=0), p(t)) was -0.30 and -0.08 for low and high quantities of COVER, respectively, when compared to estimates for my 'best' dynamic model (ψ(Disturbance+Trend+Cover), ε(Disturbance+Trend+Cover), p(.,1$^{\text{st}}$_2$^{\text{nd}}$)). Model selection results also revealed strong support for a cumulative sampling effect that resulted in decreased occupancy estimates over a sampling season (*i.e.,* DISTURBANCE effect, $w_+ = 0.99$; Table 1 and 2). For example, among transects in the high COVER category, model averaged occupancy estimates in early June were $\approx 47\%$ higher for transects in Group 2, which had never been previously surveyed, when compared to Group 1 transects (previous surveys = 6; Figure 3.2A). I also found evidence of cumulative sampling resulting in increased extinction probability; however, estimates were imprecise (Figure 3.3)

I also found strong support for models containing the TREND covariate ($w_+ = 0.87$;

Table 1 and 2) with occupancy estimates decreasing across primary periods for all transect

groups (Figure 3.2). Among transects in the high COVER category, model averaged estimates of

occupancy in May (Group 1) were ≈39% higher than those transects initiated in July (Group 3;

Figure 3.2A). Extinction probability also increased between later primary periods; however,

estimates were imprecise (Figure 3.3). Collectively, my results provide strong evidence of a

chronic disturbance effect associated with cumulative NCO surveys and seasonal decreases in

salamander occupancy. I also found evidence that cumulative sampling disturbances and

sampling later in the field season resulted in increased site extinction probabilities, although

associated estimates were imprecise.

Model selection results revealed substantial support for a short-term disturbance effect:

models that allowed detection to vary between the 1st and 2nd survey within a 24 hour period

had cumulative model weight $w_+ = 0.94$ (Table 1). As I predicted, detection probability

decreased during the second survey within a primary period ($\hat{p}_{1st} = 0.33$, 95% CI: 0.25 - 0.42;

$\hat{p}_{2nd} = 0.22$, 0.16 - 0.30; Table 2). Lastly, I found strong support for spatial variation in

occupancy and extinction probabilities among transects related to COVER (Table 2): transects

with >20 cover objects had higher occupancy estimates, but also higher extinction estimates,

than those with ≤20 cover objects (Figure 3.2 and 3.3).

3.3.2. Simulation Study

Single-season occupancy models generally showed sensitivity to violations of the closure

assumption, with the strength and direction of bias varying between simulations (Figure 3.4).

For example, when ε was high (*e.g.,* 0.75), $\hat{\psi}$ was typically positively biased for all closed

models regardless of colonization levels. The only exception was when $\gamma = 0.0$ and data were modeled with time-varying detection probabilities $\psi(.), p_t$: here, bias was slightly negative (Figure 3.4E-H). For lower values of ε, bias was generally smaller but the direction of the bias was positive when some colonization also occurred, $\gamma = 0.05$, and was negative when $\gamma = 0.0$. As expected, $\hat{\psi}$ from simulations with four primary periods had greater bias, but smaller standard errors, than those with only two primary periods (Figure 3.4; Appendix A.1). For most simulations the $\psi(.), p_t$ model yielded occupancy estimates that were less biased than the $\psi(.), p(.)$ model; however, there were several situations where the opposite was true. For example, when there were four primary periods, bias for $\hat{\psi}$ was generally greater for $\psi(.), p_t$ than $\psi(.), p(.)$ (Figure 3.4D,G,H). Bias was generally lower for moderate versus low values of p; a pattern that was consistent for all but one simulation (Figure 3.4C). The pattern of bias was nearly identical for both high and moderate levels of ψ_{int} when $\gamma = 0$, but bias was often higher for moderate levels of ψ_{int} when $\gamma = 0.05$.

3.4 Discussion

I explored the potential for bias caused by two processes commonly linked to violation of the population closure assumption in occupancy studies: 1) destructive sampling techniques or 2) sampling occurring over a time period during which organism movements result in variable occupancy status. In these cases the closure assumption is violated, causing bias in occupancy estimates obtained from standard, single-season occupancy models. Consistent with these concerns, I found evidence of a chronic decrease in occupancy, increase in local extinction, and temporary decrease in detection probability, associated with repeated sampling disturbances in my salamander system. I also found evidence for changes in seasonal availability of salamanders that was independent of the sampling process.

Although destructive sampling techniques have been acknowledged as a potential source of sampling bias in occupancy research (Smith and Petranka 2000, Bailey et al. 2004, Otto and Roloff 2011), my research is the first to explicitly test for and quantify sampling disturbance effects. I emphasize this concept by acknowledging that the effects of sampling disturbances can be both short-term and temporary, or long-term and persistent or permanent. My analysis provides evidence that destructive sampling causes short- and long-term effects on salamander detection and occupancy probabilities, respectively. I observed a 31% decrease in detection probability during the second survey within a primary period, suggesting that salamanders temporarily migrated either horizontally (*i.e.,* outside the transect width) or vertically (*i.e.,* into the leaf-litter or soil) following the first NCO survey. These organisms likely returned or were available for capture during subsequent primary periods. Kendall (1999) demonstrated that abundance estimates generated using mark-recapture analyses remain unbiased when temporary emigration occurs, if the variation in detection is modeled and there are only two sampling occasions per primary period. If I apply Kendall's (1999) results to dynamic occupancy models, then my estimates for occupancy should remain unbiased even if the species temporarily leaves the site following a sampling disturbance. Thus, by having only two surveys per primary period, and modeling heterogeneity in detection probability, I able to minimize occupancy bias. This finding is further supported by my simulation results, where little bias (<10%) occurs when the $\psi(.), p_t$ model is fit to scenarios with only two primary periods (S=2).

Importantly, I found evidence of a long-term, persistent sampling effect resulting in a chronic decrease in salamander occupancy and an increase in local extinction probabilities among primary periods. My sampling efforts caused unavoidable fragmentation of woody cover objects and reduced their overall contact with the soil and leaf litter, an outcome which is typical

for NCO surveys (Dodd 2010). My salamander analysis showed that simply modeling variation in detection probability over time (*e.g.,* including Julian data as a detection covariate) was not sufficient for reducing bias in occupancy estimates obtained from single-season models. Furthermore, biases in my simulation study were higher and more variable with more primary periods (S=4), even for the $\psi(.), p_t$ model.

More broadly, a sampling disturbance can be viewed as any act that is initiated by an investigator during the sampling process that results in increased variation, or reduced precision, of a parameter of interest (*e.g.,* occupancy or detection probability). For example, detection probabilities may increase following first detection in cases where baits or lures are used (*e.g.,* carnivore studies, Thorn et al. 2009). A similar effect can occur in volunteer-based monitoring programs when observers anticipate species that they have previously seen or heard at sample sites (Riddle et al. 2010). Alternatively, intensive monitoring at sites could decrease occupancy over time if the repeated presence of an investigator alters organism behavior or increases predation risk (*e.g.,* Bolduc and Guillemette 2003, Manning and Kaler 2011). All these processes create variation in occupancy or detection probabilities, that if not modeled appropriately lead to biased estimates of occupancy parameters. Although my analysis was limited to a single case-study, it highlights the importance of carefully considering model assumptions and sampling design, especially when investigators use invasive sampling techniques to gather species detection information.

In addition to disturbance effects, I observed strong evidence of decreased occupancy across primary sampling periods in my salamander example, presumably due to changes in seasonal availability of salamanders underneath NCOs. A decrease in salamander occupancy across time is supported by past research showing that use of cover objects by red-backed

salamanders decreases with drying soil conditions during summer months (Taub 1961, Heatwole 1962). As summer progresses, a portion of red-backed salamander populations may move underground or into the leaf-litter and are therefore unavailable for sampling using late-season NCO surveys (Bailey et al. 2004, Dodd and Dorazio 2004). Movement of wildlife in response to environmental conditions or seasonal changes in behavior is expected, yet I am aware of only one study that investigated sensitivity of occupancy models to violation of closure when species make non-random movements over the duration of a field study (Rota et al. 2009). This is problematic considering a vast majority of occupancy studies take place over multiple months (*i.e.,* a field season); a timescale where investigators may wrongfully assume closure and use a single-season model to analyze occupancy data. In their study of migratory songbirds, Rota et al (2009) determined that their study sites were likely open to changes in occupancy over timescales typical of other ornithological research. Similarly, my results highlight the importance of addressing closure in occupancy studies, even when sampling relatively sedentary organisms such as terrestrial salamanders.

The effects of both sampling disturbance and seasonal availability in my study resulted in increased local extinction probability and decreased occupancy, with little or no colonization, over the sampling season. This is analogous to emigration-only movement described by Kendall (1999) for assessing bias in mark-recapture models. Consistent with Kendall's (1999) findings, and predictions made by MacKenzie et al. (2006), my simulations revealed that failing to account for permanent species emigration within time periods where closure is wrongfully assumed can result in substantial bias in occupancy estimates. Still, my simulation also revealed situations where occupancy models are relatively robust to closure violations. This was particularly true when extinction probabilities and the number of primary periods were relatively

low. In many field studies local extinction probability may be relatively low within a single field season for non-migratory species in fairly stable habitats, where sampling methods are relatively noninvasive. The closure assumption in these situations may be appropriate. My salamander field study provides an example where local-extinction may be initially low, but dramatically increase later in the field season, and thus require both design- and model-based solutions for minimizing bias. Ultimately, I concur with suggestions made by MacKenzie et al. (2006) and Rota et al. (2009) that investigators should use phenological knowledge of their study species when establishing the length of a primary period and collect data in a manner that allows investigators to formally test for closure if violations are suspect (*e.g.,* use multiple independent observers or successive short-term sampling as demonstrated here).

Interestingly, my simulations provide some scenarios that refute the assertion of MacKenzie et al. (2006) that use of a time-dependent model, $\psi(.), p_t$, should reduce occupancy bias caused by violations of closure. Although occupancy estimates from the $\psi(.), p_t$ model were generally less biased than those from the $\psi(.), p(.)$ model, there were several cases where relative bias was higher for $\psi(.), p_t$. Occupancy estimates from the $\psi(.), p_t$ model showed higher (and negative) bias relative to the $\psi(.), p(.)$ model, for scenarios with moderate levels of extinction probability and no recolonization, especially in longer duration studies (4 primary periods). My values of N, p, ψ_{int}, and γ were chosen to reflect my biological system and are not exhaustive: it is therefore unclear as to how a time dependent model would perform across broader parameter space. My results suggest investigators should exercise caution when using a time dependent model to reduce bias caused by violations of closure and use simulations to investigate nuisances unique to their study systems.

I suggest investigators use design- and model-based approaches to address closure in species occupancy studies. By addressing closure a priori in the design phase, investigators will reduce their dependency on sophisticated modeling to reduce bias attributable to a suboptimal study design. My field and simulation studies suggest that investigators using destructive sampling techniques should minimize the number of repeated site surveys within a primary period (*i.e.,* time period when assuming closure). For example, my simulations revealed that occupancy estimates were generally less biased for single-season study designs with four site surveys compared to designs with eight surveys. This pattern was consistent regardless of whether variation in detection probability was modeled ($p(t)$) or not ($p(.)$). Thus, my salamander field study likely represents an optimal design for minimizing bias associated with temporary sampling effects, as I had only two site surveys per primary period (*i.e.,* season). I also suggest that investigators use phenological knowledge of the target species to develop sampling designs that minimize false absences associated with seasonal movement or availability. For example, when surveying red-backed salamanders, investigators should sample within a single month to minimize bias associated with non-random movements into the subterranean environment (Heatwole 1962, Otto and Roloff 2011), but allow sites >24 hr to recover from sampling disturbances. Limiting the number of repeated surveys to ≤4 within a 3-4 week primary period should minimize bias for my salamander system.   However, if surveys must be conducted over a long time span, or if >4 destructive sampling events must be used, then potential changes in occupancy over time should be accounted for within a dynamic occupancy framework, as I have done here. Investigators may also consider using spatial sub-sampling to avoid temporal bias in occupancy studies; however, spatial sub-sampling introduces its own set of assumptions that must be met to avoid bias (Kendall and White 2009). Ultimately, investigators should consider a

combination of design- and model-based strategies for minimizing estimation bias and achieving strong inference in occupancy studies.

3.5 Acknowledgements

Table 3.1. Selection results for models fit to detection of red-backed salamanders sampled using natural cover object (NCO) surveys in northern Michigan, 2009. ΔAIC_c represents the difference between AIC_c values for model i and the top-ranking model; w is the Akaike weight; K is the number of parameters; $-2\,l$ is twice the negative log-likelihood.

Model	ΔAIC_c	w	K	$-2\,l$
ψ(Disturbance+Trend+Cover), ε(Disturbance+Trend+Cover), $p(.,1^{st}\_2^{nd})$	0.00	0.82	10	806.4
ψ(Disturbance+Cover), ε(Disturbance+Cover), $p(.,1^{st}\_2^{nd})$	3.79	0.12	8	814.3
ψ(Disturbance+Trend+Cover), ε(Disturbance+Trend+Cover), $p(.,.)$	5.90	0.04	9	814.4
ψ(Disturbance+Cover), ε(Disturbance+Cover), $p(.,.)$	9.49	0.01	7	822.1
ψ(Trend+Cover), ε(Trend+Cover), $p(.,1^{st}\_2^{nd})$	12.27	0.00	8	822.8
ψ(Trend+Disturbance), ε(Trend+Disturbance), $p(.,1^{st}\_2^{nd})$	17.83	0.00	8	828.4
ψ(Disturbance), ε(Disturbance), $p(.,1^{st}\_2^{nd})$	18.05	0.00	6	832.7
ψ(Trend+Cover), ε(Trend+Cover), $p(.,.)$	18.27	0.00	7	830.9
ψ(Disturbance), ε(Disturbance), $p(.,.)$	23.74	0.00	5	840.4
ψ(Disturbance+Trend), ε(Disturbance+Trend), $p(.,.)$	23.78	0.00	7	836.4
ψ(Trend), ε(Trend), $p(.,1^{st}\_2^{nd})$	25.09	0.00	6	839.7
ψ(Cover), ε(=0), p(t)	29.04	0.00	6	822.9
ψ(Trend), ε(Trend), $p(.,.)$	31.08	0.00	5	847.8
ψ(Cover), ε(Cover), $p(.,1^{st}\_2^{nd})$	31.58	0.00	6	846.2
ψ(Cover), ε(Cover), $p(.,.)$	37.35	0.00	5	854.0
ψ(Cover), ε(=0), $p(.,1^{st}\_2^{nd})$	39.21	0.00	4	857.9
ψ(Cover), ε(=0), $p(.,.)$	44.18	0.00	3	864.9

Table 3.2. Parameter estimates for red-backed salamanders sampled using natural cover object (NCO) surveys in northern Michigan, 2009. $\hat{\beta}_{Disturbance}$, $\hat{\beta}_{Trend}$, and $\hat{\beta}_{Cover}$ are the beta estimates representing logit-linear effects of DISTURBANCE, TREND, and COVER on occupancy and extinction probabilities, respectively. $\hat{\beta}_{2nd\_Survey}$ is the beta estimate for the 2nd survey within a primary period. I report estimates and 95% confidence intervals for each of the top three models ($w > 0.01$).

Model	Occupancy		
	$\hat{\beta}_{Disturbance}$	$\hat{\beta}_{Trend}$	$\hat{\beta}_{Cover}$
ψ(Disturbance+Trend+Cover), ε(Disturbance+Trend+Cover), p(.,$1^{st}\_2^{nd}$)	-0.17	-0.20	0.98
Lower 95% Confidence Interval	-0.26	-0.36	0.11
Upper 95% Confidence Interval	-0.08	-0.04	1.86
ψ(Disturbance+Cover), ε(Disturbance+Cover), p(.,$1^{st}\_2^{nd}$)	-0.24		1.28
Lower 95% Confidence Interval	-0.34		0.35
Upper 95% Confidence Interval	-0.14		2.21
ψ(Disturbance+Trend+Cover), ε(Disturbance+Trend+Cover), p(.,.)	-0.17	-0.20	1.01
Lower 95% Confidence Interval	-0.26	-0.36	0.13
Upper 95% Confidence Interval	-0.08	-0.04	1.89

Table 2 (cont'd)

Model	Extinction			Detection
	$\hat{\beta}_{Disturbance}$	$\hat{\beta}_{Trend}$	$\hat{\beta}_{Cover}$	$\hat{\beta}_{2nd\_Suvey}$
ψ(Disturbance+Trend+Cover), ε(Disturbance+Trend+Cover), p(.,1st_2nd)	0.31	0.60	1.92	-0.55
Lower 95% Confidence Interval	0.05	0.21	0.20	-0.94
Upper 95% Confidence Interval	0.56	0.98	3.63	-0.16
ψ(Disturbance+Cover), ε(Disturbance+Cover), p(.,1st_2nd)	0.57		1.25	-0.54
Lower 95% Confidence Interval	0.22		-0.48	-0.92
Upper 95% Confidence Interval	0.91		2.99	-0.15
ψ(Disturbance+Trend+Cover), ε(Disturbance+Trend+Cover), p(.,.)	0.31	0.60	1.92	
Lower 95% Confidence Interval	0.05	0.21	0.17	
Upper 95% Confidence Interval	0.57	1.00	3.67	

Figure 3.1. Sampling lattice of 60 × 60-m cells overlaid on an aspen stand and systematically located sampling transects (in one random cell) for estimating red-backed salamander occupancy, extinction, and detection probability in northern Michigan, USA, 2009. Dark gray polygons in the background image represent unharvested canopy trees following timber harvest. Solid, dashed, and dotted lines in the foreground image represent 20-m transects initially surveyed in May, June, and July, respectively.
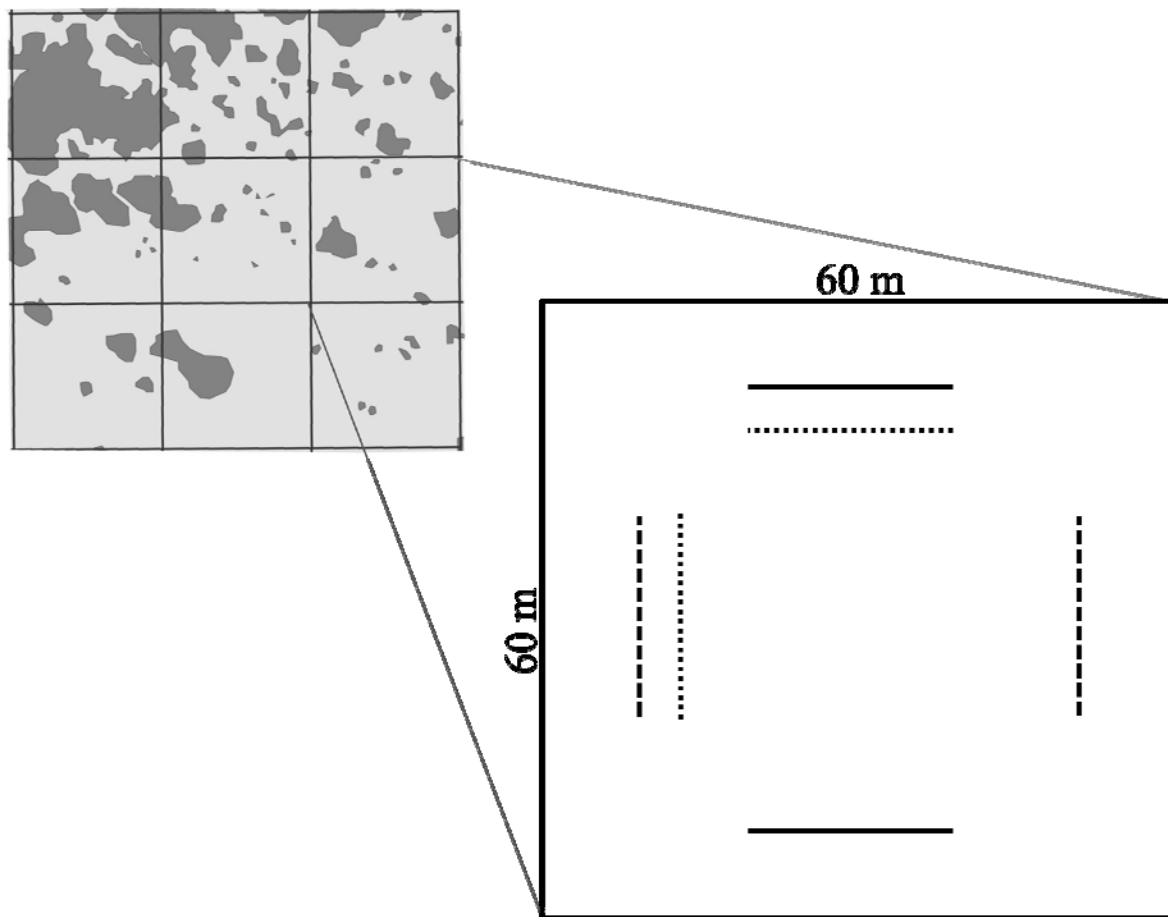
Figure 3.2. Red-backed salamander occupancy probability for transects with (a) high or (b) low levels of natural cover objects (NCO≥ 20 or NCO <20, respectively). Black circles represent Group 1 transects initiated in early May and surveyed through early July; open squares are Group 2 transects initiated in mid June and surveyed through late July; gray triangles are Group 3 transects initiated in late July and surveyed through early August. Each primary period was separated by 7-10 days. All parameter estimates are model averaged.

