University of Alberta

Local and regional demography in a migratory forest songbird and effects of forest management intensity

by

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À mes parents pour leur amour inconditionnel

ABSTRACT

The numerical response of forest birds to habitat alteration has been well documented in North America, but the underlying demographic processes driving these changes remain largely unknown. Among species sensitive to such alterations, the Ovenbird (*Seiurus aurocapilla*) shows one of the largest declines in abundance following low-intensity partial harvesting in the northern hardwood forest. The main objectives of this dissertation were to: 1) document the demographic response of the Ovenbird to partial harvesting; 2) test predictions from different conceptual models of habitat selection; 3) use stable isotope analyses to obtain estimates of natal dispersal distances, and 4) model current and future population dynamics in an intensively managed forest landscape based on alternative harvesting and climatic scenarios. I provided evidence for an ideal free distribution (IFD) in Ovenbirds based on the lack of a treatment (selection harvesting) effect on per capita productivity, daily nest survival, and post-fledging survival and a lower density and productivity per unit area in recent selection cuts compared to untreated deciduous stands. From feather samples of known origin, I showed important year and age variation in stable hydrogen isotope ratios (δ^2H_f). Using this information and a multi-isotopic approach (δ^2H_f and $\delta^{34}S_f$), I showed that almost all individuals (33/35) recruited in the breeding population would be considered residents and that only 6% of individuals would have originated from within 240 km of the study area. The study area would be a demographic sink, but I also detected source-sink dynamics within the study area. Projections of the future status of the breeding Ovenbird population over a 75-year period suggest that climate change will have more negative impacts than harvesting. Also, if population size is not maintained through immigration, a large decline in abundance is expected. This dissertation provides an important contribution to fundamental and applied avian ecology. Empirical evidence for an IFD has rarely been documented and, overall, my results suggest that the Ovenbird is more resilient to moderate alteration of its habitat than previously reported. Nonetheless, land managers should consider the numerous threats to migratory birds throughout their annual cycle, including the effects of climate change.

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CHAPTER 1: INTRODUCTION

1.1 Source-sink dynamics

A growing body of evidence suggests that many songbird populations are structured as networks of demographic sources ($\lambda > 1$) and sinks ($\lambda < 1$; λ being population growth rate; Pulliam 1996; Rodenhouse et al. 1997; Murphy 2001a). Source-sink dynamics is a relatively simple conceptual model that suggests certain areas of the landscape are demographic sources that produce more individuals than required to compensate for mortality, whereas demographic sinks do not yield enough recruits to maintain population size and decline to extinction without immigration from sources.

The study of source-sink dynamics is an area of considerable interest as alteration of demographic sources by human activities may have implications for the persistence of a species (Pulliam 1988; Tittler et al. 2006). However, source-sink dynamics are difficult to quantify because the detailed demographic information required to estimate population growth rates, generally expressed as the sum of per capita productivity (i.e. number of juveniles recruited in a breeding population) and adult survival rate (e.g. Donovan et al. 1995; Flaspohler et al. 2001; Murphy 2001a; Podolsky et al. 2007), are rarely available.

Mechanisms underlying habitat selection and the consequences of this choice on reproductive success and, ultimately, population dynamics, also remain largely unknown. Yet, such information is needed to understand source-sink dynamics. For example, an ideal free distribution suggests that density-dependent processes act irrespective of habitat quality, resulting in similar per capita productivity among habitat types whose quality appears to differ based on their productivity per unit area (Fretwell & Lucas 1970). This distribution would result in temporal rather than spatial source-sink dynamics (e.g. Nevoux et al. 2011). Alternatively, the ideal despotic distribution suggests that higher-quality habitats are selected by the most experienced and aggressive individuals, whereas other individuals choose or are forced to settle in lower-quality habitat (Fretwell & Lucas 1970). Such spatially structured populations are regulated through source-sink dynamics (Murphy 2001a,b). Despotic behavior can also lead to higher density in lower-quality habitat (Zanette 2001), which can cause crowding effects and pseudo or temporary sinks (Gilroy & Sutherland 2007). Nonideal habitat selection can also lead to demographic sinks when dominant individuals are deceived by ecological traps (Battin 2004).

Establishing whether source-sink dynamics are occurring requires habitat-specific demographic information, but also information about the spatial scale over which population processes occurs. Songbirds exhibit low fidelity to their natal site and generally disperse over tens (Tittler et al. 2006) or even hundreds of kilometres (Paradis et al. 1998; Hobson et al. 2004). Conversely, experienced breeders show high fidelity to their breeding territory (Greenwood 1980). Connectivity among populations thus mainly reflects natal dispersal movements. Empirical estimates of the extent of natal dispersal movements are required to determine the relevant spatial scale over which spatially structured breeding populations interact, source-sink dynamics should be monitored, and conservation strategies developed (Tittler et al. 2009).

1.2 Alteration of the northern hardwood forest and impacts on animal populations

To extract volume while maintaining the shade-tolerant tree species characterizing the northern hardwood forest, stands are generally managed through a partial harvesting regime removing 30 to 70% of the basal area (cross-sectional area at breast height [1.35 m] of all stems with a diameter ≥ 10 cm) at varying intervals (Gram et al. 2003; Guénette & Villard 2005; Vanderwel et al. 2009). Selection harvesting typically removes 30-40% of the basal area every 20-30 years, while more intensive treatments such as shelterwood harvesting (50-70% removal) are generally applied to improve growing stock before a selection harvesting regime.

These approaches to managing northern hardwood stands has often been considered to be ecologically sustainable as it maintains stand composition and some structure (Reader 1987; Schwartz et al. 2005, but see Angers et al. 2005). While species associated with early-seral stages usually benefit from partial harvest treatments (Heltzel & Leberg 2006; Gitzen et al. 2007; Haché et al. 2013), those associated with mature forests generally respond negatively (Edman et al. 2008; Haché & Villard 2010; Poulin et al. 2010). As the proportion of stands managed under partial harvest systems is increasing (e.g. Etheridge et al. 2006), there are growing concerns about the status of mature forest species. Several studies have documented the numerical response of forest songbirds along a gradient of habitat alteration (e.g. Guénette and Villard 2005; Vanderwel et al. 2007) or to specific harvest treatments (Campbell et al. 2007; Kardynal et al. 2011; Haché et al. 2013), but fewer have tested for effects of harvesting on reproductive success (but see Gram et al. 2003; Pérot & Villard 2009; Leblanc et al. 2011), while such effects on juvenile and adult survival remain largely unknown (but see Haché & Villard 2010; Eng et al. 2011). Given this uncertainty about habitat-specific demography in forest songbirds, the relative importance of spatial and temporal source-sink dynamics and, ultimately, the status of forest songbird populations also remain unknown.

In addition to human activities, changes in climate will have important effects on northern hardwood ecosystems (Rodenhouse et al. 1997; Groffman et al. 2012). Based on different greenhouse gas emission scenarios and climatic envelope models, large declines are projected for several neotropical migratory birds, irrespective of other human activities (Rodenhouse et al. 2008). Hence, when projecting the status of bird populations based on different human land use scenarios, it is also important to consider the anticipated effects of climate change to determine the relative importance of different threats (e.g. Coristine & Kerr 2011).

1.3 Study species

Among vertebrate species known to respond negatively to partial harvesting in eastern North America, the Ovenbird (*Seiurus aurocapilla*) is considered to be one of most sensitive (Vanderwel et al. 2009). This neotropical migratory songbird is the unique representative of the genus *Seiurus* and has a wide breeding range that extends from the eastern side of the Canadian Rockies to Newfoundland. They are found as far north as the Northwest Territories and as far south as Alabama. The eastern portion of the wintering range reaches Florida and the Caribbean islands, while its western portion extends from central Mexico to Costa Rica (Porneluzi et al. 2011). The Ovenbird forages almost exclusively on litter invertebrates (Stenger 1958; Holmes & Robinson 1988) and per capita productivity is correlated with primary productivity of northern hardwood stands (i.e. tree growth; Seagle & Sturtevant 2005). Although sensitive to habitat alteration, it remains locally abundant making it a good focal species (Lambeck 1997) for which habitat-specific demography can be measured to understand source-sink dynamics in an intensively managed forest landscape.

1.4 Study area

Most of the fieldwork for this thesis took place in the Black Brook District located in northwestern New Brunswick, Canada (47º23’N, 67º40’W). It is a 2000 km² forest privately own by J.D. Irving, Limited. Purchased in 1944, Black Brook is one of the most intensively-managed forests in Canada (Etheridge et al. 2006). It includes hardwood (25% of total area; sugar maple [*Acer saccharum*], yellow birch [*Betula alleghaniensis*], and American beech [*Fagus grandifolia*]), conifer (20%; black spruce [*Picea mariana*], white spruce [*Picea glauca*], jack pine [*Pinus banksiana*]), and mixedwood stands (18%) and spruce (*Picea* spp.) plantations (37%; see Etheridge et al. 2005 for details).

1.5 Thesis Overview

The main objectives of this dissertation were to: 1) document the demographic response of the Ovenbird to partial harvesting; 2) test predictions from different conceptual models of habitat selection; 3) use stable isotope analyses to obtain estimates of natal dispersal distances, and 4) model current and future population dynamics in an intensively managed forest landscape based on alternative harvesting and climatic scenarios. These objectives have been addressed in the following 5 chapters:

Chapter 2: Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird

The demographic response of the Ovenbird to selection harvesting was measured and predictions from conceptual models of habitat selection have been tested.

Chapter 3: Post-harvest regeneration, sciurid abundance, and postfledging survival and movements in an Ovenbird population

A model selection approach was used to compare the relative importance of selection harvesting and alternative hypotheses in explaining variation in daily postfledging survival and movements.

Chapter 4: Assigning birds to geographic origin using feather hydrogen isotope ratios (δ^2H): importance of year, age, and habitat

Several key assumptions underlying the use of hydrogen isotope ratios from feather samples to track bird movements were tested using samples of known origin.

Chapter 5: Tracking natal dispersal in a coastal population of a migratory songbird using feather stable isotope (δ^2H, $\delta^{34}S$) tracers

Two stable isotope markers were used to assign the likely natal origin of first-year breeders defending a territory in Black Brook to estimate the extent of natal dispersal and the proportion of residents vs. immigrants.

Chapter 6: Demographic response of a neotropical migrant songbird to alternative forest management and climate change scenarios

Empirical data from chapters 2, 3, and 5 and from other studies conducted in our study area were used to model population dynamics of Ovenbirds and its future status based on different harvesting and climatic scenarios.

Chapters 1 and 7 reflect my own thoughts. I use the pronoun “we” in chapters 2-6 because they were part of a collaborative work most of which is published or submitted with my co-authors.

