

**SURVIVAL AND HABITAT USE
BY POST-FLEDGING FOREST-NESTING SONGBIRDS
IN MANAGED MIXED NORTHERN HARDWOOD-CONIFEROUS FORESTS**

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*This dissertation is dedicated to
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taken countless kids with potential and curiosity, and turned them into scientists.*

ABSTRACT -- Until recently, studies of breeding migratory songbirds have been primarily limited to the nesting season. Therefore, there is very little information about songbird survival and habitat use during the post-fledging period (i.e. the time between nesting and fall migration) available to those making management decisions. I expanded on the traditional nest-monitoring study and used radio telemetry to monitor survival and habitat use of fledgling songbirds in managed northern hardwood-coniferous forests of northern-Minnesota. In addition, I used mist-nets to sample use of early-successional forest stands (regenerating clearcuts) and forested wetlands by mature forest-nesting birds during the post-fledging period. I found that many assumptions of songbird nesting studies are unreliable, including the common assumption that the presence of a family group is confirmation of a successful nest in an occupied territory. In addition, I found that annual fledgling survival can vary considerably, and does not vary consistently with nest productivity, a finding with broad implications for models of songbird population growth. Furthermore, I found that habitat used by birds during the post-fledging period can be considerably different than that used for nesting, and that post-fledging habitat use can affect fledgling survival. In addition, I found that factors commonly affecting nest productivity (e.g. edge effects) can affect fledgling survival differently. From mist-netting, I found that many mature-forest birds used non-nesting cover types during the post-fledgling period, but most of that use was by only a few species, and hatch-year birds rarely used non-nesting cover types before independence from adult care. Models of capture rates in non-nesting cover types indicated that use of non-nesting cover types by mature-forest birds was primarily related to food availability and secondarily to cover in the form of relatively dense vegetation. My results indicated that nearly every conclusion made about breeding population ecology of mature-forest birds based only on nesting data was contradicted by data from the post-fledging period. My results

clearly demonstrate that data from the entire breeding season (nesting and post-fledging) are necessary to understand songbird seasonal productivity and habitat associations.

TABLE OF CONTENTS

Acknowledgments.....	i
Dedication.....	ii
Abstract.....	iii
Table of Contents.....	v
List of Tables.....	vii
List of Figures.....	ix
CHAPTER 1: DON'T COUNT YOUR CHICKS UNLESS YOU KNOW WHERE THEY HATCHED: TESTING COMMON ASSUMPTIONS IN STUDIES OF SONGBIRD REPRODUCTIVE SUCCESS.....	1
1.1 Introduction.....	2
1.2 Methods.....	6
1.3 Results.....	11
1.4 Discussion.....	14
1.5 Tables.....	20
1.6 Figures.....	23
CHAPTER 2: SEASONAL PRODUCTIVITY IN A POPULATION OF OVENBIRDS: WHY NEST DATA ARE NOT ENOUGH...	24
2.1 Introduction.....	25
2.2 Methods.....	29
2.3 Results.....	40
2.4 Discussion.....	43
2.5 Tables.....	49
2.6 Figures.....	51
CHAPTER 3: MOVEMENTS, COVER-TYPE SELECTION, AND SURVIVAL OF FLEDGLING OVENBIRDS IN MANAGED DECIDUOUS AND MIXED-CONIFEROUS FORESTS.....	55
3.1 Introduction.....	56
3.2 Methods.....	58
3.3 Results.....	66
3.4 Discussion.....	69
3.5 Figures.....	75

CHAPTER 4: SURVIVAL OF FLEDGLING OVENBIRDS: INFLUENCES OF HABITAT CHARACTERISTICS AT MULTIPLE SPATIAL SCALES.....	81
4.1 Introduction.....	82
4.2 Methods.....	85
4.3 Results.....	90
4.4 Discussion.....	93
4.5 Figures.....	97
CHAPTER 5: EARLY SUCCESSIONAL FOREST USE BY POST-FLEDGING MATURE-FOREST SONGBIRDS IN MANAGED MIXED NORTHERN HARDWOOD-CONIFER FORESTS.....	98
5.1 Introduction.....	99
5.2 Methods.....	103
5.3 Results.....	106
5.4 Discussion.....	108
5.5 Tables.....	114
5.6 Figures.....	117
CHAPTER 6: USING INVERTEBRATE AVAILABILITY AND VEGETATION CHARACTERISTICS TO EXPLAIN USE OF NON-NESTING COVER TYPES BY MATURE-FOREST SONGBIRDS DURING THE POST-FLEDGING PERIOD..	119
6.2 Introduction.....	120
6.3 Methods.....	124
6.4 Results.....	130
6.5 Discussion.....	132
6.6 Tables.....	136
6.7 Figures.....	137
LITERATURE CITED.....	141

LIST OF TABLES

CHAPTER 1

Table 1. Estimates of Ovenbird nest success (daily survival 24) produced using 3 methods (Telemetry, Manolis, and Nest Condition), and hypothetical situations in which incorrectly determined fates were all assigned failed (Manolis Low and Nest Cond. Low) or successful (Manolis High and Nest Cond. High) fates. Each analysis was conducted using the same sample of 184 Ovenbird nests monitored during 2007 – 2008 in the Chippewa National Forest, Minnesota, USA. Standard Errors of estimates (not shown) were very similar and ranged between 0.040 – 0.042.... 20

Table 2. Distances traveled from nests by Ovenbird fledglings 1 day and 10 days following fledging during 2007 and 2008 in the Chippewa National Forest, Minnesota, USA..... 21

Table 3. Fledgling:adult, or hatch-year:after-hatch-year (HY:AHY), Ovenbird capture ratios in non-nesting forest stands during the post-fledging periods of 2006 – 2009, and HY:AHY Ovenbird population ratios estimated from nest productivity and fledgling survival during 2007 – 2008, in the Chippewa National Forest, Minnesota, USA..... 22

CHAPTER 2

Table 1. Fledged brood size and daily survival for nests and fledglings (\pm SE) for Ovenbirds nesting ≤ 100 m from clearcuts ≤ 6 years since harvest (Near YCC), nesting ≤ 100 m from clearcuts 7 – 20 years since harvest (Near OCC), and nesting > 100 m from any clearcut edge (Int. Forest) in the Chippewa National Forest, Minnesota, USA..... 49

Table 2. Intrinsic rates of growth (λ) predicted by models including our direct estimates of fledgling survival (Fledgling model) and models including an estimate of constant first-year survival (Constant S_{FY} model) commonly used in previous songbird population models. Exposure days for nests and fledglings monitored, and differences in population growth rates ($\Delta\lambda$) are presented for the entire study population and population segments nesting ≤ 100 m from clearcuts ≤ 6 years since harvest (Near YCC), nesting ≤ 100 m from clearcuts 7 – 20 years since harvest (Near OCC), and nesting > 100 m from any clearcut edge (Interior Forest) in the Chippewa National Forest, Minnesota, USA..... 50

CHAPTER 5

Table 1. Birds (after hatch year [AHY] and hatch year [HY]) associated with nesting in mature-forest, early-successional forest, and both mature and early-successional forest, captured during the post-fledging periods of 2006 – 2009 in clearcuts 2 – 10 years after harvest, and during the nesting period of 2009 in clearcuts 4 – 10 years after harvest, in the Chippewa National Forest, Minnesota..... 114

Table 2. Nests observed opportunistically during mist-netting and radio-telemetry monitoring of fledgling songbirds in regenerating clearcuts in the Chippewa National Forest, north-central Minnesota. Each of these species was classified as mature-forest nesting by 1 or more previous studies^a of clearcut use by birds during the post-fledging period..... 116

CHAPTER 6

Table 1. Best-supported and competing models ($\Delta AIC_C \leq 2.0$) describing captures of adult (AHY) and hatch-year (HY) Ovenbirds (OVEN) and American Redstarts (AMRE) in forested wetlands and regenerating clearcuts during the post-fledging period of 2009 in the Chippewa National Forest, Minnesota, USA. All models include an additional variable (not shown) for a random site effect. Model variables include: leaf litter depth (LITDEP), percent ground cover by woody debris (WOOD), canopy height (CANOPY), a quadratic canopy height term in adult Ovenbird models only (CANOPY**2), shrub-level invertebrate availability (FLYTAPE), ground invertebrate availability (PITFALL)..... 136

LIST OF FIGURES

CHAPTER 1

- Figure 1. An Ovenbird fledgling photographed 135 m from its nest, outside its presumed natal territory, and outside the 10 ha study plot containing its nest <48 h after fledging (photo by Sean Peterson)..... 23

CHAPTER 2

- Figure 1. Daily survival of Ovenbird nests (A) and fledglings (B), and seasonal productivity (fledglings raised to independence per nesting female; C) during 2007 and 2008 in the Chippewa National Forest, Minnesota, USA (Error bars depict SE, all 3 are significantly different between years)..... 51

- Figure 2. Model of weather-dependent predator-prey relationships among raptors, small mammals, and Ovenbirds based on observations in the Chippewa National Forest, Minnesota, USA. Moderate winter conditions (A) allow for relatively high abundance of small mammals, which prey heavily on Ovenbird nests and fledglings, while generalist raptors prey primarily on relatively abundant small mammals. Severe winter conditions (B) reduce abundance of small mammals, reducing their predation on Ovenbird nests and fledglings, thereby increasing Ovenbird nest productivity and fledgling abundance, while generalist raptors increase predation on relatively abundant fledglings..... 53

CHAPTER 3

- Figure 1. Minimum distances traveled by fledgling Ovenbirds within 1 day of fledging in the Chippewa National Forest, Minnesota. We estimated the maximum daily movement capability of day-zero fledglings as the intercept between the regression curve and the x-axis, rounded up to the nearest 10 m (i.e. 120 m in this case). We repeated this analysis for each fledgling age, 0 – 24 days after fledging.. 75

- Figure 2. Age-specific maximum daily movement capability for fledgling Ovenbirds, derived by repeating the analysis from Fig. 1 for fledglings aged 0 – 24 days after fledging in the Chippewa National Forest, Minnesota..... 76

- Figure 3. An example of daily estimated availability (DEA) for a fledgling Ovenbird in the Chippewa National Forest, Minnesota. Mature forest (matfor) comprised 100% of available space for this fledgling for day 1 (A). Mature forest, 7 – 20 yr-old clearcut (occ), forested wetland (forwet), and lake were within the DEA circle for day 2 (B). This process was repeated for each location during the 24-day dependent post-fledging period. Lake was removed for analysis based on the assumption that it is not used by fledgling Ovenbirds..... 77

Figure 4. Distance traveled from nests by fledgling Ovenbirds 4 days (period of highest mortality) after fledging. Distances are compared between fledglings from nests ≤ 100 m from (less), and nests > 100 m from (more) cover-types associated with higher survival (i.e. clearcuts 7-10 yr since harvest or forested wetlands at (A) a primarily deciduous mature forest site, and (B) a mixed conifer mature forest site in the Chippewa National Forest, Minnesota. Values are reported as mean, SE, and 95% CI. Differences are in the same direction, but statistically significant at only the deciduous forest site..... 79

CHAPTER 4

Figure 1. Estimated probabilities of survival for fledgling Ovenbirds that crossed at least 1 logging road (Road) or did not cross a logging road (No Road) during (A) post-fledging days 1 – 8, and (B) post-fledging days 9 – 16, during 2007 and 2008 in the Chippewa National Forest, Minnesota, USA. Values are probabilities \pm SE of surviving each 8-day period..... 97

CHAPTER 5

Figure 1. Capture rates of adult (AHY) and hatch-year (HY) mature-forest species: (A) Ovenbirds, (B) Least Flycatchers, and (C) American Redstarts captured throughout the 8 week post-fledging period, 4 July – 28 August, 2006 – 2009 in clearcuts in the Chippewa National Forest, Minnesota..... 117

CHAPTER 6

Figure 1. Study sites; (1) Pike Bay, (2) Cutfoot Sioux, and (3) Suomi Hills located in the Chippewa National Forest, north-central Minnesota, USA, where we used mist nets to sample non-mature forest cover types for use by mature-forest nesting Ovenbirds and American Redstarts during the post-fledging period, July and August, 2009..... 137

Figure 2. Mist-net captures of mature-forest songbirds in 10 non-mature-forest cover types during the post-fledging period of 2009 in the Chippewa National Forest, Minnesota, USA..... 138

Figure 3. Diagram of vegetation, invertebrate, and fruit sampling design around a pair of 12-m mist nets. Canopy height, leaf litter depth, and percent ground cover by low vegetation and woody debris were recorded in each of 16 vegetation plots during the first week of August. Vegetation density was estimated using a profile board (not shown) placed against the net perpendicular to, and viewed from, each of the 8, 5-m vegetation plots (see text). Two pitfall traps and 2 flytape traps were deployed weekly for 24 hrs between 2 consecutive days of netting..... 139

Figure 4. Invertebrates captured on flytape traps deployed in the shrub layer of 5 in the Chippewa National Forest, Minnesota, USA; mature forest (matfor), clearcuts 16 – 19 years after harvest (cc 16 – 19), clearcuts 7 – 12 years after harvest (cc 7 – 12), clearcuts 1 – 6 years after harvest (cc 1 – 6), and forested wetlands (forwet). Stands were sampled for 24 hr between 8 – 14 August 2009. Plus signs, boxes, and whiskers represent means, SE, and 95% CI, respectively. Letters confer statistically significantly different groups at the $\alpha = 0.05$ level..... 140

CHAPTER 1

DON'T COUNT YOUR CHICKS UNLESS YOU

KNOW WHERE THEY HATCHED: TESTING COMMON ASSUMPTIONS

IN STUDIES OF SONGBIRD REPRODUCTIVE SUCCESS

INTRODUCTION

Estimates of songbird reproductive success, typically limited to nest success, are used to assess habitat quality (e.g. Weinberg and Roth 1998), model population dynamics (e.g. Podolski et al. 2007), identify source and sink populations (e.g. Donovan et al. 1995), and inform conservation and management plans (e.g. Woodworth 1999). Population models are sensitive to even small changes in estimates of nest success. Therefore, estimates of vital rates and the data used to produce these estimates need to be unbiased. However, observational studies of breeding songbirds often depend on several assumptions that potentially bias results. Three of those assumptions are most critical because they deal with the determination of whether nesting attempts succeeded or failed when fledging events are not observed directly.

First, in studies of monitored nests, it is often difficult to determine the fate of a nest that is found empty on or near the expected fledge date. Nest-monitoring protocols recommend that nests be checked daily from a distance starting the day before expected fledge (Ralph et al. 1993). However, daily checks are often not possible due to weather or logistical constraints and whether observations are conducted daily or less often, it is often difficult to determine the fate of an empty nest.

Excluding nests with uncertain fates from analysis is inappropriate and causes a downward bias in nest success estimates (Manolis et al. 2000). Manolis et al. (2000) used simulation models to determine the most effective treatment of uncertain

nest fates in estimation of nest success. They found the least bias when terminating exposure (number of days a nest is observed active) with the last observation the nest was active for nests with uncertain fates. However, some bias remains if the probability of failure during the final interval differs between nests with known or uncertain fates. If the signs of failure or success are more obvious (i.e. more easily determined), or more likely to be incorrectly identified during observations of empty nests, bias in the direction of the more easily determined fate will increase as a function of the proportion of uncertain fates in a dataset. In addition, if the probability of predation increases with nestling age, even proper treatment of uncertain fates during analysis would underestimate failures and bias nest success estimates upward. As nestlings age, adult nest visitation frequency increases (Kluyver 1961), nestling vocalization type changes and volume increases (Khayutin 1985), and the reward to predators (i.e. nestling mass) increases. McDonald et al. (2009) experimentally demonstrated that begging sounds incur a risk of predation, and the predation risk increases as a function of begging activity (Haskell 1994). Therefore, the assumption that predation risk remains unchanged during the days close to fledging is tenuous.

Some studies attempt to reduce potential bias caused by uncertain fates by using more intensive field methods to limit the number of nest fates classified as uncertain (e.g. Dalley et al. 2006). This Nest Condition method uses a series of rules to make an educated guess about the fate of a nest that is empty on or near the expected fledge date. The rules differ among studies, but a typical summary follows.

If a nest is empty prior to the expected fledge date, it is assumed depredated. If a nest is empty on or after the expected fledge date, and there are signs of disturbance to the nest site (e.g. nest broken or destroyed, broken egg shells, feathers, dead young, etc.), the nest is assumed depredated. If a nest is empty on or after the expected fledge date and there is no sign of predation, or there are signs of nest success (e.g. rim of nest flattened, feces on or near rim of nest), the nest is assumed successful. These potentially subjective rules have been used to report 100% known nest fates (e.g. Dalley et al. 2006), but their reliability is untested.

A second common assumption in studies of songbird nest success is that an observation of a fledgling or family group in a presumed territory is reliable confirmation of a successful nest in that territory (e.g. Vickery et al. 1992a, Seagle and Sturtevant 2005). Many studies have circumvented the observation of nests by creating indices of reproductive activity (IRA) using observations during surveys and spot-mapping of territories (e.g. Vickery et al. 1992a). Proper application of an IRA requires observer knowledge of species-specific nesting phenology and other natural history characteristics (Vickery et al. 1992a). For example, for the species of interest, is an observation of an adult with food a sign of courtship feeding, feeding of an incubating mate, feeding of nestlings, feeding of fledglings, feeding of a brood parasite nestling or fledgling, carrying food to caching sites, or simply a prey item that requires extended handling time? Even if an observer has sufficient knowledge to interpret such activities during the nesting period, little is known about movement and habitat use for most songbird species during the post-fledging period (Anders et

al. 1998). In particular, if fledglings move off their natal territory soon after fledging, presence of fledglings near a nest is not a good indicator of nest success for that nest. Therefore, while an observation of a fledgling or family group in a territory containing a recently active nest elicits the seemingly innocuous assumption that the nest succeeded, that assumption is untested.

Another common method for assessing songbird nest success uses mist nets to sample ratios of fledglings to adults during the post-fledging period. Usually, these studies sample only areas known to be used for nesting by the study species (e.g. Dalley et al. 2009), and implicitly assume that non-nesting areas are rarely used during the post-fledging period. These methods assume that captured birds originated from nests within the sampled area, or that sampled areas are representative of all areas used by the study species during the post-fledging period. Because post-fledging movement and habitat use are poorly understood for most songbirds, this assumption also remains untested.

We studied a population of breeding Ovenbirds (*Seiurus aurocapillus*) in north-central Minnesota, USA to test these 3 common assumptions of songbird reproductive success studies: (1) the condition of an empty nest on or near its expected fledge date is a reliable indicator of nest fate, (2) presence of a fledgling or family group within a nesting territory is a reliable confirmation of a successful nesting attempt, and (3) ratios of fledglings to adults captured during the post-fledging period are reliable indicators of nest success within a local area. We monitored conditions of nests and used radio telemetry to monitor survival and

movements of juvenile Ovenbirds through expected fledge dates and the early post-fledging period. In addition, we used mist nets to sample non-nesting cover types (early-to-mid successional regenerating clearcuts and forested wetlands) for use by Ovenbirds during the post-fledging period. We expected the proportion of nests incorrectly determined by nest condition alone to be small, but still potentially a source of bias. We further expected most fledglings to remain within natal territories during the early post-fledging period. Finally, we expected fledgling and adult Ovenbirds to use non-nesting cover types infrequently, and for age ratios to be similar among cover types each year.

METHODS

Study area

Data were collected May – August, 2006 – 2009 at 3 study sites in the Chippewa National Forest (CNF) in north-central Minnesota, USA. The CNF encompasses ~600,000 ha of Cass and Itasca Counties in the northern hardwood-coniferous forest transition zone. Each study site contained mature forest stands of >50 years old and >200 ha, and a mosaic of forested wetlands, marshes, lakes, and regenerating clearcuts of various ages. Mature forest stands ranged from mostly coniferous to mostly deciduous and were primarily composed of red pine (*Pinus resinosa*), sugar maple (*Acer sacharum*), American basswood (*Tilia americana*), aspen (*Populus* spp.), birch (*Betula* spp.), white pine (*P. resinosa*), and northern white-cedar (*Thuja occidentalis*). Forested wetland stands were primarily composed of tamarack (*Larix laricina*), black ash (*Fraxinus nigra*), and alder (*Alnus* spp.).

Regenerating clearcuts were 2 – 20 years since harvest, and were primarily composed of aspen (*Populus* spp.), birch (*Betula* spp.), willow (*Salix* spp.), and red raspberry (*Rubus strigosus*).

Nest monitoring

We searched for and monitored Ovenbird nests in 8, 10-ha plots at each of 2 of the 3 study sites during the 2007 and 2008 breeding seasons. We searched each plot every 4 days and visited discovered nests at 4-day intervals. We made more frequent visits during periods of egg laying and expected hatching to predict the date of fledging. Different paths were taken to and from nests during each visit, and nests were sometimes (~10% of observations) observed remotely with binoculars to reduce disturbance of nest sites. We visited each nest 1 – 2 days before the expected fledge date, removed nestlings, and carried them in a soft cloth bag ≥ 10 m from the nest. We banded all nestlings with standard aluminum U.S. Geological Survey legbands, and attached a radio transmitter to ≥ 1 nestling from each nest. We attached transmitters using a figure-eight harness design for passerines (Rappole and Tipton 1991). The combined mass of transmitter and harness equaled 4.3 – 4.9% of nestling mass when attached. We returned nestlings to the nest within 15 minutes, and only when no known nest predators were seen or heard. We monitored the condition and location of each marked bird daily using radio telemetry. We monitored nest condition and described nests as disturbed by a predator when any sign of predation was observed (i.e. dead nestlings, broken egg shells, flight feathers, or top of nest

removed). We recorded locations of nests and fledglings using handheld GPS units (100 points averaged).

We estimated nest success by exposure (Mayfield 1961) using 3 methods: (1) Telemetry (2) Nest Condition, and (3) Manolis (Last Active-B in Manolis et al. 2000). In all 3 methods, nests that failed during laying, incubation, or early in the nestling period were treated identically as failures. In the Telemetry method, we determined nest fates based on the condition of radio-marked nestlings on or after the expected fledge date for each nest. In the Nest Condition method, we assigned a fate of failed or succeeded to each nest observed empty on or after the expected fledge date based on the condition of the nest location, and terminated exposure of each nest at the midpoint of the interval between the last active observation and the observation of the empty nest. In the Manolis method, we followed the Nest Condition method, except that we assigned fate as uncertain when we observed a nest empty on or after the expected fledge date and there was no clear sign of success or failure. In addition, in the Manolis method, we terminated exposure of each nest with a known fate at the midpoint of the interval between the last active observation and the observation of the empty nest, whereas we terminated exposure of each nest with an uncertain fate at the last active observation. Our field methods differed from the methods of Manolis (1999), in that we did not use fledgling activity near an empty nest as a sign of nest success during our study. However, the results from our Manolis method are likely unaffected by this difference in field methods, because Manolis (1999) had very few

nests for which fate was determined using fledgling activity alone (J.C. Manolis personal communication).

Ovenbirds in this population average a 4-day laying period, a 12-day incubation period, and an 8-day nestling period, with ~10% fledging on day 7 and ~10% fledging on day 9 (Streby and Andersen unpublished data). For the Nest Condition and Manolis methods, when a previously active nest was observed empty on or after day 6 of the nestling period, we used the following rules to determine nest fates based on nest site condition. If a nest was empty before day 7, we assumed the nesting attempt failed. If a nest was empty on or after day 7 and the nest was disturbed, we assumed the nesting attempt failed. If a nest was empty on or after day 7 and we found any sign of success, we assumed the nesting attempt succeeded. If a nest was empty on or after day 7 and we found no sign of predation, we assumed nestlings successfully fledged from the nest (Nest Condition method) or the nest fate was uncertain (Manolis method).

Fledgling monitoring

We measured distances from nests for each daily location of marked fledglings to determine if fledglings were inside or outside of their natal territory. Although we did not directly measure territory sizes, we recorded 5 – 15 singing males and monitored 4 – 10 simultaneously active nests per ha in some intensively searched plots. Therefore, using conservative estimates of 4 – 10 territories per ha, we determined that Ovenbird territories range from 0.10 to 0.25 ha in this population. Ovenbird territories are of similar size in other densely populated regions (e.g. Smith

and Shugart 1987). We considered fledglings outside of minimum (0.10 ha) and maximum (0.25 ha) natal territories if the distance between a fledgling and its nest was greater than the radius of a hypothetical circular territory of each size.

Mist netting

At all 3 study sites, we used mist nets to sample non-nesting (i.e. non-mature forest) cover types for use by Ovenbirds during the post-fledging periods of 2006 – 2009. Each sampled stand was adjacent to mature forest in which Ovenbirds were confirmed to nest. During 2006 – 2009 at each site, we sampled 1 regenerating clearcut of each of 2 age groups, 1 – 6 and 7 – 12 years after harvest. In 2009 at 2 of our 3 study sites, we additionally sampled 1 clearcut 13 – 20 years after harvest and 1 forested wetland. Within each stand, we erected 6 (3 pairs), 12-m, 4-shelf mist nets in 3 portions of each stand (≤ 25 m, 26 – 50 m, and > 50 m from mature forest edge). To reduce bias from differences in canopy height, we erected net-pairs end-to-end in stands with canopies ≤ 5 m, and stacked nets vertically in stands with canopies > 5 m (i.e. clearcuts 13 – 20 years after harvest, and 1 forested wetland).

We sampled each stand twice weekly from 4 July to 29 August. We opened nets 15 – 30 min before sunrise and closed them after 3 h or when weather conditions precluded safe netting and banding of birds. On several occasions, we opened nets late, or closed and reopened nets multiple times to accommodate weather events. We monitored nets at ≤ 30 -min intervals, removed entangled birds, and carried them in soft cloth bags to a banding station ≤ 200 m from capture locations. We identified species, sex, and age of each bird, referring to Pyle (1997) when necessary. We

banded each bird with a standard aluminum U.S. Geological Survey legband. We released most adult birds from the banding station, but returned juveniles and females in breeding condition to ≤ 50 m from their capture location to reduce disturbance to nesting and recently fledged family groups.

Statistical analysis

We used the Mayfield (1961) method to estimate nest success for each of the 3 methods compared in this study. For the Nest Condition and Manolis methods, we present estimates based on observed nest fates and hypothetical situations in which all incorrectly identified fates were identified as either successful (Manolis High and Nest Condition High) or failed (Manolis Low and Nest Condition Low) to demonstrate the magnitude of bias potentially produced by incorrectly identified fates. We used ArcGIS 9.3 (use of trade names does not imply endorsement by either the U.S. Geological Survey or the University of Minnesota) to measure distances between nests and fledgling locations. We report fledgling distances from nests as mean \pm SE. We compared fledgling:adult capture ratios between cover types for each year (among cover types for 2009) with χ^2 tests of independence. Tests were considered statistically significant at the $\alpha = 0.05$ level.

RESULTS

Nest Success

We monitored 184 active Ovenbird nests, 116 (63.0%) of which were active during observations 1 – 2 days prior to their expected fledge date, whereas 68 (37%) nests failed earlier in the nesting period. From the remaining 116 nests, we banded

375 nestlings and attached transmitters to 130 nestlings. Transmitters fell off of 11 nestlings in 11 nests. We found 4 of those fledged family groups, confirmed identities of banded fledglings, and re-attached transmitters. The fates of the remaining 7 nests for which transmitters fell off nestlings were uncertain. Because there was no sign of failure at those 7 nest locations, we considered them successful in the Nest Condition method, and uncertain in the Manolis and Telemetry methods.