A
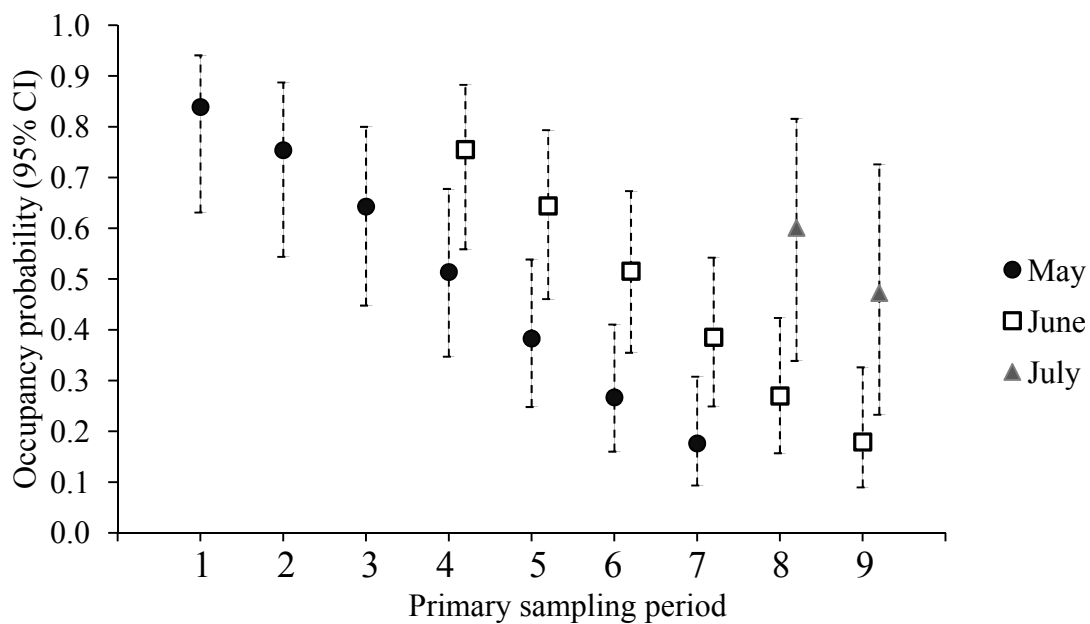
Figure 3.2 (cont'd)

B
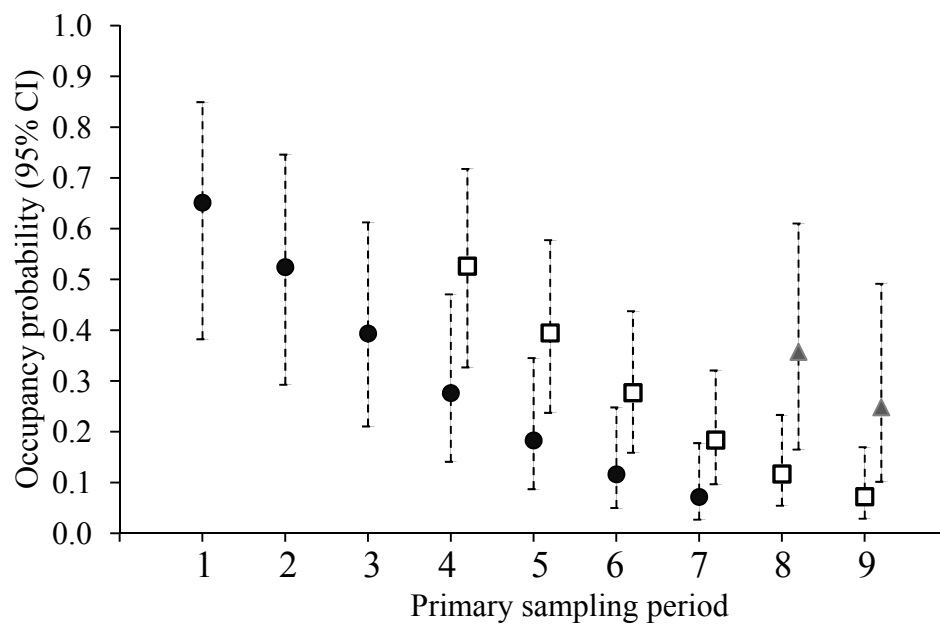
Figure 3.3. Site extinction probabilities for red-backed salamander transects with (a) high or (b) low levels of natural cover objects (NCO≥ 20 or NCO <20, respectively). Black circles represent Group 1 transects initiated in early May and surveyed through early July; open squares are Group 2 transects initiated in mid June and surveyed through late July; gray triangles are Group 3 transects initiated in late July and surveyed through early August. Each primary period was separated by 7-10 days. All parameter estimates are model averaged.

A
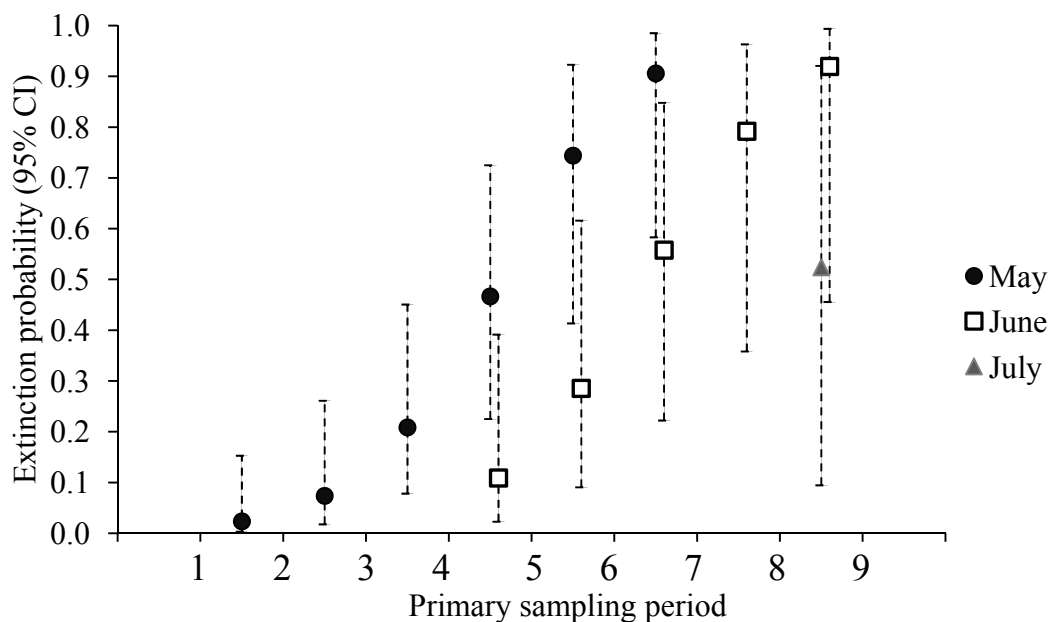
Figure 3.3 (cont'd)

B
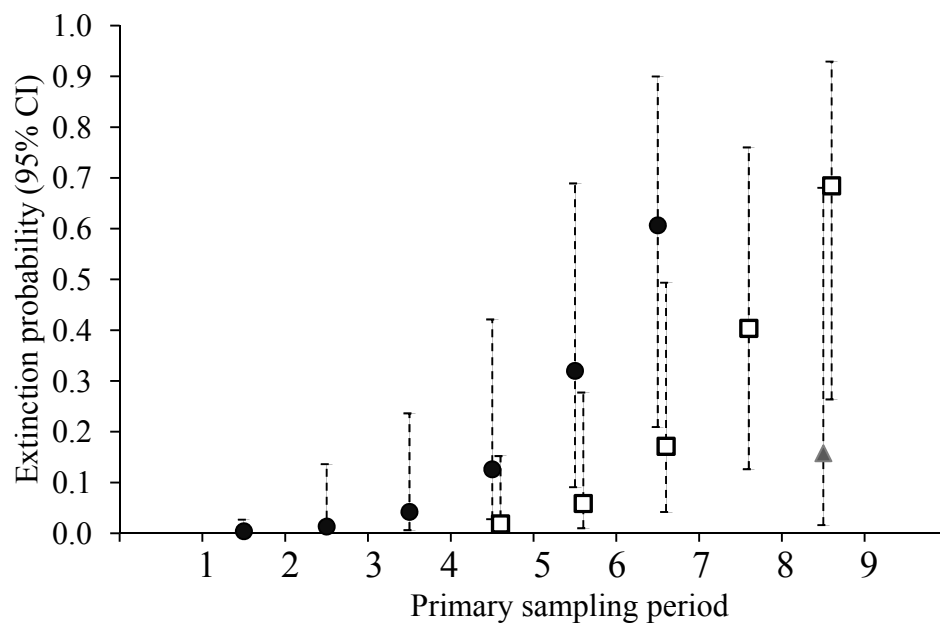
Figure 3.4. Estimates of relative bias in closed, single-season occupancy models when sites are open to local extinction events between primary periods. ψ_{int} = initial occupancy probability, S = the number of primary sampling periods (i) where the number of surveys, t = 1, 2..(2×S), γ = probability an unoccupied site at time i, becomes occupied at time $i + 1$, ε = probability an occupied site at time i, becomes unoccupied at time $i + 1$, p = probability of detecting the species during a single survey, given its presence at a site. Expected values were analyzed using time-independent ($\psi(.), p(.)$; solid line) and time-dependent ($\psi(.), p_t$; dashed line) closed occupancy models. Relative bias was calculated as bias = $(E(\hat{\psi}) - \psi_{int})/ \psi_{int})$ where $E(\hat{\psi})$ is the estimated occupancy for the closed model and ψ_{int} is the 'true' initial occupancy value.

Figure 3.4 (cont'd)

ψint = 0.4, S = 2, γ = 0.05

A

p(.) = 0.2
p(.) = 0.4
p(t) = 0.2
p(t) = 0.4

Relative bias (occupancy)

Extinction probability

ψint = 0.7, S = 2, γ = 0.05

B

Relative bias (occupancy)

Extinction probability
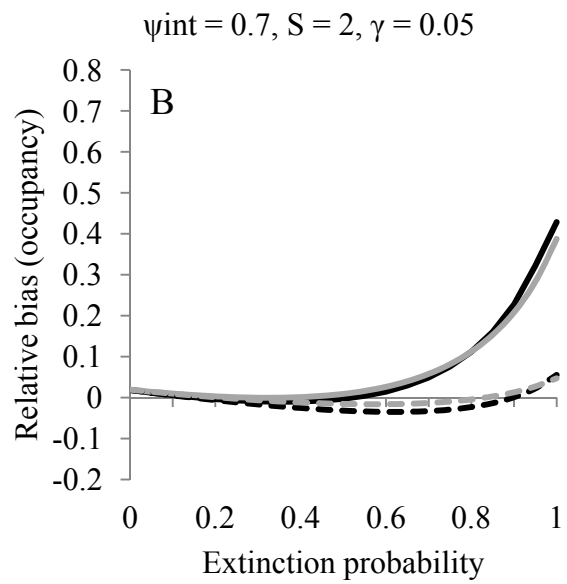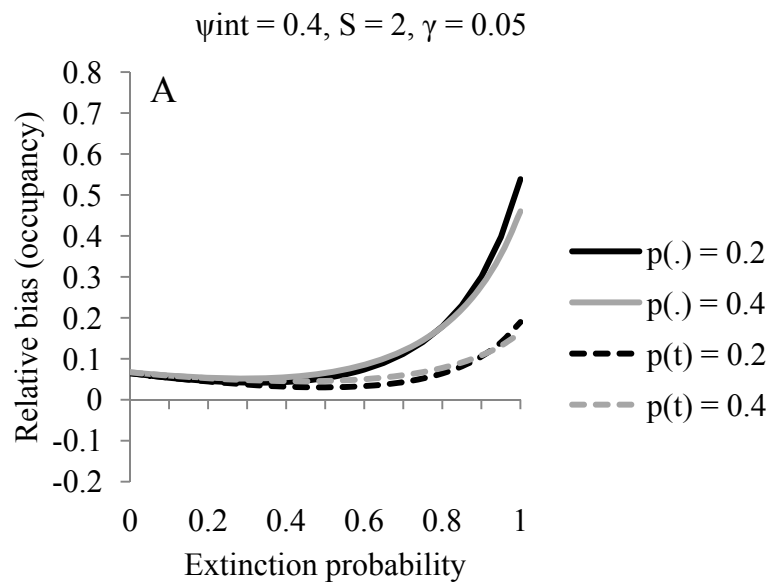
Figure 3.4 (cont'd)

Figure 3.4 (cont'd)

ψint = 0.4, S = 4, γ = 0.0   ψint = 0.7, S = 4, γ = 0.0
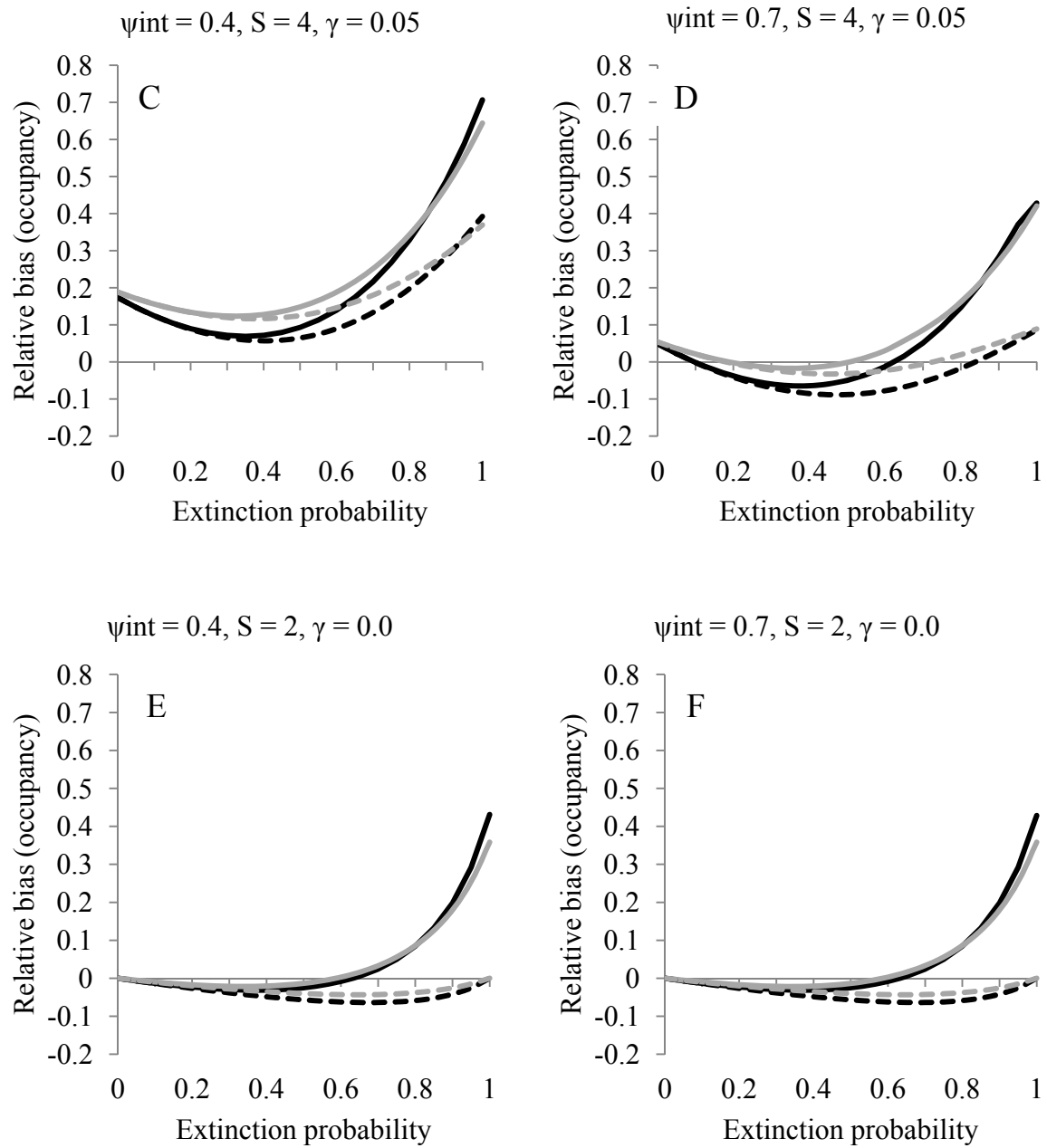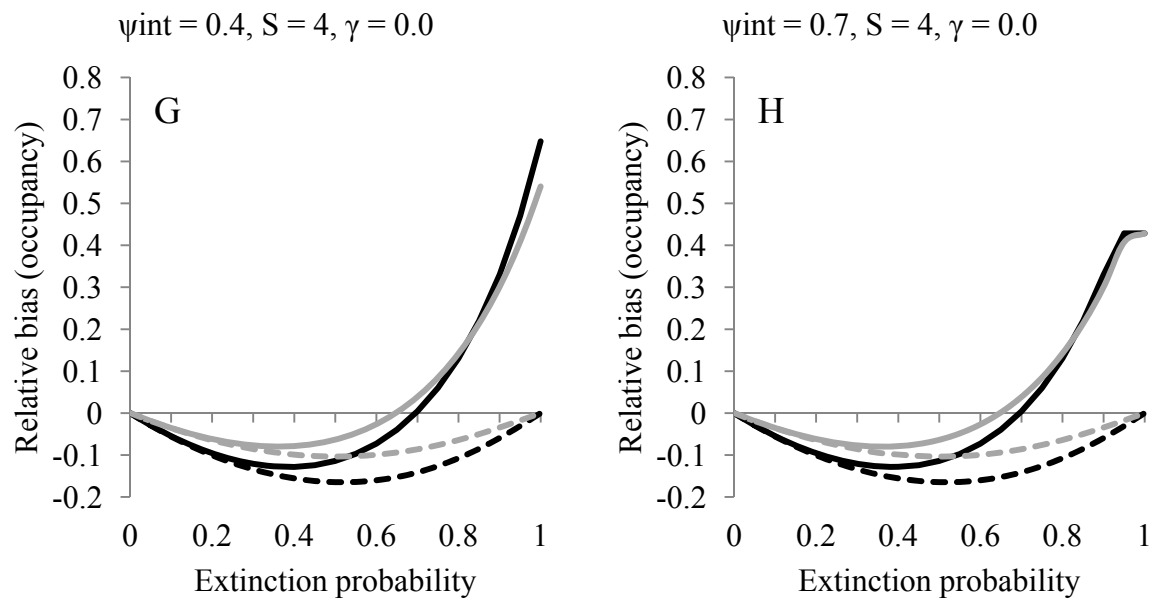
APPENDIX