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CHAPTER 2: EXPERIMENTAL EVIDENCE FOR AN IDEAL FREE DISTRIBUTION IN A BREEDING POPULATION OF A TERRITORIAL SONGBIRD

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2.1 Introduction

Population dynamics of territorial species are often described as being driven by an ideal despotic distribution (IDD), whereby more experienced/competitive individuals secure territories where their fitness is maximized (Holmes et al. 1996; Petit & Petit 1996; Murphy 2001; Calsbeek & Sinervo 2002). This scenario implies that dominant individuals force subordinates into lower-quality habitat where the subordinates achieve lower fitness. Each year, individuals from lower-quality territories try to improve their fitness by moving into higher-quality habitat, but not vice versa (e.g. Reijnen & Foppen 1994). A specific case of the IDD, the ideal preemptive distribution (IPD), suggests that individuals select the best territories known to be available, whose availability decreases rapidly with increasing density (Pulliam & Danielson 1991). Preemptive behavior tends to result in higher-quality territories being secured earlier by more experienced or dominant individuals, allowing them to achieve higher fitness than those forced to defend lower-quality territories (Sergio & Newton 2003).

Although the IDD and IPD make intuitive sense and are the processes put forward to explain source-sink dynamics (Pulliam 1988) and population regulation through site dependence (Rodenhouse et al. 1997), some authors suggest these models do not adequately describe patterns observed in the field, mainly because the assumption of constant territory size within and among habitat of different quality is rarely met (Ridley et al. 2004; Piper 2011). A key prediction from the IDD is differential per capita productivity as a function of habitat quality, which is often believed to be the outcome of despotic behavior (i.e. inter-individual differences in competitive ability) and territoriality (Ridley et al. 2004). However, some studies show that site familiarity could compensate to some degree for low habitat quality and allow individuals to achieve unexpectedly high fitness (reviewed by Piper 2011). This could lead to patterns consistent with predictions from the ideal free distribution (IFD, Fretwell & Lucas 1969), whereby density is adjusted through territory size to match local habitat quality (cf. habitat matching rules; Morris 1994). Under an IFD, population regulation is more likely to be driven by density-dependent factors acting simultaneously on different vital rates, irrespective of habitat quality (Nevoux et al. 2012 and references therein; see also Morris 1994). There is also evidence that despotic behavior may not necessarily result in an ideal despotic distribution as it may not prevent per capita productivity of individuals in good-quality habitat from being density-dependent, owing to variation in territory size (Ridley et al. 2004).

The IFD is also a simplistic model for explaining territory settlement patterns because, like the IDD, it assumes that private information does not influence habitat selection ("familiarity blindness" or "site indifference" - Schmidt 2001; Piper 2011). Site fidelity has been shown to be influenced by past reproductive success (e.g. Switzer 1997; Tremblay et al. 2007; Thériault et al. 2012). In addition, both the IDD and IFD models assume that individuals have perfect (ideal) knowledge about resource availability and density dependence functions. However, there is evidence that nonideal habitat selection by dominant individuals can occur (Arlt & Pärt 2007; Hollander et al. 2011; reviewed by Chalfoun & Schmidt 2012). Ecological traps (preference for lower-quality habitat; Battin 2004) and perceptual traps (avoidance of high-quality habitat; Gilroy & Sutherland 2007; Patten & Kelly 2010) are extreme cases of nonideal habitat selection (Pärt et al. 2007).

In spite of their relative simplicity, IDD and IFD models provide a useful theoretical framework to explore species-habitat relationships and inter-individual differences in competitive ability (Boulinier et al. 2008). For example, based on empirical models, Haugen et al. (2006) found that 40 years of variation in the distribution of pike (*Esox lucius*) in a lake composed of two basins with contrasting productivity was consistent with an IFD. The presence or absence of habitat-specific variation in per capita productivity can have very different consequences for population dynamics, not to mention conservation (Morris 2003). For example, given similar population size and habitat quality, an IDD implies that a portion of the population contributes disproportionately to population growth whereas individual contribution to population growth is more uniform under an IFD, irrespective of habitat quality. Hence, the loss of high-quality sites may have disproportionately negative effects in species following an IDD not only because the region's best territories would be lost, but it would potentially threaten the reproduction and survival of dominant individuals. Populations can also be anywhere along a "free" to "despotic" continuum owing to spatio-temporal variation in population size and habitat quality (Ridley et al. 2004). Knowing where a regional population falls along this gradient would yield insight into the effective population size of a focal species representing sensitive species .

In this study, we tested predictions of the IFD and IDD on the demographic response of the Ovenbird (*Seiurus aurocapilla*), a neotropical migratory songbird, to an experimental alteration of its habitat (selection harvesting) in five pairs of study plots (1 control, undisturbed study plot – 1 treated plot, harvested study plot) over a 6 year period (1 year pre- and 5 years post-harvest). In the same study area, Pérot & Villard (2009) found patterns in density and plot-level productivity that were consistent with an ideal free distribution, whereas Thériault et al. (2012) found no evidence that Ovenbird males preferred plots treated through selection harvesting and hence, no evidence that this treatment created ecological traps. Here, we examined the magnitude and duration of effects of selection harvesting on Ovenbird density, territory size, productivity (per unit area and per capita), and daily nest survival rate to determine whether adaptive habitat selection (sensu Morris & MacEachern 2010) occurred in response to experimental disturbance. On the basis of the IFD, we predicted a negative effect of treatment on density (through an increase in territory size) and productivity per unit area, but no treatment effect on productivity per capita. In contrast, the IDD would predict that per capita productivity will be lower in treated plots than in controls, assuming that the former represent lower quality habitat. We also estimated the abundance and biomass of litter invertebrates during the peak of the Ovenbird nestling period because they represent the main source of food exploited by Ovenbirds (Stenger 1958) and food abundance is a key component of habitat quality on both the breeding and wintering grounds (Smith & Shugart 1987; Strong & Sherry 2000; Seagle & Sturtevant 2005). We predicted that, as treated stands regenerate, the magnitude of negative treatment effects on Ovenbird demography and abundance of litter invertebrates would decrease. This, in turn, should decrease the influence of either IFD or IDD on population dynamics, as partially harvested plots gradually become functionally equivalent to controls.

2.2 Methods

2.2.1 Study area

The study was conducted in northwestern New Brunswick, Canada (47°23'N, 67°40'W), within a 2000 km^2 forest District privately owned by J.D. Irving Ltd. This intensively-managed forest landscape is characterized by hardwood stands (25% of total area; sugar maple [*Acer saccharum*], yellow birch

[*Betula alleghaniensis*], and American beech [*Fagus grandifolia*]), conifer stands (20%; black spruce [*Picea mariana*], white spruce [*Picea glauca*], jack pine [*Pinus banksiana*]), mixedwood stands (18%) and spruce (*spp*.) plantations (37%; Etheridge et al. 2005).

For 30 years, J.D. Irving Ltd has managed hardwood stands and hardwood-dominated mixedwoods using partial harvest treatments, selection harvesting being the most widely used. This treatment typically removes 30-40% of the basal area (cross-sectional area at breast height [1.35 m] of all stems with a diameter ≥ 10 cm) every 20-25 years. The creation of skid trails (5 m wide) accounts for 20% of the basal area removal, the extra 10-20% being harvested in the residual forest between skid trails (Gaetan Pelletier, J.D. Irving Limited, pers. comm.).

2.2.2 Focal species and Experimental design

The Ovenbird is considered to be one of the vertebrate species most sensitive to forest management in the northern hardwood forest (Vanderwel et al. 2007, 2009). Its fledging success has been shown to be positively correlated with the biomass of litter macroinvertebrates and productivity of mature deciduous forest stands (Seagle & Sturtevant 2005).

From 2006 to 2011, we used a Before and After-Control and Impact Paired (BACIP) design to measure the demographic response of Ovenbird to the treatment (selection harvesting), while controlling for plot and year effects. Each year, we quantified density, territory size, productivity (per unit area and per capita), and daily nest survival rates in 10 study plots (25 ha each) that are spatially paired (see Haché & Villard 2010). The average distance was 4.2 km (± 1.0 SD) between paired plots and 23.8 km (± 9.1) among pairs. In December 2006 and January 2007, one plot of each pair was treated through selection harvesting, including a 50-m band harvested around each treated plot, whereas the other plot was left intact and used as a control. Each year, we individually-marked territorial males in all study plots using unique color-band combinations, except in one pair of study plots in 2006 (*n* = 25).

Territory size and configuration were estimated using spot mapping (Bibby et al. 2000). We mapped all detections of territorial males during 8 visits to each plot and drew ellipses around clusters of detections using countersinging and locations of banded males for guidance (see Haché & Villard 2010 for details). Only territories that overlapped study plots by ≥ 25% were considered in density estimates, which were obtained by adding all territories and territory fractions (fractions estimated as overlap of 0.25, 0.33, 0.50, 0.66, and 0.75) that overlapped the study area. Throughout the breeding season, we performed systematic nest searching and balanced the effort across territories, irrespective of local density. Each nest was monitored every 2-3 days until the young fledged, the nest was depredated, or abandoned. Productivity per capita was calculated as one-half of the number of young fledged per territory. Breeding success was also attributed to banded males seen with a family group, or to territories where we saw fledglings unable to sustain flight with an unbanded adult. In those instances, the mean number of young fledged per nest in the treatment vs. control was used to estimate productivity. The proportion of males with unknown breeding status was 25.2% and it did not differ between treatment and controls (23.8% and 25.8%; Appendix A). In the analyses, we assumed that those “unknown” territories had failed (see Appendix 1 for details). Productivity per unit area (/25 ha) was estimated by adding the contribution of all breeding pairs to a given study plot. For example, a pair that produced four fledglings and had 25% of its territory overlapping a study plot was considered to have contributed 1 young to the plot’s productivity.

In four pairs of study plots, we sampled Ovenbird food items (frequency of occurrence and biomass) during the peak of the nestling period (1- 12 July) over five breeding seasons (1 year pre- and 4 years post-harvest). We collected all invertebrates (≥ 2 mm) detected in the litter of a 0.2 m^2 quadrat over a 3 min period (Willson & Comet 1996; Van Wilgenburg et al. 2001). Sampling was conducted at 60 pre-determined locations in each study plot. We then estimated the frequency of occurrence and biomass of invertebrates (all taxa), and those of ground beetles (*Coleoptera*) and land snails (*Gastropoda*) in each study plot. Stenger (1958) showed that taxa found in Ovenbird stomach contents were proportionate to their availability in the corresponding territories. We compiled data on *Gastropoda* separately because calcium limitation may have important implications for Ovenbird productivity (Pabian & Brittingham 2007). Finally, we also compiled *Coleoptera* (imagos and larvae) data separately because adults of many forest bird species have been shown to forage extensively on them (Holmes

& Robinson 1988). The biomass of each group was quantified for each study plot (see Appendix 1 for further details on the sampling method).

2.2.3 Statistical analyses

Different variables were sampled at different levels of our hierarchical experimental design. Territory size and per capita productivity were measured at the territory level, abundance of invertebrates at the quadrat level, whereas density and productivity per unit area and biomass for each group of invertebrates were measured at the study plot level. Furthermore, pairs of plots were clustered at the landscape context level. To test for treatment, year, and treatment × year interaction effects on different demographic parameters and invertebrate abundance and biomass, we used variations of linear mixed and generalized linear mixed models (Appendix 1). Appropriate hierarchical levels were included as random effects as a function of the sampling unit of each response variable. Temporal autocorrelation associated with the repeated measurement of sampling units was explicitly considered by specifying a first-order autoregressive structure to each model. To distinguish treated plots and controls for the duration of the study, the five harvested plots were also considered as treated during the pre-harvest year. Consequently, a significant treatment × year interaction was required to infer a treatment effect. Using a similar statistical analysis, we also explored heterogeneity in food abundance within treated plots by testing for a difference in the abundance of litter invertebrates in samples collected on skid trails and in the residual forest, and to determine how it evolved as stands regenerated. We then used a post-hoc multiple comparison analysis to test for treatment effects in specific years. Lastly, a logistic exposure model was used to estimate the treatment, year, and treatment × year interaction effects on daily nest survival rate (Shaffer 2004). Because only one random effect can be included in the model using this procedure, 4 *a priori* models with treatment, year, and treatment × year interaction as predictors were compared using the Akaike information criteria (AIC). The first model had no random effect, and the three others had one of the three random effects accounting for the non-independence of our sample units (i.e. nest ID, plot, and landscape context).