Using the Telemetry method, we identified 18 failed nests, 91 successful nests, and 7 nests with uncertain fates for the 116 nests that we observed active 1 – 2 days before their expected fledge date. Using the Nest Condition method, we identified 17 failed nests and 99 successful nests in the same sample of nests. Of the 99 successful nests in the Nest Condition method, 80 nests were assumed successful only because there was no sign of failure. Therefore, for the Manolis method, we identified 17 failed nests, 19 successful nests, and we assigned 80 nests uncertain fates. To demonstrate differences among the actual nest success estimates resulting from each method, we included the 68 nests that failed before the final visitation interval in each analysis (Table 1).

Of fates determined by condition of the 116 nests active during the final visitation interval, 11 (9.5%) were incorrectly identified: 6 as successful, and 5 as failed. Using telemetry, we found dead nestlings (with and without transmitters) or parts of nestlings (i.e. feathers and banded legs) under leaf litter <1 m from each of these 6 undamaged nests. The proximity of those recovered birds to their nests suggests that predation likely occurred at the nest. Although it is possible that those

birds were depredated immediately after fledging, technically meeting the definition of a successful nest, they nonetheless clearly represent a failed reproductive attempt. In addition, using telemetry, we observed 2 nests that successfully fledged on day 6, and 3 nests that were damaged or destroyed on day 7 or 8, but family groups from these nests were subsequently observed (using telemetry) alive. Because similar numbers of nest fates were incorrectly identified as successful and failed, the net bias caused by incorrectly identified fates was relatively small (Table 1). Estimates based on hypothetical situations in which all 11 incorrectly identified fates were identified as either successful (Manolis High and Nest Condition High) or failed (Manolis Low and Nest Condition Low) demonstrate the magnitude of bias potentially produced by incorrectly identified fates.

Fledgling movements

Fledglings monitored for >24 h ($n = 89$) were located 3 – 108 m ($\bar{x} = 36.4 \pm 2.54$) from their nests ≤ 24 h after fledging (Table 2). Based on estimated territories ranging in size from 0.10 – 0.25 ha, 58.4 – 74.2% of fledglings were outside of their presumed natal territory ≤ 24 h after fledging. Fledglings monitored for >10 days ($n = 41$) were located 86 – 390 m ($\bar{x} = 151.8 \pm 9.94$) from their nests, and 100% were outside of their presumed natal territories ≤ 10 days after fledging. We located 7.9% and 31.7% of fledglings outside of our 10 ha nest searching plots, ≤ 24 h and ≤ 10 days after fledging, respectively.

Fledgling:adult capture ratios

We captured 726 Ovenbirds (367 fledglings and 359 adults) in non-nesting cover types during the post-fledging periods of 2006 – 2009 (Table 3).

Fledgling:adult capture ratios were significantly different between cover types in 2006 ($\chi^2 = 4.52$, $df = 1$, $P = 0.034$) and among cover types in 2009 ($\chi^2 = 13.37$, $df = 3$, $P = 0.004$), but not different between cover types in 2007 ($\chi^2 = 0.22$, $df = 1$, $P = 0.639$) or 2008 ($\chi^2 = 1.26$, $df = 1$, $P = 0.261$). From nest productivity and fledgling survival, we estimated that fledgling:adult ratios declined from 0.92 to 0.63 in 2007 and 0.78 to 0.49 in 2008 during the period 5 – 48 days after peak fledging (Table 3). Fledgling: adult capture ratios in non-nesting cover types were consistent with estimated ratios during 2008 but not 2007.

DISCUSSION

Nest fates

In our study, using radio telemetry reduced the number of uncertain nest fates, decreasing the potential bias associated with uncertain fates, and avoided additional bias from incorrectly determined fates based on nest condition alone. Using radio telemetry, we were unable to determine fates for 4% of nests, whereas 43% of nest fates were uncertain without telemetry. Excluding nests with uncertain fates from nest success estimation is inappropriate (Manolis et al. 2000). Careful observation of the condition of empty nests is often used to determine otherwise uncertain nest fates (e.g. Dalley et al. 2006). However, in our study, nest fates were incorrectly determined for 11 (9.5%) nests for which fates were assigned based on condition of

empty nests. Although reducing the number of unknown nest fates in a sample is desirable for reducing bias, using the Nest Condition method alone to determine otherwise uncertain fates instead resulted in additional bias.

Similarities in nest success estimates produced by the 3 methods we compared obfuscate the fact that estimates from the Nest Condition and Manolis methods were biased by incorrectly identified nest fates. These methods produced similar estimates to that of the Telemetry method only because they were biased both upward and downward by incorrectly identified nest fates of similar number in each direction. When we simulated bias from the 11 incorrectly identified nest fates entirely in 1 direction (i.e. 11 successful nests were incorrectly determined to have failed, or vice versa), the Manolis estimate was biased up to 6.3%, and the Nest Condition estimate was biased up to 5.4%. Although the likelihood of all incorrectly identified fates within a sample being in 1 direction is probably low, the range of potential bias remains alarming considering the sensitivity of population models to small variation in estimates of nest success. The percent of nest fates that are incorrectly determined in a study likely varies due to differences among species' nesting ecology, and rules used to determine fates. However, it is important to note that incorrectly determined fates cause bias, not imprecision, and therefore cannot be compensated for with increased sample size.

Sensitivity analyses of songbird population models often identify nest success as 1 of the most important parameters explaining variation in population growth (e.g. Donovan and Thompson 2001). Therefore, even slightly biased estimates of nest

success have a disproportionately large effect on population growth projections in population models. Recall that we did not include observations of fledglings near a nest as a sign of success, as is typical in methods not using telemetry. Our observations of fledgling movements during this study demonstrate the potential for additional bias in nest success estimates when assuming that fledglings near a nest came from that nest. We contend that the use of radio telemetry, or other methods (e.g. cameras) that allow for certainty in assigning nest fates, is necessary for producing accurate estimates of nest success. In addition, remaining uncertain fates result in the least bias when included in analysis with exposure terminated at the day of last active observation as per the Manolis method (Manolis 2000).

Fledgling movements

Because most fledglings traveled beyond presumed natal territories within 24 h of leaving the nest, presence of a fledgling or family group within a nesting territory is not confirmation of nest success for Ovenbirds. We observed fledglings up to 390 m from their nests within 10 days of fledging, even though fledglings may not appear to be able to undertake movements of this magnitude (Fig. 1). Although an observation of a young Ovenbird fledgling or family group certainly indicates a successful nest, that successful nest may be anywhere within the surrounding 48 ha if the observed bird fledged within the previous 10 days. Ralph et al. (1993) and Martin and Geupel (1993), commonly cited sources for nest-monitoring methodology, each caution that some species move up to 100 m within hours of fledging, and that fledglings from neighboring territories may incorrectly be attributed to a nest

territory. We reiterate that caution, and suggest that observations of fledglings not be used as indicators of nest success unless fledglings can be individually identified and linked to individual nests. If fledgling activity near a nest is used as a sign of success, nest success estimates will likely be inflated, especially in areas of high nesting density.

Seagle and Sturtevant (2005) used Ovenbird territory density and observations of adults and fledglings within territories to demonstrate that Ovenbird reproductive success is predicted by forest productivity. Density alone is not a reliable indicator of habitat quality (e.g. VanHorne 1983), which has been demonstrated for many bird species (e.g. Vickery et al. 1992b). Our results demonstrated that observed fledglings may not have been produced within 10 ha study plots, and fledglings are more likely than not to be outside natal territories within 24 h of fledging. We suggest that Seagle and Sturtevant (2005) found that Ovenbird post-fledging habitat use, rather than reproductive success *per se*, was predicted by forest productivity.

Fledgling:adult capture ratios

Our 726 Ovenbird captures in non-nesting cover types were the most for any of the 71 species captured during our study. We observed Ovenbirds nesting in regenerating clearcuts as young as 17 years after harvest. However, we observed no sign of Ovenbirds nesting in forested wetlands or regenerating clearcuts younger than 17 years after harvest. Therefore, it is possible that some of the Ovenbirds captured in the 17- and 19-year-old stands sampled during 2009 had nested in those stands.

However, it is unlikely that any of the Ovenbirds using forested wetlands and younger clearcuts had nested in those cover types.

Fledgling capture rates often do not correlate with local nest success estimates (Feu and McMeeking 1991, Nur and Geupel 1993). We suggest one factor contributing to discrepancies between fledgling capture rates and nest success estimates is that netting is usually focused only in immediate areas of known nesting activity and not in non-nesting cover types (e.g. Dalley et al. 2009). For fledgling:adult capture ratios to reliably index productivity of a population, all areas used by the birds during the post-fledging period must be sampled. Fledglings and adults in our study used non-nesting cover types during the post-fledging period, and capture ratios were sometimes different among cover-types. In addition, fledgling:adult capture ratios were not consistent with fledgling:adult ratios estimated from nest productivity and fledgling survival during 1 of 2 years studied. Therefore, fledgling:adult capture ratios were not useful for assessing cover-type-specific nest success or nest success in adjacent nesting cover types in this population.

In conclusion, our results suggest that using radio telemetry or other methods of individually identifying fledglings or family groups, rather than using nest condition, improves accuracy of determination of nest fates for nest success analysis. In the absence of individual identification of fledglings or family groups, proper treatment of uncertain nest fates during analysis is more appropriate than using nest-site condition to assign fate to nests. In addition, radio telemetry or other methods of individually identifying birds to confirm nest success within a nesting territory or

larger study area provides more accurate estimates of nest success than observations of birds from nests of unknown location. Without knowledge of species-specific post-fledging movements and habitat use, an observation or capture of a fledgling or family group during the post-fledging period is no more than evidence of use of the sampled area by that species during that period.

Table 1. Estimates of Ovenbird nest success (daily survival \wedge 24) produced using 3 methods (Telemetry, Manolis, and Nest Condition), and hypothetical situations in which incorrectly determined fates were all assigned failed (Manolis Low and Nest Cond. Low) or successful (Manolis High and Nest Cond. High) fates. Each analysis was conducted using the same sample of 184 Ovenbird nests monitored during 2007 – 2008 in the Chippewa National Forest, Minnesota, USA. Standard Errors of estimates (not shown) were very similar and ranged between 0.040 – 0.042.

Method	Exposure Days	No.		No. Uncertain	Estimate	Percent Diff.
		No. Failed (no. incorrect)	Successful (no. incorrect)			
Telemetry ^a	2,569	86	91	7	0.442	0
Nest Condition ^b	2,563	85 (5)	99 (6)	0	0.445	0.67
Manolis ^c	2,531	85 (5)	19	80	0.440	-0.45
Nest Cond. Low	2,563	91 (11)	93	0	0.420	-6.25
Nest Cond. High	2,563	80	104 (11)	0	0.467	4.54
Manolis Low	2,515	91 (11)	19	74	0.416	-5.24
Manolis High	2,510	80	30 (11)	74	0.463	5.35

^a Fates determined by survival of nestlings and fledglings using radio telemetry, and nest exposure terminated on fledge date.

^b Fates determined by condition of nests found empty on or after expected fledge dates, exposure terminated at midpoint of final interval.

^c Fates determined as in Nest Condition method when predation was evident, fates of undisturbed empty nests considered uncertain, and exposure for uncertain fates terminated on date of last active observation (Last Active B from Manolis et al. 2000)

Table 2. Distances traveled from nests by Ovenbird fledglings 1 day and 10 days following fledging during 2007 and 2008 in the Chippewa National Forest, Minnesota, USA.

Days since fledging	<i>n</i>	Average distance (m) from nest \pm SE	Percent of fledglings located outside NT ^a	Percent of fledglings located outside 10-ha study plot
1	89	36.4 \pm 2.54	58.4 – 74.2 %	7.9 %
10	41	151.8 \pm 9.94	100.0 %	31.7 %

^a NT = natal territory, range of 0.10 – 0.25 ha and calculated assuming nests were located at the center of circular territories.

Table 3. Fledgling:adult, or hatch-year:after-hatch-year (HY:AHY), Ovenbird capture ratios in non-nesting forest stands during the post-fledging periods of 2006 – 2009, and HY:AHY Ovenbird population ratios estimated from nest productivity and fledgling survival during 2007 – 2008, in the Chippewa National Forest, Minnesota, USA.

Year	Cover type (years since harvest)	<i>n</i>	HY:AHY capture ratio (estimated ratio)	χ^2	df	<i>P</i>
2006	clearcuts (1 – 6)	31	0.10	5.52	1	0.034
	clearcuts (7 – 12)	72	0.25			
2007	clearcuts (1 – 6)	40	0.45 (0.63 – 0.92)	0.22	1	0.639
	clearcuts (7 – 12)	79	0.41 (0.63 – 0.92)			
2008	clearcuts (1 – 6)	91	0.66 (0.49 – 0.78)	1.26	1	0.261
	clearcuts (7 – 12)	145	0.59 (0.49 – 0.78)			
2009	clearcuts (1 – 6)	89	0.71	13.35	3	0.001
	clearcuts (7 – 12)	117	0.45			
	clearcuts (13 – 17)	35	0.57			
	forested wetlands	27	0.56			

Figure 1. An Ovenbird fledging photographed 135 m from its nest, outside its presumed natal territory, and outside the 10 ha study plot containing its nest <48 h after fledging (photo by Sean Peterson).



CHAPTER 2

SEASONAL PRODUCTIVITY IN A POPULATION OF OVENBIRDS:

WHY NEST DATA ARE NOT ENOUGH

INTRODUCTION

Reproductive output of songbird populations is traditionally measured with nest success, defined as the probability of a single nesting attempt producing at least 1 fledgling. Since Mayfield (1961, 1975) described an exposure method for estimating daily survival, increasingly robust statistical methods have been developed to accurately estimate nest success (reviewed by Johnson 2007). Murray (2000) demonstrated that nesting life-history characteristics can affect how nest success translates to nest productivity, or the mean number of fledglings produced per female within a nesting season. Making 1 or more nesting attempts following a failed attempt (re-nesting) and successfully fledging more than 1 brood in a season (multi-brooding) can compensate for low nest success (Murray 2000, Thompson et al. 2001). In addition, variation in the number of fledglings produced per successful nest can offset variation in nest success. For example, Flaspohler et al. (2001a) found that Ovenbird nest success was lower near clearcut edges than in interior mature forest, but because clutch size was higher near clearcut edges, nest productivity was similar between the 2 locations. Therefore, nest productivity is more appropriate than nest success for estimating songbird reproductive output during the nesting period (i.e. from first egg laid to fledge).

Although the nesting period is obviously an essential part of songbird reproduction, the dependent post-fledging period (i.e. after young fledge but before independence from adult care) can be as long as or longer than the nesting period (Ricklefs 1968). However, because songbirds are relatively quiet and mobile during

the post-fledging period compared to the nesting period, it is difficult to monitor survival and habitat use of individual fledglings or family groups once they leave the nest. This difficulty has resulted in a lack of information about post-fledging survival and habitat use for most songbird populations (Anders et al. 1997). In the rare case that fledgling locations are predictable (e.g. cactus wrens [*Campylorhynchus brunneicapillus*] return nightly to roost in nests during the post-fledging period), apparent fledgling survival is low during the first few days after fledging (Ricklefs 1968), suggesting that variation in fledgling survival is likely important to seasonal productivity (i.e. mean number of fledglings raised to independence per breeding female).

Both adults and fledglings of many songbirds use non-nesting areas during the post-fledging period (Pagen et al. 2000, Marshall et al. 2003). Furthermore, habitat characteristics in areas used during the post-fledging period can influence fledgling survival (e.g. King et al. 2006), suggesting that information about fledgling survival and habitat use are necessary for understanding songbird population dynamics. For more than a decade, advancements in microtechnology have made radio telemetry an available method for monitoring fledgling songbird movements and survival (Anders et al. 1997, Cohen and Lindell 2004, King et al. 2006). However, fledgling survival for most species is unstudied. Therefore, nest success, or sometimes nest productivity, remains as the reproductive parameter used to model population growth (e.g. Podolski et al. 2007), determine source-sink dynamics (e.g. Donovan et al. 1995), compare habitat quality (e.g. Weinberg and Roth 1998), and identify effects of

human activities on songbird populations (e.g. Manolis et al. 2002). Furthermore, despite the advantages of nest productivity over nest success as a measure of reproductive output, nest success remains the most commonly reported comparative estimate of this important parameter (Thompson et al. 2001). Generally, when songbird nest success is low, habitat quality is described as low (e.g. Trine 1998). When nest success is low near edges of non-nesting habitat, edges are described as negatively affecting population growth (e.g. King et al. 1996). When birds nest at high densities and nest success is low, the area is presumed to be an ecological trap (e.g. Purcell and Verner 1998). Conversely, when nest success relates positively to density, density has been purported to be a useful indicator of habitat quality (e.g. Perot and Villard 2009).

Models of songbird population growth rely primarily on nest data, and usually include fledgling survival within a broader estimate of first-year survival (e.g. Donovan et al. 1995, Podolski et al. 2007). Although these models are stochastic, mean first-year survival is usually assumed to be one-half of adult annual survival (Ricklefs 1973, Temple and Cary 1988). That estimate is derived from return rates of first-year birds with some assumption of natal philopatry. However, natal philopatry in migrant songbirds is generally low and poorly understood (Schlossberg 2009). Models including that estimate of first-year survival (one-half of adult annual survival) have been used to infer regional population growth and source-sink dynamics (e.g. Donovan et al. 1995, Porneluzi and Faaborg 1999, Podolski et al. 2007). However, conclusions based on those models require the assumption that

fledgling survival is either constant or varies consistently in direction and magnitude with nest productivity. If fledgling mortality is high and varies inconsistently with nest productivity, conclusions about seasonal productivity based solely on nest success or nest productivity will be misleading.

We studied a population of Ovenbirds (*Seiurus aurocapillus*) in a managed, forested landscape in north-central Minnesota, USA, and investigated the relative contribution of nest productivity and fledgling survival to seasonal productivity over 2 years. In addition, we tested the hypothesis that non-mature forest edges have similar effects on nest productivity and fledgling survival. Ovenbird nest success is sometimes lower near clearcut edges (Manolis et al. 2002, King et al. 1996), but that effect can be offset by increased brood size near edges (Flaspohler et al. 2001a). Ovenbird fledglings frequently use mature-forest edges and non-nesting cover types (Vitz and Rodewald 2004), and vegetation density can influence Ovenbird fledgling survival (King et al. 2006). We expected that clearcut edges may negatively influence nest productivity in our study, but that they may positively influence fledgling survival. In addition, we modeled growth for our Ovenbird population using our estimates of nest productivity and fledgling survival. We compared our models to simpler models in which we removed estimates of fledgling survival and assumed that first-year survival was one-half of adult survival. We expected that population growth estimates from our models may differ considerably from estimates from simpler models.

METHODS

Study species

Ovenbirds winter throughout Central America, southern Mexico, many Caribbean islands, and southern Florida, and breed in mature forests throughout eastern and north-central North America (Van Horne and Donovan 1994). Female Ovenbirds build distinctive dome-shaped nests on the forest floor, and likely due to high nesting densities and the relative ease of monitoring ground nests, Ovenbird nesting ecology is well studied among songbirds (Van Horn and Donovan 1994). Ovenbirds often re-nest after initial nest failure, but successfully fledge only 1 brood per year. Ovenbird nest success is highly sensitive to edges of agricultural fields and other types of anthropogenic development (Burke and Nol 2000). The effects of edges created by forest harvest (i.e. clearcuts) in predominantly forested areas are less clear, but nest success is at least sometimes negatively related to clearcut edges (e.g. Manolis et al. 2000, King et al. 2006). However, as with most songbirds, little is known about survival and habitat use of Ovenbirds during the post-fledging period (King et al. 2006).

Study area

We collected data during May – August 2007 and 2008 in the Chippewa National Forest (CNF) in north-central Minnesota, USA. The CNF encompasses approximately 600,000 ha of Cass and Itasca Counties in the transition zone from northern hardwood to boreal forest, and includes mature mixed northern hardwood-conifer forest stands interspersed with lakes, marshes, forested wetlands, and

regenerating clearcut stands (9 – 15-ha even-aged stands of primarily aspen [*Populus* spp.] with remnant mature oak [*Quercus* spp.] and white pine [*Pinus strobus*] trees and occasional large snags on our sites) of various seral stages. Mature forest stands at our sites ranged from mostly coniferous to mostly deciduous and were primarily composed of red pine (*Pinus resinosa*), sugar maple (*Acer sacharum*), American basswood (*Tilia americana*), aspen, birch (*Betula* spp.), white pine, and northern white-cedar (*Thuja occidentalis*). Forested wetland stands were primarily composed of tamarack (*Larix laricina*), black ash (*Fraxinus nigra*), and alder (*Alnus* spp.). We monitored nests on 16 randomly established 10-ha plots in mature upland forest stands in the Suomi Hills and Cutfoot Sioux areas of the CNF. Of the study plots, 12 were adjacent to 1 or 2 regenerating clearcuts, and extended 250 – 510 m from clearcut edges, and 4 were entirely >250 m from clearcut edges. Regenerating clearcuts included early successional stands ≤ 6 years since harvest (young clearcuts; primarily shrubs and saplings <2 m in height) and stands 7 – 20 years since harvest (old clearcuts; primarily aspen 2 – 15 m in height).

Data collection

We monitored Ovenbird nests following procedures modified from Martin and Geupel (1993) and Martin et al. (1997), and used in previous studies of forest-nesting birds in north-central Minnesota (Manolis 1996, Perry 1998). Starting 15 May, we intensively searched each plot every 4 days, and located nests by combining systematic searching and observations of adult behavior (e.g. singing males, flushing females, and females carrying nesting material). We recorded each nest location with

a handheld GPS unit (100 points averaged), and marked the area with flagging tape 2 – 5 m in a random direction from the nest. During nest monitoring, we approached nests from various directions and continued walking past nests to avoid attracting predators with dead-end paths (Martin and Geupel 1993). We visited each nest at 4-day intervals, and more frequently when we expected an event (i.e. laying or hatching), to help predict fledge dates. When we expected no events, and when nest positions allowed (~10% of observations), we monitored nests from >5 m using binoculars. During each nest visit, we recorded the status of nest contents (i.e. number of eggs, number of nestlings, and estimated age of nestlings) until nestlings were 1 – 2 days from fledging.

We attached radio transmitters to nestlings 1 – 2 days prior to estimated date of fledging. To minimize the chance of attracting predators to nest sites, we attached transmitters only when we could see or hear no common nest predators (e.g. eastern chipmunk [*Tamias striatus*] and red squirrel [*Tamiasciurus hudsonicus*]) nearby. We extracted all nestlings and carried them in soft cloth bags 10 – 15 m from the nest, where we weighed and banded them using standard aluminum U.S. Geological Survey legbands. We attached radio transmitters (0.67 g including harness) to ≥ 1 nestling from each nest using a figure-eight harness design (Rapolle and Tipton 1991), and then replaced nestlings in the nest. Transmitters were 4.3 – 4.9% of nestling body mass at time of attachment. We used the condition of radio-marked birds to determine fates of nests found empty on or near the expected fledge date (Chapter 1).

Radio telemetry

We used radio telemetry to monitor fledglings following procedures modified from Anders et al. (1998) and Vega Rivera et al. (1998). We located and monitored survival of radio-marked fledglings from 12 June to 11 August via ground-based telemetry. We used triangulation to estimate the location of each fledgling, and approached estimated locations and attained visual confirmation of survival or mortality. When fledglings moved beyond the range of our ground-tracking capabilities, either independently or when carried by predators, we relocated them from the air using standard aerial telemetry techniques (Mech 1983). Once a bird was relocated from the air, we determined its specific location and survival status using ground-based telemetry. We used GIS software to measure distances between nests and fledgling locations, between consecutive fledgling locations, and between fledgling locations and nearest edges of young and old clearcuts using a forest cover-type layer (U.S. Forest Service Chippewa National Forest 2007).

Predator identification

We did not directly observe any nest predation events during this study. We used condition and location of recovered fledglings and transmitters to identify predators. We identified a predator as an owl when a transmitter and corresponding legband was recovered entangled in an owl pellet (Streby et al. 2008). We identified a predator as a hawk when a transmitter was recovered in a pile of plucked feathers, when a transmitter was located in an active hawk nest, or in 1 case when a transmitter was tracked directly to a flying Broad-winged Hawk (*Buteo platypterus*). We

identified a predator as a small mammal when a fledgling was found cached underground or in a chipmunk burrow, when a transmitter and banded leg were found on a stump or low conifer branch commonly occupied by feeding chipmunks or red squirrels, or when a fledgling was found to have been chewed open and had its brain or entrails eaten.

Statistical analysis

We used PROC GENMOD (SAS Institute 1999, Appendix 2) to fit logistic exposure models (Shaffer 2004) to Ovenbird nest and fledgling survival data. For each period (nesting and post-fledging), we compared 16 candidate models including a constant survival model and all combinations of 4 explanatory variables: year (YEAR), nest initiation date (NESTIN), distance to young clearcut (DYC), and distance to older clearcut (DOC). We used Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002) to rank candidate models. We considered the best-supported model and all models with ΔAIC_c values < 2.0 to be competing models. We used the cumulative Akaike weights (w ; Burnham and Anderson 2002) of all models that included a given variable to identify the relative value of that variable for explaining variation in fledgling survival.

Because nest infestation by bird blow flies (*Trypocalliphora braueri*) apparently does not affect Ovenbird nest productivity, but can significantly lower fledgling survival (Streby et al. 2009), we included infested nests ($n = 7$), but excluded fledglings ($n = 9$) from those nests from survival analysis. We compared daily survival rates of nests and fledglings between years and among population

segments using Z-tests (Johnson 1979). From each brood for which we tracked multiple fledglings, we included 1 randomly selected fledgling in estimates of survival to avoid pseudoreplication (Pulliam 1988). However, because no 2 siblings were depredated by the same predator group (i.e. mammals or raptors), we included all fledglings when comparing predation by predator group. We compared fledgling predation by raptors and small mammals between years with χ^2 tests of independence.

We used the number of active Ovenbird nests found per hour of searching as an index of nesting density in our study population during each year. Because pairing success of male Ovenbirds is almost always $< 100\%$ (Habib et al. 2007), and can range from 0% to nearly 100% (Van Horn et al. 1995, Bayne and Hobson 2001), we believe that active nests found per unit effort is at least as accurate as point-counts for measuring relative nesting density in this species. We compared Ovenbird nesting relative densities in our study population between 2007 and 2008 with a χ^2 test of independence. We considered tests statistically significant at the $\alpha = 0.05$ level.

Population modeling

We modeled growth for 3 segments of our Ovenbird population partitioned based on proximity of nests to clearcut edges. Although edge effects on nests success can extend 300 m or more into mature forest stands (e.g. Manolis et al. 2000, Flaspohler et al. 2001b), our preliminary models of nest and fledgling survival, using the logistic exposure method with distance-to-edge as a continuous explanatory variable, indicated an apparent inflection point at ~ 100 m from clearcut edge (Streby

and Andersen unpublished data). This distance (100 m) is consistent with studies of the most common predators of ground nests in northern-hardwood forests (Fenske-Crawford and Niemi 1997), eastern chipmunk and red squirrel, for which abundance is highest within 100 m of clearcut edges (King et al. 1998). Therefore, we modeled growth for 3 segments of our Ovenbird population based on nest location: (1) ≤ 100 m from young clearcuts, (2) ≤ 100 m old clearcuts, and (3) > 100 m from any clearcut edge. We refer to these population segments as near young clearcut, near old clearcut, and interior forest, respectively.