Appendix A.1. Standard errors for occupancy estimates in closed occupancy models (*i.e.,* single-season; MacKenzie et al. 2002) when sites are open to local extinction events between primary periods. See Figure 3.4 for description of symbols and simulation overview.
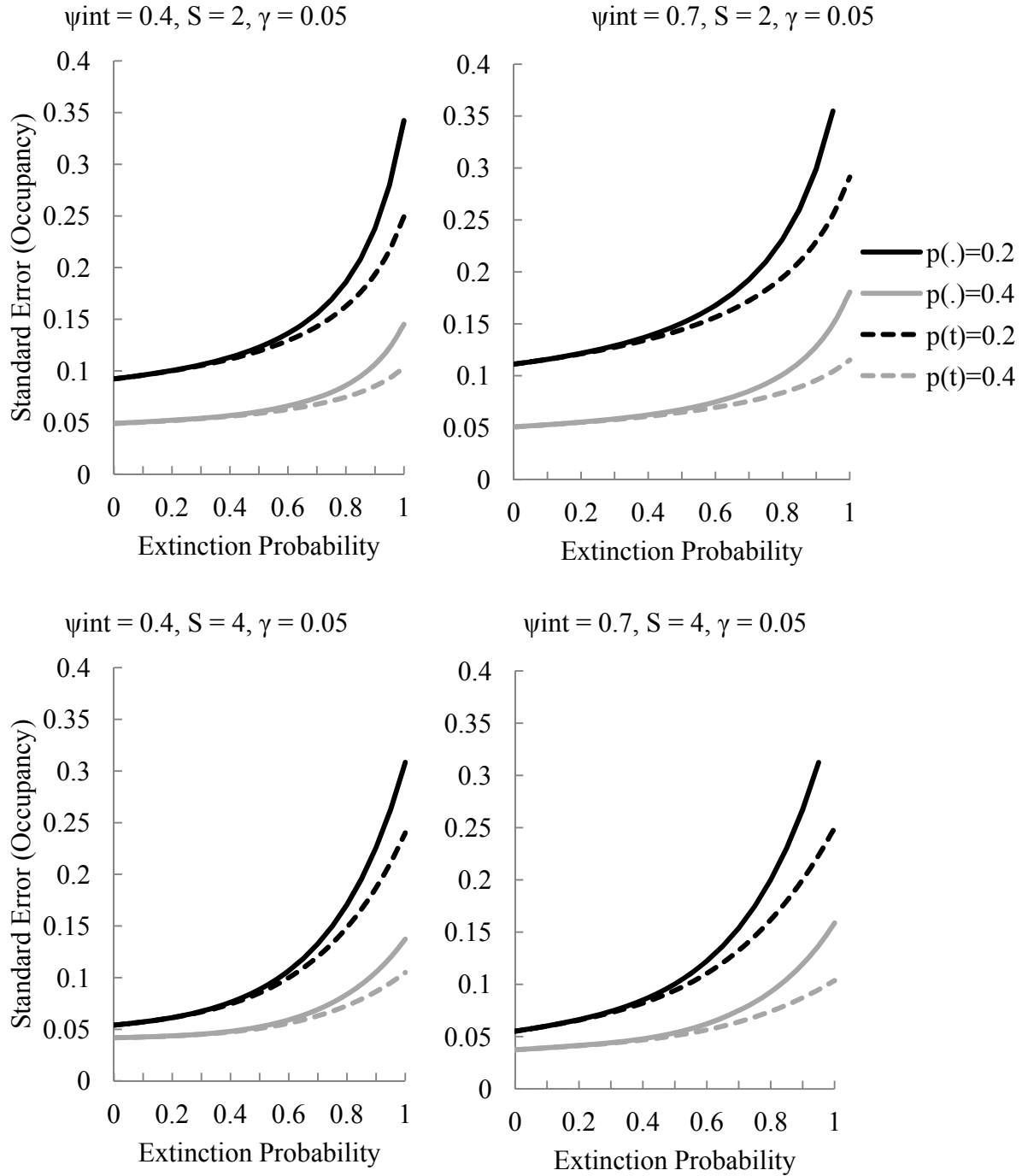
Appendix A.1 (cont'd)
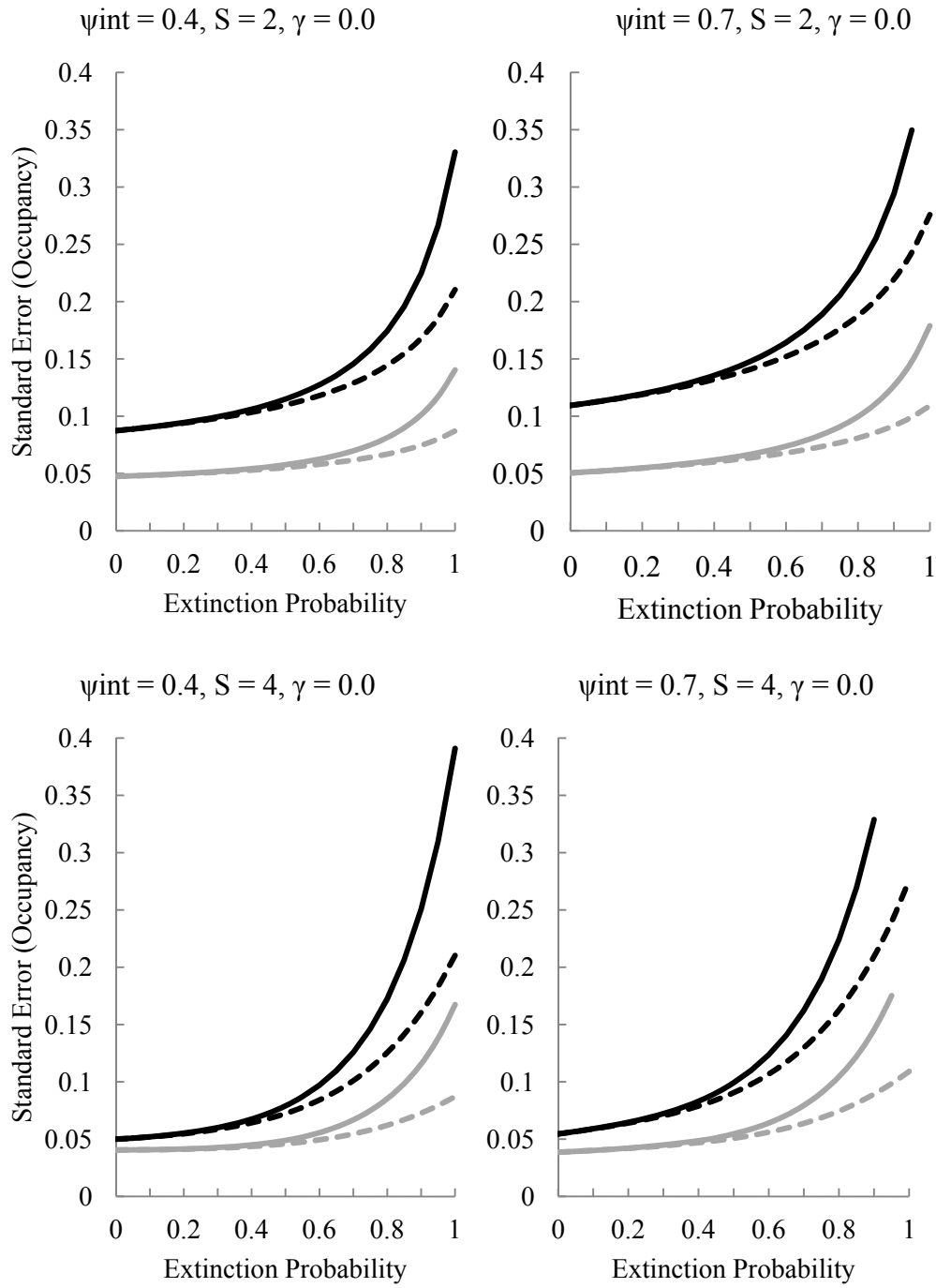
ψint = 0.4, S = 2, γ = 0.0

ψint = 0.7, S = 2, γ = 0.0

ψint = 0.4, S = 4, γ = 0.0

ψint = 0.7, S = 4, γ = 0.0

Standard Error (Occupancy)

Extinction Probability

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CHAPTER 4

SONGBIRD RESPONSE TO GREEN-TREE RETENTION PRESCRIPTIONS IN CLEARCUT FORESTS

Abstract

Green-tree retention prescriptions have been proposed as a silvicultural technique for reducing the negative impacts of clearcutting on mature forest-associated species, while still promoting habitat for early-successional species. I evaluated the effectiveness of green-tree retention for conserving mature forest-associated, generalist, and early-successional songbirds in aspen stands that were 1 to 15 years post-harvest. I compared species occupancy estimates at sites where green-tree retention levels were exceeded (>10% canopy cover), met (3-10%), or below (<3%) recommended retention guidelines. I also compared the relative importance of these levels of green-tree retention to forest stand age in explaining songbird occurrence. With the exception of Red-eyed Vireos, my results suggest that current green-tree retention guidelines are ineffective at increasing site occupancy of mature forest-associated songbirds in aspen harvest units. Additionally, site occupancy of early-successional and generalist songbirds were unaffected by these levels of retention. Rather, site occupancy probabilities for most forest birds showed a clear association with age since harvest (1-15 years); however, the strength and direction of the association varied by species. My research highlights the importance of considering forest stand age when assessing the impact of silvicultural prescriptions on forest songbirds. Future management objectives in aspen forests should reflect the value of clearcutting to early-successional and generalist bird species, while recognizing that green-tree retention as measured in my study does little to promote occupancy of the mature forest-associated bird community.

4.1. Introduction

Conservation biologists recognize habitat loss as a leading threat to worldwide

biodiversity (Schipper et al., 2008; Kraus et al., 2010). One mechanism for habitat loss that

occurs in many forests worldwide is timber harvest, specifically the silvicultural prescription

known as clearcutting. This is an even-aged management prescription that results in complete

removal of harvestable trees and has been implicated in the declines of numerous mature forest-

associated species (Thompson et al., 2003; Griesser et al, 2007; Semlitsch et al., 2009).

However, clearcutting can also serve as an effective management tool for promoting early

successional habitat or increasing habitat heterogeneity (Thompson and DeGraaf, 2001; Franklin

et al., 2002; DeGraaf and Yamasaki, 2003). Clearcutting may be particularly important for

migratory songbird species that have experienced recent population declines because of early-

successional habitat loss (Litvaitis, 1993; Brawn et al., 2001; Hunter et al., 2001). Thus,

clearcutting potentially creates a management paradox because it promotes habitat for some

wildlife species, while reduces it for others. This is problematic considering one of the main

objectives of recent forest management initiatives is to protect and conserve biodiversity within

intensively-managed ecosystems (Carey and Curtis, 1996; Sustainable Forestry Initiative, 2010;

Forest Stewardship Council, 2012).

To alleviate the negative effects of clearcutting on forest wildlife, harvest prescriptions

have been developed that include retention of canopy structure within the harvest units (*i.e.,*

structural retention). These retention prescriptions require the preservation of "biological

legacies", such as green-trees and snags, within a harvested unit, in an effort to increase stand

structural complexity and provide refugia for forest wildlife (Franklin et al., 1997; Schieck and

Song, 2006; Rosenvald and Lõhmus, 2008). In some ecosystems retention prescriptions more

closely mimic the result of natural disturbances, relative to clearcutting, and yet promote habitat

for early-successional species (DeGraaf and Yamasaki, 2003; Rosenvald and Lõhmus, 2008;

Lencinas et al., 2009).

Green-tree retention prescription have been formally integrated into state, federal, and

private management organizations through the adoption of forest practices regulations, voluntary

best management practices, and forest stewardship certification programs (Rochelle, 2008;

Elbakidze et al., 2011). Although many of these organizations share similar wildlife

conservation goals, there is substantial inter-organization variability, regarding the proposed

quantity and spatial arrangement of retained structure within harvest units. For example, the

Northwest Forest Plan in the Pacific Northwest requires that $\geq 15\%$ of the harvest unit area be

retained on all federal forest lands (summarized in Aubry et al., 1999), while the Michigan

Department of Natural Resources (MDNR) recommends 3-10% retention on state-owned lands

(Bielecki et al., 2006). This variability likely stems from differences in management agency

policies, objectives, and limited scientific information that directly relates to the management

area of interest (Rosenvald and Lõhmus, 2008). Evaluating the effectiveness of retention

guidelines can help address management questions such as 'are the current levels of retention

sufficient for conserving wildlife?' and 'do the benefits of structural retention incurred by mature

forest-associated species outweigh potential negative effects on early-successional species?'

I evaluated avian community response to structural retention guidelines implemented by MDNR in recently (1 to 15 years old) harvested aspen (*Populus* sp.) stands in Michigan. I compared species occupancy dynamics within a single breeding season at sites where green-tree retention levels were exceeded (>10%), met (3-10%), or below (<3%) the recommended guidelines. I used occupancy models (MacKenzie et al., 2006) to test the hypothesis that harvested sites with >10% green-tree retention exhibit higher occupancy by mature forest-associated songbirds within a breeding season. I also tested whether >10% green-tree retention reduced occupancy of early-successional and generalist songbird species. I then compared the relative importance of green-tree retention to forest age (1 to 15 years old) in explaining songbird occurrence across sites. Finally, my study design and modeling approach allowed me to indirectly assess how patterns in site settlement by migratory songbirds within a breeding season were related to structural retention and forest stand age.

4.2. **Methods**

4.2.1. Study Area

I conducted my study in the Cadillac-Traverse City area in the northwestern Lower Peninsula of Michigan, USA, in 2010-11. This area is characterized as a glacial outwash-plain with porous sandy soils, intermixed with ice-contact zones and moraines (Albert 1995). My study occurred on state-owned forest lands that were managed for aspen production. Within harvested stands the MDNR implemented green-tree retention prescriptions (Bielecki et al., 2006), which called for retention of 3-10% of canopy trees and retention of snags and coarse woody debris (CWD) whenever possible. Green-tree retention prescriptions consisted of single leave-tree and aggregate retention. Retained canopy trees consisted of mixed oak (*Quercus* spp.), eastern white pine (*Pinus strobus*), red maple (*Acer rubrum*), black cherry (*Prunus*

serotina), American beech (*Fagus grandifolia*), and aspen, whereas dominate understory woody plants were aspen, red maple, blackberry (*Rubus* spp.), black cherry, downy serviceberry (*Amelanchier arborea*), witch-hazel (*Hamamelis virginiana*), American beech, and hophornbeam (*Ostrya carpinifolia*). Prior to European settlement, the study landscape was dominated by eastern white and jack pine (*Pinus banksiana*) and prone to fire disturbances (Barnes and Wagner, 2004).

4.2.2. Site Selection

My initial group of candidate areas for study consisted of all state-owned aspen stands within a 4 county area that were >8 ha in size and between 1 to 15 years post-harvest. To select potential survey sites within a stand, I used HAWTH'S TOOLS (Hawth's Tools, version 3.27, http://www.spatialecology.com/htools/, accessed 1 Feb 2009) in a Geographic Information System (GIS; ArcGIS 9.1; Environmental Systems Research Institute, Redlands, CA) to overlay each aspen stand with a 60 x 60 m lattice. I eliminated all lattice cells whose borders intersected or encompassed an unharvested forest edge, active logging road, off-road recreational vehicle trail, or wetland that appeared on 2005 National Agricultural Imagery Program imagery (NAIP; Michigan Department of Information Technology 2007). For the remaining lattice cells, I digitized canopy cover of all retained green-trees within the harvest units using NAIP imagery (1998-2010 depending on stand age). I assigned each lattice cell to one of nine 'retention-age' groups defined by the amount of green-tree retention and age since harvest. I considered three levels of green-tree retention based on the proportion of canopy cover within the 60×60 m cell, which was related to the MDNR retention guidelines (Bielecki et al., 2006; <3%, 3-10%, and >10% canopy cover) and three groups for age since harvest (1-4, 5-9, and 10-15 years post-harvest).

Power approximations (Bailey et al., 2007) from a 2009 songbird pilot study revealed that my study design should include, at minimum, 153 sampling sites, split evenly between the nine 'retention-age' groups (*i.e.,* 17 sites/group). I randomly selected 17 lattice cells for each 'retention-age' group and established a point-center within each of the selected cells. This point-center represented the spatial location for my avian point-count surveys (*i.e.,* study sites). The point-center of all selected lattice cells were >250m apart and >75m from the harvest unit boundary. Once my initial site selection was complete (n=153 sites), I then randomly selected an additional 100 lattice cells. Here, all lattice cells 250m < x < 5km from a previously selected cell were included in the candidate pool. I eliminated 31 sites after initial field visits because the dominant cover-type was not aspen, the site resided within an ephemeral wetland, or it was inaccessible. My final sample size was 222 sites unequally distributed among retention-age groups.

4.2.3. Bird Sampling

To reduce travel time, I sampled 120 sites, which were in close proximity to one another, in 2010, and 102 new sites in 2011. At each site, a single observer preformed a 9-min point-count that was sub-divided into 3- 3min sub-counts. Point-counts were conducted between one-half hour after sunrise and no later than three and one-half hours after sunrise on days with appropriate weather conditions (*i.e.,* no rain, no strong winds). Detection was recorded for all songbirds seen or heard within a 50m sampling radius of the point-count center. I chose a 50m sampling distance to reduce the chance of sampling birds in adjacent forest stands (*i.e.,* reduce edge effects). All observers were trained on estimating songbird detection distances before the study commenced. Each site was initially visited in late-May and then revisited every 10-14 days. Sampling occurred in this fashion until all sites had been visited 4 times within a 2 month

time span during the breeding season (late-May to mid-July). I assigned each bird species to one of three habitat guilds (early-successional, generalist, interior forest) based on habitat preferences provided by Alsop (2001) and Poole (2005). I define Generalist bird species as those which are likely to occur in mature forests, open woodlands, early-successional forests, and scrub-shrub habitats, while interior forest species are likely to occur in mature forests with developed canopies.

4.2.4. *Habitat Covariates*

In GIS, I used NAIP imagery to quantify the proportion of canopy cover within 50m of point-center for all study sites. Although I used 60x60 m cells as the dimensions of my site selection lattice, I felt it was more biologically meaningful to align the scale of my habitat data to that of my songbird data (Smith et al. 2008). Therefore, I used the proportion of canopy cover within 50m of point center to reassign each study site to one of my nine 'retention-age' groups (Figure 4.1).

4.2.5. Model Generation and Analysis

I generated a detection history for each songbird species at each study site. Detection histories for a single species (*e.g.,* ovenbird, *Seiurus aurocapilla*) at 2 study sites might appear as:

Site 1   100   111   000   101

Site 2   010 000   110   000

where "1" represents a positive detection of ≥1 ovenbird during a 3-min survey and "0" represents non-detection. Each group of 3 numbers represents a 9-min point-count where sites were assumed closed to changes in occupancy (*i.e.,* unoccupied sites did not become occupied, or occupied sites did not become unoccupied). The 9-min point count constituted a primary-

period within a dynamic occupancy model, whereas the 3 sub-counts were temporal sampling replicates used for estimating detection probability (MacKenzie et al. 2003). I hypothesized that site occupancy status of my focal bird species may change between each primary period, which were separated by 10-14 days. Changes in occupancy within a breeding season may result from migratory birds preferentially selecting higher quality habitat as the season progresses (Betts et al. 2008). Past research has shown that migratory songbird movement (site settlement and vacancy) rates can be indirectly estimated using dynamic occupancy models (Kendall and Nichols, 2004; Betts et al., 2008; Rota et al., 2009). My study design and modeling approach allowed us to indirectly estimate how site settlement probabilities varied as a function of green-tree retention and years since harvest, for each species. I used an alternative parameterization of a dynamic occupancy model (MacKenzie et al., 2003) to estimate occupancy (ψ) within each primary period and settlement (γ: referred to as "colonization" in MacKenzie et al. 2003) probabilities between primary periods. Occupancy represents the probability that a site is occupied during a 9min point count. Settlement represents the probability that an unoccupied site during primary period i becomes occupied before primary period $i + 1$. Extinction probability [hereafter "vacancy"] is a derived parameter in this model. My results should be viewed as indirect estimates of species movement within a breeding season, as I did not determine movement from physically marked individuals (Kendall and Nichols, 2004; Betts et al. 2008).

For the model development, I tested 5 hypotheses, represented by 10 models, regarding possible differences in songbird site occupancy and settlement. My null hypothesis was that occupancy for a given species remained static and no site settlement occurred throughout the duration of my study ($\psi(.),\gamma(=0)$). My second hypothesis was that no site settlement occurred

throughout my study ($\gamma(=0)$), but site occupancy varied as a function of green tree retention level (ψ(Retention),$\gamma(=0)$) or stand age (ψ(Age),$\gamma(=0)$). My third hypothesis was that occupancy remained static $\psi(.)$, but settlement ($\gamma(.)$) occurred between primary periods and these parameters were not influenced by green-tree retention level or stand age (($\psi(.),\gamma(.)$). Fourth, I hypothesized that occupancy and/or settlement were influenced by the amount of green-tree retention within 50m of the study site. To represent this hypothesis, I constructed 3 models (ψ(Retention),γ(Retention); ψ(Retention),$\gamma(.)$; $\psi(.),\gamma$(Retention)) which allowed site occupancy and/or settlement probabilities to vary between my three retention groups: below (<3% residual canopy cover), at (3-10%), or exceeded (>10%). Strong support for models that included this structure would suggest that green-tree retention influences occupancy dynamics for a particular species. Lastly, I hypothesized that occupancy and/or settlement were influenced by the time since a stand was harvested (*i.e.,* stand age: (ψ(Age),γ(Age); ψ(Age),$\gamma(.)$; $\psi(.),\gamma$(Age)). Support for models that included this structure would suggest that stand age influences species occupancy dynamics. For my last 3 hypotheses I assumed that my collection of study sites were in a state of equilibrium with respect to occupancy- that is, the number of sites that were settled between primary periods was comparable to the number sites that were vacated (*i.e.,* stationary Markov process; MacKenzie et al., 2006 p. 208-209). Thus, my reported occupancy estimates represent an average probability of occurrence among the four primary sampling periods. I held detection probability constant for all models ($p(.)$).