2.3 Results

We monitored a total of 784 territories (458 in controls/326 in treated plots) over the six years, 721 (92%) of which were held by banded males. In total, 349 males were banded and 197 (105/92) returned for at least one breeding season. We found 229 nests (148/81). Of these, 135 (59%; 90/45) were successful. The mean number of young fledged per nest was 3.66 (± 1.1 SD, n = 85) in controls and 3.98 (± 1.1, n = 42) in treated plots (brood size was unknown for 8 successful nests). In monitored territories where no nest could be found, 212 (128/87) family groups were detected.

There was a significant treatment × year interaction effect on the density of territorial males ($F_{5,40} = 7.3$, $P < 0.001$). Significant negative treatment effects were observed for the first four years post-harvest (Figure 2.1A, Appendix 2). Territory size followed a similar pattern, with a significant treatment × year interaction effect ($F_{5,759} = 40.0$, $P < 0.001$). Territories were significantly larger in treated plots than in controls in all post-harvest years, but to a lower extent during the fifth year post-harvest (Figure 2.1B; Appendix 2). There was only a significant negative treatment effect on mean productivity per unit area ($F_{1,40} = 17.6$, $P < 0.001$). When analyses were conducted separately for each year, productivity per unit area was only significantly lower in treated plots during the first four years post-harvest (Figure 2.1C; Appendix 2). In contrast, we found no effects of treatment or year on per capita productivity (Figure 2.2A; Appendix 2), nor daily nest survival rate (Figure 2.2B). The best-ranked model estimating daily nest survival rate included landscape context as a random effect ($k = 13$, AIC = 626.86, AICw = 0.60). ΔAIC values for models with other levels of random effects or no random effect were > 2, suggesting substantially less support. Treatment effects on territory size, density, and productivity per unit area, as well as the lack of evidence for treatment effects on per capita productivity and daily nest survival rate are consistent with predictions from an IFD.

There was a significant treatment × year interaction effect ($F_{4,1912} = 15.7$, $P < 0.001$) on total abundance of litter invertebrates, with lower abundances in treated plots than in controls during the first four years post-harvest (Figure 2.3A; Appendix 2). The same treatment × year interaction effect was observed for abundance of *Coleoptera* ($F_{4,1912} = 5.1$, $P < 0.001$; Appendix 2) and *Gastropoda* ($F_{4,1912} = 3.2$, $P = 0.013$; Appendix 2). In contrast, when considering total invertebrate biomass, only year ($F_{4,24} = 4.4$, $P = 0.008$) and treatment ($F_{1,24} = 19.5$, $P < 0.001$) effects were significant. Total biomass was significantly lower in treated plots than in controls during the first four years of the study, including the pre-harvest year (Figure 2.3B; Appendix 2). Similarly, only year ($F_{4,24} = 3.6$, $P = 0.020$) and treatment ($F_{1,24} = 26.8$, $P < 0.001$) had significant effects on biomass of *Coleoptera* (Appendix 2), whereas only year was a significant predictor of biomass of *Gastropoda* ($F_{4,24} = 5.1$, $P = 0.004$; Appendix 2). However, when testing for year-specific treatment effects, the difference in biomass of *Coleoptera* was only significantly lower in treated plots than in controls during the first three years post-harvest ($P \leq 0.006$; Appendix 2). There was a significant skid trail × year interaction effect on total abundance of invertebrates ($F_{3,949} = 25.2$, $P < 0.001$; Figure 2.3C) and on the abundances of *Coleoptera* ($F_{3,949} = 2.92$, $P = 0.033$) and *Gastropoda* ($F_{3,949} = 4.4$, $P = 0.005$; Appendix 2). Total abundance of invertebrates was significantly lower in skid trails than between trails during the first two years post-harvest and the importance of this effect decreased consistently as stands regenerated (Appendix 2). A similar pattern was observed for the abundance of *Coleoptera* and *Gastropoda* (Appendix 2). The treatment effects we observed on food abundance were consistent with variations in territory size, density, and productivity per unit area, supporting the contention that food abundance is a key factor underlying the observed IFD.

2.4 Discussion

Ovenbird demographic parameters and their relationship to variations in the abundance of litter invertebrates were consistent with predictions from the ideal free distribution (IFD) (Fretwell & Lucas 1969) despite the fact that our focal species is strongly territorial. Density, through changes in territory size, was adjusted to match local habitat conditions, resulting in similar per capita productivity between treatments and controls. The fact that per capita productivity did not vary between habitat types with contrasting Ovenbird densities represents strong evidence against an ideal despotic distribution (IDD). As stands regenerated, treatment effects became weaker and they were barely detectable by the fifth year post-harvest, suggesting that treated plots were becoming functionally equivalent to controls.

Density-dependent effects on songbird territory size (Ridley et al. 2004; Sillett et al. 2004; Pons et al. 2008) or small mammal home range size (Abramsky et al. 1979; Pusenius & Schmidt 2002) have been shown in many species. The absence of post-treatment crowding in this study suggests that subordinate males could not force territorial individuals to share resources, or that they found alternative territories elsewhere in the study area. Territory size was negatively correlated with food abundance (see also Stenger 1958; Smith & Shugart 1987) and post-harvest adjustments in territory size by males banded in the pre-harvest year indicate adaptive habitat selection (see also Haugen et al. 2006; Morris & MacEachern 2010; Chalfoun & Schmidt 2012). The observed pattern is also consistent with food-value theory (Stenger 1958; Marshall & Cooper 2004), which predicts that males from treated plots would increase the size of their territory to compensate for the post-harvest decline in food abundance. This response seems to have allowed Ovenbirds to achieve similar per capita productivity, irrespective of treatment. As clearcut skid trails regained similar abundances of litter invertebrates as inter-trail forest around the fourth year post-harvest (Figure 2.3C), territory size decreased and treatment effects on demographic parameters almost all became non-significant by the fifth year post-harvest.

Although the average quality of a territory apparently did not differ between treatment and controls, the cues that are used by returning migrants to assess habitat quality and secure the resources required to attract a mate and produce young remain unclear. Site familiarity, private information (i.e. information from previous breeding experience; Piper 2011), information on predator activity (Emmering & Schmidt 2011), natal habitat preference (Davis & Stamps 2004), social information (Danchin et al. 2004; Pärt et al. 2011), or cues provided by habitat structure (James 1971; Smith & Shugart 1987) may all play a role (see ecology of information; Schmidt et al. 2010). Further studies should strive to tease apart these non-mutually exclusive factors, as exemplified by van Bergen et al. (2004), Betts et al. (2008), Mariette & Griffith (2012), and Thériault et al. (2012).

Very few studies have presented empirical evidence in support of an ideal preemptive distribution (Sergio & Newton 2003 and references therein, Zajac et al. 2006; Petty & Grossman 2010). In our study area, Thériault et al. (2012) found that male Ovenbirds returning from previous breeding seasons settled first in any given plot, alone or with a few unbanded recruits, and that settlement started 2-5 days earlier in controls than in selection cut plots. This may be seen as evidence for preemptive habitat occupancy by individuals familiar with the plots.

However, the fact that some plots were first occupied by a combination of returning males and recruits suggests that public information provided by experienced breeders is a more likely mechanism underlying habitat selection by recruits (see location cues; Danchin et al. 2004). The settlement pattern observed by Thériault et al. (2012) does not necessarily lead to a rejection of IFD predictions: higher-quality habitat may be selected first and lower-quality habitat later as density increases in controls (Giraldeau 2008). There also was no evidence for a treatment effect on apparent survival rate of male Ovenbirds during the first four years of this study (Haché & Villard 2010). The same study reports a lower recruitment rate in treated plots than in controls during the first year post-harvest. This probably reflected the increase in territory size of returning individuals in response to the treatment, because recruitment rate became similar between treated and control plots over the next two years (Haché & Villard 2010). These results and those reported in this study are all consistent with an IFD in a territorial songbird. Such a finding is somewhat unexpected for birds. Indeed, the IDD tends to receive more support than the IFD (reviewed by Rodenhouse et al. 1997, Piper 2011). Yet, there is a growing body of evidence suggesting that the IFD can indeed apply to birds (Weidinger 2000; Sebastian-Gonzalez et al. 2010; Quaintenne et al. 2011) and many other taxa (Beckmann & Berger 2003; Morris & MacEachern 2010 and references therein; Rieger et al. 2004; Haugen et al. 2006).

We showed that in a moderately altered ecosystem, individuals can adjust the size of their territory as a function of food abundance and, in turn, exhibit similar per capita productivity as their conspecifics from higher-density-habitat. This is further evidence that density can be a good indicator of productivity per unit area (Bock & Jones 2004; Pérot & Villard 2009), though not necessarily per capita (Skagen & Adams 2010). Hence, mosaics of varying habitat quality do not necessarily exhibit spatial source-sink dynamics. Temporal source-sink dynamics, where density-dependent factors act irrespective of habitat quality, also needs to be considered (Nevoux et al. 2012). Future studies should also consider that individual distributions most likely fall in a continuum between IDD to IFD rather than being either one or the other (Ridley et al. 2004). Lastly, subtle habitat-specific effects on population dynamics should be given consideration. For example, there is evidence that defending territories in habitat of lower-quality can incur a cost in terms of survival rate over long time periods (Vernouillet et al. in review). In the Ovenbird, stress levels and sex ratio in nestlings have also been shown to differ between partially harvested and control plots (Leshyk et al. 2012). Ultimately, this may reduce male fitness and, thus, population growth rates among habitat types varying in quality (Arlt et al. 2008). For these reasons, relatively subtle impacts of human activities on population dynamics deserve careful attention when considering our ever-expanding ecological footprint.