We built female-based stochastic population models in Excel® (use of trade names does not imply endorsement by either the U.S. Geological Survey or the University of Minnesota) spreadsheets for each year and segment of the sampled Ovenbird population. We built 12 models: 1 for the entire study population for each of the 2 years and both years combined (3 models), and 1 for each of the 3 population segments for each of the 2 years and both years combined (9 models). We ran 200 iterations of each model, and we allowed each parameter to vary randomly within 1 SD (unless otherwise noted) of the estimated mean for that parameter. Each of the models were structurally identical, and included adult annual survival (from Podolski et al. 2007), nest productivity, dependent fledgling survival, and independent fledgling survival (our estimates), and non-breeding season survival (calculated using our estimates and adult annual survival from Podolski et al. 2007). We compared our models to simpler models identical to our models for all parameters except that for the simpler models we replaced our estimates of independent fledgling survival and

non-breeding survival with a common estimate of first-year survival for forest-nesting songbirds equal to one-half of adult annual survival.

Model parameterization

We estimated nest success for each population segment from regression coefficients of a logistic exposure model (Shaffer 2004) that included a year and population segment interaction term. We used the same method to estimate survival for dependent fledglings (S_{DF}) originating from nests within each population segment. We used a single estimate for survival of independent (from adult care) fledglings (S_{IF}) because nest location (within a stand) is likely not relevant to survival once fledglings are capable of independently moving >1 km per day.

We used nest initiation dates (date of first egg laid) and nest failure dates in our sample and estimated probabilities of re-nesting in our study population. The range of initiation dates for nests we observed was 47 days, with nests initiated from Julian dates 137 – 183 (we refer to date 137 as day 1 of the nesting season hereafter). Ovenbirds in this population have a mean nesting period of 24 days (from first egg laid to fledge), take 4 – 9 ($\bar{x} = 7$) days to build a nest after failure, and then 2 – 3 days to lay the first egg, or initiate a subsequent nest attempt (Streby and Andersen unpublished data).

We visually assessed a frequency distribution of the initiation dates of nests we monitored, and observed a distinct peak in the first 20 days of the nesting season. We assumed that all females initiated a first nesting attempt within that 20-day period. Therefore, we estimated that first nesting attempts were active during days 1

– 43 of the nesting season (a nest initiated on day 20, if successful, would succeed on day 43). Because birds in this population take ~10 days between failure and initiation of a subsequent nesting attempt, we assumed that nesting attempts that failed after day 37 (10% of first nesting attempts we observed) did not have time to re-nest. Again because birds take ~10 days to initiate a subsequent nest after failure, we assumed that birds initiated first re-nesting attempts during days 11 – 47, second re-nesting attempts during days 22 – 47, and third re-nesting attempts during days 33 – 47. We then calculated the percent of nests we observed that were initiated during each of those time periods, and that failed after day 37 (too late to re-nest) and estimated the probability of a female re-nesting after each failed attempt in our population. From those calculations, our model assumes that 90% of females that fail during a first nesting attempt re-nest ($R_1 = 0.90$), 60% that fail during a second nesting attempt re-nest ($R_2 = 0.60$), and 30% that fail during a third nesting attempt re-nest ($R_3 = 0.30$). Although Ovenbirds can re-nest 4 or more times (Hann 1937) and can rarely successfully fledge 2 broods (Podolski et al. 2007), we determined that the length of the nesting season in our study area likely precluded >3 re-nesting attempts or double-brooding.

We observed evidence of adult female mortality (i.e. adult feathers or other remains) associated with 3 (3.5%) nest failures. We included probability of female survival during failed nesting attempts ($S_{FF} = 0.965$) as a fixed value when computing nest productivity. Because we found no effect of nest initiation date on nest success, we considered nest success constant throughout the nesting season. For each

population segment, we computed nest productivity for initial nesting attempts (P_{N0}), and first (P_{N1}), second (P_{N2}), and third (P_{N3}) re-nesting attempts as,

$$P_{N0} = NS,$$

$$P_{N1} = (1 - P_{N0}) S_{FF} R_1 NS,$$

$$P_{N2} = (1 - P_{N0} - P_{N1}) S_{FF} R_2 NS,$$

$$P_{N3} = (1 - P_{N0} - P_{N1} - P_{N2}) S_{FF} R_3 NS,$$

where NS = nest success, S_{FF} = female survival, and R = re-nesting probability.

Within each model iteration, we computed fecundity (F; mean number of female young fledged per female) for each population segment as,

$$F = (P_{N0} + P_{N1} + P_{N2} + P_{N3}) 0.5 B,$$

where B = fledged brood (i.e. mean number of fledglings produced per successful nest). Because we allowed our estimates of nest success (NS) and fledged brood (B) each to vary randomly within 1 SD, each calculation of fecundity (F) included variation from both of those parameters.

We used 0.633 (95%CI = 0.545 – 0.721) as annual adult female Ovenbird survival (S_A ; Podolski et al. 2007). Podolski et al. (2007) did not report SD for their estimate of S_A , so we allowed that parameter to vary randomly within the reported 95% CI in our models. We acknowledge that SD is a measure of the variability in the population, whereas a 95% CI is derived from SE, which describes the precision of the estimate. However, the 95% CI from Podolski et al. (2007) was the best available approximation of range for S_A .

We computed first-year survival (S_{FY}) as,

$$S_{FY} = S_{DF} S_{IF} S_{NB},$$

where S_{NB} is survival during the 9-month non-breeding season, $S_A^{(0.75)}$. This derivation of S_{NB} assumes constant adult survival within a year. Although survival likely varies among the breeding and winter seasons, and spring and fall migration, sufficient estimates are not currently available for nearly all populations of migratory songbirds (Sherry and Holmes 1995) to better inform our model.

We computed the intrinsic rate of growth (λ) from models of both years combined, each year, and each population segment as,

$$\lambda = N_{t+1} / N_t$$

where,

$$N_{t+1} = (N_t F S_{FY}) + (N_t S_A).$$

We determined the amount of uncertainty in our estimates of λ by performing 200 stochastic iterations of each model. For each of our models, we calculated the geometric mean λ from the 200 iterations (Pulliam 1996), and calculated 95% confidence intervals (Sokal and Rohlf 1981:421). For comparison to models excluding direct estimates of fledgling survival, we replicated each of our models replacing values of S_{FY} with 0.317, or $\frac{1}{2} S_A$, as per many previous songbird population growth models (e.g. Donovan et al. 1995, Porneluzi and Faaborg 1999). In addition, we calculated the coefficient of determination (r^2) from linear regressions of the parameter values and λ s from each of the 200 iterations to explore how uncertainty in each parameter related to the population growth rate.

RESULTS

We monitored 184 active Ovenbird nests, of which 91 (49%) succeeded, 86 (47%) failed, and 7 (4%) had uncertain fates. Nest construction took 4 – 9 days ($\bar{x} = 7.0$), clutch sizes ranged from 1 – 6 eggs ($\bar{x} = 4.8$), and fledged broods ranged from 1 – 6 fledglings ($\bar{x} = 4.2$). We found 90 active nests during 575 searching-hours in 2007 (0.16 nests/hour) and 94 active nests during 590 searching-hours in 2008 (0.16 nests/hour). Based on our per-unit-effort index, nesting density was nearly identical between years ($\chi^2 = 0.01$, $df = 1$, $P = 0.91$).

We monitored 109 fledglings from the 91 nests known to be successful. We removed from the sample fledglings that died associated with blow fly infection ($n = 8$; Streby et al. 2009) and 1 fledgling that died of apparent starvation that was a brood mate of a Brown-headed Cowbird (*Molothrus ater*). To avoid pseudoreplication within the remaining 89 fledglings, we randomly selected 1 fledgling from each brood for which we monitored multiple siblings. Therefore, we included 74 fledglings from 74 nests in survival analysis and population modeling. Based on observations of adult activity, we estimated that fledglings were independent of adult care ~25 days after fledging. Forty-eight of the fledglings we monitored were depredated during the 24-day dependent post-fledging period. We monitored the remaining 26 fledglings for 1 – 24 days ($\bar{x} = 12.5$) after independence from adult care.

Logistic exposure models indicated that year effects explained the most variation in both daily survival of nests and fledgling daily survival. The YEAR

variable was included in the best-supported model for each time period, and was the only variable included in all competing models. Cumulative weights for nest survival models including each variable were: year (YEAR) = 0.65, distance to old clearcut (DOC) = 0.43, distance to young clearcut (DYC) = 0.34, and nest initiation date (NESTIN) = 0.23. Cumulative weights for fledgling survival models including each variable were; YEAR = 0.57, NESTIN = 0.23, DOC = 0.20, and DYC = 0.21.

Nest daily survival was significantly lower in 2007 than 2008 ($z = 5.858$, $P < 0.001$), whereas fledgling daily survival was significantly higher in 2007 than 2008 ($z = 3.683$, $P < 0.001$; Fig. 1). Seasonal productivity was significantly higher in 2007 than 2008 ($z = 4.70$, $P < 0.001$). Nest daily survival was not significantly different among population segments within 2007 or 2008 (Table 1). However, our 2 models of nest survival with the lowest AIC_c ($S_{YEAR+DOC}$, $AIC_c = 656.30$, and $S_{YEAR+DYC}$, $AIC_c = 6567.29$) each included an effect of distance to clearcut edge, indicating a positive influence of old clearcut edges and a negative effect of young clearcut edges on nest survival. Fledgling daily survival from nests near old clearcuts and nests near young clearcuts was significantly higher ($z = 2.259$, $P < 0.025$) and lower ($z = 10.397$, $P < 0.001$), respectively, than that of fledglings from nests in mature forest in 2007. There was a similar trend in fledgling survival among population segments in 2008, but differences were not statistically significant (Table 1).

Population growth models predicted that the entire study population had positive growth in 2007 ($\lambda = 1.07$, 95% CI = 1.03 – 1.10), negative growth in 2008 ($\lambda = 0.86$, 95% CI = 0.84 – 0.89), and negative growth for both years combined ($\lambda =$

0.96, 95% CI = 0.93 – 0.99; Table 2). For both years combined, our models predicted that the population segment nesting near young clearcuts had negative growth ($\lambda = 0.80$, 95% CI = 0.77 – 0.83), the segment nesting near old clearcuts had positive growth ($\lambda = 1.09$, 95% CI = 1.06 – 1.13), and the segment nesting in interior forest was stationary, or may have experienced slight negative growth ($\lambda = 0.97$, 95% CI = 0.94 – 1.01). Using our models as standards, simpler models (without direct estimates of fledgling survival) produced predicted values of λ biased by 2 – 39% ($\bar{x} = 25\%$; Table 2). Simpler model values of λ were significantly different from our model values for 10 of 12 of the models we compared.

For our models, coefficients of determination indicated that variation in non-breeding survival explained the most variation in λ among the 200 model iterations for each year, and both years combined. Among breeding season parameters, coefficients of determination indicated that fledgling survival explained the most variation in λ . Mean coefficients of determination from entire population models of each year and both years combined were S_{NB} (0.50), S_{DF} (0.31), S_B (0.13), S_{IF} (0.04), NS (0.01), and B (0.01).

Most nest failures (90%) were caused by either predation or abandonment following partial predation. The remaining 10% of nest failures resulted from apparent abandonment. Most fledgling mortalities (95%) were caused by mammalian predators (61% of predation) and raptors (39% of predation). The remaining 5% of fledgling mortalities were caused by unknown predators or apparent starvation (i.e. dead fledgling found with no apparent injury and an empty stomach). Raptors

accounted for a significantly higher percent of fledgling predation in 2008 (50%) than in 2007 (21%; $\chi^2 = 4.19$, $df = 1$, $P = 0.04$). Based on location and condition of recovered transmitters and fledglings, mammalian predators likely included eastern chipmunks and red squirrels, although other possible mammalian predators include all of those that depredate songbird nests in this region (see Fenske-Crawford and Niemi 1997). We identified Broad-winged Hawks, Red-tailed Hawks (*Buteo jamaicensis*), Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*A. cooperii*), and Barred Owls (*Strix varia*) as fledgling predators because we tracked transmitters to their nests (each hawk species), pellets near their nest (Barred Owl), or the actual predator (1 Broad-winged Hawk).

DISCUSSION

Our results demonstrate that annual differences in songbird nest productivity can be offset by differences in fledgling survival, and that the effects of clearcut edges on fledgling survival are not necessarily similar to their effects on nest productivity. Despite statistically significantly higher nest productivity in 2008, seasonal productivity was statistically significantly higher in 2007. Furthermore, despite no significant effects of clearcut edges on nest productivity, young clearcut edges appeared to negatively affect fledgling survival, whereas older clearcut edges appeared to positively affect fledgling survival.

Our models indicated that our entire study population declined slightly over the 2-year study period. Because growth of the interior-forest population segment was stationary, it is likely that the negative effect of young clearcut edges,

specifically on fledgling survival, accounted for the overall population decline. Our study sites were selected partly based on the presence of considerable area of young clearcuts, and ~7% of our total study area was comprised by young clearcuts. The surrounding landscape (5-km radius) at each of our study sites included considerably less young clearcut (< 3%). Therefore, we do not believe the slight negative population growth on our study sites is evidence of a negative trend at larger spatial scales.

Predation was the primary cause of both nest failure and fledgling mortality during our study. Ground nests in northern Minnesota forests are depredated primarily by mammals (Fenske-Crawford and Niemi 1997), and there was no evidence that Ovenbird nests were depredated by raptors in our study. However, 39% of fledgling predation was attributable to raptors in this study. The observed differences in nest productivity and fledgling survival between 2007 and 2008 may be explained by predator community responses to weather differences between the 2 years. Spring mammal densities are limited by winter severity, and unusually cold and extended winter conditions can considerably reduce small mammal populations (Langly and Shure 1988). In our study area, 2007 winter temperatures were near decade means (NCDC; <http://www.ncdc.noaa.gov>), as were indicators of spring phenology (i.e. dates of tree leaf-out and ice-out on area lakes). In contrast, 2008 winter temperatures were 2.5 degrees C lower than decade means (coldest of the decade), and leaf-out and ice-out were 14 and 20 days later, respectively (latest of the decade) than average. Indeed, during a nearby concurrent study in northern

Minnesota, small mammal capture rates during May and June were lower in 2008 than in 2007 (Michael Rentz, personal communication).

Although mammals were likely responsible for all nest predation, raptors accounted for 39% of fledgling predation. Because raptors prey on small mammals and songbirds, our annual differences in fledgling predation rates may be explained by prey-switching in the raptor community in response to relative local prey densities. Lower densities of small mammals following a relatively severe winter likely result in reduced predation on ground-nesting songbirds, shifting the relative availability of prey-types for raptors from small mammals to songbird fledglings (Fig. 2). Because Ovenbird nesting density at our study sites was nearly identical between 2007 and 2008, and nest productivity was significantly higher in 2008, fledgling density was likely significantly higher in 2008 than in 2007. In 2007, winter conditions were moderate, Ovenbird nest productivity was similar to that of past studies in this region (e.g. Manolis et al. 2000), and 3.8 times as many fledglings were depredated by small mammals than by raptors. Conversely, 2008 winter conditions were relatively severe, Ovenbird nest productivity was significantly higher, and fledgling predation by mammals was 11% lower, whereas fledgling predation by raptors was 21% higher than in 2007.

Schmidt and Ostfeld (2003) observed a similar system in which high acorn production was followed by an increase in rodent density, which correlated with decreased nest success for forest songbirds. Despite the negative relationship between rodent density and nest success, those authors found that songbird density

was not correlated with rodent density from previous years. They concluded that songbirds may be limited by nest predation in years of high rodent densities, but limited by adult and juvenile predation by alternative predators during years of low rodent densities (Schmidt and Ostfeld 2003). Our results support that hypothesis, suggesting that prey-switching by raptors in years of relatively low mammal abundance is a potential mechanism for their observed trends. Prey-switching as a dietary response to variation in relative prey densities is common in many North American raptors (e.g. Bednarz and Dinsmore 1985, Steenhoff and Kochert 1988). However, our sample size of 2 years is small, and additional long-term studies on breeding songbird populations are necessary to determine if our observations are common.

An alternative to the prey-switching hypothesis is that there may have been, for unknown reasons, annual variation in raptor abundance in our study area, which was the case for Schmidt and Ostfeld (2003). Although we have no data about relative raptor abundance in our study area during 2007 and 2008, the prey-switching hypothesis is further supported by our observation that depredated Ovenbird fledglings were taken to the same number of raptor nests (4) in each year, but more fledglings were taken to each raptor nest in 2008 (Streby and Andersen unpublished data).

Variation in population growth was most sensitive to variation in non-breeding survival and dependent-fledgling survival both between and within years of our study. Fledglings from nests near old clearcuts had higher survival than those

from nests near young clearcuts or those in interior mature forest. These results demonstrate that edge effects are not limited to the nesting period, and effects of edges on nests and fledglings are not necessarily similar. Many fledglings from nests near old clearcuts used old clearcuts both before and after independence from adult care, and survival within those stands was relatively high (Streby and Andersen unpublished data). Therefore, there is likely a reproductive benefit from nesting near old clearcuts in this population. In addition, proximity to areas associated with high fledgling survival may be an important factor in territory and nest site selection for ovenbirds. Selection of nest sites to optimize fledgling survival over nest survival (Hypothesis 4; Refsnider and Janzen 2010) may explain weak or absent correlations between songbird nest success and nesting habitat parameters observed in many studies (see Martin 1993 for a review).

In summary, our results indicate that nest productivity is likely an inadequate measure of seasonal productivity in Ovenbirds. We suspect that nest productivity may more accurately approximate seasonal productivity in species with longer nestling periods that produce more highly developed fledglings. However, if fledgling predators are different from nest predators, as in our study, fledgling condition may not be a good predictor of differences in fledgling survival among species. In addition, we caution that nest productivity may more poorly approximate seasonal productivity in species for which multi-brooding is common. We conclude that studies of songbird productivity that do not include direct estimates of fledgling survival can produce misleading conclusions about seasonal productivity.

Consequently, we suggest that many questions about songbird population dynamics, predator-prey relationships, and territory and nest-site selection based on nest productivity alone, may require revisiting.

Table 1. Fledged brood size and daily survival for nests and fledglings (\pm SE) for Ovenbirds nesting ≤ 100 m from clearcuts ≤ 6 years since harvest (Near YCC), nesting ≤ 100 m from clearcuts 7 – 20 years since harvest (Near OCC), and nesting > 100 m from any clearcut edge (Int. Forest) in the Chippewa National Forest, Minnesota, USA.

Population segment	Year	Nest exposure days	Nest daily survival	Fledged brood size	Fledgling exposure days	Fledgling daily survival
Near YCC	2007-2008	441	0.968 \pm 0.009	4.33 \pm 0.19	104	0.933 \pm 0.023
Near OCC	2007-2008	596	0.969 \pm 0.007	4.25 \pm 0.22	229	0.969 \pm 0.011
Int. Forest	2007-2008	1604	0.966 \pm 0.004	4.19 \pm 0.15	563	0.956 \pm 0.008
Near YCC	2007	267	0.958 \pm 0.013	4.29 \pm 0.29	63	0.927 \pm 0.030
Near OCC	2007	210	0.971 \pm 0.011	4.33 \pm 0.49	108	0.992 \pm 0.005
Int. Forest	2007	671	0.948 \pm 0.012	3.83 \pm 0.32	293	0.978 \pm 0.006
Near YCC	2008	174	0.982 \pm 0.012	4.38 \pm 0.26	41	0.937 \pm 0.026
Near OCC	2008	386	0.969 \pm 0.010	4.21 \pm 0.24	121	0.944 \pm 0.021
Int. Forest	2008	933	0.978 \pm 0.005	4.36 \pm 0.15	270	0.936 \pm 0.013

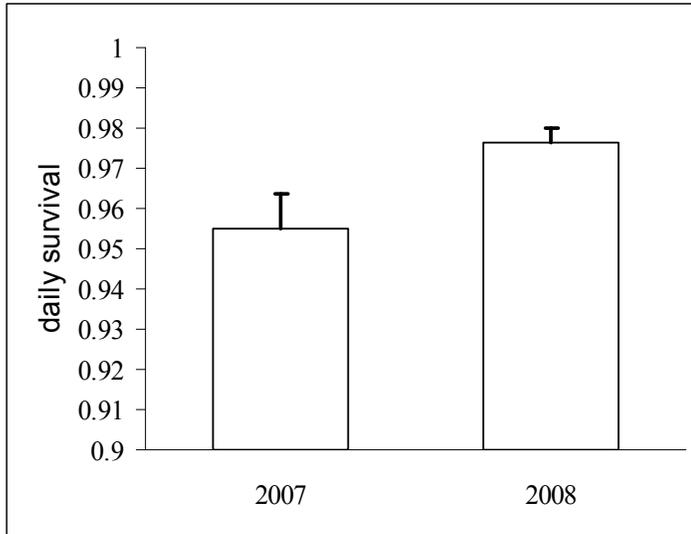
Table 2. Intrinsic rates of growth (λ) predicted by models including our direct estimates of fledgling survival (Fledgling model) and models including an estimate of constant first-year survival (Constant S_{FY} model) commonly used in previous songbird population models. Exposure days for nests and fledglings monitored, and differences in population growth rates ($\Delta\lambda$) are presented for the entire study population and population segments nesting ≤ 100 m from clearcuts ≤ 6 years since harvest (Near YCC), nesting ≤ 100 m from clearcuts 7 – 20 years since harvest (Near OCC), and nesting > 100 m from any clearcut edge (Interior Forest) in the Chippewa National Forest, Minnesota, USA.

Population Segment	Year	No. nests	Nest Productivity	λ Fledgling model (95%CI)	λ Constant S_{FY} model (95%CI)	$\Delta\lambda$
Entire population	2007 - 2008	185	0.799	0.96 (0.93 - 0.99)	1.16 (1.12 - 1.19)	0.20*
Entire population	2007	90	0.653	1.07 (1.03 - 1.10)	1.05 (1.02 - 1.08)	0.02
Entire population	2008	95	0.897	0.86 (0.84 - 0.89)	1.23 (1.19 - 1.27)	0.37*
Near YCC	2007 - 2008	26	0.848	0.80 (0.77 - 0.83)	1.19 (1.15 - 1.23)	0.39*
Near OCC	2007 - 2008	43	0.797	1.09 (1.06 - 1.13)	1.19 (1.14 - 1.22)	0.10*
Interior Forest	2007 - 2008	116	0.788	0.97 (0.94 - 1.01)	1.18 (1.14 - 1.21)	0.22*
Near YCC	2007	15	0.706	0.77 (0.75 - 0.79)	1.11 (1.08 - 1.14)	0.34*
Near OCC	2007	16	0.771	1.48 (1.41 - 1.54)	1.20 (1.15 - 1.24)	0.28*
Interior Forest	2007	59	0.593	1.01 (0.98 - 1.04)	0.99 (0.96 - 1.01)	0.02
Near YCC	2008	11	0.963	0.88 (0.84 - 0.91)	1.28 (1.23 - 1.32)	0.40*
Near OCC	2008	27	0.815	0.88 (0.85 - 0.91)	1.17 (1.13 - 1.20)	0.29*
Interior Forest	2008	57	0.913	0.87 (0.84 - 0.89)	1.26 (1.21 - 1.30)	0.39*

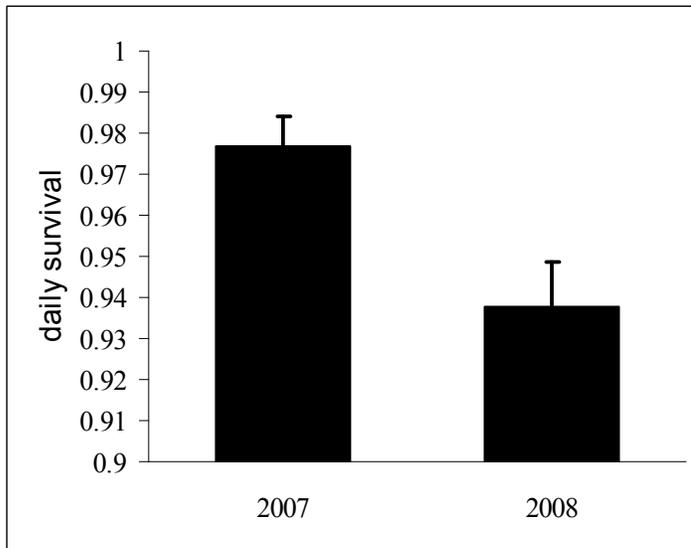
* Denotes a statistically significant difference in λ between our Fledgling model and the simpler Constant S_{FY} model at the 95% confidence level.

Figure 1. Daily survival of Ovenbird nests (A) and fledglings (B), and seasonal productivity (fledglings raised to independence per nesting female; C) during 2007 and 2008 in the Chippewa National Forest, Minnesota, USA (Error bars depict SE, all 3 are significantly different between years).