I expected the direction and strength of the relationship between occupancy and settlement, and my two covariates, RETENTION and AGE, to be different for each bird species group. For interior forest species I expected strong support for models that included RETENTION, and occupancy and settlement estimates to be positively related to green-tree

retention level. For generalist species I expected substantial model selection uncertainty and imprecise occupancy and settlement estimates with respect to RETENTION and AGE. For early-successional species I expected strong support for models that included AGE; with occupancy and settlement estimates negatively related to AGE. I also expected a negative relationship between occupancy and RETENTION for all early-successional species.

I analyzed my data using Program MARK (MARK, version 5.1, http://www.cnr.colostate.edu/~gwhite/mark/mark.htm, accessed 07 July 2010) and used Akaike's Information Criterion, adjusted for small sample size (AIC_c), to rank models (Burnham and Anderson, 2002). I used cumulative AIC weights (w_+) and evaluation of 95% confidence intervals to determine relative importance of covariates and model parameters. I report model averaged estimates and unconditional standard errors (SE) for all real parameters (Burnham and Anderson, 2002, p.149-205). Model averaging is a standard approach for conditioning inferences on *a priori* models in a candidate set (Burnham and Anderson 2002). No goodness-of-fit test for multi-season occupancy models is currently available.

4.3. Results

The mean percentage of canopy cover for my three RETENTION groups was 0.6 ± 0.09 (mean $\pm$ 1SE: Group <3%), 6.2 ± 0.3 (Group 3-10%), and 26.0 ± 1.5 (Group >10%). Green tree retention levels were >30% and >50% at 31 and 8 study sites, respectively. Although, I detected 66 bird species during this study, sufficient detection information to model occurrence existed for 20 species. For these 20 species, detection probability estimates during a 3-min sub-count ranged from 0.31-0.72 (Table 4.1). For the above species, I detected 6.5 ± 0.19 (mean $\pm$ 1SE) per site. The proportion of sites where each species was known to occur often varied between each 9-min point-count (Table 4.2).

For interior forest species, cumulative weights (w_+) for models that included

RETENTION ranged from 0.00 (Ovenbirds) to 0.99 (red-eyed vireos, *Vireo olivaceus*; Table

4.3). Model-averaged occupancy estimates were similar among all green-tree retention levels

for all interior forest species, except for red-eyed vireos, which showed a strong positive

correlation with retention (Figure 4.2A). Occupancy estimates for red-eyed vireos were

approximately 215 and 370% higher at sites that met (3-10%) or exceeded (>10%) the MDNR's

green-tree retention guidelines when compared to sites that were below (<3%) the guidelines

(Figure 4.2A). Models for two interior forest species, hermit thrush (*Catharus guttatus*) and

scarlet tanager (*Piranga olivacea*), had problems converging; therefore, parameter estimates for

these species should be interpreted with caution (Figure 4.2A and 4.3A).

Among generalist and early-successional species, support for models that included

RETENTION was generally low (12 species, w_+ <0.1; Table 4.3); however, there was moderate

support for RENTENTION models for 5 species (0.1< w_+ <0.7; Table 4.3). Among the species

for which RETENTION was moderately supported, only Baltimore orioles (*Icterus galbula*) and

rose-breasted grosbeaks (*Pheucticus ludovicianus*) exhibited occupancy estimates that varied

between the three green-tree retention groups (Figure 4.2B,C). For example, model-averaged

occupancy estimates for Baltimore orioles were approximately 44 and 36% higher at sites that

met (3-10%) or exceeded (>10%) the retention guidelines when compared to sites that were

below (<3%) the guidelines (Figure 4.2B). Estimates for rose-breasted grosbeaks were

approximately 9 and 8% higher at sites that met or exceed the retention guidelines; however,

there was substantial overlap in the 95% confidence intervals (Figure 4.2C). I did not observe

evidence of green-tree retention negatively influencing occupancy for any of my study species

(Figure 4.2). Collectively, I observed little evidence that green-tree retention promotes occupancy of interior forest species, or inhibits occupancy of early-successional and generalist species, respectively.

Cumulative weights (w_+) for models containing stand AGE were >0.75 for 4 of 5 early-successional, 7 of 10 generalist, and 1 of 5 interior forest species (Table 4.3). I observed little support for models that included AGE for Baltimore orioles, red-eyed vireos, and scarlet tanagers (w_+ <0.10; Table 4.3). There was substantial inter-specific variation in occupancy estimates with relation to my three stand age classes (Figure 4.2). For example, occupancy estimates declined with increasing stand age for all early-successional species; however, the most dramatic decline occurred between the 5-9 year and 10-15-year age class of sites (Figure 4.2D). Occupancy estimates for golden-winged warblers (*Vermivora chrysoptera*) were similar for 1-4 year and 5-9 year sites, but decreased by approximately150% and 135% when compared to 10-15 year sites, respectively. Some generalist species, such as brown-headed cowbirds (*Molothrus ater*), exhibited occupancy estimates that declined with harvest age, and yet Nashville warblers (*Oreothlypis ruficapilla*), another generalist species, showed a positive response (Figure 4.2B,C). Collectively, my results provide evidence that songbird occupancy dynamics are often influenced by stand age within the first 15 years of harvest in aspen forests.

I found strong evidence that occupancy status of my study sites changed between primary periods for all species: models where site settlement probability was fixed at 0.0 (*i.e.,* occupancy was static across all primary periods) received no weight (Table 4.3). Furthermore, the probability that an unoccupied site became occupied during a later primary period (*i.e.,* settlement) was strongly related to harvest age for many species, and related to green-tree retention for red-eyed vireos (Figure 4.3). For example, site settlement estimates for red-eyed

vireos were greater by 130 and 370% for sites that met or exceeded the retention guidelines when compared to sites that were below the guidelines (Figure 4.3A). Settlement for most early-successional species showed a negative response to increasing stand age, while generalist and interior forest species showed mixed responses, respectively (Figure 4.3).

4.4. Discussion

Green-tree retention prescriptions have been proposed as a silvicultural technique for reducing the negative impacts of clearcutting on interior forest species while still promoting habitat for early-successional species and maintaining a sustainable timber industry (Franklin et al., 1997; DeGraaf and Yamasaki, 2003; Rosenvald and Lõhmus, 2008). Although structural retention prescriptions are being implemented into forestry certification programs (e.g., Bielecki et al., 2006; Rochelle, 2008; Elbakidze et al., 2011), there is relatively little scientific information regarding wildlife response to these prescriptions. My results provide somewhat conflicting evidence that green-tree retention levels observed in this study are effective at increasing site occupancy of interior forest songbirds, at least in aspen clearcuts <15 years old. With the exception of red-eyed vireos, I did not observe strong evidence of any species exhibiting increased occupancy probabilities at sites that met or exceeded the MDNR's green-tree retention guidelines when compared to sites with retention levels below the guidelines. Rather, site occupancy probabilities for most songbirds showed a clear association with age since harvest (1-15 years), with the strength and direction of the association varied by species. Occupancy estimates for Baltimore orioles and rose-breasted grosbeaks were higher at sites with 3-10% and >10% retention when compared to sites with <3% retention; however, the strength of the response was relatively weak. A meta-analysis of green-tree retention studies by Rosenvald and Lõhmus (2008) showed that the strength and direction of wildlife response to retention is often

conditional on retention quantity, cover-type, and the focal wildlife taxa, making comparisons across studies difficult. Similarly, my findings contradict other studies which documented a positive response of songbirds to green-tree retention, relative to clearcutting (*e.g.*, Merrill et al., 1998; Atwell et al., 2008; Söderström, 2009), but support other studies that did not observe an effect (reviewed in Rosenvald and Lõhmus, 2008). Sites that exceeded the MDNR's retention guidelines had an average of 25% canopy cover: a quantity of retention comparable to other studies that documented positive responses of songbirds to retention quantity (Atwell et al., 2008; Söderström, 2009). The landscape matrix of my study area consists of mixed northern hardwoods and conifer forests (Barnes and Wagner, 2004). Therefore the relative benefit of retention within my small (20-80 ha) harvest units may be reduced because forested habitat is a dominant feature in the landscape. It is unclear how the ecological role of structural retention may change in landscapes with different land-use conditions or within larger harvest units than those observed here. These relationships warrant further study.

4.4.1. Interior Forest Bird Response to Green-tree Retention

Several interior forest species, such as Black-throated Blue Warblers (*Setophaga caerulescens*) and Northern Parula (*Setophaga americana*), were rarely detected at my study sites, even though they were present on the landscape. Lack of detection information precluded us from including these species in my analysis. Furthermore, occupancy estimates for three of my interior forest species were low, and the reliability of these estimates were suspect for Hermit Thrushes and Scarlet Tanagers. These findings suggest that interior forest species rarely occurred within my clearcuts, regardless of green-tree retention. Although inferred rarity of interior-forest species in clearcuts seems like an obvious finding, I note that a main objective of green-tree retention prescriptions is often to provide refugia for species that require mature forest

(*i.e.,* life-boating; Franklin et al., 1997; Rosenvald and Lõhmus, 2008). Quantities of structural retention that I observed appear inadequate for promoting occupancy of many interior forest species in aspen clearcuts, except for Red-eyed Vireos. Twedt and Somershoe (2009) reported that densities of Red-eyed Vireos were lower in stands where variable retention prescriptions were applied, relative to untreated control stands. The objective of my study was to determine how occupancy of forest birds varied across three levels of green-tree retention that correspond to current MDNR guidelines, rather than comparing retention harvest to untreated "control" stands. Thus, my study shows that occupancy of Red-eyed Vireos is higher at sites where retention exceeded MDNR guidelines; however, it is unclear how occupancy at high retention sites compares to mature forest.

A variety of environmental factors, interacting at multiple spatial and temporal scales, influence the occurrence of forest birds within a landscape (Sirami et al. 2008, Lesak et al. 2011, McDermott et al. 2011). Therefore identifying appropriate scales of forest management is of interest to natural resource managers. My analysis suggests that occupancy of most interior forest species is influenced by factors other than structural retention within harvest units. Consistent with this finding, McDermott et al. (2011) found that stand-level habitat factors, such as stand age and landform type, provided greater utility for predicting occurrence of late-successional birds in harvested forests when compared to within-stand vegetation factors. This suggests that management efforts for conserving interior forest bird should be focused at the stand and landscape scales, rather than the within-stand scale which was the focus of my study. My analysis did not include other within-stand habitat factors that could potentially influence occurrence of interior-forest birds such as green tree composition and size, and other habitat structures such as vertical snags (Poulin 2002, Remm et al., 2006, Jayapal et al. 2009). Canopy

green trees provide the only significant form of vertical structure within my harvest units: a feature that influences forest bird habitat selection and is of primary interest to forest management (Whelan, 2001; Poulsen, 2002; King et al., 2006). Thus, I feel my choice of green tree retention quantity as my primary habitat variable is justified, and acknowledge that other aspects of structural retention merit further study.

4.4.2. Competing Hypotheses: Songbird Response to Tree Retention, Relative to Stand Age

I assessed evidence for multiple, competing hypotheses by evaluating songbird response to stand age, relative to varying green-tree retention levels, using an information theoretic (IT) approach. As with other studies that use IT, my inferences are conditional on the candidate model set (Burnham and Anderson, 2002). Had I not considered stand age (*i.e.,* AGE models) in my analysis, then evidence for a positive influence of retention on occupancy of interior forest species would have been greater. This result highlights the importance of critical thinking and incorporating knowledge about the study system into development of *a priori* models. This was particularly true for all early-successional species, which showed a strong, negative response to years since harvest.

Young aspen clearcuts with green-tree retention are used by a distinct avian community that require open or disturbed habitat for breeding (Merrill et al., 1998; DeGraaf and Yamasaki, 2003; Atwell et al., 2008). Clearcutting may serve as an effective management tool for creating early-successional habitat in landscapes where natural disturbances, such as fire, have been suppressed (Litvaitis, 1993; Brawn et al., 2001; Hunter et al., 2001). Collectively, my results corroborate those of Vanderwel et al. (2007), Campbell et al. (2007) and Donner et al. (2010) who stressed the importance of considering forest temporal dynamics when assessing the impact of silvicultural prescriptions on forest songbirds, even within the first 15 years following harvest.

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4.4.3. Songbird Detection Probability and Intra-breeding Season Movement

Failure to account for species detection has been cited as a leading source of uncertainty in wildlife-habitat research and monitoring programs (MacKenzie, 2005; Kéry and Schmidt, 2008; Watson et al. 2008). Even small amounts of observation error attributable to imperfect detection can bias results from aural point-count surveys if it is unaccounted for within an estimation framework (Etterson et al., 2009, McClintock et al., 2010). Consistent with this concern, I detected 66 species during this study, but had sufficient detection information to model occurrence patterns for just 20. Furthermore, detection probability for these 20 study species was always less than 1. Most studies investigating songbird response to timber harvesting use organism counts (incorrectly called abundance) or detection/non-detection (presence-absence or richness) data of multiple species as the response variable: data which are uncorrected for detection probability and thus possess an unknown level of bias (Kéry and Schmidt, 2008; McClintock et al., 2010). Future wildlife-forestry research should explicitly acknowledge this source of observation error and take steps to minimize potential bias in abundance, occupancy, or richness estimates by incorporating detection uncertainty into the modeling framework (Yoccoz et al. 2001, Royle et al., 2005; MacKenzie et al., 2006).

I also observed evidence that the occupancy status of my study sites changed throughout the field season, presumably due to non-random movement of songbirds between primary periods. Although my analysis does not allow for direct inferences regarding species movements (Kendall and Nichols, 2004), it does suggest that habitat selection by my study species may occur as an iterative process, where sites with more suitable habitat conditions are more likely to be settled as the breeding season progressed. Migratory birds arriving on a landscape must make initial habitat selection choices based on limited knowledge of current conditions; however, these

choices may be refined as additional habitat information is gained (Hutto, 1985; Betts et al., 2008). Accordingly, my analysis revealed that site settlement probabilities within a breeding season were associated with stand age for many species and with green-tree retention for red-eyed vireos. For example, site settlement probabilities for all of my early-successional species were lower on 10-15yr forest stands when compared to 1-4yr stands. Although telemetry and banding studies provide more direct evidence of species habitat selection, my study supports the growing use of patch occupancy models for inferring habitat selection dynamics of migratory birds in managed forests (Kendall and Nichols, 2004; Betts et al. 2008; Donner et al. 2010). Furthermore, my results corroborate those of Rota et al. (2009) who stress the importance of accounting for non-random movement of songbirds during point-count studies which span the length of a breeding season.

4.4.4. *Conclusions*

My findings create a dilemma for resource managers using clearcutting with green-tree retention prescriptions for conserving songbirds in young aspen stands in Michigan. With the exception of Red-eyed Vireos, I found little evidence of green-tree retention influencing songbird occupancy when compared to the influence of forest succession within the first15 years of harvest. This pattern was consistent for all species guilds, including early-successional species, for which I hypothesized a negative association with green-tree retention. Based on these results, I do not support the notion that green-tree retention guidelines implemented by the MDNR are effective for promoting occupancy of most interior forest songbirds in harvested aspen stands. As with all scientific research, extrapolating these results to other systems should be done with caution. This is especially true for managed forests where green tree retention prescriptions may be greater than the quantities observed in my study (Aubry et al., 1999;

Hickey et al., 2001; Lance and Phinney, 2001; Martínez Pastur et al., 2009). For example, in some managed forests of Southern Patagonia, approximately 30% of the harvest area is retained as aggregate retention (Martínez Pastur et al., 2009). My study provides limited insight regarding the effectiveness green-tree retention within other forest systems where retention levels are higher than those observed here. However, retention levels observed in my study are comparable to other forest certification regulations in Finland, Norway, and Sweden and some portions of the Pacific Northwest (Arnott and Beese 1997; Aubry et al., 2004; Gustafsson et al. 2010). Because there is a high degree of inter-agency variability in management objectives related to, and application of, structural retention prescriptions, I feel it is prudent to provide management recommendations based on the observed evidence. If resource managers wish to promote occupancy of early-successional and generalist songbirds, then my results suggest that clearcutting, with limited structural retention, is a viable management option, particularly within the first 10 years of harvest. Although there is concern that canopy retention may reduce habitat quality for some early-successional birds (Tittler et al., 2001; McDermott and Wood, 2011), my study shows that <25% retention over a 0.78ha area did not result in lower occupancy of early-successional species. If forest management objectives also include conservation of red-eyed vireos, then my results suggest that green-tree retention patches should provide ≥25% canopy cover within a 0.78ha area. However, it is unlikely that management goals for many interior forest songbirds will be accomplished solely through green-tree retention at the forest stand scale. Rather, successful management of these species may require conservation of entire stands of late-successional forests within actively managed landscapes.

4.5. Acknowledgements

APPENDIX

Appendix B.1 Methodology for calculating the proportion of canopy cover at study site.

To estimate the proportion of canopy cover of each 50m radius site, I digitized canopy cover of

all retained green-trees within the harvest units using 2010, 2009, 2005, and 1998 NAIP

(National Agricultural Imagery Program) imagery. The age of the harvest unit dictated which

year of NAIP imagery I used. For example, if harvest of a stand was completed in 2003, then I

used 2005 NAIP imagery to map retention. To digitize canopy cover, I created a new shapefile

in a Geographic Information System (GIS; ArcGIS 9.1; Environmental Systems Research

Institute, Redlands, CA) to represent canopy cover provided by retained green-trees. I used the

SKETCH tool in ArcEditor to draw the canopy cover polygons into the new shapefile.   I then

used the INTERSECT function in Arc Toolbox (ArcGIS 9.1; Environmental Systems Research

Institute, Redlands, CA) to intersect the canopy cover polygon shapefile with separate polygon

shapefile that represented the boundary of 50m radius site.   I used the AREA function in

HAWTH'S TOOLS (Hawth's Tools, version 3.27, http://www.spatialecology.com/htools/) to

calculate the proportion of canopy cover within each site. For example, if area of canopy cover

within a site was $1260m^2$ then the proportion of canopy cover at that site was $\{1260m^2 / [\pi \times$

$(50m\ radius)^2]\}$ or 0.16. This was the value which I used to group my study sites for analysis in

Chapter 4 (*i.e.,* assign the site to one of three green-tree retention groups based on the MDNR

retention guidelines (<3%, 3-10%, and >10% canopy cover)).

Figure 4.1. Number of songbird sampling sites, stratified by green-tree retention level and years since harvest. 'Green-Tree Retention Level' represents sites where the proportion of canopy cover within a 50m radius around the point-count station was below (<3%), at (3-10%), or exceeded (>10%) retention guidelines implemented by the MDNR in harvested aspen stands (Bielecki et al., 2006). 'Years Since Harvest' is the age of the site at the time sampling occurred.

Figure 4.2. Site occupancy estimates for 20 songbird species detected at 222 sites in young aspen stands from the northern Lower Peninsula of Michigan, USA, 2010-2011. Occupancy represents the probability that a site is occupied during a 9min point count. Green Tree Retention (%) is the percent canopy cover within a 50m radius of an avian point-count site; <3, 3-10, and >10% represent green tree retention levels that were below, met, or exceeded MDNR retention guidelines (Bielecki et al., 2006). Years Since Harvest is the age of the forest stand at the time of sampling.   All parameter estimates are model averaged.   A = Interior Forest[e], B-C = Generalist[f], and D = Early-successional[g] species.