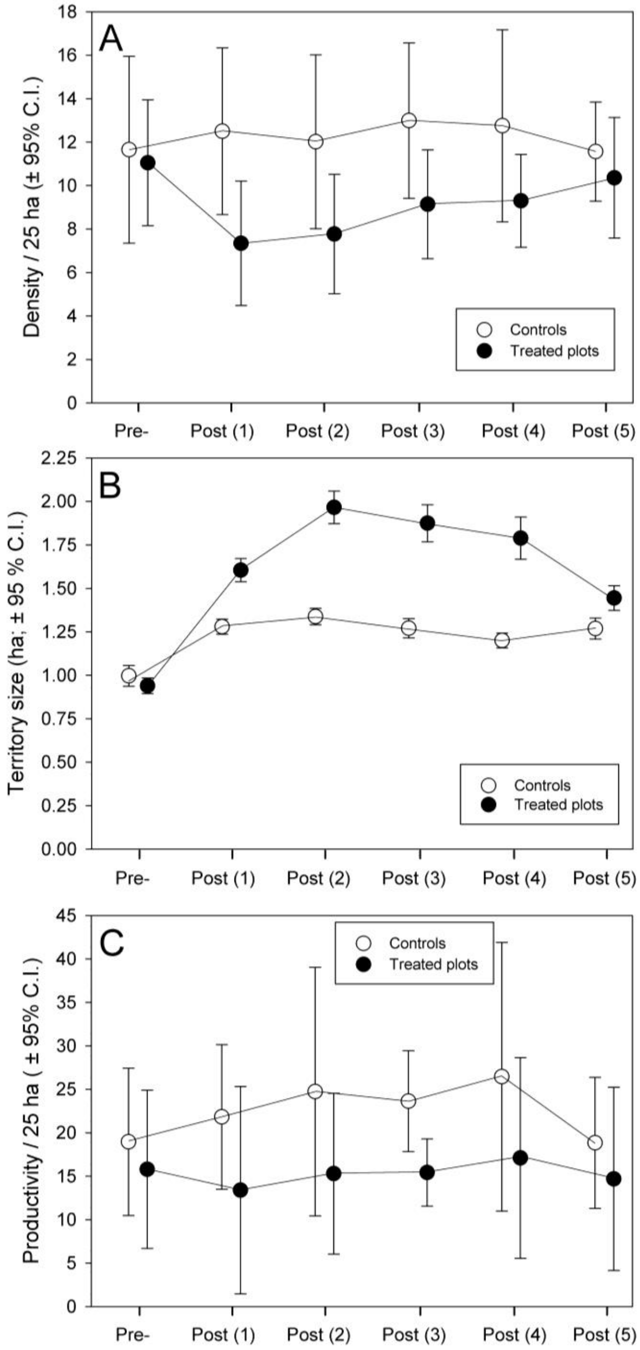

Figure 2.1. Mean (± 95% C.I.) density (A) and territory size (B) of territorial males and productivity per unit area (number of young fledged per 25 ha; C) in plots treated by selection harvesting and in controls one year pre-harvest and the first five years post-harvest.

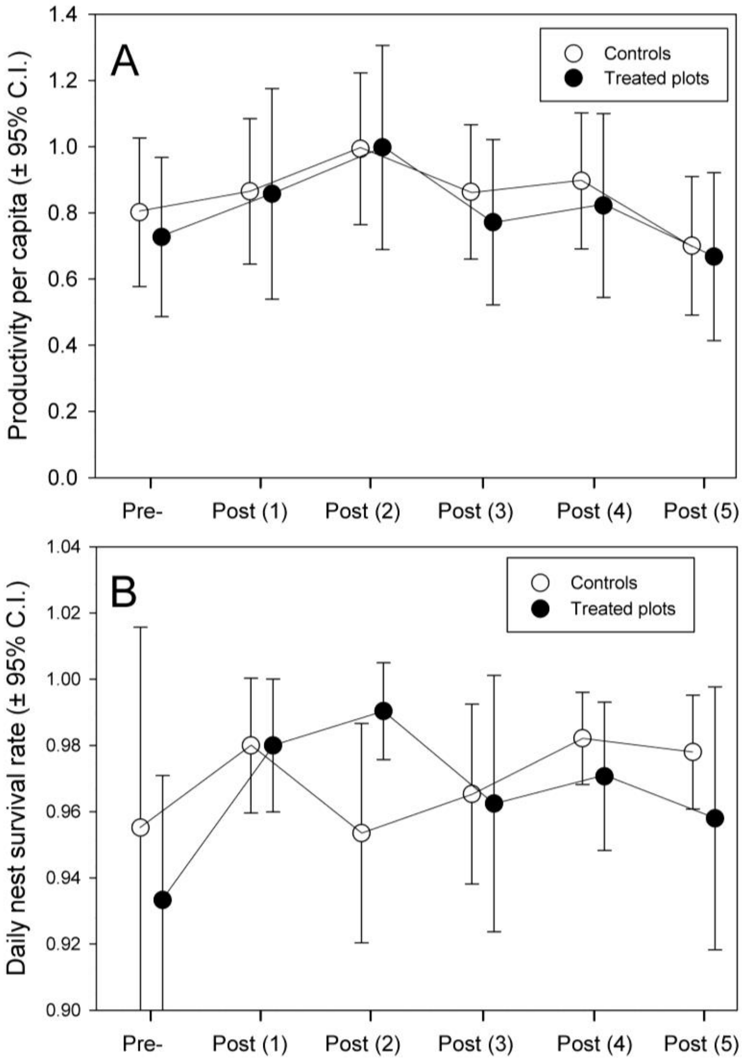

Figure 2.2. Mean (± 95% C.I.) productivity per territorial male (A) and estimated mean daily nest survival rate (B) in treated plots and controls one year pre-harvest and the first five years post-harvest.

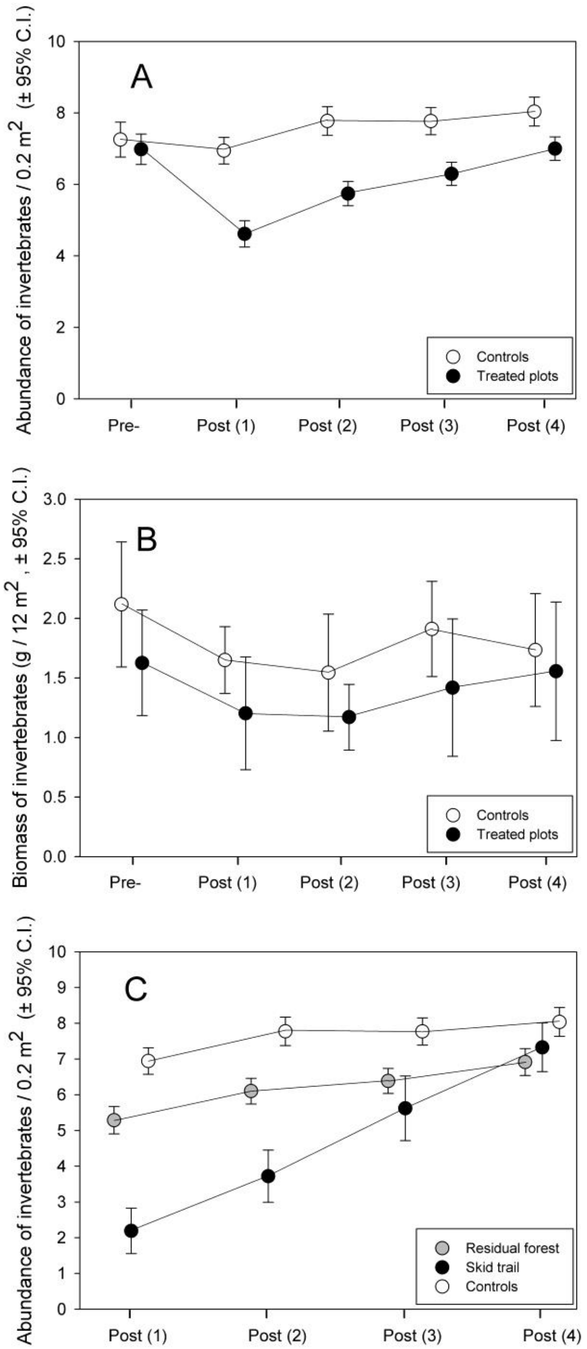

Figure 2.3. Mean (± 95% C.I.) abundance of invertebrates (A; per sampling point) and total biomass of invertebrates (B; per study plot) in treated plots and controls and mean (± 95% C.I.) abundance of invertebrates (C) per sampling point in skid trails vs. inter-trail forest in treated plots and in controls.

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CHAPTER 3: POSTHARVEST REGENERATION, SCIURID ABUNDANCE, AND POSTFLEDGING SURVIVAL AND MOVEMENTS IN AN OVENBIRD POPULATION

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3.1 Introduction

Postfledging survival is an important aspect of songbird demography (Anders & Marshall 2005). Recent studies have documented juvenile survival rates during the first few weeks postfledging for many forest songbird species and a wide range of survival estimates has been reported (e.g. 0.19 - 0.77; Powell et al. 2000; Fink 2003; Rush & Stutchbury 2008; Vitz & Rodewald 2011). Sources of this variation are not well understood but likely include species-specific life history and behavior, geographical location, methods, sample size, and environmental variability. For a given species, variation in postfledging survival has mainly been attributed to: 1) concealment procured in vegetation; 2) predator abundance; and 3) body condition of fledglings.

Higher juvenile survival has been reported in areas with dense ground cover. Authors have suggested that concealment from predators is crucial (hereafter, “concealment hypothesis”; King et al. 2006; Vitz & Rodewald 2011). However, other studies have reported no differences in postfledging survival between control plots and plots altered by harvest treatments resulting in denser shrub cover (Moore et al. 2010; Eng et al. 2011). This lack of consistency suggests that vegetation cover may interact with the predator species assemblage or other factors (e.g. food abundance) in different regions. There is also evidence for important annual variation in postfledging survival. This variation has been linked to fluctuations in predator abundance ("predator abundance hypothesis"; Schmidt et al. 2008; Streby & Anderson 2011). Finally, body condition may be an important predictor of postfledging survival ("body condition hypothesis"; Vitz & Rodewald 2011; Mitchell et al. 2011). Fledglings in better condition should be able to sustain flight earlier, thus shortening the critical stage of low mobility when they are most vulnerable to predators (Naef-Daenzer et al. 2001). Although there is a growing body of evidence in support of all of these factors, their relative importance in the same system has rarely been tested. Without simultaneously testing these alternative hypotheses, our ability to make realistic predictions of how fledgling survival is influenced by environmental variation and therefore its contribution to per capita productivity and population dynamics will remain limited.

Postfledging survival is often estimated as a population level rate, but choices made by individuals ultimately determine whether they survive. In forest ecosystems, studies on different species have shown that fledglings from mature forests often disperse to early-seral forests or to other patches with a dense shrub cover during the postfledging period (Vitz & Rodewald 2006; Streby et al. 2011a; Chandler et al. 2012). Dense cover may reduce predation risk and should offer similar benefits to adults that are molting and less mobile (Anders et al. 1998; Vega Rivera et al. 1999; Pagen et al. 2000; Bayne & Hobson 2001). Shrubby cover may also provide access to food sources that are less abundant in more open understories (Vitz & Rodewald 2007; Streby et al. 2011b; Chandler et al. 2012). Although the apparent convergence of postfledging movements toward areas with a dense shrub cover has been shown in several studies, how far and when fledglings move to such patches is still unknown. Another key uncertainty (but see Vitz & Rodewald 2010; Streby & Anderson 2013a) is whether fledglings originating from habitat with sparse shrub cover have higher movement rates, and whether these movements are directed toward dense vegetation relative to young fledged in areas with denser shrub cover. The body condition of nestlings has also been shown to be positively correlated with postfledging movement rate (Naef-Daenzer & Grüebler 2008; Vitz & Rodewald 2010) and although a similar positive relationship would be expected in response to predator abundance, to our knowledge this prediction remains untested.