A



B



C

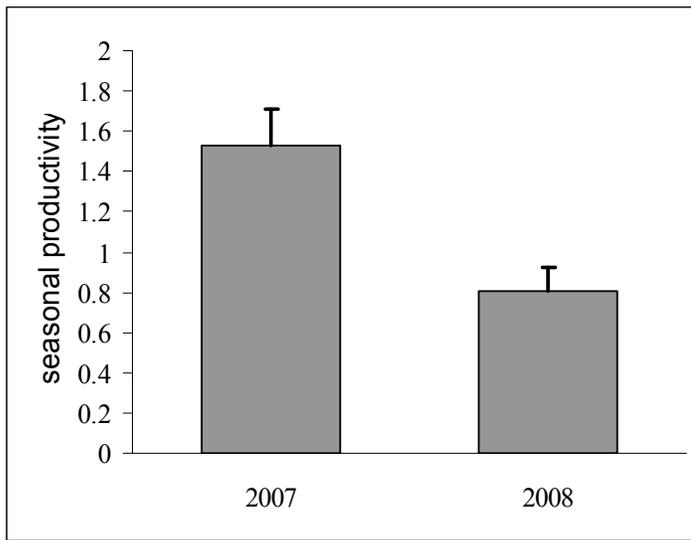
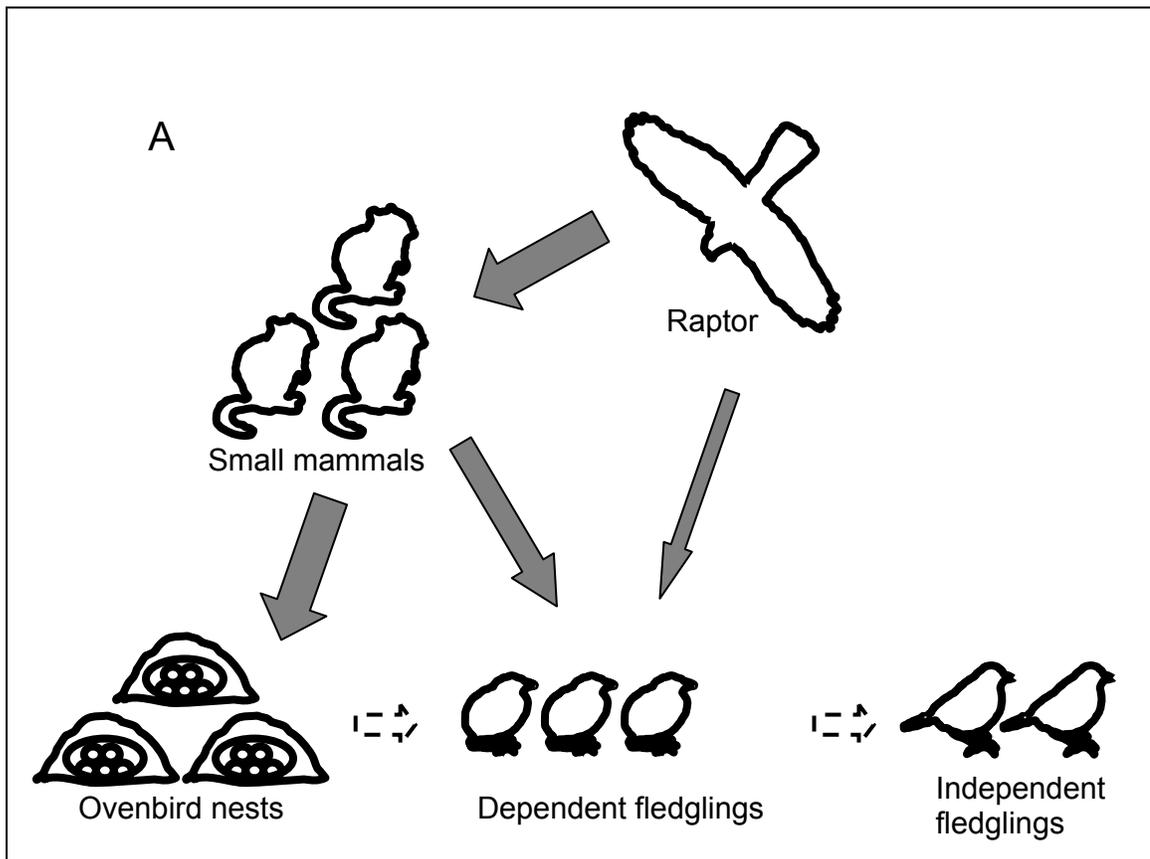
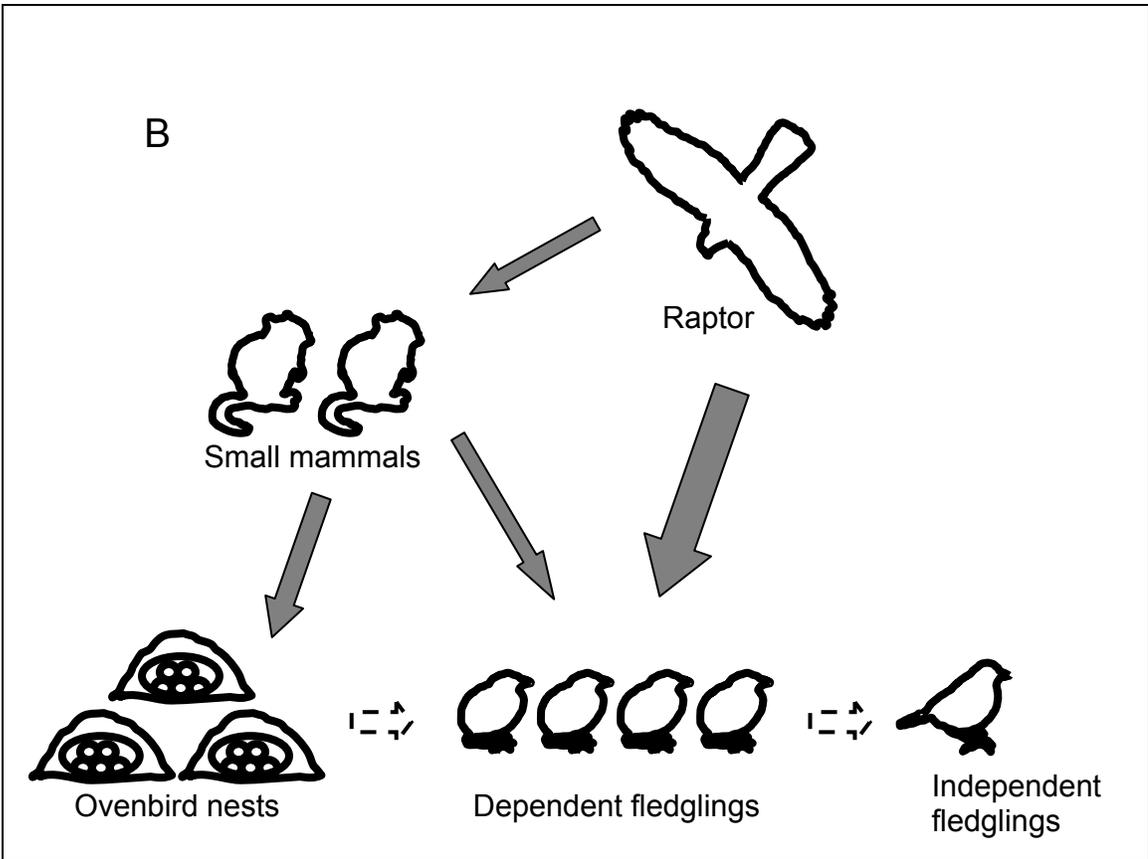


Figure 2. Model of weather-dependent predator-prey relationships among raptors, small mammals, and Ovenbirds based on observations in the Chippewa National Forest, Minnesota, USA. Moderate winter conditions (A) allow for relatively high abundance of small mammals, which prey heavily on Ovenbird nests and fledglings, while generalist raptors prey primarily on relatively abundant small mammals. Severe winter conditions (B) reduce abundance of small mammals, reducing their predation on Ovenbird nests and fledglings, thereby increasing Ovenbird nest productivity and fledgling abundance, while generalist raptors increase predation on relatively abundant fledglings.





CHAPTER 3
MOVEMENTS, COVER-TYPE SELECTION, AND SURVIVAL
OF FLEDGLING OVENBIRDS IN MANAGED DECIDUOUS
AND MIXED-CONIFEROUS FORESTS

INTRODUCTION

Compared to studies of adult songbird home-range and territory use (Vega Rivera et al. 1999, Norris and Stutchbury 2001, Fraser and Stutchbury 2004, Leonard et al. 2008) studies of fledgling songbird spatial habitat use are uncommon. Studies based on point counts and mist-netting report that many species of forest-nesting songbirds use early successional (regenerating clearcut) cover types during the post-fledgling period (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2007), the time between nesting and fall migration. These observations have fueled debate about the relative value of non-nesting cover types, specifically clearcuts, to populations of forest-nesting birds (Vitz and Rodewald 2007), because clearcuts are often associated with decreased nest productivity in adjacent mature forest (e.g. Manolis et al. 2000, Manolis et al. 2002). However, it is not known how use of non-nesting cover types is related to fitness, and some cover types may be used, even though they are negatively related to survival (e.g. ecological traps).

Point counts and mist nets are useful for detecting cover-type use by songbirds. However, point counts during the post-fledging period must rely heavily on visual detection and identification of birds, because vocalizations decline after broods fledge (Bicknell 1884). Therefore, detectability of songbirds during post-fledging point counts is likely to vary among stands that differ in vegetation density and canopy height, and comparing bird abundance among cover types is complicated when detectability is not constant (Caughley 1977). It is also difficult to use mist nets to sample statistically comparable areas for bird use in cover types that differ greatly

in canopy height, because capture rates will be biased in taller vegetation toward birds that concentrate activity near the ground. For example, it is common to sample an early successional stand with a canopy height of approximately 2.5 m using standard mist nets (e.g. Vitz and Rodewald 2007). However, to sample a statistically comparable area of mature forest with a canopy height of 25 m presents a serious logistical challenge (Marshall et al. 2003). Therefore, while point counts and mist nets can detect cover type use, their utility is limited for comparing relative use or selection between cover types with different vegetation structure.

Radio telemetry is a useful method for monitoring fledgling songbird movements and habitat use (Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002, Fink 2003, Cohen and Lindell 2004), and avoids the detectability issues associated with point counts and mist nets. Monitoring individual fledglings throughout development allows for analysis of cover-type selection using methods designed for radio telemetry data (e.g. compositional analysis [Aebischer et al. 1993]). However, few studies have integrated both space use and availability (e.g. Lang et al. 2002) or considered the relationship between habitat selection patterns and survival (King et al. 2006, Berkeley et al. 2007) for fledgling songbirds.

We used radio telemetry to study movement, cover-type selection, and survival for fledgling Ovenbirds (*Seiurus aurocapillus*) at 2 managed forested sites in north-central Minnesota. Ovenbirds nest on the ground nearly exclusively in mature forest (Van Horn and Donovan 1994), but use at least some non-nesting cover types during the post-fledging period (e.g. Marshall et al. 2003, Vitz and Rodewald 2007).

Our goal was to determine if non-nesting cover types (i.e. non-mature forest) were selected more than mature forest, and if survival was different in those cover types than in mature forest. We hypothesized that fledglings would use non-nesting cover types more than expected based on availability, and that survival within those cover types would be higher than survival in mature forest. We further hypothesized that early post-fledging movements by fledglings from nests near cover types associated with high survival would be directed toward those cover types and would be shorter than movements by fledglings from nests farther from those cover types.

METHODS

Study area

We studied Ovenbirds at 2 sites in the Chippewa National Forest (CNF), Itasca County, Minnesota. The CNF is located in the transition zone from northern hardwood to northern coniferous forest, and mature forest stands in the CNF range from entirely deciduous to entirely coniferous dominant trees. Mature forest stands at our sites were interspersed with lakes, marshes, forested wetlands, regenerating clearcut stands (9 – 15 ha even-aged stands with remnant mature oak [*Quercus* spp.], white pine [*Pinus strobus*] and occasional large snags) of various seral stages, and logging roads (unpaved roads ranging from open to entirely closed forest canopy cover). Our first site (hereafter: deciduous site) was located in the Suomi Hills region of the CNF, and mature stands at that site were comprised primarily of sugar maple (*Acer saccharum*), American basswood (*Tilia americana*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), big-tooth aspen (*P.*

grandidentata), and red maple (*A. rubrum*). Our second site (hereafter: mixed site) was located in the Cutfoot Sioux region of the CNF, and mature stands at that site ranged from nearly entirely red pine (*Pinus resinosa*) to mixed stands of approximately a 1:1 ratio of red pine to deciduous trees. Mature stands at that site had a relatively dense and heterogeneous understory of sugar maple and hazel (*Corylus* spp.).

Radio telemetry

We monitored movements and survival of fledgling Ovenbirds from monitored nests at each site during the 2007 – 2008 breeding seasons. For detailed description of nest monitoring and transmitter attachment methods, see Chapter 2. We used radio telemetry to monitor fledglings following procedures modified from Anders et al. (1998) and Vega Rivera et al. (1998). We relocated fledglings daily from 12 June to 11 August via ground-based telemetry. We first used triangulation to estimate the location of each fledgling, and then attained visual confirmation of survival or mortality by approaching estimated locations on foot. When fledglings moved beyond the range of ground-based telemetry, either under their own power or by that of a wide-ranging predator, we relocated them from the air using standard aerial telemetry procedures (Mech 1983). We recorded each nest and fledgling location with a handheld GPS unit (100 points averaged, estimated error <10 m) and noted the cover type of the occupied location. We measured distances from nests to non-nesting cover types and measured minimum daily distances travelled by

fledglings (i.e. straight-line distance between subsequent daily locations) using geographic information system (GIS) software.

Cover-type classification and delineation

We used aerial photographs and cover-type layers (U.S. Forest Service Chippewa National Forest 2007) for each study site in a GIS, and edited polygons and descriptive attributes of cover types within our study sites based on extensive ground-truthing (i.e. we visited >1,000 locations throughout our study sites and confirmed or adjusted cover type classification and delineation). We reclassified all cover types into 5 classes: (1) mature forest, (2) young clearcut, (3) older clearcut, (4) forested wetland, (5) road, and (6) lake. We classified upland cover types as mature forest (stands ≥ 50 years after harvest), young clearcut (successional stands ≤ 6 years after harvest, composed primarily of dense shrub ground cover), and older clearcut (successional stands 7 – 20 years after harvest, composed primarily of sapling aspen trees). We classified tamarack bogs and all ephemeral wet forested stands as forested wetland. We classified all open water and permanently wet open areas as lake. We did not include lake in analyses because open water was not used by fledgling Ovenbirds. Excluding lake, and depending on the position of arbitrarily delineated site boundaries, our deciduous site comprised approximately 69% mature forest, 17% older clearcut, 7% young clearcut, 5% forested wetland, and 2% road, and our mixed site comprised approximately 58% mature forest, 27% forested wetland, 8% older clearcut, 6% young clearcut, and 1% road.

Compositional analysis

We compared cover-type availability with cover-type use using COMPANA (compositional analysis) in the ADEHABITAT package (Calenge 2006) in Program R. Compositional analysis can be used to compare proportions of space available with proportions of space used by radio-tracked animals (Aebischer et al. 1993). As originally proposed, that method involves first determining a minimum convex polygon home range for each animal, and then comparing proportions of cover types within home ranges to those available within the study area. Then, the proportions of cover types available within home ranges are compared with those used by animals during individual observations.

The statistical procedure of compositional analysis is appropriate for fledgling songbird radio telemetry data. However, spatial habitat selection analyses, including the method proposed by Aebischer et al. (1993), are intended for studies of animals for which entire study areas constitute available space, and an entire home range is available for use at all times. Martin et al. (2008) demonstrated that apparent differences in spatial habitat selection between 2 female black bears (*Ursus americanus*) - 1 with a dependent cub, and 1 lone bear - were not present when considerations were made for differences in movement capability associated with the dependent cub. Those same assumptions about space availability are not valid for fledgling songbirds, for which movement capability is limited but increases throughout development. First, the assumption that a home range is selected from all space within a study area is not valid for fledglings, because there is certainly space

within a study area that is not available to a fledgling early in the post-fledging period, but becomes available as the fledging ages and movement capability increases. For the same reason, a home range, defined as the “area repeatedly traversed by an animal during a specified time period,” (Kenward 2001:208) is not applicable to space used by dependent fledgling songbirds. A home range derived from daily locations of a fledgling songbird throughout the dependent post-fledging period (from nest to independence) is almost certain to include space that was not available to the bird early in that period. In either case, considering space to be available when it actually is not will potentially bias spatial habitat selection results toward the selection of areas relatively close to nests. For songbirds that nest exclusively in 1 cover type, results may therefore be biased toward the nesting cover type. Therefore, modified methods are needed for estimating available space for animals with limited and variable movement capability so that compositional analysis can be appropriately applied. Here, we develop such a method for analyzing space use by fledgling Ovenbirds.

Daily estimated availability of cover types

Because it is unlikely that fledglings move in straight lines from 1 daily location to the next, minimum daily distance between locations on successive days does not accurately reflect movement capability. Therefore, we used the frequency distribution of minimum daily distances (grouped by 10 m intervals) for all fledglings of similar age (i.e. days after fledging) to estimate maximum movement capability for fledglings of each age (Fig. 1). We fit a quadratic regression curve to the frequency

distribution of minimum daily distance traveled from day t to day $t + 1$, and used the right intercept of that curve and the x-axis as our estimate of age-specific maximum daily movement capability (rounded up to the nearest 10 m). If the regression curve crossed the x-axis at a distance lower than the greatest minimum daily distance traveled by a fledgling, we instead used that greatest minimum daily distance as the estimated maximum movement capability. We repeated this analysis to estimate maximum movement capability for fledglings of each age from 0 – 24 days after fledge (Fig. 2). This method assumes that all fledglings of similar age are capable of traveling a similar distance. Another possible method for estimating maximum movement capability is the Bounded-count Estimator, or 2 times the highest value minus the second-highest value (Johnson et al. 2007). A linear regression of the results from our quadratic method with those from the Bounded-count Estimator indicated that the 2 methods produced nearly identical estimates ($r^2 = 0.99$, $F_{1,24} = 2381.14$, $P < 0.01$) for our dataset.

Using GIS software, we overlaid nest and fledgling locations onto the cover-type layer. We used our estimates of age-specific maximum daily movement capability as radii for circles (i.e. GIS buffers) of daily estimated availability (DEA) of space around each fledgling location. The DEA circle for age zero was drawn around the nest, and subsequent DEA circles were drawn around subsequent fledgling locations (Fig. 3). We then measured the area of each cover type within each DEA circle, and calculated proportions of available cover types. We assumed that lake was not available for use by fledgling Ovenbirds. Therefore, we removed lake contained

within a DEA circle, and recalculated proportions for the remaining available cover types. For each fledgling, we calculated the proportional availability of each cover type for the entire post-fledging period as the mean of all daily proportional availabilities. We thereby standardized cover type availability by age-specific movement capability.

Ovenbirds primarily occupy ground litter, shrubs, and low understory vegetation (Van Horn and Donovan 1994), and understory vegetation density can influence fledgling Ovenbird movements and survival (King et al. 2006). Therefore, we analyzed cover-type selection separately for the 2 study sites because of apparent differences between sites in understory vegetation density of mature forest stands. The understory of the mature forest stands at the coniferous site had large areas of dense hazel that were not present at the deciduous site. To quantify this difference for statistical comparison, we estimated understory vegetation density at 50 randomly selected points within mature forest stands at each site using a profile board method modified from MacArthur and MacArthur (1961). We used a 2 m x 0.25 m board divided into 8 squares to measure the density of vegetation at successive 25-cm intervals ranging from ground level to 2 m above ground. We viewed the board from 10 m in a randomly selected direction and estimated the percent of each square obscured by vegetation. We then turned the board 90 degrees and repeated the procedure from a second direction. We used the mean of the 16 cover estimates as the estimate of understory vegetation density at each point.

Statistical analysis

For cover-type selection analysis, we randomly selected 1 fledgling from each nest for which we tracked multiple siblings to avoid pseudoreplication (within-brood cover type use was very similar). We excluded fledglings that were depredated within 24 hr of fledging from compositional analysis because we had no data about cover-type use for those animals. We analyzed cover type selection separately for fledglings that survived through the dependent post-fledging period and for fledglings that were depredated during that period. For each fledgling group (survived or depredated) we used compositional analysis and ranked cover types from most selected to least selected and reported statistically significant (i.e. $P < 0.05$) differences in among-cover-type selection (Λ ; Aebischer et al. 1993). We also used compositional analysis to compare cover-type availability between fledglings that survived and those that were depredated. For availability analysis, we randomly removed either depredated or surviving fledglings to achieve balanced sample size for compositional analysis. We limited our comparisons of availability to the first 8 post-fledging days because few fledglings were depredated after 8 days, and availability is only comparable for fledglings of similar age.

We ranked cover-types based on mean daily survival ($1 - \text{mortalities} / \text{number of fledgling locations in a cover type}$) for fledglings using each cover type, and compared survival among cover types with χ^2 tests of independence. For each site we compared movements (i.e. distance traveled from nest) in the first 4 post-fledging days (the highest mortality period) between fledglings from nests ≤ 100 m from non-

nesting cover types associated with higher survival and fledglings from nests >100 m from those cover types. We selected that distance because 100 m is the apparent distance between nests and edges within which fledgling survival is affected by non-nesting cover types (Chapter 2). We compared distances traveled from nests using a 2-tailed *t*-test for unequal samples. We tested for directional orientation of fledgling movements using the Rayleigh test for circular uniformity with a specified mean direction (Durand and Greenwood 1958). For that analysis, we standardized the specified mean direction among fledglings by converting to North (0 degrees) the direction from each nest to the nearest non-nesting cover type associated with higher survival. We compared understory vegetation density between the 2 study sites with a 2-tailed Student's *t*-test. All tests were considered significant at the $\alpha = 0.05$ level.

RESULTS

We attached transmitters to 109 fledglings from 91 successful Ovenbird nests. After we randomly selected 1 fledgling from each brood with >1 radio-marked fledgling, removed birds that slipped out of their harness or were depredated within 1 day of fledging ($n = 23$), and removed birds that died associated with blow fly infection ($n = 8$; Streby et al. 2009) or of apparent starvation ($n = 1$), 62 fledglings from 62 nests remained for analysis (31 from each site). Of the 31 fledglings monitored at the deciduous site, 15 survived to independence and 16 were depredated during the dependent post-fledging period. Of the 31 fledglings monitored at the mixed site, 14 survived to independence and 17 were depredated during the same period.

Fledgling daily survival was different among cover types ($\chi^2 = 43.45$, $df = 4$, $P < 0.01$), and cover type-specific daily survival ranked as: (1) older clearcut ($S = 1.00$, $n = 106$), (2) forested wetland ($S = 0.98$, $n = 53$), (3) mature forest ($S = 0.96$, $n = 699$), (4) young clearcut ($S = 0.80$, $n = 5$), and (5) road ($S = 0.50$, $n = 6$), where n is the number of fledgling locations recorded in each cover type. We therefore considered the older clearcut and forested wetland cover types to be associated with higher survival, and the young clearcut and road cover types to be associated with lower survival in analysis of fledgling movements.

Mature forest understory density was significantly higher ($t = 2.44$, $df = 98$, $P = 0.02$) at the mixed site ($\bar{x} = 48.9\%$) than at the deciduous site ($\bar{x} = 39.7\%$).

Heterogeneity in mature forest understory density was also larger at the mixed site ($V = 0.76$) than at the deciduous site ($V = 0.57$). Based on that confirmation of our presumption about differences in understory vegetation density and heterogeneity, and therefore the likelihood that birds used mature forest stands differently between sites, we proceeded by conducting analyses separately for each site.

Fledgling movements

At the deciduous site, fledglings from nests ≤ 100 m from non-nesting cover types associated with higher survival moved shorter distances from nests in the early post-fledging period than did fledglings from nests > 100 m from those cover types ($t = 3.11$, $df = 24$, $P < 0.01$; Fig 4). Regardless of nest location at the deciduous site, fledglings directed movements toward the nearest non-nesting cover type associated with higher survival: fledglings from nests ≤ 100 m from a higher-survival cover type

($u = 2.91$, $df = 11$, $P < 0.01$), and from nests >100 m from a higher-survival cover type ($u = 3.57$, $df = 7$, $P < 0.01$).

At the mixed site, fledglings from nests ≤ 100 m from non-nesting cover types associated with higher survival moved similar distances to those from nests >100 m from those cover types ($t = 1.38$, $df = 16$, $P < 0.18$; Fig. 4). Fledglings did not consistently direct movements toward the nearest higher-survival non-nesting cover type at the mixed site: fledglings from nests ≤ 100 m from a higher-survival cover type ($u_{0.05,8} = 0.79$, $df = 8$, $P = 0.22$) and from nests >100 m from a higher survival cover type ($u_{0.05,18} = 0.33$, $P < 0.50$).

Cover-type selection

Fledglings that survived the post-fledging period at the deciduous site selected ($\Lambda = 0.05$, $P < 0.01$) mature forest and older clearcuts significantly more than forested wetland and road, and selected against young clearcut relative to all other cover types. Depredated fledglings at the deciduous site selected ($\Lambda = 0.11$, $P < 0.01$) mature forest and road more than older clearcut and forested wetland, and selected against young clearcut relative to all cover types except forested wetland. At the deciduous site, there were significantly different proportions of cover types available to birds that survived than to those that were depredated ($\Lambda = 0.08$, $P < 0.01$). Birds that survived had more older clearcut available, whereas birds that were depredated had more young clearcut and road available.

Fledglings that survived the post-fledging period at the mixed site selected ($\Lambda = 0.03$, $P < 0.01$) mature forest significantly more than all other cover types, which

they used relative to availability (although statistically similarly) in the order: older clearcut > forested wetland > young clearcut > road. Depredated fledglings at the mixed site also selected ($\Lambda = 0.05$, $P < 0.01$) mature forest more than all other cover types, which they used relative to availability (although statistically similarly) in the order: road > older clearcut > forested wetland > young clearcut. At the mixed site, there were significantly different proportions of cover types available to birds that survived than to those that were depredated ($\Lambda = 0.07$, $P < 0.01$). Birds that were depredated had more young clearcut available, whereas birds that survived had more of all other cover types available.

DISCUSSION

Fledgling Ovenbirds at our study sites in north-central Minnesota used all available cover types during the dependent post-fledging period, and they used those cover types non-randomly. Fledglings selected mature forest as much as or more than each non-nesting cover type during our study. However, some non-nesting cover types were selected more than others at both sites, and that pattern differed between fledglings that survived and those that were depredated at the deciduous site.

Fledgling Ovenbird survival in older clearcuts and forested wetlands was higher, and survival in young clearcuts and on roads was lower, than in mature forest. Whether fledglings used non-nesting cover types seemed to be influenced by the availability of dense areas of understory vegetation within mature forest, the only apparent difference in vegetation structure between mature-forest stands at our study sites.

Fledgling movements at the deciduous site were directed toward cover types

associated with higher survival, and distances moved differed depending on proximity of nests to those cover types. However, distance and direction of fledgling movements at the mixed site were independent of non-nesting cover type proximity.

We observed differences in availability of cover types between surviving and depredated fledgling Ovenbirds. At both study sites, depredated fledglings had more young clearcut available than did surviving fledglings in the early post-fledging period, suggesting that nesting near young clearcuts increased the probability of fledgling depredation. Conversely, surviving fledglings at the deciduous site had higher older clearcut availability than did depredated fledglings, suggesting that nesting near older clearcuts increased the probability of fledgling survival at that site.

In addition to differences in cover type availability, there were differences in cover type selection between surviving and depredated fledglings. Not only did surviving fledglings at the deciduous site have higher availability of older clearcuts, but they also used that cover type at a higher rate than others relative to availability. However those differences in older clearcut availability and selection were not apparent at the mixed site. The difference in understory vegetation density between study sites may explain the difference in cover-type selection. Based on cover-type-specific survival rates, it is likely that birds use older clearcuts and forested wetlands to reduce exposure to predation. Presumably, the higher vegetation density of those cover types provides increased cover for fledglings compared to the relatively open mature-forest understory. However, where dense and heterogeneous understory is

available, that understory vegetation may be used by fledglings similarly to older clearcuts and forested wetlands.

A key difference between surviving and depredated fledglings at both sites was the selection of roads. Roads at our sites were unpaved logging roads under open or partially closed forest canopy. Roads ranked last (mixed site) and second-to-last (deciduous site) in cover-type selection by fledglings that survived, but ranked second in selection by depredated fledglings at both sites. Roads were the least available cover type to all fledglings, and we observed only 6 fledglings on roads, and 6 others in dense vegetation beside roads within forest. However, of those 12 fledglings, 4 were tracked to hawk nests the following day. Throughout our study, we regularly observed Broad-winged Hawks (*Buteo platypterus*), Cooper's Hawks (*Accipiter cooperii*) and Sharp-shinned Hawks (*A. striatus*) coursing roads at heights of ~3-5 m, and we occasionally observed plucked feathers of passerines, woodpeckers (Picidae), and Ruffed Grouse (*Bonasa umbellus*) on those roads. Our observations suggest that remnant logging roads are common hunting grounds for some hawks, and may therefore be areas of lower survival for fledgling songbirds compared to surrounding adjacent forest.