A
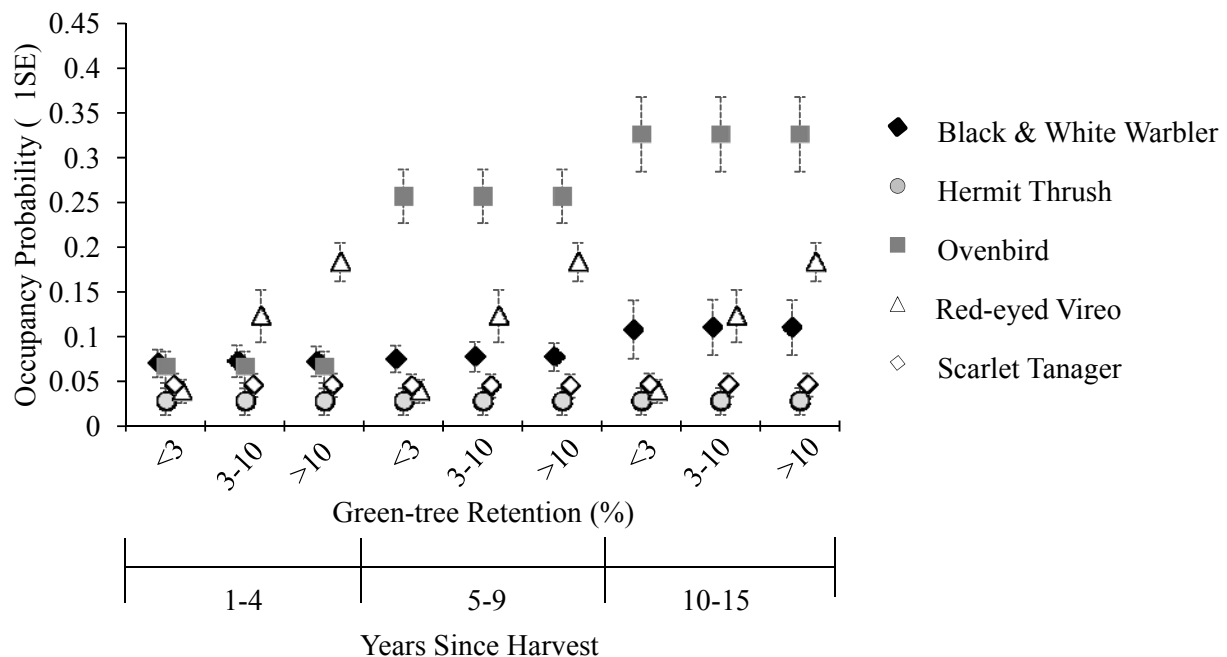
Figure 4.2 (cont'd)

B
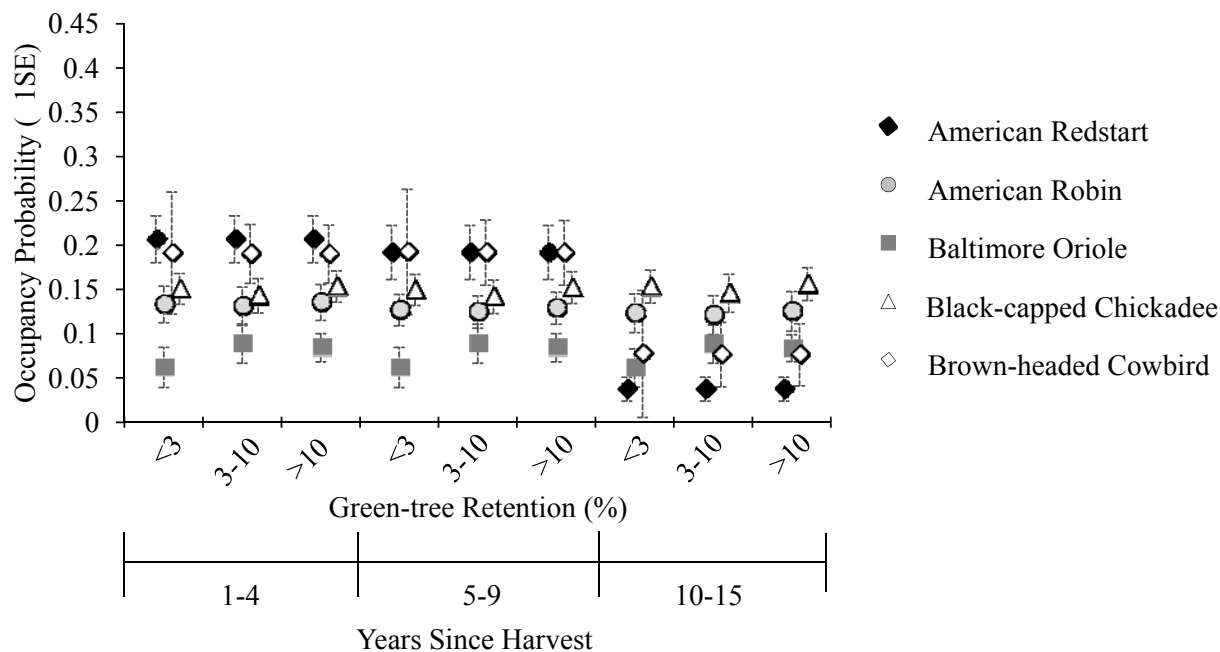
C
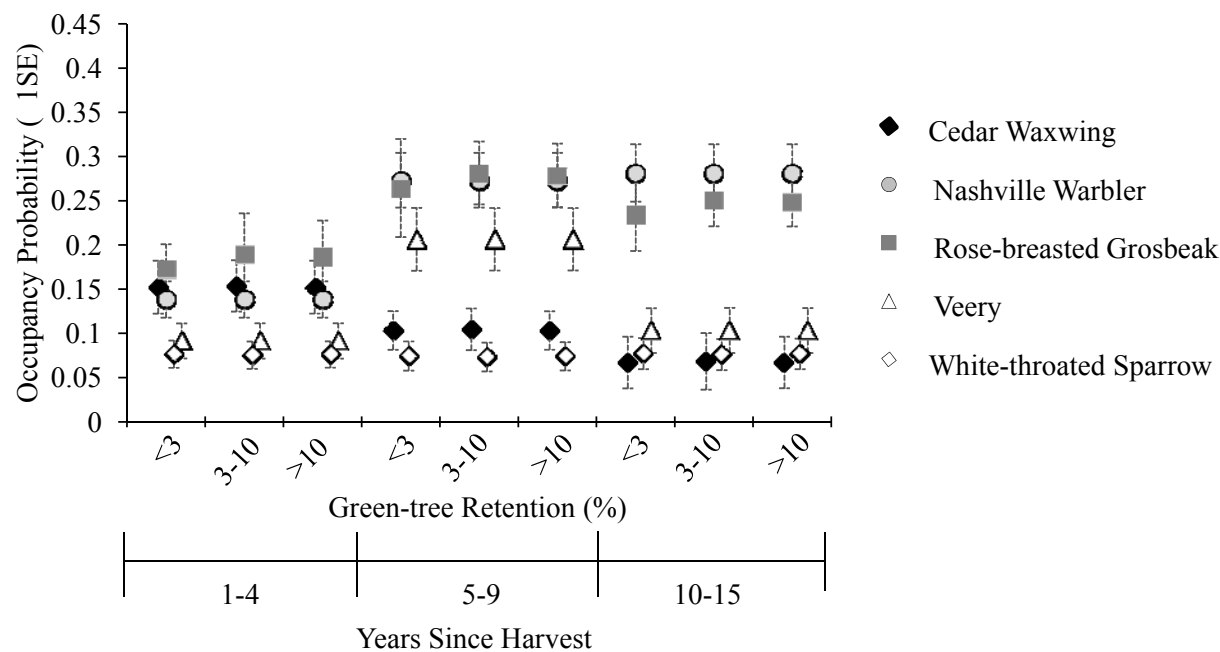
Figure 4.2 (cont'd)

D

[e] Interior forest birds; black-and-white warbler (*Mniotilta varia*), hermit thrush (*Catharus guttatus*), ovenbird (*Seiurus aurocapillus*), red-eyed vireo (*Vireo olivaceus*), scarlet tanager (*Piranga olivacea*)

[f] Generalist birds: American redstart (*Setophaga ruticilla*), American robin (*Turdus migratorius*), Baltimore oriole (*Icterus galbula*), black-capped chickadee (*Poecile atricapillus*) brown-headed cowbird (*Molothrus ater*), cedar waxwing (*Bombycilla cedrorum*), Nashville warbler (*Oreothlypis ruficapilla*), rose-breasted grosbeak (*Pheucticus ludovicianus*), veery (*Catharus fuscescens*), white-throated sparrow (*Zonotrichia albicollis*)

[g] Early-successional; chestnut-sided warbler (*Setophaga pensylvanica*), common yellowthroat (*Geothlypis trichas*), eastern towhee (*Pipilo erythrophthalmus*), golden-winged warbler (*Vermivora chrysoptera*), indigo bunting (*Passerina cyanea*)

Figure 4.3. Site settlement estimates for 20 songbird species detected at 222 sites in young aspen stands from the northern Lower Peninsula of Michigan, USA, 2010-2011. Settlement is the probability that an unoccupied site during primary period *i* becomes occupied before primary period *i* + 1. Green Tree Retention (%) is the percent canopy cover within a 50m radius of an avian point-count site; <3, 3-10, and >10% represent green tree retention levels that were below, met, or exceeded MDNR retention guidelines (Bielecki et al., 2006). Years Since Harvest is the age of the forest stand at the time of sampling.   All parameter estimates are model averaged.   A = Interior Forest[e], B-C = Generalist[f], and D = Early-successional[g] species.

A
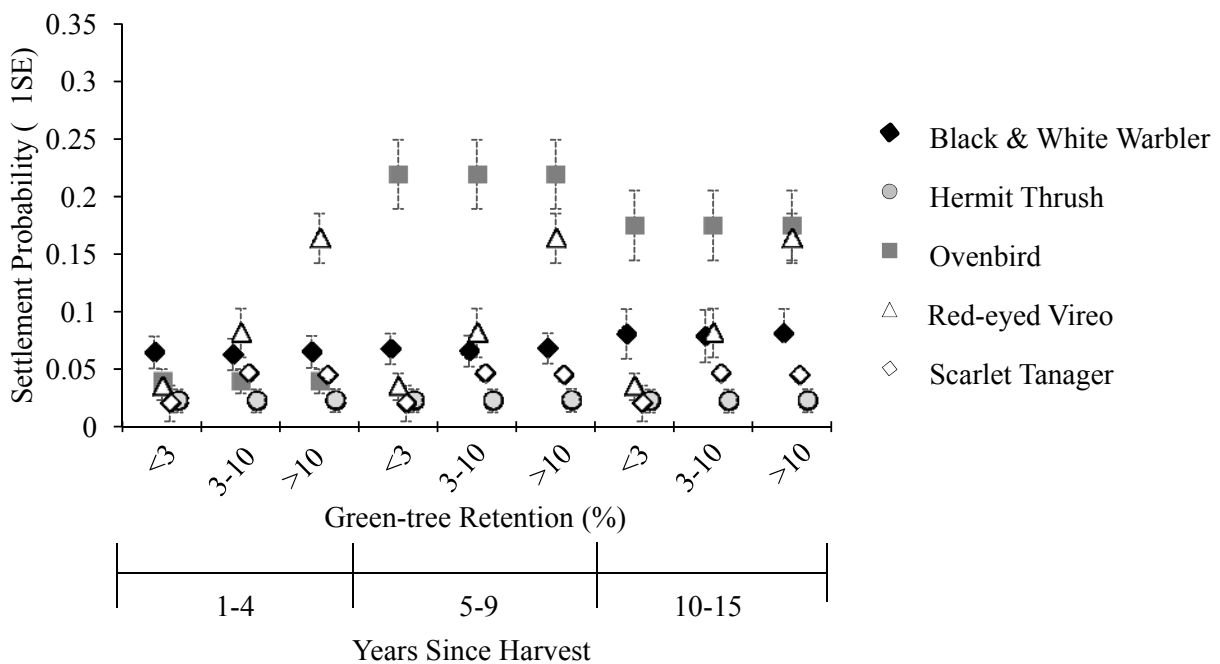
Figure 4.3 (cont'd)

B
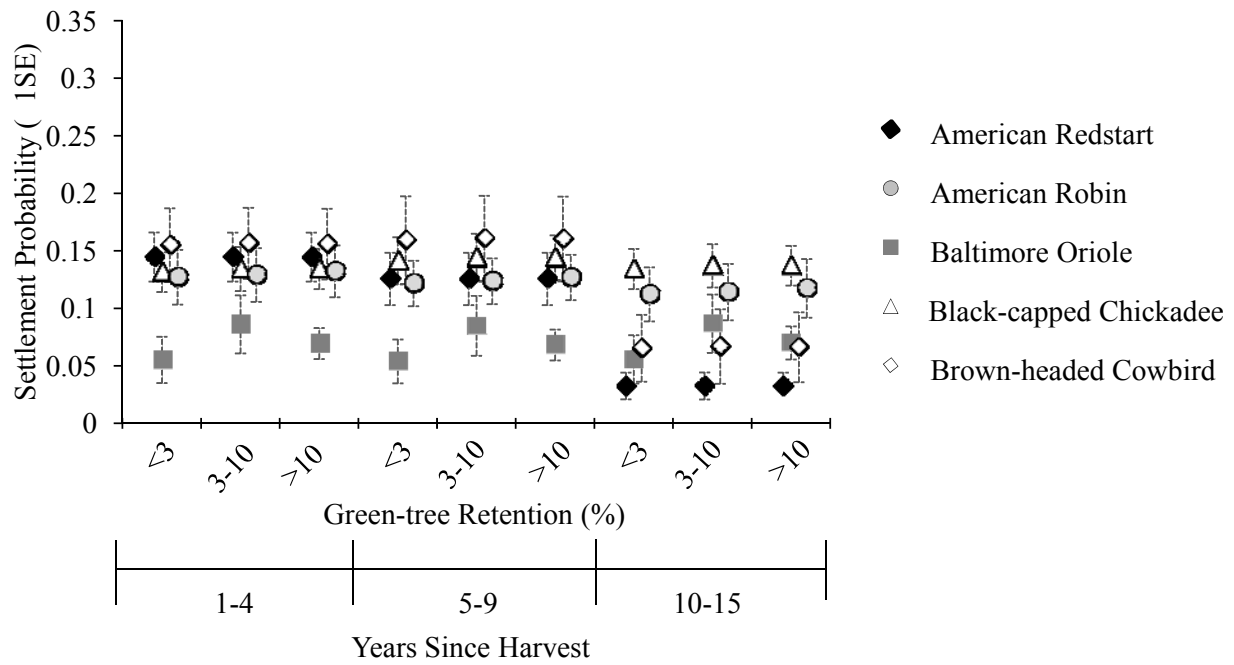
C
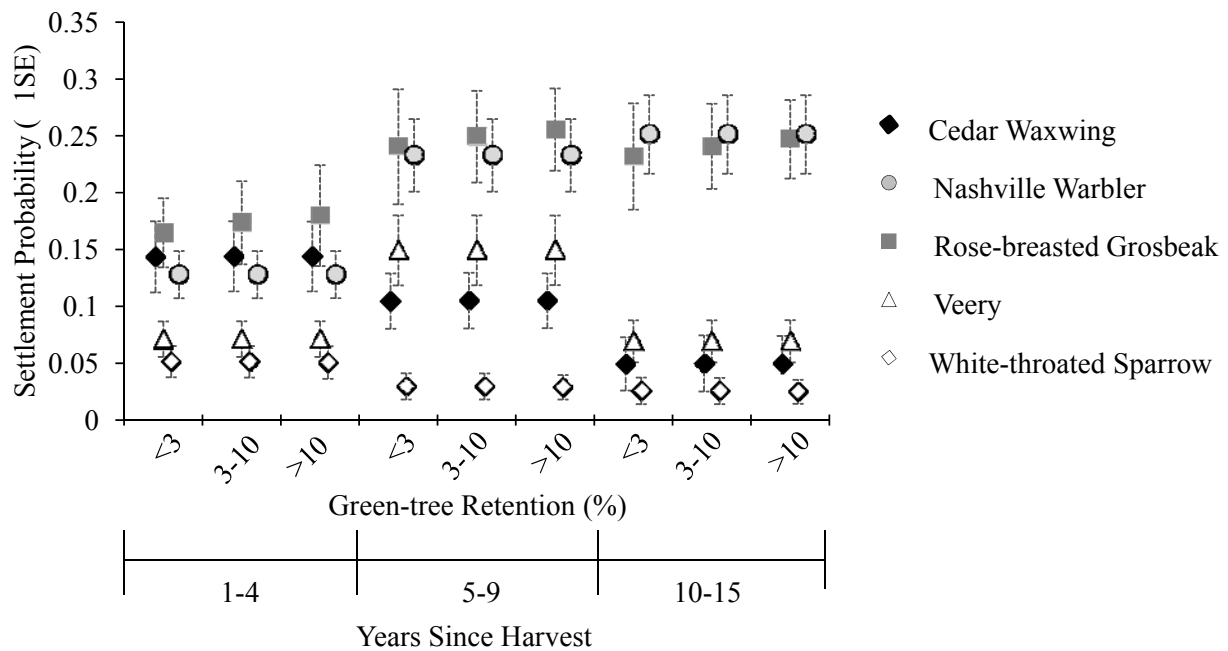
Figure 4.3. (cont'd)

D

[e] Interior forest birds; black-and-white warbler (*Mniotilta varia*), hermit thrush (*Catharus guttatus*), ovenbird (*Seiurus aurocapillus*), red-eyed vireo (*Vireo olivaceus*), scarlet tanager (*Piranga olivacea*)

[f] Generalist birds: American redstart (*Setophaga ruticilla*), American robin (*Turdus migratorius*), Baltimore oriole (*Icterus galbula*), black-capped chickadee (*Poecile atricapillus*) brown-headed cowbird (*Molothrus ater*), cedar waxwing (*Bombycilla cedrorum*), Nashville warbler (*Oreothlypis ruficapilla*), rose-breasted grosbeak (*Pheucticus ludovicianus*), veery (*Catharus fuscescens*), white-throated sparrow (*Zonotrichia albicollis*)

[g] Early-successional; chestnut-sided warbler (*Setophaga pensylvanica*), common yellowthroat (*Geothlypis trichas*), eastern towhee (*Pipilo erythrophthalmus*), golden-winged warbler (*Vermivora chrysoptera*), indigo bunting (*Passerina cyanea*)

Table 4.1. Estimated detection probability and standard error estimates ($\hat{p} \pm 1SE$) for 20 songbird species detected in harvested aspen stands in the northern Lower Peninsula of Michigan, 2010-11. $\hat{p}$ is the estimated probability of detecting the species during a 3 minute point-count, given it was present within a 50m radius of point-count site.

Species	$\hat{p}$	1SE	Scientific Name
Interior Forest			
Black-and-white warbler	0.60	0.04	*Mniotilta varia*
Hermit thrush	0.68	0.06	*Catharus guttatus*
Ovenbird	0.70	0.02	*Seiurus aurocapillus*
Red-eyed vireo	0.62	0.03	*Vireo olivaceus*
Scarlet Tanager	0.50	0.06	*Piranga olivacea*
Generalist			
American redstart	0.72	0.02	*Setophaga ruticilla*
American robin	0.43	0.04	*Turdus migratorius*
Baltimore oriole	0.51	0.05	*Icterus galbula*
Black-capped chickadee	0.56	0.03	*Poecile atricapillus*
Brown-headed cowbird	0.31	0.04	*Molothrus ater*
Cedar waxwing	0.37	0.04	*Bombycilla cedrorum*
Nashville warbler	0.65	0.02	*Oreothlypis ruficapilla*
Rose-breasted grosbeak	0.61	0.02	*Pheucticus ludovicianus*
Veery	0.60	0.03	*Catharus fuscescens*
White-throated sparrow	0.52	0.05	*Zonotrichia albicollis*

Table 4.1 (cont'd)

Species	$\hat{p}$	1SE	Scientific Name
Early-successional			
Chestnut-sided warbler	0.66	0.03	*Setophaga pensylvanica*
Common yellowthroat	0.70	0.03	*Geothlypis trichas*
Eastern towhee	0.61	0.03	*Pipilo erythrophthalmus*
Golden-winged warbler	0.62	0.04	*Vermivora chrysoptera*
Indigo bunting	0.62	0.02	*Passerina cyanea*

Table 4.2. The proportion of 222 study sites where the target species was known to occur (*i.e.* positive detection) during 4, 9-minute point-counts. Each point-count was separated by 10-14 days. "Combined" represents the proportion of sites where the species was detected at least once during any of the 4 point-counts.

Species	Proportion of sites with known occurrence				
	1st	2nd	3rd	4th	Combined
Mature forest-associated					
Black-and-white warbler	0.11	0.09	0.08	0.05	0.23
Hermit thrush	0.02	0.02	0.03	0.03	0.08
Ovenbird	0.21	0.15	0.19	0.21	0.42
Red-eyed vireo	0.05	0.14	0.11	0.17	0.34
Scarlet tanager	0.03	0.03	0.03	0.05	0.12
Generalist					
American redstart	0.12	0.14	0.18	0.17	0.34
American robin	0.05	0.13	0.11	0.12	0.35
Baltimore oriole	0.08	0.09	0.07	0.04	0.23
Black-capped chickadee	0.10	0.13	0.11	0.20	0.42
Brown-headed cowbird	0.12	0.14	0.07	0.10	0.34
Cedar waxwing	0.02	0.05	0.13	0.14	0.29
Nashville warbler	0.33	0.21	0.16	0.14	0.57
Rose-breasted grosbeak	0.31	0.23	0.22	0.10	0.59
Veery	0.04	0.10	0.17	0.18	0.30
White-throated sparrow	0.06	0.07	0.05	0.08	0.15
Early-successional					
Chestnut-sided warbler	0.18	0.16	0.19	0.16	0.34
Common yellowthroat	0.10	0.09	0.10	0.16	0.23
Eastern towhee	0.12	0.14	0.22	0.23	0.44
Golden-winged warbler	0.09	0.12	0.07	0.02	0.18
Indigo bunting	0.15	0.25	0.27	0.27	0.50

Table 4.3. Ranking of candidate occupancy models for 20 songbird species detected at 222 sites in young aspen stands from the northern Lower Peninsula of Michigan, USA, 2010-2011. 'Retention' is the percent canopy cover within a 50m radius of a avian point-count site, assigned to 1 of 3 classifications: sites where retention levels were below (<3%), at (3-10%), or exceeded (>10%) MDNR retention guidelines (Bielecki et al., 2006). 'Age' is the number of years post-harvest, assigned to 1 of 3 classifications: 1-4, 5-9, or 10-15 years post-harvest. I report the complete model set for Black-and-white Warblers, but report only models accounting for 0.80 of the total Akaike weight (w_i) for all other species. Cumulative model weights (w_+) for Retention (Reten) and Age are also reported.