In this study, our goal was to address some of these gaps in our understanding of postfledging ecology. Specifically, we set out to test predictions from the concealment, body condition, and predator abundance hypotheses to determine which factor or combination thereof best explained postfledging survival and movement in an Ovenbird (*Seiurus aurocapilla*) population from an intensively-managed forest landscape. The Ovenbird is a songbird generally associated with closed-canopy deciduous forest with a relatively sparse understory (Porneluzi et al. 2011). The study was conducted during two breeding seasons in plots treated 4 and 5 years earlier through selection harvesting, and in control plots. Shrub cover was denser in treated plots than in controls (22.8% and 32.1% for the fourth and fifth year postharvest, respectively; Haché et al. 2013a). Hence, according to the concealment hypothesis, we predicted higher postfledging survival and lower movement rates in treated plots than in controls. Because food density was higher in controls than in treated plots during the fourth year postharvest (by 10-60%, depending on invertebrate taxa; Haché et al. 2013b), we predicted higher postfledging survival/longer movements in controls than in treated plots, in accordance with the body condition hypothesis. Alternatively, individuals in good body condition may exhibit low movement rates if they fledged from an area of high food abundance, while individuals in poor body condition might exhibit higher movement rates as they search for areas of high food abundance. Finally, based on the predator abundance hypothesis, we predicted that spatial and temporal variation in predator abundance would be a better predictor of postfledging survival/movement rates than concealment from the vegetation or body condition of fledglings.

3.2 Methods

3.2.1 Study area

The study was conducted in a forest owned by J.D. Irving Ltd. (Black Brook District) located in northwestern New Brunswick, Canada (47º23'N, 67º40'W). The study area is dominated by spruce plantations (37%), along with forest stands characteristic of the Acadian region such as shade-tolerant hardwoods (25%), spruce-fir (20%), and mixedwood stands (18%) (Etheridge et al. 2006). The Black Brook District is considered to be one of the most intensively-managed forest landscapes in Canada (Montigny & MacLean 2005). Hardwood stands are generally managed through partial harvesting. Among the different silvicultural prescriptions (e.g. strip-cutting, patch-cutting, shelterwood), selection harvesting has been the most frequently used method since the early 1980s. Approximately 20% of the basal area (sum of the cross-sectional area at breast height [1.3 m] of all trees within a study plot) is removed by the creation of skid trails and an additional 10-20% is selectively harvested within the remaining forest strips. Skid trails are ca. 5 m wide and 20 m apart (see Figure 3.2 in Haché & Villard [2010] for an aerial photo).

3.2.2 Experimental design and data collection

In 2006, we selected five pairs of experimental plots (25 ha each; 1 treated plot and 1 control per pair) to measure the demographic response of the Ovenbird to selection harvesting. All plots were located within northern hardwood stands dominated by sugar maple (*Acer saccharum*). These plots have not been disturbed for at least 30 years and were dominated by trees 120-150 years of age. Paired plots were located 3-6 km apart and the mean distance between pairs of plots was 23.8 km (± 9.1 SD). Plots from a pair had to be close enough to avoid plot-specific landscape effects, yet far enough to avoid an influence of treatment effects on controls. Selection harvesting was applied to each treated plot and to a ca. 50-m band around each plot during the winter of 2006-2007. This study was based on data collected during the fourth (2010) and fifth (2011) years postharvest. See Haché & Villard (2010) for further details on the experimental design.

When nestlings were 6-7 days old, one (2010 and 2011) or two (2011) individuals per brood were weighed to the nearest 0.1 g and fitted with a ~ 0.5-g (0.48-0.52 g) radio-transmitter (BD-2N, Holohil Systems Ltd.). In 2011, two individuals per brood were monitored to increase sample size. We used nestling body mass as a proxy for body condition. Studies have often used ratios or residual indices, but body mass alone can provide a reasonable, easily measured estimate of fat content (Labocha & Hayes 2012) and may be more appropriate than indices that are unverified (Schamber et al. 2009). Transmitters were fitted using the harness technique developed by Hallworth et al. (2009). We relocated each fledgling every two days after fledging to determine its status (dead or alive) until day 14 and record its GPS location. Visual contact was required to determine the fate of each individual. To avoid disturbing family groups, we returned to each location later in the season (in July) to quantify microhabitat characteristics. Specifically, we measured litter depth and estimated shrub cover at all locations where fledglings were relocated, as well as 10 m north, southeast, and southwest of each location. We measured litter depth down to the mineral soil (to the nearest 0.5 mm) and estimated shrub cover (0.1 to 1.3 m high within a 2.5 m radius) using a semi-quantitative scale (0-10, 10-25, 25-50, 50-75, 75-90, and 90-100%). For each individual, we measured the distance between locations for every two-day interval and between the nest and the location of each individual on day 14 using ArcGIS 10. Fledglings were monitored during the "dependent period" when adult care is provided (ca. 24 days in Minnesota; Streby & Anderson 2013a). By day 14, fledglings can sustain flight over relatively long distances (> 10 m; S. Haché, M.-A. Villard, & E.M. Bayne, pers. observ.).

Haché et al. (2013b) estimated the density of Coleoptera, Gastropoda, and total invertebrates at 60 locations per study plot by counting all litter invertebrates (≥ 2 mm) detected within a 0.2 × 1.0 m quadrat over 3 minutes in 2010. Here, we also included the density of Lepidoptera larvae because softer food items represent a high proportion of the diet of fledglings (Streby et al. 2013). The three other groups of invertebrates are important items in the diet of adults, if not fledglings (Stenger 1958; Holmes & Robinson 1988; Pabian & Brittingham 2011; Streby et al. 2013) and they should at least influence the ability of adults to care for their young (via adult body condition) and, consequently, postfledging survival and movement. Owing to logistical constraints, invertebrate sampling took place in only four pairs of study plots.

Shrub cover and litter depth were estimated at 400 locations in four treated plots and two controls using the same approach described above to generate plot-level estimates (Haché et al. 2013a). We had to limit the number of study plots owing to logistical constraints. Lastly, in 2010 and 2011, Villard et al. (2012) estimated the relative abundance of two important predators on nests and fledglings: eastern chipmunk (*Tamias striatus*; King et al. 2006; Schmidt et al. 2008) and red squirrel (*Tamiasciurus hudsonicus*; Ball et al. 2009). Relative abundances of these predators were expressed as the mean number of detections per plot on the basis of eight spot mapping visits during the Ovenbird's breeding season.

3.2.3 Statistical analyses

To determine the relative importance of different habitat characteristics and spatio-temporal variation in abundance of predators on daily postfledging survival, we compared the importance of ten *a priori* models using Akaike's information-theoretic approach for model selection. Daily postfledging survival estimates were calculated using logistic-exposure models with a random effect (Shaffer 2004). To produce these models, we used the PROC NLMIXED procedure in SAS 9.2 (SAS Institute 2008). We accounted for our hierarchical experimental design by considering study plots ("Plot") as a random effect. To our knowledge, all studies measuring postfledging survival have shown important effects of number of days since fledging on survival rates, with most mortality occurring within the first four days and being negligible after 10 days. Consequently, all models presented include "Age" as a fixed effect (2, 4, 6, … , and 14 days). A model with Age as the only predictor was considered our null model because we were only interested in knowing whether models including the predictors of interest (i.e. Year, Abundance of eastern chipmunks, Abundance of red squirrels, Treatment, Litter depth, and Shrub cover) better explained variation in survival than a model including Age as single predictor. A model with both variables measured at individual locations (i.e. Litter depth + Shrub cover) was used to compare the relative importance of microhabitat. However, individuals found dead might have been carried by a predator and these locations may not reflect where predation occurred. Because most mortality occurred during the first four days postfledging, when little movement was observed, we used values of shrub cover and litter depth from the previous visit. Similar models were also generated using vegetation measurements from locations where young were found dead and both approaches yielded qualitatively similar results. Hence, we only reported the former models. Another model including plot-level abundances of both predators was considered as an “Abundance of rodent predators” model. Lastly, a model comprising all predictors was included as our full model. All 10 *a priori* models were run with and without a squared term for Age to determine whether a non-linear relationship would better predict daily postfledging survival rate. Models without the squared term provided a better fit to the data, so we present results from these models.

Villard et al. (2012) detected a significant year effect (2006-2011) on both rodent predators, but no significant treatment effect. Here, we present results from multiple comparison analyses testing for a year effect (2010 vs. 2011) on the abundance of eastern chipmunks, red squirrels, and both rodent predators. Haché et al. (2013b) tested for effects of treatment, year, and year × treatment interaction effects on density of Coleoptera, Gastropoda, and total invertebrates. Similarly, we used a generalized linear mixed effect model (GLMM) with a negative binomial distribution to test for a treatment effect on density of Lepidoptera larvae (with Plot as a random effect). We used a Chi-square test to determine whether fledglings originating from the same brood could be considered as independent sampling units by comparing the number of events where only one individual died, both individuals died, and both lived, to what would be expected by chance alone.

We tested the effects of the same predictors (i.e. 10 *a priori* models) on the distance between successive locations using linear mixed models (LMM; fledglings [FID] nested within Plot was used as a random effect for this and other models below). Because Age has been identified as important factor influencing fledgling movement (Vitz & Rodewald 2010; Streby & Anderson 2013a), the model containing Age as the only predictor was considered our null model. Again, because the distance over which predators can travel with their prey is unknown, only distances among locations where individuals were found alive were used. The same statistical approach was applied to determine whether there were Treatment, Year, and Treatment × Year interaction effects on the distance between locations of individuals on day 14 and the nest from which they fledged. We used a LMM to test for Treatment, Year, and Treatment × Year interaction effects on body condition. Also, using a LMM, we tested whether body condition was a good predictor of the number of days a fledgling would live and the distance between successive locations. We had to apply a logarithmic transformation to distance between successive locations to meet the assumptions of normality and equal variances. LMM and GLMM were generated using the PROC MIXED and PROC GLIMMIX procedures, respectively, in SAS. We report mean values ± 95% C.I.

3.3 Results

Transmitters were fitted on a total of 65 nestlings from 49 nests. Reliable data from the entire period (until death or when individuals reached 14 days) were obtained for 55 fledglings. Transmitter failure or loss of harness (eight individuals) and uncertain predation outcomes (two individuals; fledglings from the same brood found dead within 1 m of their undisturbed nest) explain the discrepancy in sample size. However, observations made prior to transmitter loss were used in the analyses (4 individuals). In 16 cases, two nestlings from the same brood were fitted with a transmitter. In five instances, only one of the two individuals was found dead. Only twice were both young from the same nest found dead at the same visit. In 6 instances, siblings were found > 100 m apart after 4 or 6 days. Thus, nestlings represented independent sampling units ($\chi^2_2 = 2.5$, $p = 0.29$).