A common criticism of habitat selection studies using individual locations of animals is that locations are likely serially autocorrelated, or not statistically independent (De Solla et al. 1999). However, autocorrelation in animal movement studies is not undesirable (De Solla et al. 1999, Martin et al. 2008). In fact, the inherent autocorrelation in such studies contains ecologically important information

that should be integrated, not removed (Martin et al. 2008). For example, the concept of a home range not only includes, but requires, autocorrelation of locations within a landscape (De Solla et al. 1999). Locations of fledgling songbirds, for which movement capability is low and increases with age, are potentially highly autocorrelated. Our analysis implicitly assumes autocorrelation of fledgling locations, and integrates that autocorrelation by allowing availability to vary with each daily location and with age-specific fledgling movement capability. A second common criticism of habitat selection studies is that estimates of availability are often defined by arbitrary study area or legal boundaries (Cooper and Millspaugh 1999). Available space should be defined using biological knowledge and information about the movement capability of the studied animals (Martin et al. 2008). Our method also accounts for that issue by standardizing availability by age-specific movement capability.

It is important to consider how fledgling movement and space use choices are made. Individual fledglings probably choose specific cover objects or perches, and those choices likely influence survival. However, at larger scales, as in the current study, fledgling space use is largely dependent on choices made by adults, especially early in the post-fledging period. Studies of fledgling movement patterns suggest that adult songbirds may have 2 movement strategies for rearing broods. Birds that rear their young within presumed nesting territories are described as following a stationary strategy, while birds that move their young from the natal territory are following a drifting strategy (Anders et al. 1998, Vega Rivera et al. 2000, White and Faaborg

2008). Birds following the drifting strategy have been reported as moving significantly farther from nests than birds following the stationary strategy (White and Faaborg 2008). However, that is circular reasoning, because a statistical difference in distance traveled between 2 groups is meaningless when the groups are first classified based on distance traveled. It is more appropriate to group birds based on an *a priori* ecologically based hypothesis, and then test for movement differences between groups. The same is true for directional orientation of fledgling movements. In our study, fledglings did not move in any distinct compass direction at either site, but movements were directed toward cover types in which survival was highest.

Proposed explanations for brood movement patterns include whether adults attempt a subsequent brood (Vega Rivera et al. 2000) and whether the birds occupy landscapes fragmented by undesirable cover types (Fink 2003). There may also be differences in movements between adult males and females when broods are split (Vega Rivera et al. 2000). Our results demonstrated that proximity of nests to brood-rearing areas associated with higher fledgling survival can influence both distance and direction of fledgling movements during the early post-fledging period. Therefore, birds with nesting territories that include, or are adjacent to, brood-rearing areas associated with higher fledgling survival (which may be non-nesting cover types) may move shorter distances than birds nesting farther from those areas. This hypothesis is supported by observations that Dicksissel (*Spiza americana*) fledgling survival is significantly correlated with high density of forbs at the nest site (Berkeley et al. 2007), Swainson's Thrush (*Catharus ustulatus*) fledglings use dense thickets

near nests within 1 to 2 days of fledging (White and Faaborg 2008), and White-throated Robins (*Turdus assimilis*) move more quickly from pasture into forest than from coffee plantation into forest, presumably due to a lack of cover in pastures (Cohen and Lindell 2004). In addition, White and Faaborg (2008) reported that some Swainson's Thrush broods were led by adults to areas of abundant fruit, suggesting that food availability, in addition to cover, may be an important factor in brood-rearing habitat selection. If future studies continue to explore relationships between spatial habitat-use patterns and fledgling survival, rather than separating the 2, they will provide more useful information about habitat requirements and population responses to management actions to better inform management decisions.

Figure 1. Minimum distances traveled by fledgling Ovenbirds within 1 day of fledging in the Chippewa National Forest, Minnesota. We estimated the maximum daily movement capability of day-zero fledglings as the intercept between the regression curve and the x-axis, rounded up to the nearest 10 m (i.e. 120 m in this case). We repeated this analysis for each fledgling age, 0 – 24 days after fledging.

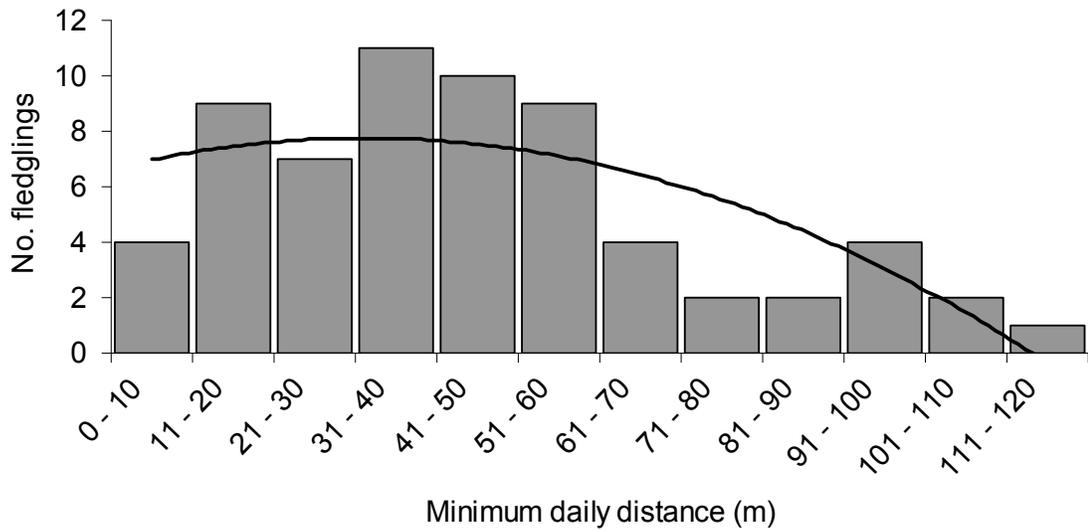


Figure 2. Age-specific maximum daily movement capability for fledgling Ovenbirds, derived by repeating the analysis from Fig. 1 for fledglings aged 0 – 24 days after fledging in the Chippewa National Forest, Minnesota.

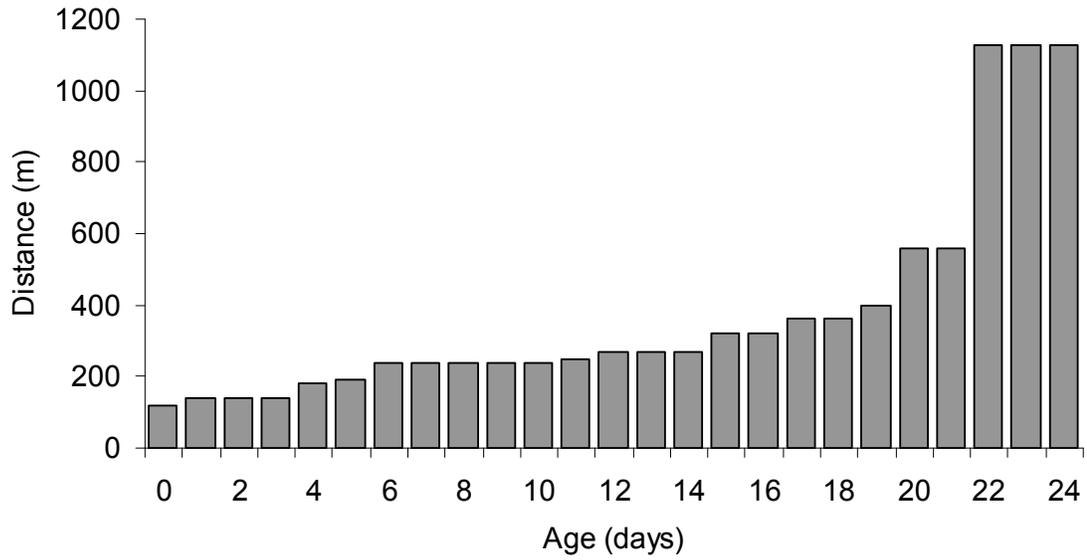
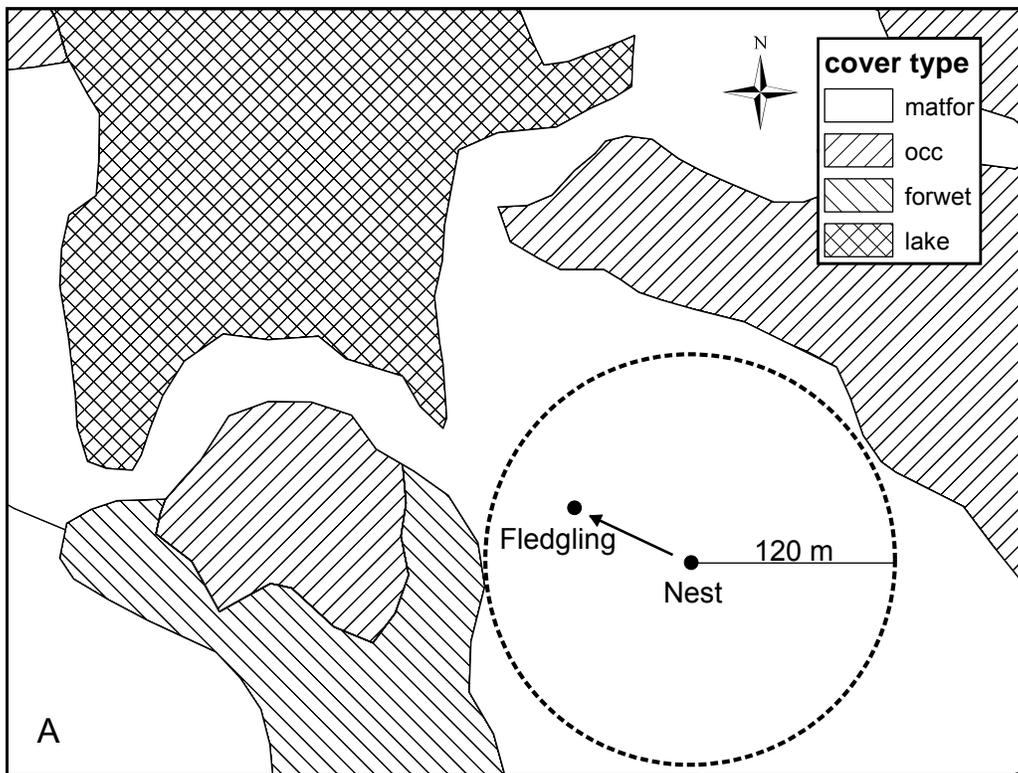


Figure 3. An example of daily estimated availability (DEA) for a fledgling Ovenbird in the Chippewa National Forest, Minnesota. Mature forest (matfor) comprised 100% of available space for this fledgling for day 1 (A). Mature forest, 7 – 20 yr-old clearcut (occ), forested wetland (forwet), and lake were within the DEA circle for day 2 (B). This process was repeated for each location during the 24-day dependent post-fledging period. Lake was removed for analysis based on the assumption that it is not used by fledgling Ovenbirds.



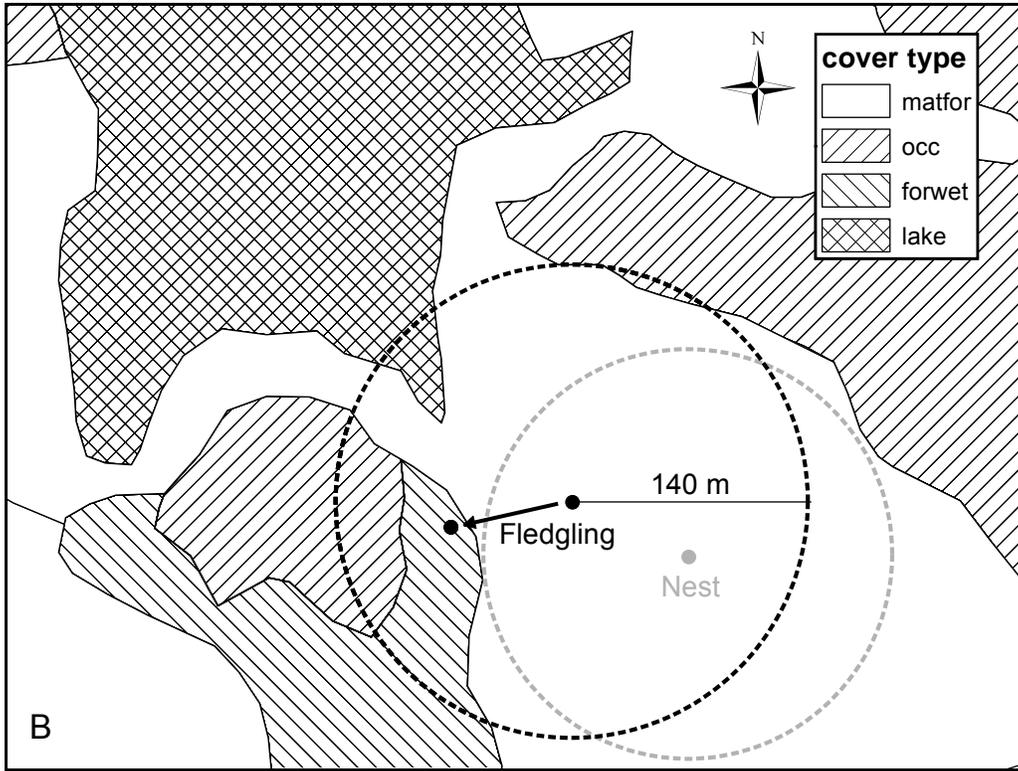
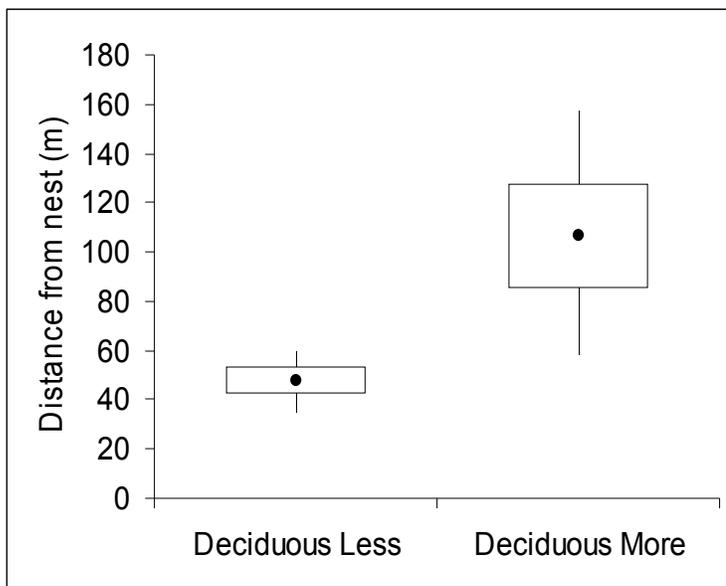
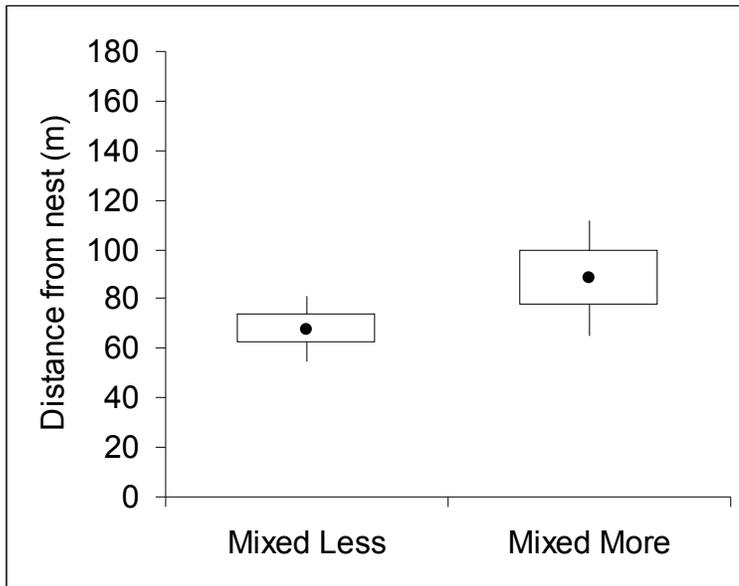


Figure 4. Distance traveled from nests by fledgling Ovenbirds 4 days (period of highest mortality) after fledging. Distances are compared between fledglings from nests ≤ 100 m from (less), and nests >100 m from (more) cover-types associated with higher survival (i.e. clearcuts 7-10 yr since harvest or forested wetlands at (A) a primarily deciduous mature forest site, and (B) a mixed conifer mature forest site in the Chippewa National Forest, Minnesota. Values are reported as mean, SE, and 95% CI. Differences are in the same direction, but statistically significant at only the deciduous forest site.

A



B



CHAPTER 4

SURVIVAL OF FLEDGLING OVENBIRDS: INFLUENCES OF HABITAT CHARACTERISTICS AT MULTIPLE SPATIAL SCALES

INTRODUCTION

Many species of songbirds that breed in North America have experienced apparent long-term population declines (Peterjohn and Sauer 1994), highlighting the importance of demographic studies that focus on identifying the factors that influence population dynamics. For most songbirds, nest success remains the most commonly estimated measure of reproductive output, and song territories delineated using point-counts or spot-matting often provide the only information available about species-habitat associations. However, nest success without consideration for fledged brood size and re-nesting probabilities can be a misleading indicator of nest productivity (Thompson et al. 2001). In addition, nesting territories delineated by mapping song perches can significantly underestimate space use by breeding adults (e.g. Hanski and Haila 1988, Anich et al. 2009) or for rearing fledged young (e.g. Anders et al. 1998, Vega Rivera et al. 1998, King et al. 2006). Studies of fledgling survival and habitat use can improve estimates of reproductive success (Anders et al. 1997) and characterizations of species-habitat relationships (King et al. 2006). Recent studies using radio telemetry to monitor survival of Mallard (*Anas platyrhynchos*) and Ovenbird (*Seiurus aurocapillus*) fledglings (mallards after independence from adult care, and dependent fledgling Ovenbirds) suggest that population growth for at least some birds is more sensitive to fledgling survival than to any other life stage (Amundson 2010, Chapter 2).

Because population growth can be very sensitive to fledgling survival, information about the post-fledging period is important for understanding population

dynamics and species habitat requirements. Although several studies have demonstrated that for many songbirds, habitat use is different during the post-fledging period than during nesting (e.g. Anders et al. 1998, Pagen et al. 2000, Marshall et al. 2003), to our knowledge, only 2 studies have directly related habitat characteristics to fledgling survival. King et al. (2006) found that fledgling Ovenbirds used areas with more dense vegetation than that of unused sites, and that fledgling survival increased significantly with density of occupied vegetation. In an analyses of stand-level space use by fledgling Ovenbirds, we found that survival was relatively low in or near recently clearcut stands and on logging roads, moderate in core mature forest, and relatively high in or near forested wetlands and mid-successional (i.e. 7 – 20 years since harvest) regenerating clearcut stands (Chapters 2 and 3). Fledgling songbird habitat use has typically been studied at 1 of those 2 scales: either micro-scale, in which habitat characteristics are sampled within several meters of fledgling locations (e.g. litter depth, food availability, vegetation density, and ground cover), or meso-scale, in which habitat characteristics are measured at larger spatial scales (e.g. cover type, patch size, and distance to edge). Few studies have incorporated habitat characteristics from multiple spatial scales, and to our knowledge, no study has compared the relative influence of habitat characteristics from multiple scales on fledgling songbird survival.

For habitat management activities to positively influence population growth, it is necessary to understand which habitat characteristics most strongly affect survival and productivity. Our objectives in the current study were to determine which habitat

characteristics, both micro- and meso-scale, influenced fledgling Ovenbird survival, and to examine the relative importance of habitat characteristics from those spatial scales to fledgling survival. Ovenbirds nest in mature forest, but commonly use non-mature forest cover types during the post-fledging period (e.g. Marshall et al. 2003, Vitz and Rodewald 2006). In our previous analyses of fledgling Ovenbird survival relative to meso-scale habitat characteristics, we found that proximity of nests to non-nesting cover types had significant effects on fledgling survival (Chapter 2), and that use of non-nesting cover types by fledglings was non-random (Chapter 3). For our current analysis we included similar meso-scale variables in addition to several micro-scale vegetation and food availability variables sampled at fledgling locations.

Fledgling songbirds are most vulnerable to predation in the few days immediately after leaving the nest (Ricklefs 1968, Anders et al. 1997, Berkeley et al. 2007), and fledgling Ovenbirds are primarily dependent on food provided by adults during that period (Streby and Andersen unpublished data). Therefore, among micro-scale variables, we expected food availability to have little influence on fledgling survival, but ground cover and understory vegetation density to be important to fledgling survival during the early post-fledging period. However, because most fledgling songbird mortalities are from predation (Sullivan 1989, Anders et al. 1997, Cohen and Lindell 2004, King et al. 2006), and because densities and home-ranges of mammalian and avian predators vary at relatively large spatial scales, we expected meso-scale variables to better explain fledgling survival than micro-scale variables.

METHODS

Study area

We studied fledgling Ovenbirds at 2 sites in the Chippewa National Forest (CNF), Itasca County, Minnesota. The CNF is located in the transition zone from northern hardwood to northern conifer forest. Both of our sites were characterized by extensive mature forest interspersed with forested wetlands, tamarack (*Larix laricina*) bogs, lakes, and successional regenerating clearcuts ranging from 2 – 20 years since harvest. At our sites, mature forest stands (in which Ovenbirds nested) were comprised primarily of sugar maple (*Acer saccharum*), American basswood (*Tilia americana*), red pine (*Pinus resinosa*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), big-tooth aspen (*P. grandidentata*), and red maple (*A. rubrum*), with a patchy understory of sugar maple, red maple, and hazel (*Corylus* spp.).

Radio telemetry

We used radio telemetry to monitor habitat use and survival of fledgling Ovenbirds from nests we monitored during the 2007 – 2008 breeding seasons. For a detailed description of nest monitoring and transmitter attachment methods, see Chapter 2. We attached a transmitter to ≥ 1 fledgling per successful nest, and we relocated fledglings daily from 12 June to 11 August via ground-based telemetry. We first used triangulation to estimate the location of each fledgling, and then attained visual confirmation of survival or mortality. When fledglings moved beyond the range of ground-based telemetry, either under their own power or by that of a wide-

ranging predator, we relocated them from the air using standard aerial telemetry procedures (Mech 1983). We recorded each nest and fledgling location with a handheld GPS unit (100 points averaged, estimated error <10 m) and noted the cover type of the occupied stand.

Micro-scale habitat parameters

We sampled vegetation characteristics and invertebrate abundance and activity at fledgling locations every fourth day, starting with the first day, after fledglings left the nest. We centered a 1-m radius plot on each fledgling location, within which we visually estimated percent ground cover (below 0.25 m) by vegetation (GVEG) and by woody debris (GWOOD). In addition, we measured litter depth (LITDEP) at 3 locations within each plot, and used the mean of those measurements for analysis.

We estimated vegetation density, or lateral cover (LATCOV), around each plot using a profile board method modified from MacArthur and MacArthur (1961). We divided a 2 x 0.25-m board into 8, 0.25 x 0.25-m squares, and painted the squares alternately orange and white. One observer held the board vertically at a fledgling location, while a second observer viewed the board from a distance of 10 m in a randomly selected direction and estimated the percent of each square obscured by vegetation (random directions were selected consecutively from a list generated by computer). We then turned the board 90 degrees to the right and repeated the process. We used the mean of the 16 estimates (8 from each direction) as a single estimate of lateral cover around each fledgling location.

Ovenbirds are insectivores and forage primarily on the ground (VanHorne and Donovan 1994). Therefore, we sampled food availability in terms of abundance and activity of ground invertebrates using 2 methods at each fledgling location plot. First, we collected leaf litter samples covering 0.25 m², down to the humus layer, from each plot. We sifted through each litter sample immediately following collection, removed all visible invertebrates, and stored them in 50% ethanol solution. Second, we sampled ground invertebrate activity in each plot using a pitfall trap. For each pitfall trap, we used a 473-ml plastic cup, with ~50 ml of 50% ethanol solution, buried such that the top of the cup was flush with the ground surface. We deployed each pitfall trap immediately following fledgling observation, collected trap contents after 24 hours, and stored them in a 50% ethanol solution. We counted and identified (to Order) invertebrates from each leaf litter and pitfall sample, dried each sample for 24 hr in a drying oven, and measured dry mass to within 0.0001 g. We used dry mass of invertebrates collected from litter samples as an estimate of micro-scale invertebrate abundance (INVABUN), and dry mass of invertebrates captured in pitfall traps as an estimate of micro-scale invertebrate activity (INVACT).

We did not collect micro-scale data at nest locations within the 24-hr period preceding fledging for 2 reasons; because the fledge date is not precisely predictable (Chapter 1) and to avoid forcing the brood to fledge prematurely due to data collection activities around the nest. Therefore, because our survival model paired habitat data from the first day of a 4-day period with fledgling fates from that period, we could not include birds that died in the first 24 hours after fledging in analysis.

Meso-scale habitat parameters

At each fledgling location, we recorded the cover type (e.g. mature forest, forested wetland, logging road, etc.) occupied by the fledgling and the distance between fledgling locations and each non-nesting cover type. We defined stands ≤ 6 yr since harvest as young clearcuts, and stands 7 – 20 yr since harvest as older clearcuts. Regenerating clearcuts in this region tend to transition from low shrub-dominated (primarily *Rubus*, *Salix*, and *Corylus*) stands to stands dominated by fast-growing aspen saplings around 5 – 7 years after harvest. We defined all forested stands in which the ground was ephemerally or permanently covered with water (e.g. black ash stands, tamarack bogs, and alder thickets) as forested wetlands. Based on cover type-specific Ovenbird fledgling survival estimates from our previous analyses (Chapter 3), we grouped older clearcuts and forested wetlands as high-survival cover types (HIGHCOV), and we grouped young clearcuts and logging roads as low-survival cover types (LOWCOV). We used GIS software to measure the minimum distance between each fledgling location and each of the cover-type categories. We recorded distance to edge as 0 if a fledgling was at the edge of or using any of the non-nesting cover types.

Results from our previous meso-scale analyses suggested that logging roads (unpaved roads ranging from open to entirely closed forest canopy cover) are associated with high mortality for fledgling Ovenbirds (Chapter 2). However, our method of observing fledglings once per day likely under-represented fledgling use of the relatively small area of logging roads. Therefore, for our current analysis we

created a binomial meso-scale variable called road crossing (ROADX), in which we used daily locations to determine if a fledgling crossed a logging road at least once during the 4-day interval between vegetation samples. For each fledgling, we gave a 4-day interval a value of 1 if we recorded any 2 locations within that interval on opposite sides of a logging road, and a value of 0 if not.

Statistical analysis

Before analysis, we tested for correlations between variables for which we expected relationships. We expected LITDEP to have a significant positive correlation with INVABUN and INVACT because those variables are commonly reported as highly correlated (e.g. Haskell 2000). In addition, we expected a negative correlation between our LOWCOV and ROADX variables. Because young clearcuts are usually associated with logging roads at our study sites, it is reasonable to expect that fledglings closer to young clearcuts and logging roads were more likely to cross logging roads than fledglings farther from those cover types.