Species[b]	Model	ΔAIC_c[a]	w	K	$-2\,l$	w_+ Reten	w_+ Age
Interior Forest							
Black-and-white warbler	ψ(Age),γ(Age),p(.)	0.00	0.34	7	733.8	0.18	0.67
	ψ(Age),γ(.),p(.)	0.23	0.30	5	738.1		
	ψ(.),γ(.),p(.)	1.69	0.15	3	743.6		
	ψ(Retention),γ(.),p(.)	3.02	0.07	5	740.9		
	ψ(.),γ(Retention),p(.)	3.13	0.07	5	741.0		
	ψ(Retention),γ(Retention),p(.)	4.73	0.03	7	738.5		
	ψ(.),γ(Age),p(.)	4.94	0.03	5	742.8		
	ψ(Age),γ(=0),p(.)	140.38	0.00	4	880.3		
	ψ(.),γ(=0),p(.)	143.15	0.00	2	887.1		
	ψ(Retention),γ(=0),p(.)	146.20	0.00	4	886.1		
Hermit thrush	ψ(.),γ(.),p(.)	0.00	0.85	3	287.7	0.02	0.13
Ovenbird	ψ(Age),γ(Age),p(.)	0.00	1.00	7	1320.8	0.00	1.00
Red-eyed vireo	ψ(Retention),γ(Retention),p(.)	0.00	1.00	7	997.5	1.00	0.00

Table 4.2 (cont'd)

Species[b]	Model	ΔAIC_c [a]	w	K	$-2\,l$	w_+ Reten	w_+ Age
Scarlet tanager	ψ(.),γ(Retention),p(.)	0.00	0.68	5	383.7	0.68	0.04
	ψ(.),γ(.),p(.)	1.78	0.28	3	389.5		
Generalist							
American redstart	ψ(Age),γ(Age),p(.)	0.00	1.00	7	1136.8	0.00	1.00
American robin	ψ(.),γ(.),p(.)	0.00	0.41	3	953.5	0.24	0.35
	ψ(Age),γ(Age),p(.)	1.98	0.15	7	947.4		
	ψ(.),γ(Age),p(.)	2.30	0.13	5	951.7		
	ψ(.),γ(Retention),p(.)	2.92	0.10	5	952.4		
	ψ(Retention),γ(.),p(.)	3.20	0.08	5	952.6		
Baltimore oriole	ψ(Retention),γ(Retention),p(.)	0.00	0.43	7	674.7	0.66	0.09
	ψ(.),γ(.),p(.)	1.13	0.25	3	683.9		
	ψ(.),γ(Retention),p(.)	2.51	0.12	5	681.2		
Black-capped chickadee	ψ(.),γ(.),p(.)	0.00	0.24	3	1171.6	0.37	0.39
	ψ(.),γ(Age),p(.)	0.17	0.22	5	1167.7		
	ψ(Retention),γ(.),p(.)	0.21	0.22	5	1167.7		
	ψ(Age),γ(.),p(.)	1.50	0.11	5	1169.0		
	ψ(.),γ(Retention),p(.)	2.08	0.09	5	1169.6		
Brown-headed cowbird	ψ(Age),γ(Age),p(.)	0.00	0.88	7	929.0	0.02	0.94
Cedar waxwing	ψ(Age),γ(Age),p(.)	0.00	0.83	7	780.9	0.04	0.92
Nashville warbler	ψ(Age),γ(Age),p(.)	0.00	0.99	7	1567.5	0.00	1.00
Rose-breasted grosbeak	ψ(Age),γ(Age),p(.)	0.00	0.70	7	1636.3	0.21	0.76
	ψ(Retention),γ(Retention),p(.)	3.09	0.15	7	1639.4		
Veery	ψ(Age), γ(Age),p(.)	0.00	0.92	7	1026.7	0.01	0.96
White-throated sparrow	ψ(.),γ(Age),p(.)	0.00	0.64	5	584.2	0.08	0.79
	ψ(.),γ(.),p(.)	3.10	0.14	3	591.3		
	ψ(Age),γ(Age),p(.)	3.50	0.11	7	583.6		

Table 4.2 (cont'd)

Species[b]	Model	ΔAIC_c [a]	w	K	$-2\,l$	w_+ Reten	w_+ Age
Early-successional							
Chestnut-sided warbler	ψ(Age),γ(Age),p(.)	0.00	1.00	7	1247.7	0.00	1.00
Common yellowthroat	ψ(.),γ(Retention),p(.)	0.00	0.31	5	890.4	0.42	0.49
	ψ(.),γ(Age),p(.)	0.35	0.26	5	890.8		
	ψ(Age),γ(Age),p(.)	0.81	0.21	7	887.2		
	ψ(.),γ(.),p(.)	2.43	0.09	3	896.9		
Eastern towhee	ψ(Age),γ(Age),p(.)	0.00	1.00	7	1360.5	0.00	1.00
Golden-winged warbler	ψ(Age),γ(Age),p(.)	0.00	0.86	7	662.3	0.02	0.95
Indigo bunting	ψ(Age),γ(Age),p(.)	0.00	1.00	7	1637.1	0.00	1.00

[a] ΔAIC_c = difference from the Akaike's Information Criterion best model, adjusted for small sample size: K = no. of parameters; $-2\,l$ is twice the negative log-likelihood.

[b] See Table 1 for scientific names.

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CHAPTER 5

OCCURRENCE AND SURVIVAL OF A TERRESTRIAL SALAMANDER FOLLOWING HABITAT DEGRADATION: CAN WE AMELIORATE THE EFFECT OF TIMBER HARVEST?

Abstract

Habitat degradation resulting from anthropogenic activities poses immediate and prolonged threats to biodiversity, particularly among declining amphibians. Most studies infer amphibian response to habitat degradation by correlating patterns in species occupancy or abundance with an ecological effect, often with little regard to the demographic process underlying these patterns. I used correlative and experimental evidence to evaluate how retention of vertical green trees (CANOPY) and coarse woody debris (CWD) influenced terrestrial salamander occupancy and survival in clearcut forests. I observed little evidence that terrestrial salamander occupancy was related to structural retention within harvested forests: cumulative weight of models was 0.36 and 0.37 for CANOPY and CWD, respectively and model parameters consistently overlapped 0. However, salamander survival within recently harvested forests was positively influenced by CANOPY and CWD retention ($\hat{\beta}_{Canopy}$= 0.73 (0.27 – 1.19; 95%CI) and $\hat{\beta}_{CWD}$ = 1.01 (0.53 – 1.50). In some instances, estimated salamander survival was higher at harvested sites with high levels of structural retention compared to older (40-60 year-old) forests. I demonstrated that organismal pattern (occupancy) and process (survival) can function independently in response to habitat change. My study emphasizes the importance of quantifying population vital rates when evaluating mitigation techniques presumed beneficial to wildlife.

Status: I intend to submit this manuscript to Ecological Applications.

5.1. Introduction

Anthropogenic habitat degradation is a primary threat to global biodiversity (Foley et al. 2005; Schipper et al. 2008; Krauss et al. 2010). For example, > 30% of amphibian species are at risk of extinction and habitat degradation is cited as a leading cause of amphibian declines (Stuart et al. 2004; Wake and Vredenburg 2008; Hof et al. 2011). In forested systems, degradation via timber harvesting poses both short- and long-term threats to forest biota (Ferraz et al. 2003; Gibson et al. 2011). Most researchers agree that timber harvesting has a negative effect on forest amphibian abundance (Petranka et al. 1993; Ash 1997; Knapp et al. 2003, Homyack and Haas 2009), thus amphibians are useful candidates for studying this form of habitat degradation on wildlife.

Limited knowledge exists on how timber harvesting influences amphibian population vital rates because most observational and experimental studies use indices like species richness (counts of the number of species), relative abundance (counts of individuals within a species), or occurrence (counts of occupied sites) as the response variable (reviewed in deMaynadier and Hunter 1995; Cushman 2006). Use of these population indices for inferring response to habitat degradation has been criticized for several reasons (*e.g.,* Cushman 2006, Welsh et al. 2008). First, assessing changes in abundance or occupancy does not provide adequate information on how population vital rates or life-history characteristics change as a consequence of habitat condition (Van Horne 1983; Yoccoz et al. 2001). When inferring species response to a particular habitat condition or ecological effect, researchers implicitly assume a positive, and

often linear, relationship exists between species occurrence, or abundance, and habitat (Van Horne 1983). Support for this assumption may be tenuous if amphibians exhibit metapopulation or source-sink dynamics (Carlson and Edenhamn 2000, Marsh and Trenham 2001, Heard et al. 2012). Furthermore, patterns in species occurrence and abundance are a dictated by population process such as survival, reproduction, and movement. Hence, studies that directly assess the influence of habitat degradation on survival, reproduction, and movement of organisms should yield greater inferential power that those which assess population indices (Yoccoz et al. 2001; Williams et al. 2002).

Second, raw counts of individuals or species are often incorrectly referred to as (relative) abundance, or richness data; however, these data are not corrected for probability of encounter (*i.e.,* detection probability; MacKenzie and Kendall 2002, Kéry and Schmidt 2008). Failure to account for detection probability has been cited as a leading source of uncertainty in research investigating amphibian response to timber harvest and other habitat relationships (Bailey eta l. 2004a, Mazerolle et al. 2005, Pellet and Schmidt 2005, Kroll 2009). These authors stress that count data that are uncorrected for detection probability possess an unknown level of uncertainty, and therefore should be viewed as indices of abundance or richness, which in turn, are indices of population processes. Over the past decade, a myriad of statistical techniques have been developed to estimate species occupancy and abundances from replicate count data (*e.g.,* MacKenzie et al. 2002, Royle 2004, Royle and Dorazio 2004). These estimation techniques are generally preferred over traditional Generalized Linear Models (GLM) because they account for imperfect detection probability (Kéry and Schmidt 2008, Archaux et al. 2012). Thus, ecologists now possess the tools for generating unbiased estimates of occupancy and abundance from count

data which can be collected relatively quickly over broad spatial scales to address ecological and management questions.

I used correlative and experimental approaches to investigate red-backed salamander (*Plethodon cinereus;* RBS) response to residual forest structure, such as coarse woody debris and vertical green trees, within harvested forests. These structures were purposefully left to potentially ameliorate the negative effects of clearcutting on forest wildlife (Franklin et al. 1997). First, I studied how patterns in salamander occupancy were related to retention of green trees (CANOPY) and coarse woody debris (CWD) within a managed, forested landscape (560,000ha). Second, I quantified how salamander survival was influenced by CANOPY and CWD within timber harvest areas. For both studies, I used hierarchical models that account for observation error associated with imperfect detection. By focusing my study on the same species, forested areas, and time period I was able to evaluate if occupancy and survival measurements yielded similar inferences regarding amphibian response to structural retention. Hence, my study informs the current debate over which population parameters are most useful for assessing amphibian response to habitat degradation (Cushman 2006; Welsh et al. 2008, Kroll et al. 2009).

5.2. Methods

5.2.1. Study Species

Red-backed salamanders (RBS) are a terrestrial, lung-less amphibian distributed in woodlands throughout eastern North America (Petranka 1998, p. 336). RBS are recognized as critical components of forested ecosystems through their contribution to the detrital food web, forest biomass and potentiality serve as an indicator species (Davic and Welsh 2004). Like all Plethodontids, respiration in RBSs occurs cutaneously, making them prone to desiccation. As a result, RBS has been utilized in many forest management studies and its negative response to

clearcutting has been well documented (*e.g.,* Petranka et al. 1993; Ash 1997; Homyack and Haas 2009).

5.2.2. Study Area

I conducted my study across a 560,000 ha area in the northwestern Lower Peninsula of Michigan, USA, in 2010-11. My study occurred on state-owned forest lands that were managed for aspen (*Populus* spp.) production by the Michigan Department of Natural Resources (MDNR). In Michigan, aspen is typically harvested via clearcutting on a 50-70 year rotation. Within harvested stands (where a stand is defined as an area with homogenous vegetation and management focus) the MDNR implemented green-tree retention prescriptions to provide refugia for wildlife following timber harvesting (Franklin et al. 1997). These prescriptions called for retention of 3-10% of the pre-harvest green-tree basal area (i.e., the cumulative surface area covered by a cross-section of tree stems at ground level), arranged throughout the stand as single leave-trees or aggregated into retention patches (Bielecki et al. 2006). Harvested areas also contained varied amounts of CWD that was unequally distributed throughout the harvest areas as part of the logging contract specifications. Additional study area details can be found in Otto and Roloff (2011).

5.2.3. Salamander Occupancy

My candidate areas for study consisted of all state-owned aspen stands within a 4 county area that were >8 ha in size and between 1 to 5 years post-harvest. To select potential survey sites within a stand, I used HAWTH'S TOOLS (Hawth's Tools, version 3.27, http://www.spatialecology.com/htools/) in a Geographic Information System (GIS; ArcGIS 9.1; Environmental Systems Research Institute, Redlands, CA) to overlay each aspen stand with a 60 x 60 m lattice. I used orthophotos from the 2010 National Agricultural Imagery Program (NAIP;

http://www.mcgi.state.mi.us/mgdl) to digitize canopy cover of all retained green-trees within the sampling lattice over each forest stand. I assigned each cell of the lattice to one of three groups (>25%, 10-25%, and <10% canopy cover) and then randomly selected 40 cells from each group. To maintain site independence, I ensured that all selected cells were >200m apart. I selected an additional 30 cells within 40-60 year old aspen stands that were adjacent to my harvested stands. I eliminated 16 cells after initial field visits because the dominant cover-type was not aspen. My final sample size for harvested cells was 107, with varying levels of green-tree retention, and 27 for the 40-60 year-old cells. Hereafter, I refer to the subset of cells used for this study as sites.

Within each selected site I identified 33, 20 x 2m transects which were oriented north to south and spaced ≥5m apart. From the 33 transects I randomly selected, with replacement, 3 transects for salamander sampling. Selected transects were treated as spatial replicates for estimating salamander detection probability (MacKenzie et al. 2002; Kendall and White, 2009). Each transect was surveyed once unless it was selected with replacement, in which case it was surveyed again 12-16 days later. For each transect survey, one observer searched for RBSs under cover objects >4 cm diameter and >15 cm long. Observers tallied the number of cover objects they search along each transect.

I generated detection histories of RBSs for each site and used single-season occupancy models (MacKenzie et al. 2002) to test predictions regarding salamander occupancy and detection. I started with a general hypothesis that salamander occupancy probability was lower in 1-5 year-old sites when compared to 40-60 year-old sites. I included this hypothesis so that my results were comparable to other amphibian-forestry studies (Petranka et al. 1993; Ash 1997; Knapp et al. 2003). I also hypothesized that salamander occupancy at harvested sites would be positively related to structural elements, such CANOPY and CWD, that were purposefully

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retained during timber harvest to provide refugia for forest wildlife (Franklin et al. 1997; Rosenvald and Lõhmus 2008). To represent my hypotheses, I constructed models where salamander occupancy (ψ) varied linearly on the logit scale as a function of CANOPY within the 60 x 60m cell (logit(ψ_i) = $\beta_0 + \beta_1$(CANOPY$_i$)), or the cumulative number of CWD objects encountered during surveys along the three transects (logit(ψ_i) = $\beta_0 + \beta_1$(CWD$_i$)). I hypothesized that CANOPY and CWD could operate independently, or as additive effects on occupancy (ψ(CANOPY + CWD)). Although I stratified canopy cover into different categories during site selection, I treated CANOPY as a continuous variable for all analyses. I predicted that salamander detection probability would be constant across time, as all transects within a site were sampled at the same time and all sites were sampled within a single month. However, I was concerned that variable quantities of downed wood along transects could influence the ability of my field observers to detect salamanders. Hence, I constructed a model where detection probability (p) varied as a function of CWD encountered along transect j (CWD$_j$; logit(p_j) = $\beta_2 + \beta_3$(CWD$_j$). I note the distinction between CWD$_i$, a site covariate, which is the total number of cover objects encountered among all 3 surveyed transects within a site, and CWD$_j$, a detection covariate, which is the number of cover objects along transect j within a site (j = 1,2,3).

5.2.4. Salamander Survival

I selected a subset of 6, 1-5 year-old stands that were sampled during my occupancy study. These stands were selected to represent variation in green tree retention levels. I used a 30 x 30m sampling lattice and stratified (i.e., >25%, 10-25%, and <10% canopy cover) random selection to identify 36 cells for study. All cells were >50 m apart. I also selected 9 cells, spaced

$\geq$ 50m apart, within two, 40-60 year-old aspen stands that were adjacent to my 1-5 year-old stands.

In early May of 2010 and 2011 I erected a 3 x 3m salamander enclosure at the center of each 30 x 30 m lattice cell (total = 45 cells). Enclosures were constructed of aluminum flashing 50cm high and buried 12-15cm into the ground. The top of each fence was bent inward at 90° to prevent salamander escape. CWD that extended beyond the enclosure boundary were cut and those portions external to the enclosure were removed prior to fence construction. I tested the effectiveness of this enclosure design for preventing salamander escape over the top by adding 12 RBSs to a $0.09m^2$ replica enclosure, placed in a covered plastic container with air holes, over a 3 day period. No salamanders escaped from the replica during this time.

In mid-May, I added 10 adult RBSs that were individually marked with visual implant elastomere (VIE; Northwest Marine Technology, Shaw Island, Washington; Grant 2008) to each enclosure. These salamanders were captured within 1km of my study stands and added to the enclosure within 24 hours of capture. Release locations within an enclosure were randomly assigned. Marked salamander density within the enclosures ($\approx 1.1m^2$) was comparable to observed densities in mature forests in northern Michigan (Heatwole 1962).

In mid-June, I searched enclosures for marked salamanders on three successive visits, separated by 3.0 ± 1.2 days (mean $\pm$ 1 standard deviation). Prior to each search, enclosures were gridded into $1m^2$ sections to ensure searches were performed systematically. Observers thoroughly searched their assigned $1m^2$ area by examining leaf litter and underneath and within pieces of CWD for marked salamanders. When performing searches, observers placed all leaf-litter and CWD in plastic tubs that were assigned to each $1m^2$ area until nothing remained inside

the enclosure except for rooted herbaceous and woody vegetation, and mineral soil. Observers

placed leaf-litter and CWD back in the enclosure after searching was complete and attempted to

reconstruct the micro-habitat to pre-sampling conditions. All captured salamanders were held in

coolers until the sampling event was complete, and then identified by their unique VIE marking,

measured, and re-released into the enclosure at the point of capture. I did not mark any

unmarked salamanders that were captured inside the enclosures (mean number of captured,

unmarked salamanders per enclosure = 4.9). My sampling and handling protocols were

approved by the Michigan State University Animal Care and Use Committee (Animal Use Form

no. 07/08-118-00).

I used the Huggins parameterization of the robust design population model (Pollock

1982, Bailey et al. 2004b) to estimate individual salamander survival (S_i), initial capture (p_t) and

recapture probabilities (c_t). Here, I used subscript "i" to denote that survival estimates apply to

individual salamanders, as opposed to estimates from occupancy models which apply to

individual sites. My robust design framework consisted of two primary periods: a salamander

additions period and a capture/recapture period. During the additions period, marked

salamanders were added to the enclosure, as described above. After one month, I searched

through all enclosures for marked salamanders on three successive visits (*i.e.,* 3 secondary

periods during primary period 2). Thus, $\hat{S}$ represents the probability that a marked salamander

survived from mid-May (primary period 1) until mid-June (primary period 2) and was available

for capture during primary period 2. Initial capture (p_t) is the probability that a marked

salamander was captured for the first time during visit t of the second primary period ($t = 1, 2, 3$).

Recapture (c_t) is the probability a marked salamander was recaptured during visit t, conditional

on it being captured at least once before during a previous visit (note: $c_1 = 0$). My design

contained only two primary periods, which prevented estimation of emigration between primary

periods. I therefore fixed emigration (γ) at 0 for all models.

I hypothesized that salamander survival probability in 40-60 year-old sites would be

higher than survival in 1-5 year-old sites, given the literature suggesting that amphibians are

negatively impacted by timber harvest (*e.g.,* deMaynadier and Hunter 1995; Semlitsch et al.