We found 70% (21/30) of dead fledglings cached in shallow depressions in mineral soil covered by leaf litter. In one instance, remains were found in an eastern chipmunk burrow and twice, they were found on the top of conifer snags with no evidence of feathers having been plucked (i.e. raptor or corvid predation unlikely), suggesting predation by red squirrel or another small mammal. If this is correct, then raptors or corvids were responsible for 20% (6/30) of mortalities. There was no evidence for a treatment effect on sciurid abundance (Villard et al. 2012), but it varied widely between years: eastern chipmunk and red squirrel abundances were 8.3 and 2.5 times higher, respectively, in 2010 than in 2011 (Figure 3.1). However, there was only a trend for a Year effect on the abundance of eastern chipmunk ($t_{40} = 1.9$, $p = 0.07$) and it was only statistically significant when abundances of both rodent predators were pooled ($t_{40} = 2.4$, $p = 0.02$; red squirrel: $t_{40} = 1.2$, $p = 0.25$).

Of the 55 fledglings whose fate was known, 45.5% (25/55) were still alive on day 14 and 60% (18/30) cases of mortality occurred during the first two days postfledging, while the other 12 cases occurred between days 2 and 10 (Figure 3.2). For the fledglings with known fate and those whose transmitters lasted beyond day 2, we recorded 231 events (dead or alive based on visual contact; Table 3.1). The model explaining variation in daily postfledging survival rate that had the lowest AIC value was Age + Abundance of red squirrels (Plot) (Table 3.2 and Figure 3.3A). Another model (Age + Abundance of red squirrels + Abundance of eastern chipmunks (Plot)) had a ΔAIC < 2.0, suggesting competition among top models. However, there was little evidence suggesting that eastern chipmunk was an important variable as the ΔAIC for this model was equivalent to the penalty associated with adding this extra parameter to our best-ranked model. Although it had a relatively large ΔAIC (4.08), the Age + Year (Plot) model performed better than the null model (ΔAIC = 6.31; Figure 3.3B). There was only weak support for any of the 6 other candidate models.

Body weight did not differ significantly between years (13.5 ± 0.7 g [n = 20] and 14.3 ± 0.7 g [n = 30] in 2010 and 2011, respectively; $F_{1,36} = 3.5$, $P = 0.07$) and there was no Treatment nor Treatment × Year interaction effects (Ps > 0.37). In 2010, densities of Coleoptera, Gastropoda, and total invertebrates were 1.1, 1.6, and 1.4 times higher, respectively, in controls than in treated plots (Haché et al.

2013b). However, there was no Treatment effect on the density of Lepidoptera larvae (treated plots = 0.20 ± 0.07, controls = 0.16 ± 0.05, $F_{1,472} = 0.31$, p = 0.576). There was also no evidence that nestling body condition was a good predictor of fledgling survival ($n = 50$, $F_{1,38} = 1.3$, $P = 0.26$).

We recorded 199 distances among successive locations (two-day intervals) occupied by fledglings. The model explaining variation in movement between subsequent locations with the lowest AIC value was Age (Plot[FID]) (Table 3.3). The ΔAIC for the second best-ranked model was 4.7 suggesting little support for effects of habitat variables (Figure 3.4) and abundance of predators. However, there was a trend for a positive effect of body condition on movement between subsequent locations ($F_{1,142} = 3.9$, $P = 0.05$). In control plots, the mean distance between nests from which fledglings were radio-tracked and the closest stand with dense ground cover (i.e. plantation < 10-yr old or recently harvested hardwood stand [< 10-yr post-harvest]) was only 284.6 m ± 44.0 m. Nonetheless, only three individuals moved away from the stand in which they fledged and they moved in > 10-yr old plantations or a coniferous riparian area with open ground cover. Although some movements covered relatively long distances (maximum: 355 m), fledglings generally remained in the vicinity of their nest during the first two weeks postfledging. Mean distances between the nest and location on day 14 were 138.5 m ± 53.4 m in treated plots ($n = 10$) and 212.2 m ± 125.7 m in controls ($n = 15$), but there was no treatment effect on total distance moved ($F_{1,17} = 1.0$, $P = 0.34$).

3.4 Discussion

Our data provide strong support for the predator abundance hypothesis to explain variation in fledgling survival. Postfledging movement rate, however, was not influenced by habitat variables, predator abundance, or body condition. The three best-ranked models suggest that spatio-temporal variation in abundance of sciurid predators was a key factor influencing fledgling survival. However, only plot-level abundance of red squirrels had an important predictive effect; the model with plot-level abundance of eastern chipmunks as the single predictor received poor support. The third best-ranked model only included a year effect. Daily survival rate in year_x was inversely related to the abundance of both red squirrels and eastern chipmunks which, again, is consistent with the predator abundance hypothesis. Although shrub cover was significantly denser in treated plots than in controls in both years, there was no evidence for an effect of selection harvesting on postfledging survival or movement, hence there was no support for the concealment hypothesis. The absence of treatment-specific variation in body mass prevented us from experimentally testing the body condition hypothesis. However, there was no evidence that body condition influenced postfledging survival or movements.

Unlike effects of concealment in vegetation and body condition, the influence of predator abundance on postfledging survival and movements has rarely been tested. Not surprisingly, the relative influence of concealment vs. predator abundance remains poorly understood. Perceived predation risk induces antipredation responses (site selection and foraging behavior) that can reduce substantially the number of young fledged (Zanette et al. 2011). Our results provide no evidence that movement rate of fledgling Ovenbirds was altered by the abundance of rodent predators, but we cannot rule out the possibility that altered behavior of adults (e.g. foraging behavior) resulted in fledglings being disproportionally more vulnerable to predation in areas of high rodent density. A seasonal decline in the postfledging survival of Great and Coal Tits (*Parus major* and *P*. *ater*) has been attributed to higher abundance of predators later in the season (Naef-Daenzer et al. 2001). Fisher & Davis (2011) and Vitz & Rodewald (2011) have also suggested that spatial variation in predator abundance could be an important predictor of postfledging survival. However, to our knowledge, only Schmidt et al. (2008) have explicitly tested effects of predator abundance on postfledging survival in songbirds. They found that survival rate of juvenile Wood Thrushes (*Hylocichla mustelina*) was higher in years with intermediate rodent abundance. They interpreted this relationship as a functional response of raptors to changes in rodent abundance. The same rodent-raptor interaction was also proposed to explain the year effects observed on Ovenbird postfledging survival by Streby & Anderson (2011).

In this study, most predation on fledglings was associated with rodents (24/30), especially during the first 4 days, when they cannot sustain flight. Of the six predation cases attributed to raptors or corvids, three occurred between day 4 and 10. Some fledglings for which transmitter failure was assumed might have been predated by raptors and carried outside the range of our receivers, whereas other fledglings might have died from disease or exposure and subsequently been scavenged by rodents. Nonetheless, the fact that in 63% (24/38) of all instances of mortality or transmitter failure, carcasses were found in shallow depressions in mineral soil covered by leaf litter, in a chipmunk burrow, or predated without evidence of plucked feathers suggests that rodents and other small mammals were the prominent predators of fledglings in this study. Although rodent abundance in 2010 was high, it may have been insufficient to generate a shift in raptor diet towards a higher proportion of rodents. For example, we detected 4.3 times more eastern chipmunks and 3.4 times more red squirrels in the same study plots in 2007 than in 2010 (Villard et al. 2012). Forest-specialist raptors might also be present at lower densities in our study area as a result of intensive forest management (Olsen et al. 2006; Vanderwel et al. 2009; Harrower et al. 2010). Concealment might also be more important for fledgling survival and movement when density of raptors (visual predators) is high and olfactory predators such as rodents (Rangen et al. 2000; Colombelli-Négrel & Kleindorfer 2009) are kept at low densities.

Although a year effect on fledgling survival is consistent with an effect of annual variation in predator abundance, annual variation in other biotic or abiotic factors could also be invoked. For example, drought intensity had a strong negative effect on postfledging survival in Lark Buntings (*Calamospiza melanocorys*; Yackel Adams et al. 2006). However, there was no major change in food density in control plots from 2006-2011 (Haché et al. 2013b) and, according to a local weather station, there was no substantial variation in mean temperature (17.3 vs. 16.5°C) nor total precipitation (142.9 vs. 144.5 mm) in June and July

2010 vs. 2011 (Environment Canada 2012). Also, the observed pattern might have been influenced by density-dependent effects on predation risk through apparent competition. Density of Ovenbird males was lower in treated plots than in controls in 2010, but it was similar in 2011 and there was no evidence for a year effect (Haché et al. 2013b). In the same study plots, four bird species had higher densities in 2011 than 2010, but four other species showed no year effect (Haché et al. 2013a). However, except for the Ovenbird, we do not know whether these changes in density are correlated with the number of young fledged. Future studies should investigate the relative importance of density-dependence (conspecifics and heterospecifics) on fledgling survival.

Plot-level abundance of red squirrels, but not that of eastern chipmunks, had an important effect on Ovenbird postfledging survival, irrespective of year. Considering that eastern chipmunk detections were 20% higher than those of red squirrel and that the chipmunk is a known predator of fledglings (King et al. 2006, Schmidt et al. 2008), this result was unexpected. In the same study area, Poulin & Villard (2011) showed a negative relationship between daily nest survival rate of Brown Creepers (*Certhia americana*) and the proportion of cone-producing spruce plantations within a 2-km radius of the study plots. They suggested that spruce cone production may increase local abundance of red squirrels and in turn, affect nest survival in years of low cone crops. In this study, higher plot-level abundance of red squirrels was indeed found in plots located near older plantations or coniferous riparian areas (S. Haché & M.-A. Villard, unpubl. data). Hence, landscape structure may influence Ovenbird fitness (see also Burke & Nol

2000). Vitz & Rodewald (2011) mentioned that regional variation in predator abundance could explain the wide differences in postfledging survival reported among studies for a given species. Based on our results, spatial variation in predator abundance may also affect postfledging survival over relatively fine spatial scales.

Previous studies on songbird postfledging survival within partially-harvested northern hardwood forests also did not report evidence for harvesting effects (Moore et al. 2010; Eng et al. 2011). Spatial heterogeneity in shrub cover within old, untreated northern hardwood forests (gap-phase dynamics; Runkle 1985) may provide sufficient concealment against visual predators. Similarly, movements appeared not to be altered by post-harvest regeneration in our plots (see also Berkely et al. 2007; Vitz & Rodewald 2010). Movements of fledglings from controls were not directed toward harvested areas or young plantations, as was predicted based on previous studies (Vitz & Rodewald 2006; Streby et al. 2011a; but see Chandler et al. 2012). However, it should be noted that in Minnesota, the peak in capture rate of hatch-year Ovenbirds in clearcuts occurred around the second week of August (Streby et al. 2011a), whereas our monitoring ended during the last week of July. Hence, we cannot rule out the importance of early-seral stands for juvenile Ovenbirds later in the season (see also Streby & Anderson 2012).

In our study area, the forestry company uses herbicides to control deciduous regeneration shortly after planting spruce, which reduces the amount and diversity of food (fruits and invertebrates) available to songbirds and, consequently, may reduce the attractiveness of this habitat to songbirds hatched in nearby hardwood stands. Indeed, an experimental reduction of food abundance in recent clearcuts (5-12 years old) lowered the frequency of occurrence of mature-forest birds (Major & Desrochers 2012). Streby & Anderson (2013a, b) found that Ovenbird postfledging survival rate was lower in young clearcuts and when crossing roads than in older ‘‘sapling-dominated clearcuts’’ (but see Vitz & Rodewald 2013). Interestingly, in this study, the three individuals that moved outside their natal stand went in old coniferous stands after crossing a road, but limited sample size prevents us from making strong inferences.