We used the logistic exposure method (Shaffer 2004) to model fledgling survival with both meso- and micro-scale explanatory variables. The logistic exposure method was designed to estimate daily survival of nests monitored at intervals, and to examine the explanatory value of categorical and continuous variables on variation in daily survival of nests. The logistic exposure method is therefore convenient and appropriate for the analysis of similarly collected data about fledgling survival. We used survival (i.e. whether a fledgling survived a 4-day interval) as the response variable, and the meso- and micro-scale habitat data we

collected on the first day of each interval as explanatory variables. We developed a set of a priori candidate models based on biologically relevant combinations of our variables. We developed a set of 19 candidate models that included a constant survival model, 7 combinations of meso-scale variables, and 11 combinations of micro-scale variables.

We used Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002) to rank candidate models. The best-supported model and all models with ΔAIC_c values <2.0 were considered competing models. We did not consider models with one additional parameter, but otherwise identical to the best-supported model, to be competing models regardless of ΔAIC_c values, because the additional parameter in such models is generally uninformative (Arnold 2010). We included each variable in the same number of candidate models, and we used the cumulative Akaike weights (w ; Burnham and Anderson 2002) of all models that included a given variable to identify the relative value of that variable for explaining variation in fledgling survival.

RESULTS

We attached transmitters to 109 fledglings from 91 successful Ovenbird nests. We randomly selected 1 fledgling from each brood for which we radio-marked >1 fledgling to avoid pseudoreplication (Hurlbert 1984), removed from analysis birds that slipped out of their harness or were depredated within 1 day of fledging, and removed birds that died due to blow fly infection ($n = 8$; Streby et al. 2009) or of apparent starvation due to a Brown-headed Cowbird (*Molothrus ater*) brood mate (n

= 1). We included the remaining 62 fledglings from 62 nests in analysis. Because 53 (94.6%) of all (including multiply marked broods and blowfly-infected fledglings) fledgling Ovenbird mortalities we observed occurred during the first 16 days after fledging, we limited our survival analysis to those 16 days. Furthermore, fledgling Ovenbirds transition from primarily hopping along the ground and low vegetation and relying entirely on adult care for food, to flying short distances and occasionally gathering their own food approximately 5 – 8 days after fledging. Therefore, because a fledgling's ability to elude a predator and gather food appeared to increase throughout the study period, we modeled fledgling survival separately for post-fledging days 1 – 8 and 9 – 16.

We recorded 533 daily locations for 62 fledglings during the 16-day period (or shorter for fledglings that did not survive 16 days) we studied, and collected micro-scale habitat data at 175 of those locations. There were no significant correlations between any of our explanatory variables. Of particular interest was the lack of correlation between LITDEP and INVABUN ($r^2 < 0.01$, $F_{2,174} < 0.50$, $P = 0.48$), between LITDEP and INVACT ($r^2 < 0.01$, $F_{2,174} < 0.93$, $P = 0.34$), and between ROADX and LOWCOV ($r^2 < 0.01$, $F_{2,174} < 0.01$, $P = 0.98$), all of which we expected to be highly correlated.

Ovenbird fledgling survival during the first 8 post-fledging days was best explained by the model including only the ROADX variable. Fledglings that crossed a logging road at least once in the first 8 days ($n = 35$) were 50% less likely to survive ($S = 0.31$) that period than fledglings for which there was no evidence of crossing a

logging road ($n = 27$, $S = 0.62$; Fig. 1). Cumulative weights indicated that ROADX was the strongest meso-scale predictor of Ovenbird fledgling survival ($w = 0.67$), followed by LOWCOV ($w = 0.43$), which had a negative effect on fledgling survival, and HIGHCOV ($w = 0.40$), which had a positive effect on fledgling survival.

All models that included meso-scale variables outperformed all models that included micro-scale variables in explaining variation in survival during days. Among the micro-scale variables, the ground cover and understory vegetation density variables had the highest cumulative weights; GVEG ($w = 0.06$), GWOOD ($w = 0.06$), and PROFILE ($w = 0.05$). However, cumulative weights of each micro-scale variable were small compared to cumulative weights of each meso-scale variable during the first 8 post-fledging days.

Fledgling survival during days 9 – 16 after fledging was also best explained by the model that included only the ROADX variable. During that period, fledglings that crossed a logging road at least once were 34% less likely to survive ($S = 0.58$) through day 16 than fledglings that did not cross a road ($S = 0.89$). Cumulative weights indicated that ROADX was the strongest ($w = 0.52$) meso-scale predictor of Ovenbird fledgling survival, followed by HIGHCOV ($w = 0.31$), which had a positive effect on fledgling survival, and LOWCOV ($w = 0.27$), which had a negative effect on fledgling survival during days 9 – 16.

The model that included only the PROFILE variable was among the competing models of fledgling survival during days 9 – 16 after fledging. Cumulative weights indicated that PROFILE was the strongest ($w = 0.22$) micro-scale

variable for explaining Ovenbird fledgling survival during this period, followed by INVACT ($w = 0.14$) and INVABUN ($w = 0.12$). Although micro-scale variables received more cumulative weight in the 9 – 16 day period models than the 1 – 8 day period models, those weights were again smaller than cumulative weights of each meso-scale variable.

DISCUSSION

Micro-scale habitat characteristics, such as vegetation density and ground cover, can influence fledgling Ovenbird survival (King et al. 2006). Among only the micro-scale variables in our study, ground cover by vegetation and by woody debris best explained fledgling survival during the first 8 post-fledging days, and understory vegetation density best explained fledgling survival during days 9 – 16. Those results are consistent with the behavior of fledgling Ovenbirds we observed during those periods (Streby and Andersen unpublished data). During the first 8 days after fledging, fledglings were most commonly observed on the ground, often under woody debris, and their exact locations were sometimes not known until adults arrived to feed them. During days 9 – 16, observations of fledglings perching and flying through understory trees and shrubs were more common.

Although micro-scale habitat characteristics may influence fledgling Ovenbird survival, our results suggest that meso-scale habitat characteristics are much more important. In our study, fledgling use of logging roads and fledgling proximity to non-nesting cover types had a substantially larger influence on survival than vegetation density, ground cover, or food availability in the immediate vicinity of

fledglings. Crossing a logging road (ROADX) or being within close proximity of a logging road or young clearcut (LOWCOV) each negatively affected fledgling survival during our study, whereas being within close proximity of or using older clearcuts or forested wetlands (HIGHCOV) positively affected survival. Our finding that logging roads were the habitat feature with the greatest influence on fledgling survival is especially important because logging roads had no apparent effect on Ovenbird nest productivity during our study (Streby and Andersen unpublished data) or that of King and Degraff (2002). This result exemplifies the importance of including the post-fledging period when determining the effects of habitat characteristics on songbird population productivity.

We expected our ROADX and LOWCOV variables to be significantly negatively correlated, but we found no correlation between those variables. Many birds fledged from nests ≤ 5 m from logging roads, but moved away from the roads in the first few days after fledging without crossing them. Therefore, our results suggest that although the use of mature forest near young clearcuts and logging roads negatively affects fledgling Ovenbird survival, the specific use of logging roads by fledglings presents a separate and greater risk of mortality. This may be because hawks (*Buteo* spp. and *Accipiter* spp.) regularly course logging roads throughout our study sites (Chapter 3), and a fledgling Ovenbird is probably in the greatest danger of detection by a road-coursing hawk only when the fledgling is in the open space of the road. We also expected litter depth to be highly correlated with invertebrate activity and abundance, which has been reported in previous studies (e.g. Haskell 2000).

However, litter depth was not significantly correlated with invertebrate counts or dry mass from litter samples or pitfall samples collected during our study. We therefore caution that litter depth may not be reliable as an index of food availability for ground-foraging insectivorous birds in mixed northern-hardwood conifer forests.

We did not include nestling mass as an explanatory variable in our survival analysis. Nestling mass has been hypothesized to be an index of nestling condition, and relative mass has been investigated for its potential influence on fledgling survival (e.g. Anders et al. 1997) and movements (e.g. Vitz and Rodewald 2010). When we weighed nestlings during banding and transmitter attachment, we observed that the mass of individual Ovenbird nestlings varied up to 8.0% depending on whether the nestling defecated before weighing (Streby and Andersen unpublished data). Because of this large short-term variation in nestling mass caused by frequent feeding and defecating, we caution that nestling mass may not be a reliable indicator of nestling condition in small birds. This phenomenon may contribute to findings that nestling mass often correlates weakly (Vitz and Rodewald 2010) or not at all (Anders et al. 1997) with fledgling survival and movement capabilities.

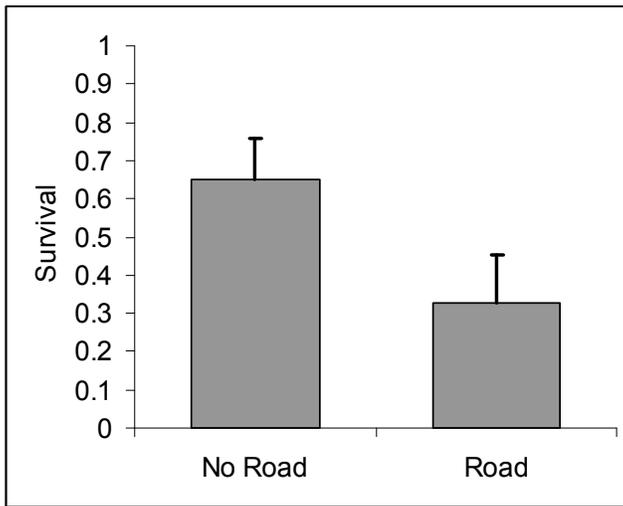
Management implications

Our finding that meso-scale habitat characteristics have a greater influence on fledgling Ovenbird survival than do micro-scale habitat characteristics, suggests that common forest management practices (usually conducted at the stand level) have larger effects on Ovenbird fledgling survival than natural smaller-scale variation in habitat characteristics. Agencies and landowners are not likely to make management

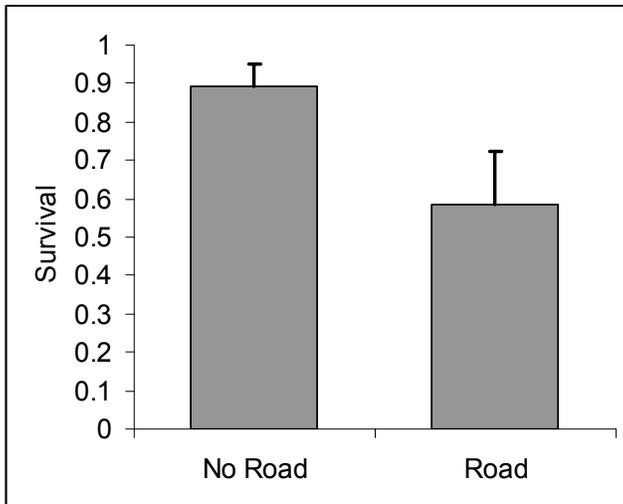
decisions based solely on Ovenbird habitat needs. However, if remnant logging roads present areas of high predation for Ovenbird fledglings, they likely have similar effects on other songbirds as well as game birds such as American Woodcock (*Scolopax minor*) and Ruffed Grouse (*Bonasa umbellus*). This may be important to investigate, because Ruffed Grouse habitat management often includes creation and maintenance of trails (e.g. Berner and Gysel 1969) and we observed plucked grouse feathers on logging roads during our study. Logging roads, many of which extend for kilometers through mature forest, and some of which remain unused for decades, are very slow to regenerate because the soil is greatly compacted by logging trucks and other machinery. We suggest that assisted revegetation of abandoned logging roads, in the form of tilling soil and possibly seeding, could positively impact populations of ground dwelling birds in primarily forested landscapes.

Figure 1. Estimated probabilities of survival for fledgling Ovenbirds that crossed at least 1 logging road (Road) or did not cross a logging road (No Road) during (A) post-fledging days 1 – 8, and (B) post-fledging days 9 – 16, during 2007 and 2008 in the Chippewa National Forest, Minnesota, USA. Values are probabilities \pm SE of surviving each 8-day period.

A



B



CHAPTER 5

EARLY SUCCESSIONAL FOREST USE

BY POST-FLEDGING MATURE-FOREST SONGBIRDS

IN MANAGED MIXED NORTHERN HARDWOOD-CONIFER FORESTS

INTRODUCTION

Forest harvest (e.g. clearcutting) in predominantly forested landscapes creates temporary cover-type heterogeneity, which is accompanied by increased breeding bird diversity (e.g. Conner and Adkisson 1975). However, there is an ongoing debate about the effects of clearcuts on adjacent mature-forest bird communities. In addition to the obvious temporary loss of nesting habitat, negative effects of clearcuts on nesting success in adjacent mature forest appear to be common (Manolis et al. 2000). However, many studies detecting increased predation near clearcut edges have been conducted using artificial nests, and the consistency of clearcut edge effects on natural nests is unclear (e.g. Hanski et al. 1996, Vitz 2003, Chapter 2). In addition, when present in natural populations, edge effects on nest success may sometimes be compensated for by increased brood size (Flaspohler et al. 2001a). In contrast, there are relatively pervasive and often strong effects of edges and forest patch size on nesting success in predominantly agricultural landscapes (e.g. Robinson et al. 1995, Hoover et al. 1995). Further confounding the issue, studies using mist nets, point counts, and radio telemetry have found that adult and hatch-year birds of many mature-forest species use regenerating clearcuts during the post-fledging period (i.e. after young leave nests, but before migration; Anders et al. 1998, Pagen et al. 2000, Marshall et al. 2003, Vega Rivera et al. 2003, Fink 2003, Vitz and Rodewald 2006). During the post-fledging period, songbird habitat use can be substantially different from that used for nesting (e.g. Anders et al. 1998, King et al. 2006), birds can be exposed to additional predator species (e.g. Streby et al. 2008), and mortality of

young birds can be high (Ricklefs 1968, Anders et al. 1998, King et al. 2006), especially during the first few days after leaving the nest. Therefore, songbird survival and habitat associations during the post-fledging period may be as important to managers and conservationists as parameters associated solely with nest productivity (e.g. Anders et al. 1998, King et al. 2006).

An important first step in understanding the potential influence of clearcuts on mature-forest birds during the post-fledging period is to determine which species, and to what degree, use clearcuts after nesting. Studies using mist-nets to sample bird use of clearcuts in Missouri (Pagen et al. 2000), Virginia and West Virginia (Marshall et al. 2003), and Ohio (Vitz and Rodewald 2006) have each reported that adult and hatch-year mature forest-nesting birds use clearcuts during the post-fledging period. In each of those studies, most mature-forest bird captures were of a relatively small number of species, suggesting that clearcuts are not used similarly by all mature-forest birds. However, differences in capture rates among species may also reflect differences in population abundance or productivity. Of mature-forest species commonly captured in Missouri clearcuts, few were captured during the nesting period, but capture rates of some species, such as Ovenbird (*Seiurus aurocapillus*) and Red-eyed Vireo (*Vireo olivaceus*) increased significantly during the post-fledging period (Pagen et al. 2000). In Virginia and West Virginia, adult Worm-eating Warblers (*Helmitheros vermivorus*) banded in entirely mature forest territories were later captured in clearcuts, some with dependent fledglings (Marshall et al. 2003). During the post-fledging period in Ohio, mature-forest birds used clearcut interior

more than edges (Vitz and Rodewald 2006), and that use was generally associated more with vegetation structure than fruit availability (Vitz and Rodewald 2007).

Previous studies of clearcut use by mature forest-nesting birds have focused on spatial variables, such as comparing capture rates between mature forest and clearcuts, or among areas within clearcuts, or among clearcuts differing in total area. An overlooked and potentially important component of post-fledging use of clearcuts by mature forest birds is time. For example, when does clearcut use begin relative to completion of nesting, and how does clearcut use vary throughout the post-fledging period? Although each of the aforementioned mist-netting studies reports capture rates during a time range that the authors define as the post-fledging period, none directly compares the timing of captures to the nesting phenology of local populations. Differences in capture rates between studies may reflect differences in periods sampled, relative to breeding phenology. For example, 71% of mature forest birds captured by Vitz and Rodewald (2006) in south-east Ohio were hatch-year birds, compared to only 29% of birds captured by Marshall et al. (2003) in neighboring West Virginia and Virginia. It is possible that there were large differences in productivity or habitat selection between forest bird communities in those studies. However, Vitz and Rodewald (2006) sampled clearcuts through 16 August, whereas Marshall et al. (2003) ceased sampling on 31 July. If clearcut use by hatch-year mature-forest birds increases throughout the post-fledging period - a reasonable hypothesis considering abundance and movement capabilities of hatch-year birds both increase throughout the post-fledging period - the difference between

those studies may be an artifact of sampling design. However, neither Vitz and Rodewald (2006) nor Marshall et al. (2003) reported temporal variation in capture rates during the sampling period. Furthermore, the relatively dense vegetation cover and abundance of food resources have been hypothesized to potentially increase survival of birds that use clearcuts during the post-fledging period. Considering the relatively high predation risk to recently fledged birds (e.g. Ricklefs 1963, Anders et al. 1997, King et al. 2006), it is important to make a distinction between clearcut use by dependent (under adult care) and independent hatch-year birds of mature forest-nesting species.

We studied use of clearcuts by birds in the managed Chippewa National Forest of north-central Minnesota. The mixed northern hardwood-conifer forests of northern Minnesota, Wisconsin, Michigan, and south-central Canada host some of the highest densities of forest-nesting songbirds in North America. However, to our knowledge, there are no published studies of clearcut use by songbirds during the post-fledging period in this region. Our first objective was to determine if mature-forest birds in this region follow the commonly reported pattern of clearcut use during the time between nesting and the onset of fall migration. We hypothesized that adult and hatch-year birds of many mature-forest species would use clearcuts during the post-fledging period. In addition, we were specifically interested in when clearcuts would be used by hatch-year Ovenbirds banded as nestlings in mature forest adjacent to clearcuts. We hypothesized that we would capture those and other hatch-year birds

early in the post-fledging period and at a constant or increasing rate throughout the post-fledging period.

METHODS

Mist netting

We used mist nets and sampled bird use of 6 early successional, regenerating clearcuts ranging from 2 – 10 years after harvest and from 9 – 15 ha in area. Sampled stands were located within primarily mature forest areas of the Chippewa National Forest in north-central Minnesota. For a detailed description of the study sites, see Chapter 2. The clearcuts we sampled ranged in vegetation composition from primarily red raspberry (*Rubus* sp.) shrubs and aspen (*Populus* spp.) saplings of 1 – 2 m in the youngest stands to primarily aspen saplings of 4 – 6 m interspersed with red maple (*Acer rubrum*), hazel (*Corylus* spp.), pussy willow (*Salix discolor*), and other less abundant trees and shrubs in the 10 year-old stands. Mean canopy height in the sampled stands, measured during 2008, ranged from 1.8 m to 5.1 m.

Between 28 June and 4 July each year, we cleared (during 2006) and re-cleared (during 2007 – 2009) vegetation to create net lanes approximately 1.5 m wide and 15 m long, and set pairs (2 nets on 3 poles) of 12-m, 4-shelf mist-nets (32 mm mesh) at 3 locations within each clearcut: (1) ≤ 25 m from mature forest edge, (2) 26 – 50 m from mature forest edge, and (3) > 50 m from mature forest edge. We generally oriented each pair of nets such that 1 net per pair was approximately perpendicular to mature forest edge, and 1 was approximately parallel to edge. Each year, we sampled clearcuts for 8 weeks between 4 July – 28 August, and opened nets 15 – 30 minutes

before sunrise and closed them between 0830 and 1000 or when conditions such as rain or high winds potentially placed undue stress on birds.

We sampled 2 clearcuts each day, and sampled each clearcut twice per week for a total of 16 netting occasions in each clearcut each year. We monitored nets at intervals ≤ 30 minutes and removed entangled birds. We carried birds in soft cloth bags to a bird-banding station located centrally to the 2 sampled clearcuts (< 200 m from nets). We identified the species, sex, and age of each bird (weighing and measuring when necessary) according to Pyle (1997) and banded all birds except Ruby-throated Hummingbird (*Archilocus colubris*) using standard aluminum U.S. Geological Survey legbands. We released adult birds from the banding station immediately following banding and carried hatch-year birds and females in breeding condition (i.e. with a brood patch) back for release < 25 m from the point of capture. We returned hatch-year birds to near the point of capture in case they were dependent on adult care, and may otherwise not be found by adults. We returned females in breeding condition to near the point of capture to minimize time away from the nest in case they were incubating a late clutch. During all netting, when a bird was captured more than once during 1 day, we included only the first capture in analysis to optimize the utility of our captures as a measure of abundance by reducing the influence of localized individual activity. We standardized capture rates by captures per 100 net hours for temporal comparisons.

Nesting cover type classification

We classified species based on nesting cover-type associations as mature-forest birds (those that nest nearly exclusively in mature forest), early-successional birds (those that nest nearly exclusively in early successional forest or shrubby areas) and forest-generalist birds (those that commonly nest in both mature forest and early successional forest, or nest predominantly in edge vegetation or lowland forested wetland; Table 1). We initially classified birds based on nesting cover-type associations used in previous, similar studies (i.e. Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006). However, our observations suggested that multiple species categorized in those studies as mature forest-nesting species nested in the clearcuts we sampled (Table 2). While clearing net lanes and erecting mist-nets during late June of each study year, we opportunistically searched the surrounding vegetation for nests of early successional species (e.g. Golden-winged Warbler [*Vermivora chrysoptera*]) of management concern. During those searches, we observed nests of birds commonly considered to be mature-forest species. We found 7 Rose-breasted Grosbeak (*Pheucticus ludovicianus*) nests, 2 Veery (*Catharus fuscescens*) nests, 2 Red-eyed Vireo nests, a Scarlet Tanager (*Piranga olivacea*) nest, and an American Robin (*Turdus migratorius*) nest, each within 20 m of our nets. Those species were considered mature-forest birds by 1 or more of Pagen et al. (2000), Marshall et al. (2003), and Vitz and Rodewald (2006). Each of those species is described as sometimes or commonly nesting in early-successional forest (Poole 2005) and we observed nests of all of those species, except Veery, in mature forest

during a concurrent nest-monitoring study. We therefore classified all 5 of those species as forest generalists.

Because we observed nests of species often categorized as mature-forest birds in our clearcuts, we expanded our study in 2009, and used mist nets to sample 4 of the original 6 clearcuts during the nesting season, 22 May – 3 July. We used the same methods for mist netting during that period, except that we returned female birds to <25 m from capture locations to minimize time they spent away from active nests.

Nestling banding

During 2006 – 2008 we searched for and monitored Ovenbird nests in mature forest adjacent to the clearcuts we sampled, and banded nestlings before they fledged. For a detailed description of nest monitoring and nestling banding methods, see Chapter 2.

RESULTS

During 4 years and 9,376 net hours during the post-fledging period, we captured 4,556 birds, of which 1,746 (38.3%) were of 28 mature-forest species, 1,659 (36.4%) were of 18 early successional species, and 1,151 (25.3%) were of 18 species that we classified as forest generalist species. Of mature-forest bird captures, 75.5% were of 4 species: Ovenbird ($n = 660$), American Redstart (*Setophaga ruticilla*; $n = 315$), Least Flycatcher (*Empidonax minimus*; $n = 226$), and Black-and-white Warbler (*Miniotilta varia*; $n = 118$). The remaining 24.5% of mature-forest bird captures were of 24 species for which captures ranged from 2 – 67 ($\bar{x} = 17.8$; Table 1).

During 2006 – 2008, we banded 424 nestling Ovenbirds that subsequently fledged from nests located 5 – 920 m from the nearest clearcut where we captured birds with mist nets. The mean fledge date for those birds was 21 June \pm 7 days (SD), and fledgling Ovenbirds in this population are last attended by adults \sim 24 days after fledging (Streby and Andersen unpublished data). Therefore, we assumed that a majority of hatch-year Ovenbirds was independent of adult care by \sim 14 July of each year. Of the 226 hatch-year Ovenbirds we captured in clearcuts during 2006 – 2008, only 1 was a bird we banded as a nestling, 30 days earlier in a nest 565 m from the capture net. Of the 340 hatch-year Ovenbirds we captured in clearcuts during all 4 years, we captured 2 (0.5%) during the first week (4 – 10 July), and 16 (4.7%) during the second week (11 – 17 July) of mist-netting. Therefore, \sim 95% of the hatch-year Ovenbirds we captured in clearcuts were likely independent of adult care.

Capture rates of adult Ovenbirds were highest during the first week of mist-netting, whereas capture rates of hatch-year Ovenbirds were highest during weeks 6 – 8 (Fig. 1a). Similarly, capture rates of adult Least Flycatchers were highest during the second and third weeks of mist-netting, whereas capture rates of hatch-year Least Flycatchers were highest during weeks 5 – 8 (Fig. 1b). We captured adult American Redstarts at a relatively constant rate throughout the post-fledging period. However, we captured very few hatch-year American Redstarts before August, when capture rates peaked during the last 3 weeks of mist-netting (Fig. 1c).

In 432 net hours in 4 of the clearcuts during the nesting season of 2009, we captured 345 birds of 33 species, of which 74 (21.4%) were of 13 mature-forest

species, 181 (52.5%) were of 10 early-successional species, and 90 (26.1%) were of 10 generalist species. During that period, we did not capture any hatch-year mature-forest birds. Of the mature forest birds we captured during the nesting season, 60.0% were in apparent breeding condition, as determined by the presence of a brood patch or cloacal protuberance. Of the early-successional birds and generalist birds we captured, 76.7% and 67.9%, respectively, were in apparent breeding condition.

DISCUSSION

Our finding that mature-forest birds constitute a substantial portion of birds using clearcuts during the post-fledging period is consistent with that of previously studied forested regions in eastern North America (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006). Of the 28 mature-forest species we captured, 4 species comprised 75.5% of those captures. Those 4 species (Ovenbird, American Redstart, Least Flycatcher, and Black-and-white Warbler) are among the most common mature-forest birds in this region (Danz et al. 2008), which suggests that the differences in captures among species may reflect differences among local abundance, assuming equal capture probabilities among species. However, point counts of breeding birds in the Chippewa National Forest suggest that those 4 species comprise considerably less than 75% of mature forest birds (Danz et al. 2008), assuming equal detection probability. In fact, Hermit Thrush (*Catharus guttatus*) and Pine Warbler (*Dendroica pinus*) were the ninth and tenth most common of 103 species recorded during those surveys in 2007, whereas we captured only 52 Hermit Thrushes and 7 Pine Warblers in our entire 4-year study. Therefore, we believe that

the differences in captures among forest nesting species in our study may reflect both differences in abundance and differences in cover-type selection among species.

Vitz and Rodewald (2006) suggested that the use of clearcuts by hatch-year mature-forest birds may increase survival because of the relatively abundant cover and food resources in clearcuts, and that seems to be true for hatch-year Ovenbirds in clearcuts 7 – 20 years after harvest (Chapter 3). We agree that those habitat characteristics probably attract adult birds and independent hatch-year birds with well-developed flight and foraging capabilities. However, the temporal pattern of our capture rates of hatch-year mature-forest birds, in the context of local nesting phenology, suggests that clearcuts are rarely used by hatch-year birds during the time when they are most vulnerable to predation. In fact, we estimate that 95% of hatch-year Ovenbirds we captured in clearcuts were independent of adult care. This finding is supported by our concurrent radio telemetry study of fledgling Ovenbirds at the same sites, in which clearcuts ≤ 6 years after harvest were used less than expected based on availability by fledglings prior to independence (Chapter 3). Wood Thrush (*Hylocichla mustelina*) fledglings in Missouri followed a similar pattern, whereby they used mid- to early-successional forest stands only after independent dispersal from family groups (Anders et al. 1998). Because hatch-year mature-forest birds seem to use clearcuts primarily after independence of adult care, we caution that the simultaneous capture of hatch-year and adult conspecific mature-forest birds in a clearcut – a common event during our study – is not reliable evidence of family groups using clearcuts, as suggested by Marshall et al. (2003).