2009). I also predicted that salamanders within enclosures with higher quantities of CWD would

exhibit higher survival rates because these structures trap moisture on the forest floor and may

reduce risk of amphibian desiccation (Rittenhouse et al. 2008). I modeled CWD quantity as a

continuous covariate on salamander survival (logit $(S_i) = \beta_0 + \beta_1 \times CWD_e$) where CWD_e equaled

the total number of CWD objects within the enclosure which contained salamander *i*. I also

hypothesized that salamander survival would be higher within enclosures that were shaded by

retained green-trees. To represent this hypotheses, I modeled CANOPY as a continuous

covariate on salamander survival (logit$(S_i) = \beta_2 + \beta_3 \times CANOPY_e$) where CANOPY equaled the

amount of canopy cover within the 30 x 30m cell in the enclosure that contained salamander *i*.

As with the occupancy analysis, I modeled survival probability as a function of a single covariate

only (S(CANOPY) or S(CWD)), or as an additive effect (S(CANOPY + CWD)).

I explored whether capture and recapture probabilities were equal and constant across

time ($p(.)$). Although seldom acknowledged, perfect or constant capture probabilities are often

implicitly assumed by investigators who use organism counts to infer amphibian response to an

ecological effect (Pellet and Schmidt 2005, Kroll 2009). For contrast, I also hypothesized that

capture and recapture probabilities may decrease through time because previous sampling

disturbances caused salamanders to be temporarily unavailable for sampling during later surveys ($p(t)$). This hypothesis is based on previous work which suggests salamanders temporarily emigrate from sites following habitat disturbances caused by sampling (Bailey et al. 2004a; Otto and Roloff 2011).   I note the distinction between emigration that occurs between primary periods ("γ" in traditional Robust Design models), which I fixed at "0", and temporary emigration that occurs within a primary period, between surveys.   Although my enclosures restricted horizontal movements of salamanders, temporary unavailability could still occur if salamanders moved vertically into the subterranean environment following a sampling disturbance. My final hypothesis was based on the prediction that salamanders may exhibit a behavioral response to being captured, thereby resulting in lower recapture probability during subsequent surveys (*i.e.,* trap response). I represented this hypothesis by including an additive constant on recapture probability, which allowed initial capture and recapture probabilities to be different ($p(.) = c(.)+b$; Lukacs 2007). I also considered a similar model where initial capture and recapture probabilities differed and varied across time ($p(t) = c(t)+b$).

5.2.5 Data Analysis

I analyzed the occupancy data using R (version 2.12.1, http://www.r-project.org/; R Development Core Team 2011) with the add-in package unmarked (Fiske and Chandler 2011). I analyzed survival data using Program MARK (MARK, version 5.1, http://www.cnr.colostate.edu/~gwhite/mark/mark.htm). For both studies I used Akaike's Information Criterion, adjusted for small sample size (AIC_c), to rank models (Burnham and Anderson 2002). I changed the effective sample size for the survival analysis to represent the number of field enclosures (n= 45), rather than the number of salamanders (n= 450). I used cumulative AIC weights (w_+) and evaluation of 95% confidence intervals to determine relative

importance of covariates and model parameters. I report model averaged estimates and unconditional 95% confidence intervals for all real parameters. For my occupancy study, I report confidence intervals for all 40-60 year-old sites based on the profile likelihood approach because estimates often resided on the 0-1 boundary (Gimenez et al. 2005).

5.3. Results

Covariates CANOPY and CWD were weakly, negatively correlated for my occupancy (df = 132, correlation coefficient = -0.36 (-0.56 – -0.16; 95% CI), R^2 =0.09) and survival (df = 43, -0.63 (-1.04 – -0.21), R^2 =0.18) studies.

5.3.1. Salamander Occupancy

As predicted, occupancy estimates for RBSs were higher for 40-60 year-old sites ($\hat{\psi}_{40-60yr}$ $_{Stands}$ = 1.0, 0.79 – 1.0; 95%CI) when compared to harvested sites ($\hat{\psi}_{1-5yr\ Stands}$ = 0.57, 0.41 – 0.72). Weights for models that included the effect of CANOPY and CWD on occupancy were 0.32 and 0.38, respectively (Table 1). Although my structural retention covariates, CANOPY and CWD, both showed a positive relationship with salamander occupancy (Figure 5.1), the effect size (i.e., the associated beta estimates) was small and the 95% confidence intervals overlapped zero. For example, salamander occupancy estimates for sites with 50% canopy retention were only 15% higher than sites with 0% canopy retention (Figure 5.1). Collectively, the evidence does not suggest that patterns in salamander occupancy were related to structural retention attributes within my 1-5 year-old clearcut aspen stands.

Estimated detection probability for RBSs was <1.0 for all candidate models (range = 0.27 – 0.49). I observed evidence that salamander detection probability was higher along transects that contained higher quantities of downed wood (cumulative AIC$_c$ weights; $w+$ = 0.56; Table

1). However, the confidence intervals for CWD_j overlapped zero for all models that included this covariate and the effect size was small. For example, my top ranking model estimated detection probability as a function of CWD_j (Table 1), and the beta parameter associated with CWD_j was 0.23 (-0.03 – 0.49; 95%CI).

5.3.2. Salamander Survival

Observers took an average of 83 minutes (range = 47-184) to search through an enclosure during a sampling visit. I had 270 detections of marked salamanders during the three visits. Of these detections, 265 were made while searching underneath leaf-litter and CWD, and 5 were from salamanders found in the bottom of the plastic tubs at the end of the sampling event.

Model-averaged salamander survival estimates were 0.62 (0.50 – 0.72) and 0.49 (0.36 – 0.63) for 1-5 and 40-60 year-old sites, respectively. Substantial evidence ($w+ = 0.99$ for CANOPY and CWD; Table 2) indicated that green tree retention and CWD both positively influenced salamander survival from mid-May until mid-June in clearcut harvest stands (Figure 5.2A,B,C). For my top-ranking model, S(CANOPY + CWD + Control), p(t), beta parameter estimates were 0.73 (0.27 – 1.19; 95%CI) and 1.01 (0.53 – 1.50) for CANOPY and CWD, respectively (Figure 5.2A,B). In many cases, estimated survival was higher for 1-5 year-old sites that contained high levels of canopy cover or CWD (Figure 5.2C) compared to an 'average' 40-60 year-old site ($\hat{S}_{40\text{-}60yr\ Stands}$ = 0.49, 0.36 – 0.63; 95%CI).

Survival models that assumed constant detection probabilities of RBSs were not supported ($w+ = 0.00$; Table 2). Rather, initial capture probabilities of marked salamanders were approximately 50% lower in the second and third site visits when compared to the first visit (Figure 5.3). The estimated probability of capturing a marked salamander at least once during

the 3 visits was 0.78 (*i.e.,* $1 - \prod_{t\,=\,1}^{3}(1 - p_t)$). Model-averaged recapture probabilities were

slightly lower than initial capture probabilities (Figure 5.3), but the effect was not strong as

models with the capture probability structure p(t)=c(t)+b garnered only 0.30 of the cumulative

model weight (*w+ =* 0.30; Table 2).

5.4. Discussion

Ultimately, population processes such as survival, reproduction, and movement

determine patterns in species occupancy, richness, and abundance (Williams et al. 2002).

Response variables like occupancy and abundance may not be effective for determining faunal

response to habitat alteration because they are indirect representations of demographic processes

(Van Horne 1983; Yoccoz et al. 2001; Williams et al. 2002). However, an appealing

characteristic of occupancy and abundance studies is that they can be conducted over broader

spatial and shorter temporal scales, thereby increasing the breadth of inference and applicability

to management. My inferences regarding RBS response to structural retention in aspen clearcuts

were largely conditional on my state variable of interest. Whereas I found no support for a

correlation between structural retention and RBS occupancy, I found strong evidence for a

positive effect of retention on individual RBS survival probability.

5.4.1. Does Structural Retention Promote Occupancy?

I observed higher estimates of salamander occupancy in 40-60 year-old sites when

compared to 1-5 year-old sites, which is consistent with other studies that show patterns in

amphibian counts are positively correlated with time since timber harvest (Petranka et al. 1993;

Ash 1997; Knapp et al. 2003). Salamander occupancy probability was not strongly related to

green-tree or CWD retention level within my young aspen clearcuts. Rather, occupancy

estimates for 1-5yr old sites were always 33-48% lower than 40-60 yr old sites, regardless of

structure retention levels. I selected occupancy as one of my state variables because a primary

goal of structural retention prescriptions is to ensure that faunal populations persist within a

forest patch following timber harvest (Franklin et al., 1997; Rosenvald and Lõhmus, 2008).

Thus, occupancy, or presence-absence, is proposed as a useful state-variable for assessing

wildlife response to this mitigation technique. Furthermore, the spatial extent of my study was

consistent with the scale at which forest resources are managed and extracted. This is an

important consideration because the spatial scale of past amphibian-forestry studies that assessed

occupancy or abundance has often been limited to few experimental forest stands (e.g., Ash

1997, McKenny et al. 2006, Patrick et al. 2006, Todd and Rothermel 2006). Inferring broad-

scale impacts based on limited spatial extent and site replication is a common issue in research

on the effects of timber harvest on forest diversity (Bennett and Adams 2004), even though the

potential pitfalls of doing so in amphibian-habitat research have been discussed (Dodd and

Dorazio 2004; Mazerolle et al. 2007; Kroll 2009).

5.4.2. Does Structural Retention Promote Survival?

In contrast to my occupancy results, I found that retention of vertical green-trees and

coarse woody debris had a strong effect on salamander survival in young aspen clearcuts. Past

research has shown that clearcutting negatively impacts amphibian survival (Rothermel and

Semlitsch 2006; Todd and Rothermel 2006; Rittenhouse et al. 2008). However, the role of

structural retention for reducing these impacts is less clear (Rosenvald and Lõhmus 2008). An

enclosure study by Rittenhouse et al. (2008) showed that amphibian survival over 30 hours in

clearcuts was higher when enclosures were deployed in brushpiles compared to enclosures

deployed in open areas with no microhabitat refugia. My study differs from Rittenhouse et al.

(2008) in both the area encompassed by the enclosure ($0.07m^2$; Rittenhouse et al. 2008, $9m^2$; my

study) and the time over which survival was estimated (30 hours; Rittenhouse et al. 2008, $\approx$1 month; my study). My research shows that leaving structural elements, such as vertical green trees and horizontal CWD, within young clearcuts may ameliorate the observed negative impacts of clearcutting on amphibian survival (Rothermel and Semlitsch 2006; Todd and Rothermel 2006; Rittenhouse et al. 2008). Various combinations of retention can be used to yield comparable survival estimates, ranging from an emphasis solely on CWD or green trees to a combination of CWD and green trees (Figure 5.2C).

5.4.3. Probability of Encounter

My analyses highlight the importance of accounting for imperfect detection probability when assessing the effects of anthropogenic disturbance on amphibian populations; salamander detection probabilities at both the species and individual level were always <1.0, sometimes <0.3. This finding is significant considering count data, which are uncorrected for detection probability, are commonly used to infer amphibian response to timber harvest and other anthropogenic disturbances (*e.g.,* deMaynadier and Hunter 1995, Todd and Rothermel 2006, Homyack and Haas 2009). The importance of accounting for bias caused by limited detectability of target species has been emphasized (MacKenzie and Kendall 2002, Bailey et al. 2004a, Kéry and Schmidt 2008); however, ecologists have been slow to apply these analytical tools to amphibian research (Dodd and Dorazio 2004, Mazerolle et al. 2007, Kroll 2009). Indeed, results from my survival analysis suggest that raw counts of recaptured individuals are likely to underestimate true survival because marked individuals went undetected during sampling events. Even though I implemented several design-based approaches for increasing capture rates (*i.e.,* housing salamanders in enclosures, repeated and intensive sampling), my survival analysis revealed that capture and recapture probabilities were surprisingly low. Thus, my study does not

support the notion that design-based approaches alone can eliminate bias caused by limited detectability of amphibians.

5.4.4. Conclusions

Single pattern- or process-based response variables are often used to assess the impacts of anthropogenic disturbance on biological diversity; seldom are they jointly evaluated in the same ecological system (Todd and Rothermel 2006, Welsh et al. 2008). Inferential power of studies that directly assess demographic processes, such as survival, is generally greater than studies that assess demographic indices, such as occupancy or abundance; however, strength typically comes at the expense of inferential breadth.   Ecologists often fail to recognize that understanding demographic processes at a small number of sites is of little utility to resource managers concerned with broad-scale anthropogenic impacts (Yoccoz et al. 2001). Similarly, managers do not often acknowledge the importance of understanding the underlying demographic processes that result in changes in population indices over space and time.

My research shows that structural retention harvest, when done at relatively small spatial scales, can reduce the negative impacts of clearcutting on terrestrial salamanders by lowering mortality rates. This provides resource managers with direct evidence that alternative forest management can positively influence salamander population dynamics. However, when viewed at larger spatial scales (*i.e.,* species occupancy across a landscape), I found little evidence that structural retention resulted in higher site occupancy by RBSs, at least within the first 5 years following timber harvest. These seemingly conflicting results may highlight the scale-dependent nature of my two response variables: ecological processes that drive patterns of salamander occurrence likely operate at spatial scales beyond those observed in this study. Indeed, the composition and configuration of the landscape matrix may be an equal or better predictor of

amphibian patch occupancy than within-patch habitat conditions (*e.g.,* Joly et al. 2001, Marsh and Trenham 2001, Otto et al. 2007). Although species occupancy is often used as the response variable in wildlife-forestry research (e.g., Rosenvald and Lõhmus 2008, Welsh et al. 2008, Kroll et al. 2008), my study suggests that the spatial resolution of this variable may be too coarse to effectively assess the impact of small-scale mitigation techniques, such as structural retention, on wildlife populations.

Another potential explanation for these conflicting results is the difference in the temporal scales of both studies. My occupancy study represents a snapshot of a population that was subjected to an anthropogenic disturbance event that occurred 1to 5 years previous, whereas my survival study was conducted over just one month. Thus, although structural retention may increase salamander survival over one month, this benefit may be negated over a longer temporal period in clearcuts.

One final compelling explanation for my conflicting results is that patterns in salamander occurrence within clearcuts were largely influenced by population movement dynamics, rather than mortality. Some amphibians will emigrate from (*i.e.,* evacuation hypothesis; Semlitsch et al. 2008, Peterman et al. 2011) or may go deep underground (*i.e.,* subterranean retreat hypothesis; Petranka et al. 1993) following timber harvesting events. Thus, lower occupancy estimates for my 1 to 5 year stands could reflect behavioral avoidance of salamanders to clearcuts, regardless of the local availability of structural retention. However, in my enclosure experiment, I restricted the horizontal movements of salamanders; thereby eliminating their ability to seek refugia in adjacent forest stands and instead, forced them to select microhabitat refugia within the enclosure. This explanation is consistent with the observed weak correlation between salamander occupancy and structural retention and the strong effect of structural

retention on salamander survival. Although my enclosure experiment shows that salamanders can survive in clearcuts when habitat refugia are provided, it is unclear if these salamanders would choose to remain in clearcuts, if given the option (Semlitsch et al. 2008, Rittenhouse et al. 2009, Todd et al. 2009). My mark-recapture study provides anecdotal evidence that salamanders will make vertical movements into the subterranean environment to escape anthropogenic disturbances to the forest floor: estimated capture probabilities were lower for the second and third enclosure sampling events than the first.

Regardless of potential mechanism(s), my study suggests that broad-scale conservation goals for terrestrial salamanders, and other forest-obligate species, will not be accomplished by simply retaining structure within individual harvest units. Rather, successful conservation efforts for these species may also require conservation of late-successional forests as part of managed landscapes. In the foreseeable future, habitat degradation will continue to be a dominant force in the global biodiversity and sustainability crisis (*e.g.,* Stuart et al. 2004; Schipper et al. 2008). Hence, developing research and monitoring programs that assess broad-scale changes in population patterns, and the demographic processes underlying these changes, should be a shared goal of ecologists and resource managers alike.

5.5. Acknowledgements

APPENDIX

Appendix C.1 Methodology for calculating the proportion of canopy cover at study site.

To estimate the proportion of canopy cover of each 50m radius site, I digitized canopy cover of all retained green-trees within the harvest units using 2010, 2009, 2005, and 1998 NAIP (National Agricultural Imagery Program) imagery. The age of the harvest unit dictated which year of NAIP imagery I used. For example, if harvest of a stand was completed in 2003, then I used 2005 NAIP imagery to map retention. To digitize canopy cover, I created a new shapefile in a Geographic Information System (GIS; ArcGIS 9.1; Environmental Systems Research Institute, Redlands, CA) to represent canopy cover provided by retained green-trees. I used the SKETCH tool in ArcEditor to draw the canopy cover polygons into the new shapefile.   I then used the INTERSECT function in Arc Toolbox (ArcGIS 9.1; Environmental Systems Research Institute, Redlands, CA) to intersect the canopy cover polygon shapefile with separate polygon shapefile that represented the boundary of 50m radius site.   I used the AREA function in HAWTH'S TOOLS (Hawth's Tools, version 3.27, http://www.spatialecology.com/htools/) to calculate the proportion of canopy cover within each site. For example, if area of canopy cover within a site was $1260m^2$ then the proportion of canopy cover at that site was $\{1260m^2 / [\pi \times$ $(50m\ radius)^2]\}$ or 0.16. I used this value as continuous site covariate in my Chapter 5 analysis (*i.e.,* CANOPY).

Table 5.1. Ranking of candidate occupancy models for red-backed salamanders detected at 134 sites located in aspen stands from the northern Lower Peninsula of Michigan, USA, 2010-2011. ψ and p represent site occupancy and detection probability, respectively. All models include a "Control" covariate, noting whether a site was located in a recently harvested (1-5 years post-harvest) or 40-60 year-old aspen stand. CANOPY represents the green-tree retention covariate, while CWD_i and CWD_j represent coarse woody debris covariates for each site and transect within a site, respectively.

Model	$\Delta AIC_c{}^a$	w	K	$-2\,l$
ψ(Control),p(CWD_j)	0.00	0.26	4	394.9
ψ(Control),p(.)	0.91	0.16	3	397.9
ψ(CWD_i + Control),p(.)	1.37	0.13	4	396.3
ψ(CANOPY + Control),p(CWD_j)	1.53	0.12	5	394.2
ψ(CWD_i + Control),p(CWD_j)	1.53	0.12	5	394.3
ψ(CANOPY + Control),p(.)	2.55	0.07	4	397.4
ψ(CANOPY + CWD_i + Control),p(.)	2.77	0.07	5	395.5
ψ(CANOPY + CWD_i + Control),p(CWD_j)	3.00	0.06	6	393.5

[a] ΔAIC_c = difference from the Akaike's Information Criterion best model, adjusted for small sample size, K = number of parameters, $-2\,l$ is twice the negative log-likelihood.

Table 5.2. Ranking of candidate robust design models for 450 red-backed salamanders within field enclosures deployed in aspen stands, Lower Peninsula of Michigan, 2010-2011. All models include a "Control" covariate, denoting whether the salamander was detected in 1-5 or 40-60 year-old sites. "CANOPY" represents the amount of green-tree canopy cover above each salamander enclosure, while "CWD" represents the number of coarse woody debris objects within each enclosure. p and c represent initial capture and recapture probability of marked salamanders, respectively. b is an additive constant for recapture probability.

Model	$\Delta \text{AIC}_c{}^a$	w	K	$-2\,l$
S(CWD + CANOPY + Control), p(t)	0.0	0.68	7	1219.8
S(CWD + CANOPY + Control), p(t) = c(t) + b	1.6	0.30	8	1217.6
S(CWD + Control), p(t)	9.0	0.01	6	1230.8
S(CWD + CANOPY + Control), p(.) = c(.) + b	9.7	0	6	1231.5
S(CWD + Control), p(t) = c(t) + b	11.6	0	7	1230.6
S(CWD + Control), p(.) = c(.) + b	22.9	0	5	1247.4
S(Control), p(t) = c(t) + b	27.8	0	5	1252.3
S(CANOPY + Control), p(t)	28.7	0	6	1250.5
S(Control), p(t)	29.0	0	5	1253.5
S(CANOPY + Control), p(t) = c(t) + b	31.4	0	7	1250.3
S(CANOPY + Control), p(.) = c(.) + b	42.7	0	5	1267.2
S(CWD + CANOPY + Control), p(.)	73.5	0	5	1297.9
S(CWD + Control), p(.)	82.6	0	4	1309.6
S(CANOPY + Control), p(.)	100.0	0	4	1327.0
S(Control), p(.)	100.2	0	3	1329.6

[a] ΔAIC_c = difference from the Akaike's Information Criterion best model, adjusted for small sample size: K = no. of parameters; $-2\,l$ is twice the negative log-likelihood.

Figure 5.1. Occupancy probability for red-backed salamanders in 1-5 year-old clearcut aspen stands in the northern Lower Peninsula of Michigan, 2010-2011, explained as a function of (A) percent of site area that was covered by green tree canopy retention, and (B) the number of coarse woody debris objects at each site. All estimates were generated using model averaging.