A positive effect of body mass on songbird juvenile survival has often been reported (e.g. Perrins 1965; Nur 1984; Naef-Daenzer et al. 2001; Suedkamp Wells et al. 2007; Mitchell et al. 2011), but many other studies reported no relationship (e.g. Anders et al. 1997; Hovick et al. 2011; Rivers et al. 2012; Streby & Anderson 2013b). Here, the selection harvest treatment did not influence nestling body mass shortly before fledging and although movements tended to increase with body mass, there was no significant relationship between body mass and postfledging survival, irrespective of the treatment.

Postfledging survival is an important component of songbird demography and this critical part of their life cycle must be incorporated in population growth and viability analyses. Our results indicate that in the Ovenbird, a species typically associated with closed-canopy deciduous forest with a relatively open understory, moderate habitat alteration through selection harvesting may not influence survival or movements of fledglings. Effects of spatio-temporal variation in predator abundance on postfledging and nestling survival rates differ, highlighting the importance of stage-specific survival estimates (Schmidt et al. 2008; Streby & Anderson 2011). Future studies should explore effects of landscape configuration on juvenile survival and address the complex relationships between yearly variations in predator abundance and associated trophic cascades (Yang 2004; Schmidt et al. 2008; Schmidt & Ostfeld 2008). Such information about spatio-temporal variation in predation risk during the postfledging period is needed if we are to accurately model songbird population dynamics.

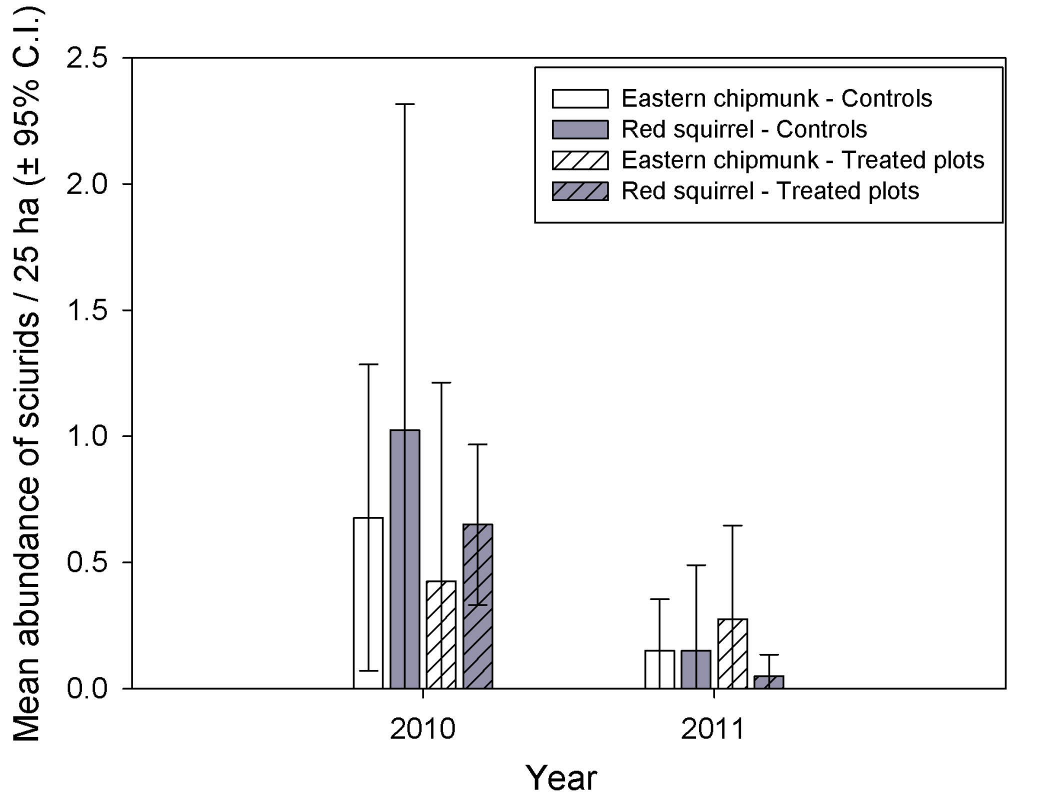

Figure 3.1. Mean abundance (± 95% C.I.) of eastern chipmunks and red squirrels in plots treated by selection harvesting and controls during the two years of the study.

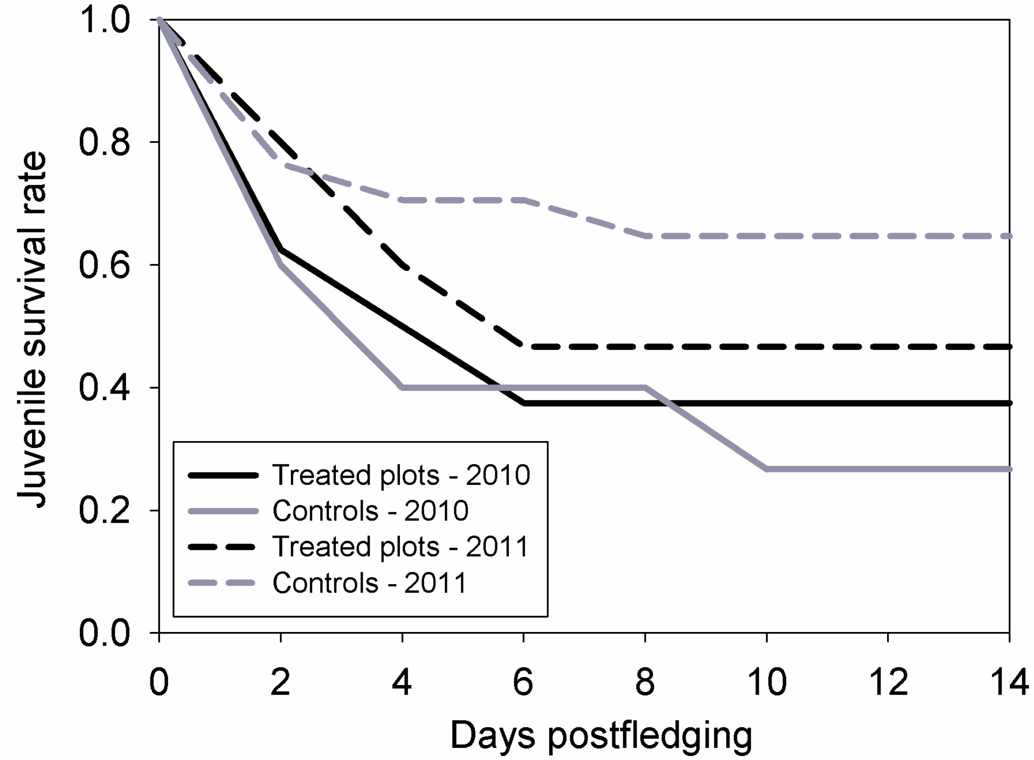

Figure 3.2. Cumulative postfledging survival rates of Ovenbirds as a function of treatment for both years.

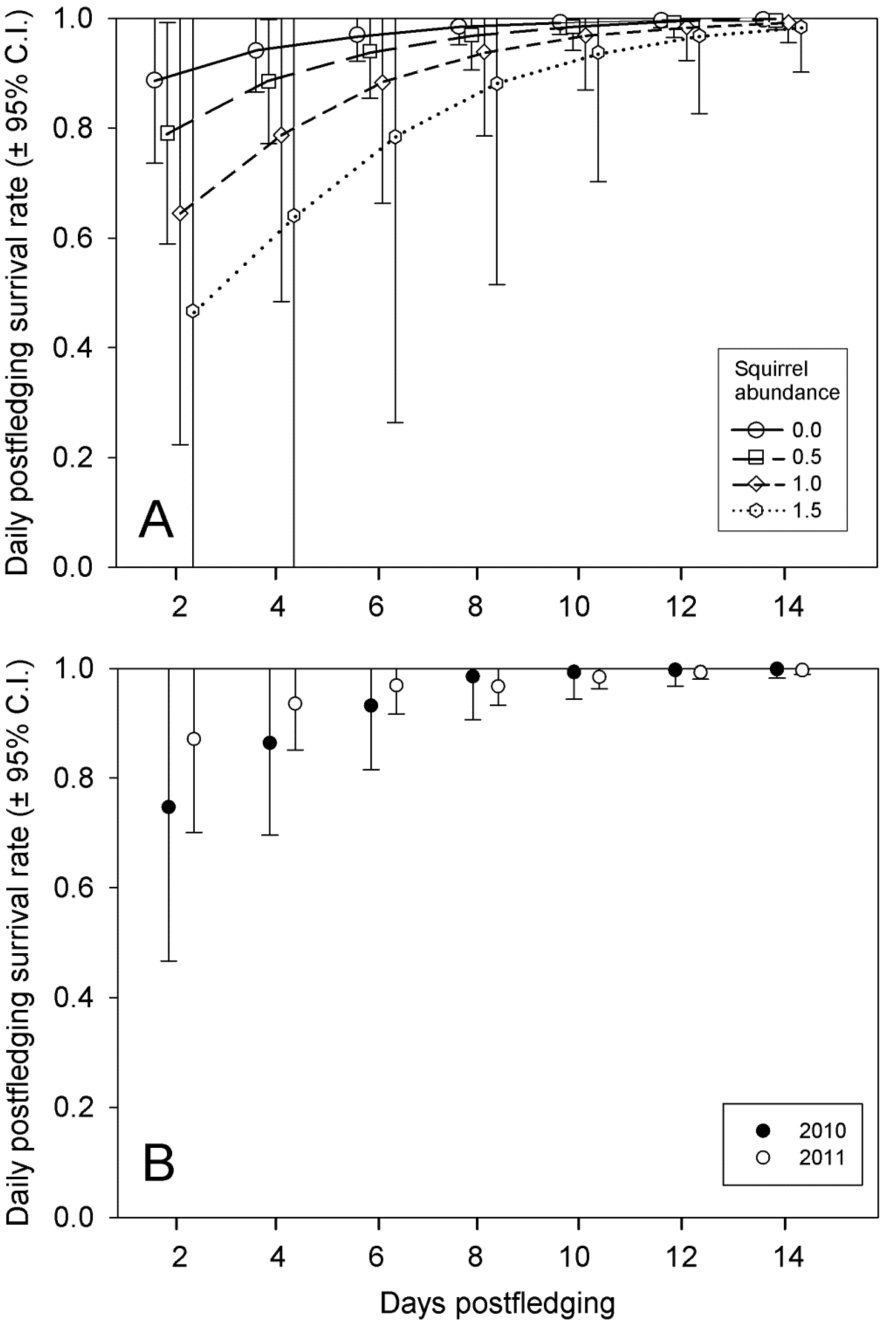

Figure 3.3. Predicted daily postfledging survival estimates in Ovenbirds as a function of age and abundance of red squirrels (mean number of detections per visit; A) or year (B).