It would be difficult to make comparisons of clearcut use by mature-forest birds between our study and previous studies even if we followed identical protocols, because of differences in forest structure and regeneration patterns and forest-bird communities. But, in addition to inconsistencies between our nest observations and classifications of nesting cover-type associations in previous studies, there were also inconsistencies in classifications among those previous studies. For example, Vitz and Rodewald (2006) included American Redstart and Hooded Warbler (*Wilsonia citrina*) as mature-forest species in south-east Ohio. However, Marshall et al. (2003) considered American Redstarts and Hooded Warblers forest generalists in West Virginia, whereas other studies in West Virginia considered Hooded Warblers and American Redstarts as mature-forest species (e.g. Baker and Lacki 1997). Unless species are consistently classified, or regional differences in classification are justified, we caution that it is inappropriate to make comparisons about numbers of mature-forest species using clearcuts in different study areas (e.g. Vitz and Rodewald 2006), especially when most species comprise very few captures. It is also important to acknowledge that there is a gradual transition from the post-fledging period to migration, both within and among species, which is exemplified by our late-August captures of Wilson's Warblers (*Wilsonia pusilla*), a species that does not nest in our study sites (Ammon et al. 1999).

Because we sampled clearcuts in a different forested bioregion, it is possible that our high nesting-season capture rates and observations of mature-forest birds nesting in clearcuts reflect regional differences in nesting cover-type associations.

Vitz and Rodewald (2006) reported little activity by mature-forest birds in clearcuts during the nesting season in south-east Ohio, and concluded that their post-fledging captures were therefore not a consequence of birds nesting in clearcuts. However, territoriality and differences in activity rates between the nesting period and the post-fledging period likely limit the efficacy of using surveys to compare abundance between the 2 periods. Pagen et al. (2000) concluded from point counts and mist netting during both the nesting and post-fledging periods that some mature forest birds likely nested in the 9- to 10-year-old clearcuts they sampled in the Missouri Ozarks. They detected mature-forest birds in clearcuts during the nesting season using mist nets, but detected them infrequently or not at all in those stands during point counts. We suggest that a possible explanation is that male birds of some species sing from high perches in mature forest edge – perches that are not available in many regenerating clearcuts – but females may choose nest locations in the relatively dense vegetation of adjacent clearcuts. During our concurrent nest-monitoring study, Veeries sang almost exclusively from mature-forest edge and interior forest (HMS personal observation). However, we found no Veery nests during intensive searching of those mature-forest stands, but found 2 nests opportunistically in clearcuts.

Not knowing which species are nesting in clearcuts emphasizes 1 major limitation of using mist nets alone to assess space use by birds. Although sample size per-unit-effort with mist nets is considerably superior to nest monitoring and radio telemetry, deciphering results requires substantially more speculation. During the

nesting season of 2009, 21.4% of our captures were of mature-forest birds. It is possible that some of those birds were non-breeding individuals that were avoiding competition from territorial birds in mature forest. Indeed, 40% of those mature-forest birds did not have either a brood patch or a cloacal protuberance (signs of breeding condition), compared to 23.3% of early- successional birds captured during the same period. It is also possible that the mature-forest birds in breeding condition were nesting in adjacent mature forest and using clearcut stands as a portion of their home range for predator avoidance or to exploit food resources. However, we cannot rule out the possibility that many of the mature-forest birds we captured were nesting in clearcuts. In fact, our nest observations confirm that some individuals of some mature-forest birds were certainly nesting in clearcuts. Regardless, clearcuts were at least a portion of the breeding home ranges of many birds of several mature-forest species, some of which are commonly described as forest-interior, or edge-sensitive species, including Ovenbird, Scarlet Tanager, and Wood Thrush.

Our nest observations and nesting-season captures suggest that the age, or seral stage, at which regenerating clearcuts are first recolonized for nesting by many mature-forest species is earlier than generally assumed. As further evidence, we also observed Hermit Thrush, Wood Thrush, and Ovenbird nests in 16 – 19 year-old clearcuts during our concurrent nest-monitoring study (Table 2). The phenomenon of mature-forest birds nesting in regenerating clearcuts does not diminish the potential importance of clearcuts to those species during the post-fledging period. Rather, it

suggests that the utility of clearcuts to at least some mature-forest species extends to the nesting period as well.

In summary, mature-forest birds use early-successional clearcut stands during the post-fledging period in managed mixed northern hardwood-conifer forests of north-central Minnesota, although that use is predominantly by only a few species. The percent of our mist-net captures comprised by mature-forest birds was as high as, or higher than, in studies of other forested regions, even after we removed 5 species from that group that nested in our clearcuts. We caution that nesting cover-type associations for many migratory songbirds may not be as clear-cut as have been suggested in previous studies. Although mature forest is often defined based on a minimum age or canopy height, “mature forest” birds colonize regenerating stands as they mature, not after they mature, and such colonization may occur earlier than is commonly assumed. An important management consideration for the impact of clearcuts on forest-bird populations may be the rapidity with which species of concern recolonize regenerating stands, and how well they reproduce within those stands. Intensive nest monitoring studies in clearcuts of various ages may improve the current understanding of species nesting cover-type associations, and productivity within those cover types.

Table 1. Birds (after hatch year [AHY] and hatch year [HY]) associated with nesting in mature-forest, early-successional forest, and both mature and early-successional forest, captured during the post-fledging periods of 2006 – 2009 in clearcuts 2 – 10 years after harvest, and during the nesting period of 2009 in clearcuts 4 – 10 years after harvest, in the Chippewa National Forest, Minnesota.

Species	Post-fledging 2006 – 2009 Total (AHY, HY)	Nesting season 2009
<i>Mature-forest species</i>		
American Redstart (<i>Setophaga ruticilla</i>)	315 (184, 131)	11
Black-and-white Warbler (<i>Miniotilta varia</i>)	118 (61, 57)	6
Blackburnian Warbler (<i>Dendroica fusca</i>)	16 (7, 9)	0
Black-capped Chickadee (<i>Parus atricapillus</i>)	67 (42, 25)	1
Black-throated Green Warbler (<i>Dendroica virens</i>)	19 (14, 5)	0
Blue Jay (<i>Cyanocitta cristata</i>)	13 (12, 1)	2
Canada Warbler (<i>Wilsonia canadensis</i>)	59 (43, 16)	1
Eastern Wood-pewee (<i>Contopus virens</i>)	12 (10, 2)	0
Hermit Thrush (<i>Catharus guttatus</i>)	52 (18, 32)	4
Least Flycatcher (<i>Empidonax minimus</i>)	226 (73, 153)	4
Northern Waterthrush (<i>Seiurus noveboracensis</i>)	18 (5, 13)	0
Ovenbird (<i>Seiurus aurocapillus</i>)	660 (320, 340)	12
Ruby-throated Hummingbird (<i>Archilocus colubris</i>)	73 (52, 21)	14
Wood Thrush (<i>Hylocichla mustelina</i>)	12 (10, 2)	0
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)	31 (6, 25)	4
Total*	1746 (885, 861)	74
<i>Early successional species</i>		
American Goldfinch (<i>Archilochus colubris</i>)	15 (15, 0)	0
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	608 (440, 168)	89
Common Yellowthroat (<i>Geothlypis trichas</i>)	29 (18, 11)	2
Golden-winged Warbler (<i>Vermivora chrysoptera</i>)	161 (108, 53)	30
Gray Catbird (<i>Dumetella carolinensis</i>)	72 (36, 36)	1
Indigo Bunting (<i>Passerina cyanea</i>)	22 (18, 4)	4
Mourning Warbler (<i>Oporonis philadelphia</i>)	141 (92, 49)	25
Nashville Warbler (<i>Vermivora ruficapilla</i>)	328 (96, 232)	20
Song Sparrow (<i>Melospiza melodia</i>)	74 (37, 37)	3
Wilson's Warbler (<i>Wilsonia pusilla</i>)	30 (7, 23)	1
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	168 (81, 87)	6
Total*	1659 (956, 703)	181

<i>Forest generalist species</i>		
American Robin (<i>Turdus migratorius</i>)	18 (9, 9)	1
Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)	11 (8, 3)	1
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	53 (37, 16)	0
Purple Finch (<i>Carpodacus purpureus</i>)	13 (9, 4)	1
Red-eyed Vireo (<i>Vireo olivaceus</i>)	424 (378, 46)	5
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	118 (96, 22)	32
Scarlet Tanager (<i>Piranga olivacea</i>)	30 (17, 13)	3
Swainson's Thrush (<i>Catharus ustulatus</i>)	32 (31, 1)	1
Tennessee Warbler (<i>Vermivora peregrina</i>)	58 (36, 22)	0
Trail's Flycatcher (<i>Empidonax</i> sp.)	39 (20, 19)	15
Veery (<i>Catharus fuscescens</i>)	311 (216, 95)	23
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	17 (7, 10)	8
Total*	1150 (879, 271)	90

* totals include species with fewer than 10 captures listed below

Species with <10 captures include mature forest species: Blue-headed Vireo (*Vireo solitarius*), Brown Creeper (*Certhia americana*), Downy Woodpecker (*Picoides pubescens*), Golden-crowned Kinglet (*Regulus satrapa*), Hairy Woodpecker (*Picoides vellosus*), Yellow-rumped Warbler (*Dendroica coronata*), Northern Flicker (*Colaptes auratus*), Northern Parula (*Parula americana*), Pine Warbler (*Dendroica pinus*), Orange-crowned Warbler (*Vermivora celata*), Red-breasted Nuthatch (*Sitta canadensis*), Ruby-crowned Kinglet (*Regulus calundula*), White-breasted Nuthatch (*Sitta carolinensis*), Winter Wren (*Troglodytes troglodytes*), Yellow-throated Vireo (*Vireo flavifrons*), early successional species: Chipping Sparrow (*Spizella passerine*), Clay-colored Sparrow (*Spizella pallida*), Olive-sided Flycatcher (*Contopus cooperi*), Savannah Sparrow (*Passerculus sandwichensis*), White-crowned Sparrow (*Zonotrichia leucophrys*), Yellow Warbler (*Dendroica petechia*), forest generalist species: Baltimore Oriole (*Icterus galbula*), Connecticut Warbler (*Oporornis agilis*), Magnolia Warbler (*Dendroica magnolia*), Philadelphia Vireo (*Vireo philadelphicus*), Swamp Sparrow (*Melospiza georgiana*).

Table 2. Nests observed opportunistically during mist-netting and radio-telemetry monitoring of fledgling songbirds in regenerating clearcuts in the Chippewa National Forest, north-central Minnesota. Each of these species was classified as mature-forest nesting by 1 or more previous studies^a of clearcut use by birds during the post-fledging period.

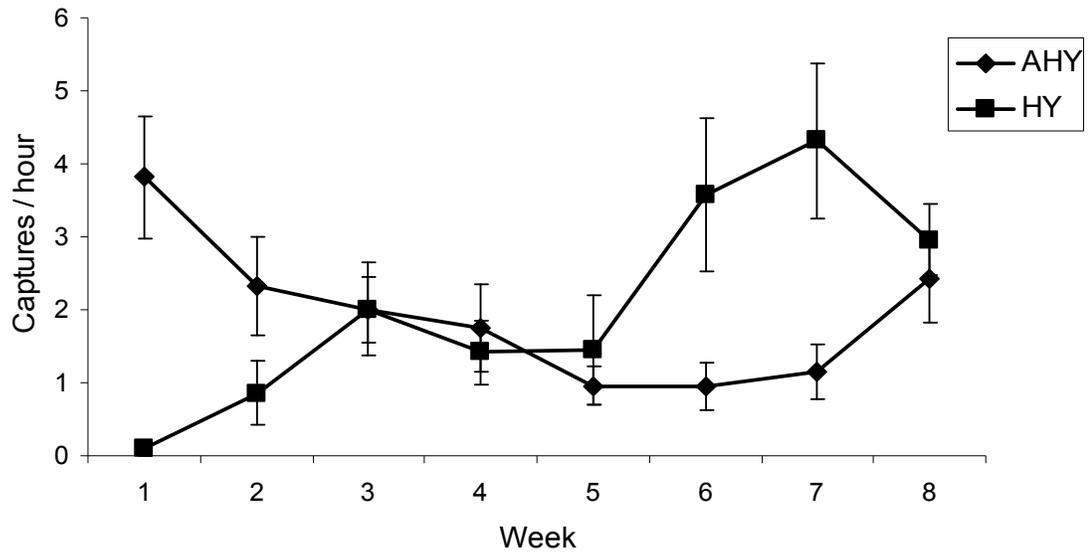
Species	Number of nests	Age of youngest clearcut
Red-eyed Vireo	2	3 years
Rose-breasted Grosbeak	7	7 years
Veery	2	7 years
American Robin	1	7 years
Scarlet Tanager	2	7 years
Hermit Thrush ^b	2	15 years
Wood Thrush ^b	3	15 years
Ovenbird ^b	7	17 years

^a Previous studies cited include Pagen et al. (2000), Marshall et al. (2003), and Vitz and Rodewald (2006).

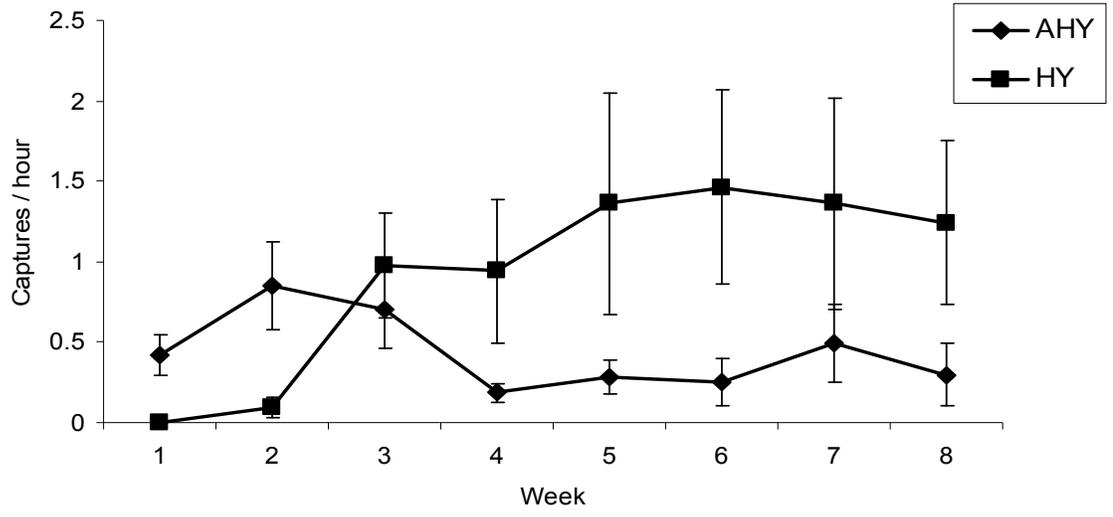
^b Species classified as mature-forest birds in those previous studies and in our study.

Figure 1. Capture rates of adult (AHY) and hatch-year (HY) mature-forest species: (A) Ovenbirds, (B) Least Flycatchers, and (C) American Redstarts captured throughout the 8 week post-fledging period, 4 July – 28 August, 2006 – 2009 in clearcuts in the Chippewa National Forest, Minnesota.

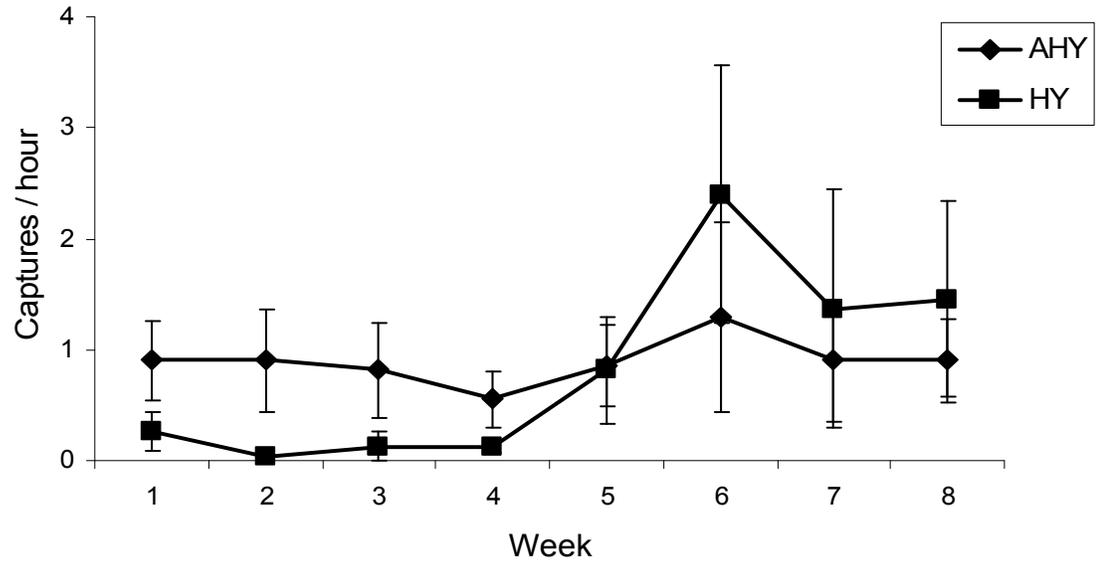
A



B



C



CHAPTER 6

USING INVERTEBRATE AVAILABILITY

AND VEGETATION CHARACTERISTICS TO EXPLAIN

USE OF NON-NESTING COVER TYPES BY MATURE-FOREST

SONGBIRDS DURING THE POST-FLEDGING PERIOD

INTRODUCTION

Many species of migratory forest-nesting songbirds have experienced population declines during recent decades (Peterjohn and Sauer 1994). Studies identifying and investigating potential causes of these declines on wintering grounds (e.g. Sillit and Holmes 2002), along migratory routes (e.g. Yong et al. 1998), and particularly on North American breeding grounds (e.g. Manolis et al. 2002) have been numerous. In largely fragmented North American forests, nesting habitat loss, increased nest predation, and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) likely are the dominant factors that contribute to forest songbird population declines (Robinson et al. 1995). However, in primarily forested landscapes, the effects of natural edges between mature forest and forested wetlands, and the temporary fragmentation of mature forest by timber harvest, are less certain. Increased nest predation can be present near clearcut edges (e.g. Fenski-Crawford and Niemi 1997, Manolis 1999), and can extend as far as 300 m into mature forest (Manolis et al. 2000, Flaspohler et al. 2001b). However, a majority of studies that have detected edge effects on nest success in managed, primarily forested landscapes have used artificial nests (Manolis et al. 2000), which do not reliably represent natural nests (Burke et al. 2004). When detected in natural populations, clearcut edge effects on nest success can be compensated for by increased brood size (Flaspohler et al. 2001a). Furthermore, fledgling survival can be increased when mid-successional clearcuts are used by birds during the post-fledging period, the time between nesting and fall migration (Chapter 2).

Radio telemetry studies of Wood Thrush (*Catharus gutatus*), Scarlet Tanager (*Piranga olivacea*), Swainson's Thrush (*C. ustulatus*), and Ovenbird (*Seiurus aurocapillus*) movements have found that those mature-forest species increase use of non-nesting areas such as early- to mid-successional clearcuts, riparian areas, and forested wetlands during the post-fledging period (Anders et al. 1998, Vega Rivera et al. 2003, White et al. 2005, King et al. 2006, Chapter 2). Although the extent to which some mature-forest species nest in non-mature forest cover types is unclear (Chapter 5), studies using mist nets to sample these cover types suggest that use of regenerating clearcuts and forested wetlands by many mature-forest species increases during the post-fledging period (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006, Chapter 5).

For purposes of managing forests and forest songbird populations, it is important to understand reasons why forest-nesting birds use non-mature forest cover types during the post-fledging period, and the effects that this use has on songbird population dynamics. Hypothesized explanations for the use of non-nesting cover types include predator avoidance in relatively dense vegetation, and greater food availability in early successional stands (Marshall et al. 2003). Only 1 study has explicitly investigated these hypotheses by using vegetation parameters and fruit abundance to model capture rates of forest-nesting birds in non-mature forest stands (Vitz and Rodewald 2007). Vitz and Rodewald (2007) concluded that vegetation structure was generally more important than food abundance for explaining forest bird capture rates in early successional regenerating clearcuts. They found that birds

used areas of higher canopy and less dense low vegetation within clearcuts 2 – 7 years after harvest in Ohio. Because canopy height increases and density of low vegetation generally decreases as clearcut stands regenerate, Vitz and Rodewald's (2007) results suggest that forest birds may use older successional clearcut stands at higher rates than the younger stands they sampled.

Vitz and Rodewald (2007) found that fruit abundance was a stronger predictor than vegetation structure of capture rates of Scarlet Tanagers, the only primarily frugivorous species in their study. Because the other 6 species Vitz and Rodewald (2007) studied were insectivores, it is possible that those birds were selecting areas based on food parameters that were not measured. Due to reduced vertical vegetation stratification in clearcuts relative to mature forest, invertebrate density is much more concentrated within a few meters of the ground in clearcuts (Su and Woods 2001). This relative density of food resources may attract mature-forest insectivorous birds into stands with lower canopy after nesting. Although forest invertebrate abundance generally declines immediately following forest harvest, their abundance and species richness tend to increase linearly during the first 20 years of succession (Niemela 1997). That relationship is consistent with Vitz and Rodewald's (2007) finding that mature-forest birds used areas of higher canopy within young clearcuts. Furthermore, harvest-induced reductions in forest invertebrate abundance are less pronounced in smaller harvested stands (e.g. Niemela et al. 1988), which may explain why capture rates of forest-nesting birds are higher in relatively small, early successional stands (Vitz and Rodewald 2006). However, to our knowledge, no study has directly

investigated the value of invertebrate availability for explaining use of non-mature forest cover types by mature-forest birds during the post-fledging period.

We investigated post-fledging use of non-nesting cover types, including regenerating clearcut stands and forested wetlands, by adult and hatch-year Ovenbirds and American Redstarts in a managed, northern hardwood conifer forest landscape in north-central Minnesota. Ovenbirds and American Redstarts are insectivorous, and they feed nearly exclusively insects to their young, as do most passerines in North America (Gill 2007). Ovenbirds and American Redstarts nest primarily in mature forest, although American Redstarts sometimes nest in early successional forest stands and mature forest edges (Sherry and Holmes 1997). We selected these 2 species because they were the most commonly captured mature-forest species in a previous study we conducted of post-fledging use of clearcuts and forested wetlands (Chapter 5).

Our first objective was to determine whether food resources (i.e. invertebrate availability) or vegetation characteristics were more important in explaining post-fledging use of non-nesting cover types by Ovenbirds and American Redstarts. Second, we compared invertebrate availability between the stands we sampled and adjacent mature forest, to determine whether invertebrate availability was higher in non-mature forest cover types during the post-fledging period. Third, we examined the relationship between fruit abundance and invertebrate availability during the post-fledging period in non-mature forest stands. Because many invertebrates are attracted to fruits (Sallabanks and Courtney 1992), fruit abundance may be a useful index of

invertebrate availability during the post-fledging period. To our knowledge, this hypothesis has not been tested. We expected birds to use non-nesting cover types for cover and for food, and therefore expected captures of adult and hatch-year birds of both species to be related to vegetation characteristics and invertebrate availability. Although invertebrate abundance generally increases as clearcut stands regenerate, we expected invertebrates to be most concentrated in the relatively low vegetation of young clearcuts. We expected invertebrate availability to be positively associated with fruit abundance regardless of cover type.

METHODS

Mist netting

At 3 study sites located across the Chippewa National Forest in north-central Minnesota (Fig. 1), we used mist nets to sample a total of 10 non-nesting (i.e. non-mature forest) stands for use by Ovenbirds and American Redstarts during the post-fledging period of 2009. At each site, we sampled 1 regenerating clearcut of each of 2 age groups; 1 – 6 and 7 – 12 years after harvest. At 2 of the 3 study sites, we additionally sampled 1 clearcut 16 – 19 years after harvest and 1 forested wetland. Each stand we sampled was adjacent to mature forest in which both study species were known to breed. All stands we sampled were 9 – 15 ha in area except 1 forested wetland which was 2.5 ha. Clearcuts 1 – 6 years after harvest were dominated primarily by *Rubus* shrubs, and aspen (*Populus* spp.) and pussy willow (*Salix discolor*) saplings 1 – 4 m tall. Clearcuts 7 – 12 years after harvest were dominated by aspen saplings 3 – 7 m tall with fewer low shrubs. Clearcuts 16 – 19 years after

harvest were dominated by aspen saplings 8 – 15 m tall, with relatively open understory of maple (*Acer* spp.) and American basswood (*Tilia americana*), with very little shrub-layer vegetation. The forested wetlands we sampled were dominated by black spruce (*Picea mariana*), tamarack (*Larix laricina*), and alder (*Alnus* spp.) that ranged in height from 2 – 14 m, and ground cover of sedges, sphagnum (*Sphagnum* spp.) mats, and shallow open water.

Within each stand, we erected 6 (3 pairs), 12-m, 4-shelf mist nets (32 mm mesh) in 3 locations: ≤ 25 m, 26 – 50 m, and > 50 m from mature forest edge. To reduce bias from differences in canopy height, we erected net-pairs end-to-end in stands with canopies ≤ 5 m, and stacked nets vertically in stands with canopies > 5 m (i.e. both clearcuts 16 – 19 years after harvest, and 1 forested wetland). We sampled each stand twice weekly (on 2 consecutive days) for eight weeks, from 4 July to 27 August. We opened nets 15 – 30 min before sunrise and closed them after 3 h or when weather conditions (i.e. high wind, rain, or temperatures below 0°C) precluded safe netting and handling of birds. On several occasions, we opened nets late, or closed and reopened nets multiple times to accommodate weather events and maintain 3 h of netting.

We monitored nets at ≤ 30 -min intervals, removed entangled birds, and carried them in soft cloth bags to a banding station ≤ 200 m from capture locations. We identified species, sex, and age of each bird, referring to Pyle (1997) when necessary. We banded each bird, except Ruby-throated Hummingbirds (*Archilochus colubris*), with a standard aluminum U.S. Geological Survey legband. We examined the gape

and feces (when graciously offered during handling) of birds for signs of fruit consumption, including red stained gape or seeds in feces.

Vegetation sampling

Between 1 and 7 August, we sampled vegetation characteristics around each pair of mist nets in each stand we sampled. Around each pair of nets, we established 16, 0.75-m radius circular plots (Fig. 2). On each side of each pair of nets, we established 4 plots 2 m from the nets, and 4 plots 5 m from the nets. Within each plot, we visually estimated canopy height and percent ground cover (from ground to 0.25 m above the ground) by vegetation and by woody debris. In addition, we measured leaf litter depth at the center of each plot. We used the mean of the 16 values for each parameter as the value of that parameter for each pair of nets. We estimated vegetation density around each pair of nets using a profile-board method modified from MacArthur and MacArthur (1961). We divided a 2 x 0.25-m board into 8, 0.25 x 0.25-m squares, and painted the squares alternately orange and white. We stood the board vertically against the nets at 4 locations, directly facing the vegetation plots. We viewed the board from each of the 8 5-m vegetation plots and estimated the percent of each square obscured by vegetation. We used the estimates from all squares from all samples, and produced 1 estimate of mean vegetation density for each pair of nets.