A

Figure 5.1. (cont'd)

B

Y-axis: Occupancy Probability (95%CI)

X-axis: Number of Coarse Woody Debris Objects/Site
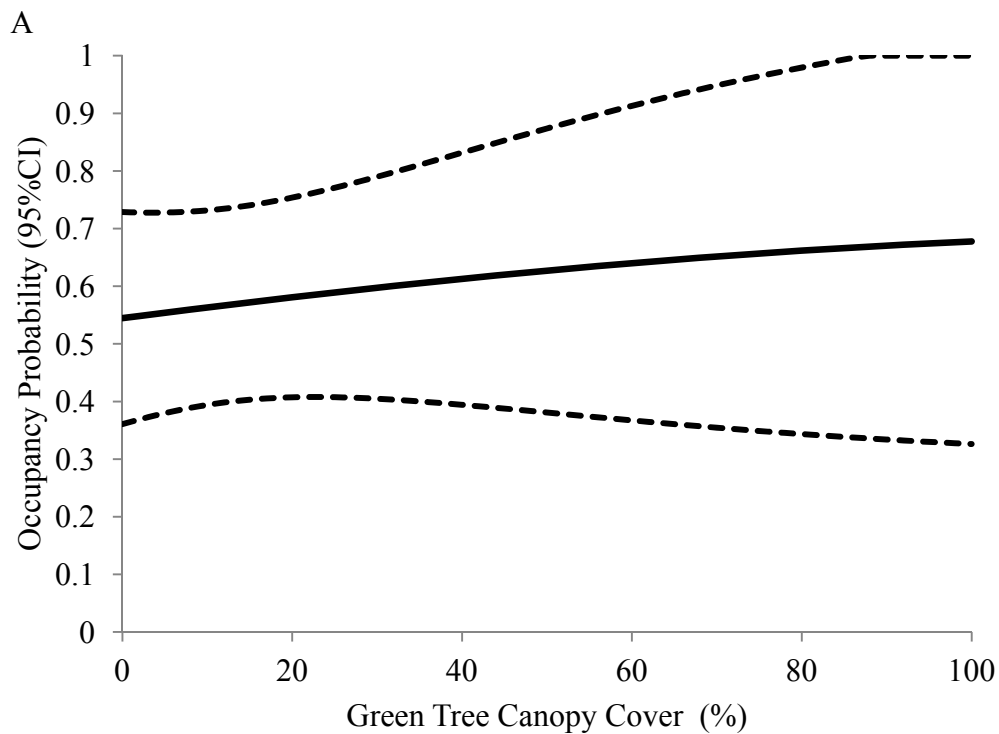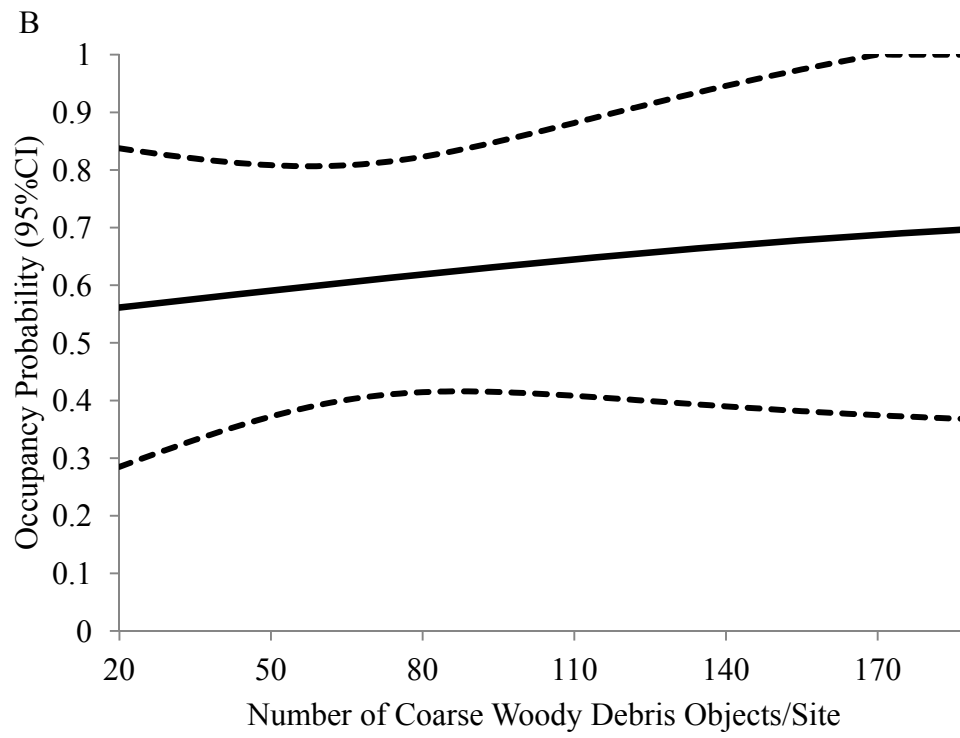
Figure 5.2. Estimated salamander survival probability in the northern Lower Peninsula of Michigan, 2010-2011, explained as a function of (A) percent residual canopy cover found above a field enclosure, (B) the number of coarse woody debris objects within a field enclosure, (C) or both variables. Survival is the probability that a marked salamander *i* survived 1 month in a field enclosure located in an aspen stand that was 1-5 years post harvest. All estimates were generated using model averaging.

A

Figure 5.2. (cont'd)

B
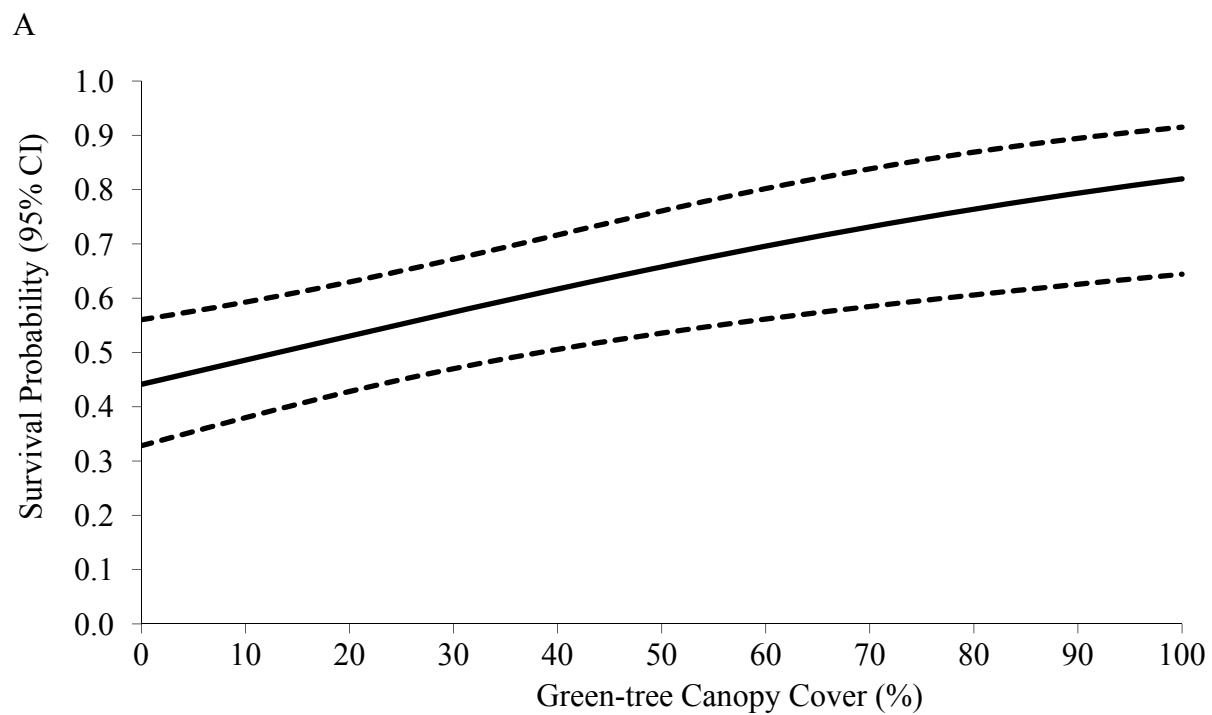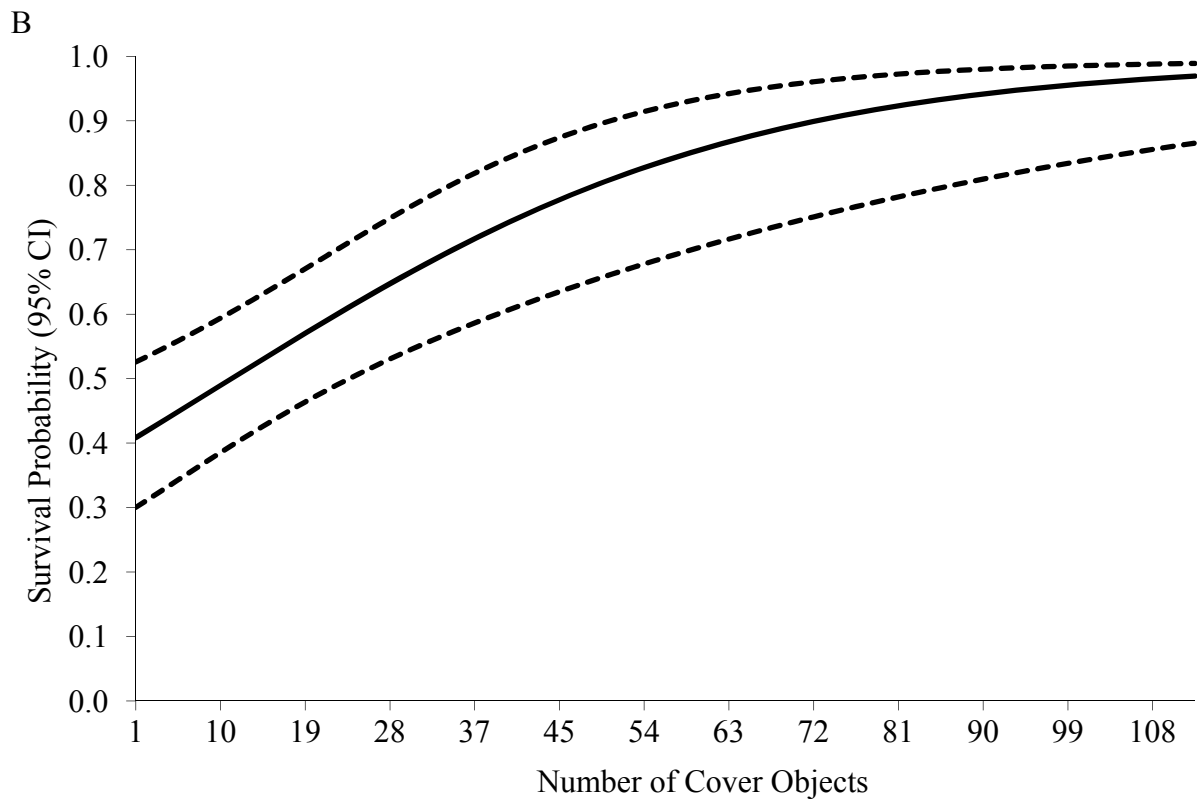
Figure 5.2 (cont'd)

C
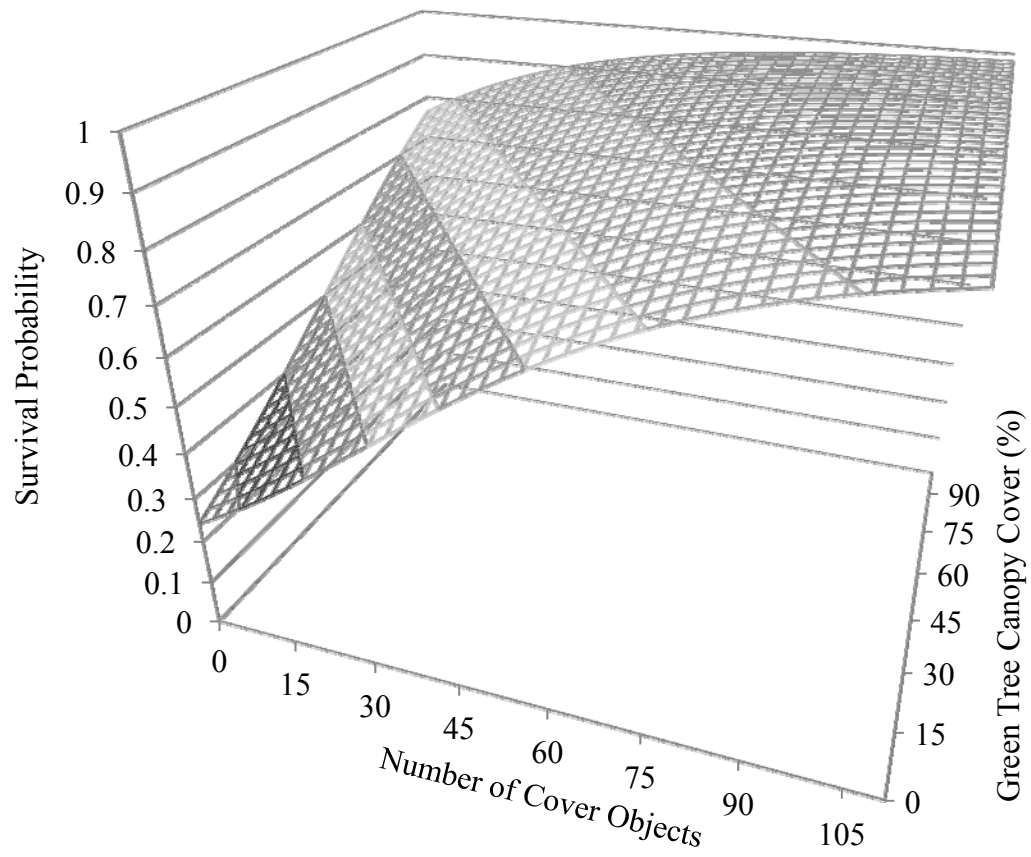
Figure 5.3. Model-averaged estimates of initial capture (p) or recapture (c) probability of salamanders during 3 sampling events (visits) in mid-June, northern Lower Peninsula of Michigan, 2010-2011. Initial capture (p_t) is the probability that a marked salamander is captured for the first time during visit t, conditional on it surviving and being available for capture. Recapture (c_t) is the probability a marked salamander is recaptured during visit t, conditional on it being captured at least once before during a previous visit.
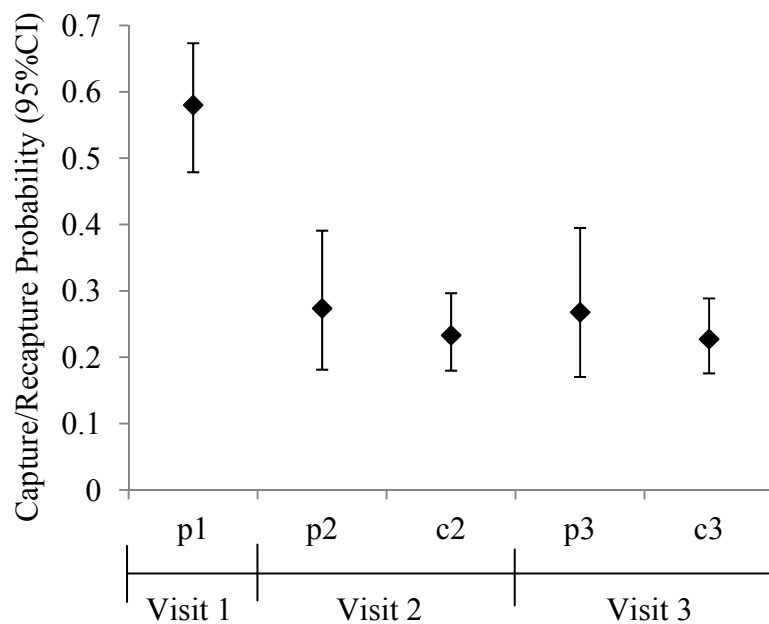
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CONCLUSIONS

The overarching theme of my dissertation involves the development and implementation of a conservation research program for studying the impacts of anthropogenic disturbances, specifically timber harvesting, on forest wildlife. Although the primary objective of my dissertation is to assess the effectiveness of structural retention (*i.e.,* canopy green trees and coarse woody debris) for conserving wildlife in Michigan's harvest forests, it also provides valuable insight to other areas of ecology and wildlife management. A strength of my dissertation is that it shows how pilot data can be used to design future wildlife research projects with strong inferential power and reduced estimation bias. It also highlights how statistical models can be used to decouple biological process from observational sampling error: a problem that is ubiquitous in observational wildlife studies. My capstone chapter (Chapter 5) serves as a cautionary reminder that scientific inference is conditional on the selected response variable(s) and stresses that joint evaluation of population indices, such as species occupancy, and population processes, such as survival, provides a more holistic view of biological reality.

In Chapter 1 I used species occupancy models and multiple trapping methodologies to estimate detection probabilities of forest-floor wildlife. I used parameter estimates from my initial analysis to explore alternative study design tradeoffs for sampling two shrew species. Although I captured 25 species, I could reliably detect (detection probability >0.15) only northern short-tailed shrews (*Blarina brevicauda*) and pygmy and masked shrews (*Sorex* spp.) using drift fences and red-backed salamanders (*Plethodon cinereus*) using visual encounter surveys (VES). This research demonstrated the need to incorporate species detectability when comparing the effectiveness of different trapping methodologies and highlights the utility of power analyses for exploring study design tradeoffs for research and monitoring programs.

In Chapter 2 I compared the effectiveness of natural cover object (NCO) and leaf litter surveys for detecting red-backed salamanders in harvested forests. Both NCO and leaf litter surveys performed well in their ability to detect *P. cinereus* and produced similar site occupancy estimates; however, leaf litter searches took 3 times longer to complete. My simulation study revealed the time required to complete leaf litter surveys limited the number of sampling sites, which reduced statistical power for detecting a 25% change in salamander occupancy between two groups of sites. Chapters 1 and 2 illustrate how pilot data can be used to design occupancy studies that possess strong inferential power.

Analyses from Chapter 3 revealed general sensitivity of estimates from single-season occupancy models to violations of closure. I observed a chronic decrease in salamander occupancy associated with cumulative sampling and non-random salamander movements over the entire field season. My simulations showed that estimation bias was minimal when extinction probability or the number of sample occasions was relatively low. This research highlights the importance of addressing closure in occupancy studies. I provide multiple solutions, using both design- and model-based frameworks, for minimizing bias associated with non-random changes in occupancy and repeated sampling disturbances. This research should appeal to researchers who are currently designing occupancy studies and are concerned if their design is consistent with occupancy model assumptions. Results from Chapter 3 also provided guidance for development of candidate models and statistical analyses for Chapters 4 and 5.

In Chapter 4 I evaluated the effectiveness of green-tree retention for promoting occupancy of interior forest, generalist, and early-successional songbirds in aspen stands that were 1 to 15 years post-harvest. I estimated songbird occurrence at 222 sites where green tree retention was exceeded, met, or below recommended retention guidelines established by the

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MDNR. Contrary to my initial expectation, results suggest that current green-tree retention guidelines are ineffective at promoting site occupancy of most forest songbirds in aspen harvest units. Rather, site occupancy probabilities for most forest birds showed a clear association with age since harvest (1-15 years); however, the strength and direction of the association varied by species. My research suggests it is unlikely that management goals for many interior forest songbirds will be accomplished solely through green-tree retention at the forest stand scale. I provide natural resource managers with recommendations based on alternative management objectives for forest songbirds.   Future management objectives in aspen forests should reflect the value of clearcutting to early-successional and generalist bird species, while recognizing that green-tree retention as measured in my study does little to promote occupancy of the interior forest bird community.

Chapter 5 highlighted the importance of coupling large-scale distributional studies with more focused demographic research. Inferential power of studies that directly assess demographic processes, such as survival, is generally greater than the inferential power from studies that assess population indices, such as occupancy; however, strength typically comes at the expense of inferential breadth. My research shows that structural retention harvest, when evaluated at relatively small spatial scales, reduces the negative impacts of clearcutting on terrestrial salamanders by lowering mortality rates. This provides resource managers with direct evidence that alternative forest management can positively influence salamander population dynamics. However, when viewed at larger spatial scales (*i.e.,* species occupancy across a landscape), I found little evidence that structural retention resulted in higher site occupancy by red-backed salamanders, at least within the first 5 years following timber harvest. Thus, results from Chapter 5 corroborate those of Chapter 4, which suggested that broad-scale conservation

goals for terrestrial salamanders, and other forest-obligate species, will not be accomplished by simply retaining structure within individual harvest units.   Rather, successful conservation efforts for these species likely require conservation of late-successional forests as part of managed landscapes. In the foreseeable future, habitat degradation will continue to be a dominant force in the global biodiversity and sustainability crisis. Hence, developing research and monitoring programs that assess broad-scale changes in population patterns, and the demographic processes underlying these changes, should be a shared goal of ecologists and resource managers alike.