Food sampling

We used 2 trapping methods, flytape and pitfall traps, to sample invertebrates at each pair of nets during each week of netting. Although traps may not directly

sample invertebrate availability for songbirds, we considered captures of invertebrates to be an index to availability. Availability is a function of abundance and accessibility, and for invertebrates to be captured in a trap, they must be present (abundance) and active (accessible). On the first of 2 consecutive days of netting within a stand, we deployed 2 pitfall traps and 2 flytape traps at each pair of nets (Fig. 2). We used a 473-ml plastic cup with ~50 ml of 50% ethanol solution for each pitfall trap. We set 1 pitfall trap at the center of each net, such that the top of the cup was level with the ground. We used a 10 x 1-cm strip of attractant-free flytape for each flytape trap. We attached each flytape trap to a small branch that protruded into the net lane 1 – 2 m above the ground. We collected and counted the contents of each pitfall trap and flytape trap 24 hr after deployment (i.e. after the second of 2 consecutive mornings of netting). We used the number of invertebrates captured in pitfall traps as an index of ground invertebrate availability. We used the number of invertebrates captured on flytape traps as an index of shrub-level invertebrate availability. In addition, each week we counted all ripe fruit within 1.5 m of each pair of nets (Fig. 2). To compare between our sampled stands and adjacent mature forest stands, we established 1, 25 x 3-m transect in a mature forest stand at each site during 8 – 14 August (week selected arbitrarily). We counted fruit and deployed 7 flytape traps (24 hr) in each mature forest transect.

Statistical analysis

Before analysis, we tested variables for normality and linearity. One variable, canopy height, had an apparent non-linear relationship with captures of adult

Ovenbirds. We therefore included an additional quadratic term for canopy height in models of adult Ovenbird captures. Vegetation density and ground-vegetation cover each correlated strongly and negatively with canopy height. Therefore, of those 3 variables, we used only canopy height in models of bird captures.

We modeled captures of each of 4 groups of birds: adult Ovenbirds, hatch-year Ovenbirds, adult American Redstarts, and hatch-year American Redstarts. Because the use of non-nesting cover types by adult and hatch-year mature-forest birds is not necessarily temporally similar (Chapter 5), and most groups were not captured throughout the entire 8-week period (Fig. 3), we included in models only data from weeks in which birds of the group in question were captured. For example, in models of hatch-year American Redstart captures we included only data from weeks 5 – 8. No hatch-year American Redstarts were captured before August. Therefore, including data from weeks 1 – 4 in an analysis intended to compare habitat use within non-nesting cover types would likely yield erroneous results for explanatory variables that increase or decrease throughout the 8-week sampling period. Using the same logic, we included only data from weeks 2 – 8 in hatch-year Ovenbird models, weeks 1 – 8 in adult American Redstart models, and weeks 1 – 5 in adult Ovenbird models.

Because all sampling events were equal in length (6 hr), counts of birds captured were equivalent to capture rates for each sampling event. Therefore, we used counts of birds captured in each pair of nets per week as the response variable in Poisson regression in PROC NLMIXED (SAS Institute 2008). For each species we

developed a set of a priori candidate models based on biologically relevant variables. Ovenbirds typically occupy ground litter and low vegetation, and forage primarily on the ground, and secondarily in shrub-level and understory vegetation (Van Horne and Donovan 1994). Therefore, we included ground-level and shrub-level variables in models of Ovenbird captures. We developed 14 candidate models for Ovenbirds that included ground invertebrate availability (Pitfall), shrub-level invertebrate availability (Flytape), litter depth (Litdep), percent ground cover by woody debris (Wood), and canopy height (Canopy). American Redstarts occupy all available vegetation from near ground to canopy, and forage primarily from foliage and secondarily from the air (Sherry and Holmes 1997). Because American Redstarts use the ground for brief prey attacks, but otherwise use the ground rarely, we included ground level invertebrates, but not litter depth or woody debris in models of American Redstart captures. We developed 6 candidate models for American Redstarts that included Pitfall, Flytape, and Canopy. Because the 10 sampled stands were located at 3 sites separated by approximately 25 km, we included a random Site effect in all models.

We used Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002) to rank candidate models. The best-supported model and all models with ΔAIC_c values <2.0 were considered competing models. We did not consider models with one additional parameter, but otherwise identical to the best-supported model, to be competing models regardless of ΔAIC_c values, because the additional parameter in such models is generally uninformative (Arnold 2010). We included each variable in the same number of candidate models, and we

used the cumulative Akaike weights (w ; Burnham and Anderson 2002) of all models that included a given variable to identify the relative support for that variable for predicting bird captures.

To test if food availability was higher in non-mature forest cover types than in mature forest, we used Student's t -tests and compared invertebrate counts from sampling in each stand with invertebrate counts sampled simultaneously in adjacent mature-forest stands. It was not necessary to statistically compare fruit abundance, because we found no fruit in mature forest transects. To test the reliability of fruit abundance as an index of invertebrate availability in non-mature forest stands, we used linear regression and compared fruit counts with Pitfall and Flytape counts. We considered results of statistical tests significant at the $\alpha = 0.05$ level.

RESULTS

We captured 253 (102 adult and 151 hatch-year) Ovenbirds, and 92 (51 adult and 41 hatch-year) American Redstarts during 1,440 net-hours (pairs of nets). Around our nets, we counted 5,627 ripe fruits, captured 6,200 invertebrates in pitfall traps, and captured 5,783 invertebrates on flytape traps. Most fruits (>90%) were *Rubus*, including American red raspberry (*R. idaeus*), dwarf red raspberry (*R. pubescens*), and common blackberry (*R. allegheniensis*). Pitfall samples included representatives of 23 invertebrate orders, but >90% of pitfall contents were of 5 orders: Hymenoptera, Coleoptera, Diptera, Araneida, and Orthoptera. Flytape traps sampled dipterans, hemipterans (leafhoppers), hymenopterans, and adult and larval

lepidopterans. Flytape traps therefore captured both flying and flightless shrub-level invertebrates.

Adult Ovenbird captures were best explained by the model including all vegetation structure variables (Canopy, Wood, and Litdep), and a competing model that included both invertebrate availability variables and vegetation structure variables (Table 1). Cumulative weights indicated that percent woody debris cover ($w = 0.97$) and canopy height ($w = 0.84$) were the strongest predictors of adult Ovenbird captures. There were 5 competing models of hatch-year Ovenbird captures (Table 1), all of which included the Flytape variable. Cumulative weights indicated that shrub-level invertebrate availability ($w = 0.84$) was the strongest predictor of hatch-year Ovenbird captures, with >50% more cumulative weight than the second strongest predictor, leaf litter depth ($w = 0.55$). In general, Ovenbird captures were highest in areas of relatively high canopy and relatively high shrub-level invertebrate availability.

Adult American Redstart captures were best explained by the model including Flytape and Canopy (Table 1). Cumulative weights indicated that shrub-level invertebrate availability ($w = 0.99$) was the strongest predictor of adult American Redstart captures, followed very closely by canopy height ($w = 0.98$). There were 3 competing models of hatch-year American Redstart captures, each of which included the Flytape variable. Cumulative weights indicated that shrub-level invertebrate availability was the strongest predictor of hatch-year American Redstart captures ($w =$

1.00). In general, American Redstart captures were highest in areas of relatively high shrub-level invertebrate availability and relatively low canopy height.

Shrub-level invertebrate availability was significantly higher both in clearcuts 1 – 12 years after harvest and in forested wetlands than in mature forest, but was similar between clearcuts 16 – 19 years after harvest and mature forest (Fig. 4). Among non-mature-forest cover types, shrub-level invertebrate availability was highest in 7 – 12 yr-old clearcuts. Fruit abundance explained very little variation in either Pitfall ($r^2 < 0.01$, $F = 0.67$, $df = 1,239$, $P = 0.41$) or Flytape ($r^2 < 0.01$, $F < 0.01$, $df = 1,239$, $P = 0.96$) invertebrate availability estimates. Clear signs of fruit consumption, including red-stained gape and seeds in feces were common in adult frugivorous birds we captured (e.g. Rose-breasted Grosbeak [*Pheucticus ludovicianus*]). However, we did not observe signs of fruit consumption for any Ovenbirds or American Redstarts, suggesting that these species were not exploiting fruit resources in non-nesting cover types during the period we sampled.

DISCUSSION

Our results support the hypothesis that both food availability and vegetation structure influence use of non-nesting cover types by mature-forest-nesting birds during the post-fledging period, but that food availability is generally the stronger predictor of that use. There are clearly potential advantages for predator avoidance in the relatively dense vegetation of regenerating clearcuts and forested wetlands compared to mature forest. Although we found in a previous study that fledgling Ovenbirds experience higher survival in some non-nesting cover types (Chapter 3),

the developmental conditions of birds we captured in this study suggested that few hatch-year birds used these cover types until after independence from adult care. If non-nesting cover types were used primarily for predator avoidance, we would expect to capture adult and hatch-year birds in these stands throughout the post-fledging period, and those captures would relate strongly to vegetation parameters. However, the patterns of our captures of adult and hatch-year birds suggested that these stands were used primarily for food acquisition, possibly for migratory preparation. Most adult captures were in July and most hatch-year captures were in August, and those captures generally related most strongly to food availability rather than vegetation structure.

Of the 2 invertebrate variables we measured, we expected Ovenbird captures to be more strongly related to ground invertebrate availability because they are described as a ground-foraging species (Van Horn and Donovan 1994). However, adult and hatch-year Ovenbirds were more strongly related to shrub-level invertebrate availability, suggesting that Ovenbirds may forage more commonly in the shrub layer when using non-mature forest stands than they do in mature forest. In mature forest, where shrub-layer vegetation is patchy and relatively uncommon, Holmes and Robinson (1988) reported that 29% of Ovenbird prey attacks occurred on foliage of shrubs and understory trees. If Ovenbirds forage in shrubs based on availability, it is likely that they forage more commonly in the relatively abundant shrubs in the stands we sampled. Indeed, during a radio-telemetry study, hatch-year Ovenbirds were

observed more commonly in shrubs and small trees in non-mature forest stands than when they were in mature forest (Streby and Andersen unpublished data).

Our results are complementary to those of Vitz and Rodewald (2007), who concluded that vegetation structure rather than fruit abundance explained use of clearcuts by Ovenbirds, American Redstarts, and other mature-forest nesting songbirds. However, we demonstrated the importance of including species-appropriate food resources in habitat-use models. Because invertebrates can be attracted to fruits (Sallabanks and Courtney 1992), it may seem valid to assume fruit abundance is a reasonable index of invertebrate availability. However, we found no relationship between fruit abundance and invertebrate availability during our study.

As expected, we observed fruit abundance to be highest in the youngest clearcuts and fruit was nearly absent from forested wetlands, clearcuts 16 – 19 years after harvest, and in mature forest. In cover types where fruit was present, fruit abundance consistently increased during July and then decreased during August. Conversely, invertebrate availability was highest in regenerating clearcut stands 6 – 12 years after harvest, and varied considerably both temporally and spatially within the stands we sampled. We therefore note that it is necessary to concurrently sample highly variable food resources and bird availability, at similar scales, to meaningfully ascertain a relationship between the two.

Our study emphasizes the importance of expanding the scale of breeding-migratory-bird studies to include the post-fledging period to better understand species-habitat relationships. Some non-mature forest cover types (i.e. early

successional clearcuts) have negative effects on mature-forest birds during the nesting season, including temporary loss of nesting habitat and sometimes decreased nest success near edges (e.g. Manolis et al. 2000 and 2002). However, the resources provided to mature forest-nesting birds in non-mature-forest cover types must also be considered in management and conservation planning. Our study supports previous assertions that non-mature-forest cover types may provide important resources for forest-nesting birds during the post-fledging period. Our study also emphasizes the importance of considering the effects of regenerating clearcuts during all stages of succession. Dependent fledgling Ovenbird survival may be low near early successional clearcuts (Chapter 2). However, results of this study suggest that mid-successional clearcuts and forested wetlands provide greater food resources than mature forest during the weeks preceding fall migration, which may improve pre-migratory condition and increase survival during migration.

Table 1. Best-supported and competing models ($\Delta AIC_C \leq 2.0$) describing captures of adult (AHY) and hatch-year (HY) Ovenbirds (OVEN) and American Redstarts (AMRE) in forested wetlands and regenerating clearcuts during the post-fledging period of 2009 in the Chippewa National Forest, Minnesota, USA. All models include an additional variable (not shown) for a random site effect. Model variables include: leaf litter depth (LITDEP), percent ground cover by woody debris (WOOD), canopy height (CANOPY), a quadratic canopy height term in adult Ovenbird models only (CANOPY**2), shrub-level invertebrate availability (FLYTAPE), ground invertebrate availability (PITFALL).

Bird Group	model	K	AIC _c	ΔAIC_C	w_i
OVEN AHY	C _{LITDEP + WOOD + CANOPY + CANOPY**2}	6	280.79	0.00	0.52
	C _{FLYTAPE + PITFALL + WOOD + CANOPY + CANOPY**2}	7	281.93	1.14	0.29
OVEN HY	C _{FLYTAPE + LITDEP + CANOPY}	5	477.67	0.00	0.19
	C _{FLYTAPE + LITDEP + WOOD}	5	477.68	0.01	0.19
	C _{FLYTAPE + PITFALL}	4	478.02	0.35	0.16
	C _{FLYTAPE}	3	478.39	0.72	0.13
	C _{FLYTAPE + PITFALL + LITDEP + WOOD + CANOPY}	7	479.14	1.47	0.09
AMRE AHY	C _{FLYTAPE + CANOPY}	4	230.16	0.00	0.74
AMRE HY	C _{FLYTAPE + CANOPY}	4	156.57	0.00	0.38
	C _{FLYTAPE}	3	157.53	0.96	0.24
	C _{FLYTAPE + PITFALL}	4	157.98	1.41	0.18

Figure 1. Study sites; (1) Pike Bay, (2) Cutfoot Sioux, and (3) Suomi Hills located in the Chippewa National Forest, north-central Minnesota, USA, where we used mist nets to sample non-mature forest cover types for use by mature-forest nesting Ovenbirds and American Redstarts during the post-fledging period, July and August, 2009.

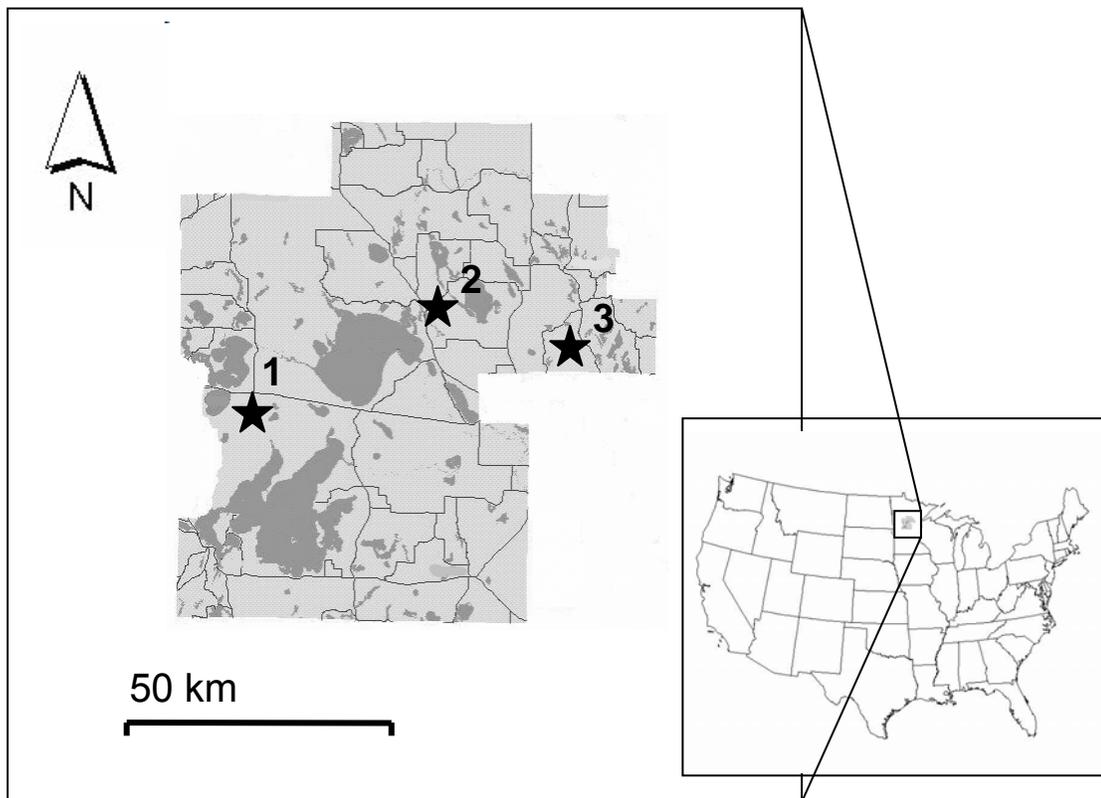


Figure 2. Mist-net captures of mature-forest songbirds in 10 non-mature-forest cover types during the post-fledging period of 2009 in the Chippewa National Forest, Minnesota, USA.

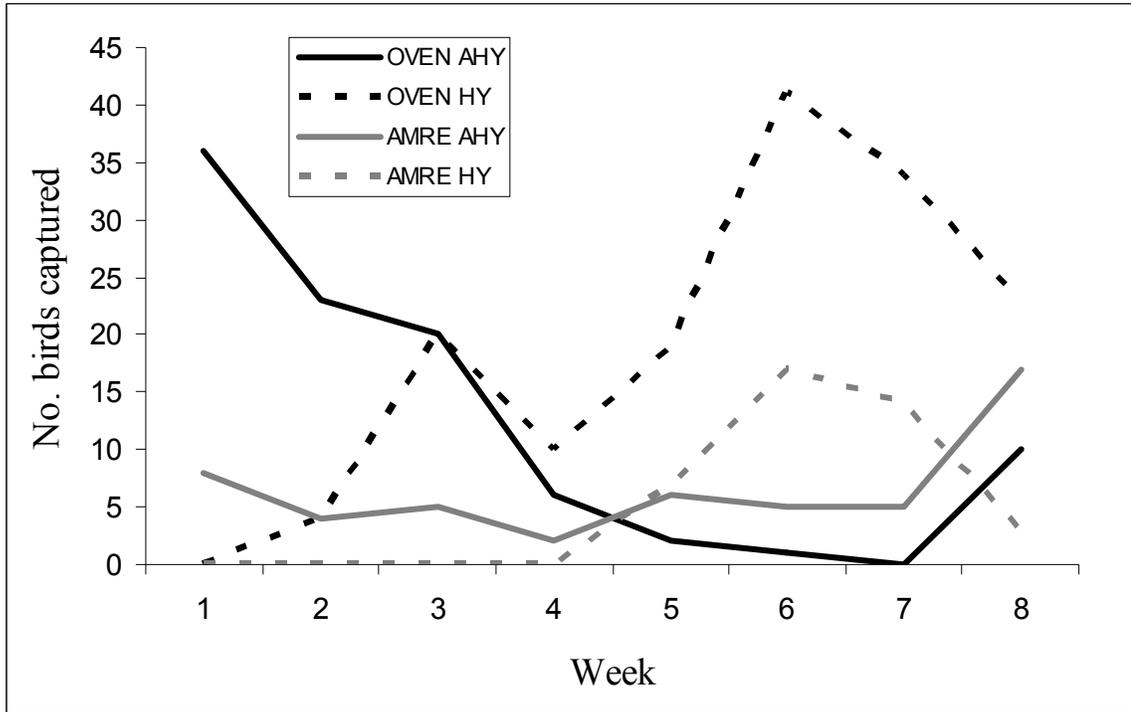


Figure 3. Diagram of vegetation, invertebrate, and fruit sampling design around a pair of 12-m mist nets. Canopy height, leaf litter depth, and percent ground cover by low vegetation and woody debris were recorded in each of 16 vegetation plots during the first week of August. Vegetation density was estimated using a profile board (not shown) placed against the net perpendicular to, and viewed from, each of the 8, 5-m vegetation plots (see text). Two pitfall traps and 2 flytape traps were deployed weekly for 24 hrs between 2 consecutive days of netting.

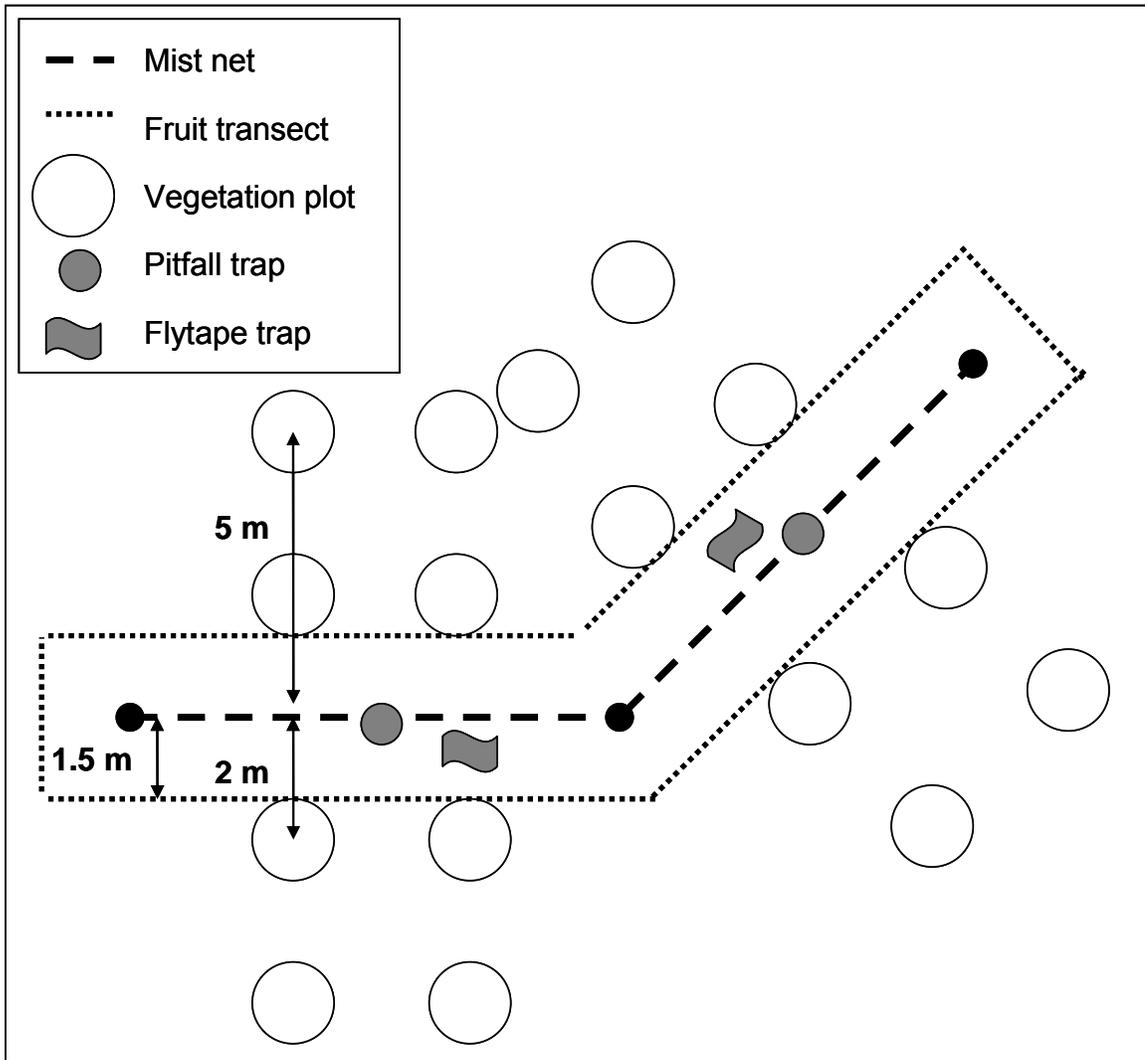
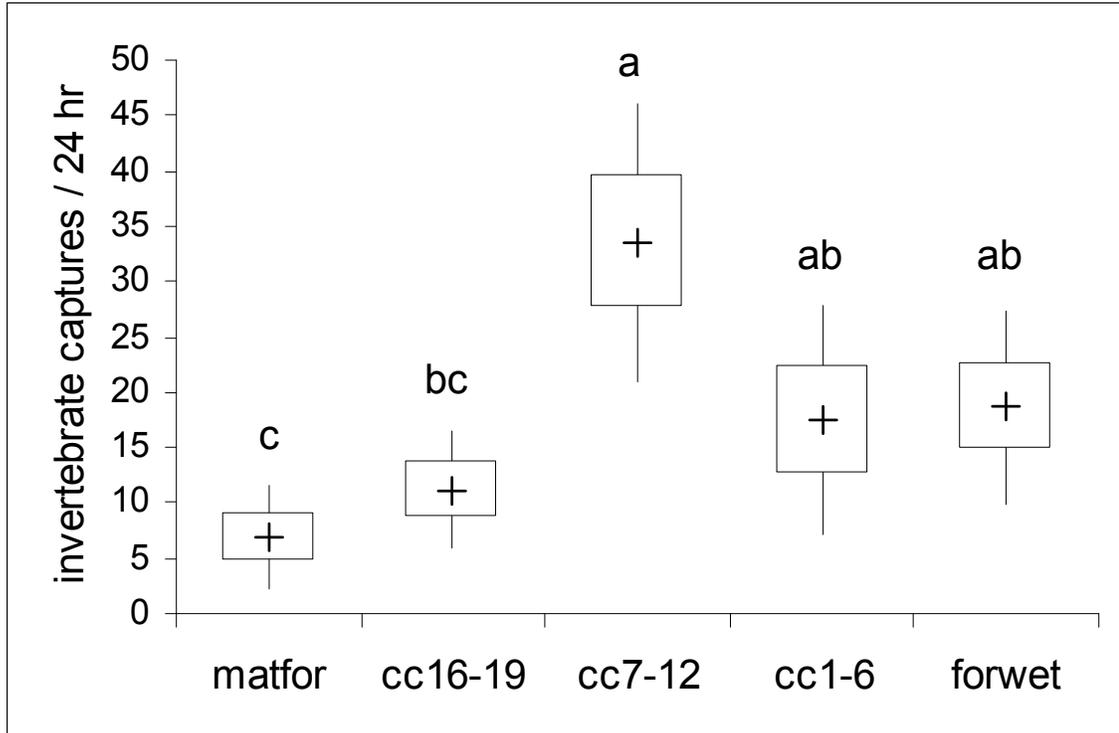


Figure 4. Invertebrates captured on flytape traps deployed in the shrub layer of 5 in the Chippewa National Forest, Minnesota, USA; mature forest (matfor), clearcuts 16 – 19 years after harvest (cc 16 – 19), clearcuts 7 – 12 years after harvest (cc 7 – 12), clearcuts 1 – 6 years after harvest (cc 1 – 6), and forested wetlands (forwet). Stands were sampled for 24 hr between 8 – 14 August 2009. Plus signs, boxes, and whiskers represent means, SE, and 95% CI, respectively. Letters confer statistically significantly different groups at the $\alpha = 0.05$ level.



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