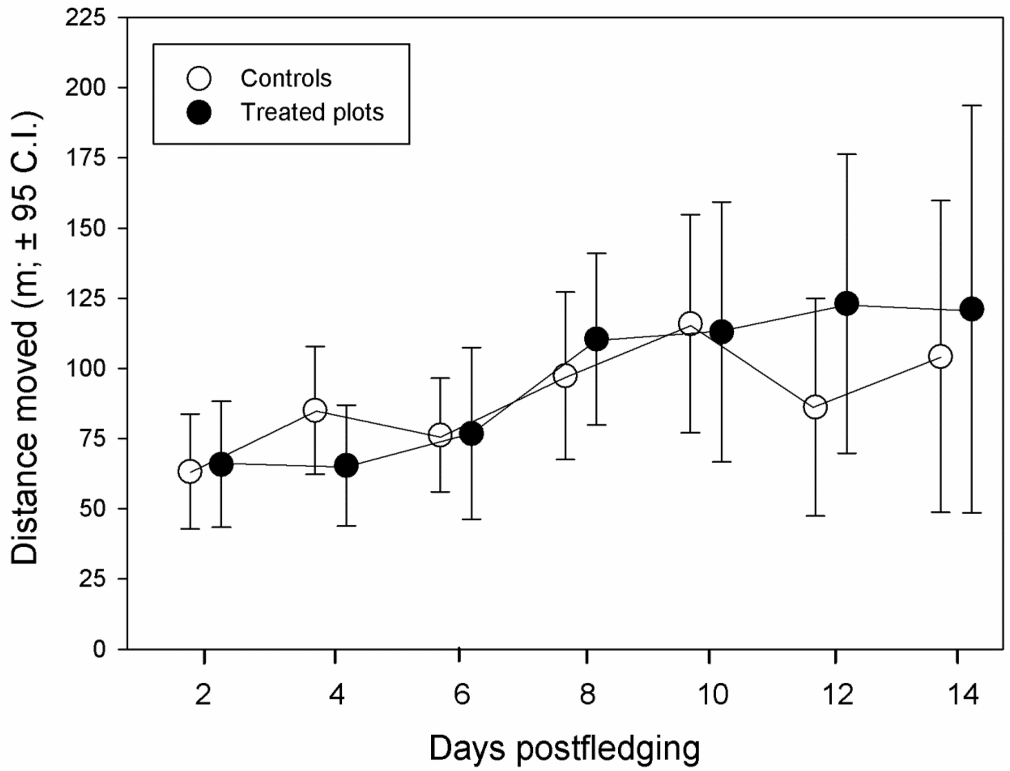

Figure 3.4. Movements of juvenile Ovenbirds during the first two weeks postfledging in treated plots and controls. For example, a value recorded at day 4 is the distance between locations occupied on days 2 and 4.

Table 3.1. Number of nestlings fitted with a radio-transmitter and postfledging observations (dead or alive) for each study plot and both years of the study. For four nestlings, data were available prior to transmitter loss.

STUDY PLOT	STUDY PLOT PAIR	TREATMENT	# OF NESTLINGS (2010/2011)	# OF OBSERVATIONS (2010/2011)
A	1	SELECTION CUT	0/4	0/7
B	1	CONTROL	3/3	16/9
C	2	SELECTION CUT	3/4	10/28
D	2	CONTROL	5/2	11/14
E	3	SELECTION CUT	3/2	9/14
F	3	CONTROL	4/10	11/50
G	4	SELECTION CUT	2/6	4/16
H	4	CONTROL	1/4	7/16
I	5	SELECTION CUT	1/0	7/0
J	5	CONTROL	2/0	2/0
TOTAL			24/35	77/154

Table 3.2. Results from 10 *a priori* models used to generate daily postfledging survival estimates from 231 observations of Ovenbirds (n = 59) in northwestern New Brunswick. Models are ranked from the lowest to the highest AIC values (Akaike's information criterion). K is the number of parameters, Dev is the deviance, ΔAIC is the AIC value relative to the top-ranked model, W is model weight, RESQ is abundance of red squirrels, and EACH is abundance of eastern chipmunks. Note that all models included Plot as a random effect.

Model description	*K*	Dev	AIC	ΔAIC	W
Age + RESQ (Plot)	4	137.3	145.3	0	0.55
Age + RESQ + EACH (Plot)	5	137.1	147.1	1.88	0.22
Age + Year (Plot)	4	141.3	149.3	4.08	0.07
Age (Plot)	3	145.6	151.6	6.31	0.02
Age + Treat + Year + Lit + Shrub + RESQ + EACH (Plot)	9	134.2	152.2	6.96	0.02
Age + Lit (Plot)	4	144.6	152.6	7.34	0.01
Age + Shrub (Plot)	4	144.8	152.8	7.58	0.01
Age + Treat (Plot)	4	145.4	153.4	8.12	0.01
Age + EACH (Plot)	4	145.5	153.5	8.26	0.01
Age + Lit + Shrub (Plot)	5	144.0	154.0	8.71	0.01

Table 3.3. Results from 10 *a priori* models testing for effects on the distance between subsequent locations (n = 199) from 41 Ovenbirds in northwestern New Brunswick. Only distances from individuals found alive have been used in these analyses. Models are ranked from the lowest to the highest AIC values (Akaike's information criterion). K is the number of parameters, Dev is the deviance, ΔAIC is the AIC value relative to the top-ranked model, W is model weight, RESQ is abundance of red squirrels, and EACH is abundance of eastern chipmunks. Note that all models included fledgling ID nested within Plot as a random effect.

Model description	*K*	Dev	AIC	ΔAIC	W
Age (Plot[FID])	4	141.4	149.4	0.0	0.79
Age + RESQ (Plot[FID])	5	144.1	154.1	4.7	0.07
Age + Treat (Plot[FID])	5	144.7	154.7	5.3	0.06
Age + Year (Plot[FID])	5	145.0	155.0	5.6	0.05
Age + EACH (Plot[FID])	5	145.9	155.9	6.5	0.03
Age + RESQ + EACH (Plot[FID])	6	148.6	160.6	11.2	0.00
Age + Shrub (Plot[FID])	5	151.4	161.4	12.0	0.00
Age + Lit (Plot[FID])	5	151.8	161.8	12.4	0.00
Age + Lit + Shrub (Plot[FID])	6	161.7	173.7	24.3	0.00
Age + Treat + Year + Lit + Shrub + RESQ + EACH (Plot[FID])	10	174.5	194.5	45.1	0.00

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CHAPTER 4: ASSIGNING BIRDS TO GEOGRAPHIC ORIGIN USING FEATHER HYDROGEN ISOTOPE RATIOS (δ^2H): IMPORTANCE OF YEAR, AGE, AND HABITAT

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4.1 Introduction

Recent studies aiming to assign the origin of individuals or populations of migratory animals have emphasized the advantages of intrinsic markers that circumvent the need for recapturing previously marked individuals (Hobson 2011). Contaminants, parasites, pathogens, trace elements, and genetic markers have all been suggested as potential intrinsic markers (reviewed by Hobson & Norris 2008; Hobson 2008; Bensch et al. 2009; Coiffait et al. 2009; Rodríguez et al. 2011). Stable isotope measurements of animal tissues are frequently used to quantify animal movement because biogeochemical information inherent in isotope values is transferred from the base of food webs to animal tissues (Hobson & Wassenaar 2008). Assignment of an individual to geographic origin using this approach is based on the premise that spatial patterns of several elements (i.e. isoscapes) are known or can be modeled (West et al. 2010).

The stable isotope ratios of H ($^2H/^1H$, depicted as δ^2H) are particularly useful for assigning individuals to approximate location because the processes that create variance in these isotopes in the hydrosphere are relatively well understood at continental scales (Clark & Fritz 1997; Bowen et al. 2005; West et al. 2010). For many migratory bird species in North America, moulting occurs on the breeding grounds (Pyle 1997) prior to migration and δ^2H value of feathers (δ^2H_f) obtained elsewhere can be used to place birds on δ^2H_f isoscapes (e.g. Hobson et al. 2009a, b). Recent advances in analytical approaches such as Bayesian or likelihood-based assignment techniques now integrate several sources of error (Wunder 2010) when determining the spatial origin of birds as a function of their isotopic signature. However, which covariates should be included in such models remains unclear for most species owing to limited studies looking at within and between individual variance in δ^2H_f from birds of known origin (Smith et al. 2008; Hobson 2011).

Numerous assumptions are made when using isotopes to assign birds to specific moulting locations. First, the underlying amount-weighted mean growing season δ^2H in precipitation from the long-term Global Network of Isotopes in Precipitation (GNIP; δ^2H_p) database (IAEA/WMO 2001) is assumed to correctly model δ^2H. Compared to studies conducted in coastal regions, those based on feather samples collected in central North America tend to more closely match predictions from the GNIP model (Lott et al. 2003; Wunder et al. 2005; reviewed by Hobson 2008). While this difference may reflect the fact that studies conducted closer to oceanic coasts have mainly featured "problematic groups of birds" (i.e. shorebirds and raptors; Lott et al. 2003; Wunder et al. 2005) it may be more likely that some coastal effects on δ^2H_p have not been properly modeled owing to more important annual variations in δ^2H_p. A second assumption is that differences among individuals from the same part of a breeding range do not reflect differential timing in growth (Wassenaar & Hobson 2006; Reudink et al. 2008). Understanding the amount of within and between feather variation in individual birds is important for testing this assumption (Wassenaar & Hobson 2006; Paxton et al. 2007; Smith et al. 2008; Bortolotti 2010; but see Kelly et al. 2002 and Mazerolle et al. 2005). A third assumption is that all individuals of a species show the same isotoptic signature if they grew their feathers in the same region. However, differences between adults and juveniles (i.e. hatch-year) have been shown (Meehan et al. 2003; Langin et al. 2007; Betini et al. 2009) suggesting that this assumption needs to be explicitly tested, especially when using stable isotopes for studying age-specific dispersal questions.

In this study, our objectives were to determine factors influencing intra- and inter-individual variability in δ^2H_f from known origin Ovenbirds (*Seiurus aurocapilla*) in a coastal forest of eastern Canada. From 2006 to 2011, we monitored a subpopulation of individually-marked Ovenbirds in New Brunswick to study the effects of selection harvesting on demographic parameters including recruitment and dispersal (Haché & Villard 2010). To confirm the validity of using δ^2H_f measurements to study recruitment and dispersal dynamics in Ovenbird populations, we tested for age (nestling vs. adult) and year (2005-2011) effects. Based on results from Langin et al. (2007) on American Redstarts

(*Setophaga ruticilla*), we predicted that nestlings will have a lower δ^2H_f than adults and that this effect will vary among years due to differential departures of local climate and δ^2H_p from the long-term GNIP average (Van Wilgenburg et al. 2012). We also tested for effects of microclimate. Because single-tree selection harvesting opens the canopy, which in turn can increase average temperatures on the forest floor (Mladenoff 1987; Vance & Nol 2003), we hypothesized that nestlings from harvested stands would experience greater evapotranspiration than those from control stands. Betini et al. (2009) found that nestling Tree Swallows (*Tachycineta bicolor*) from sites with higher ambient temperatures had higher δ^2H_f values. Hence, we predicted that nestlings from harvested stands (i.e. grown under semi-open canopies) will have a higher δ^2H_f than nestlings from untreated (closed canopy) stands. We also hypothesized that δ^2H_f would vary among feather types (here, primaries vs. rectrices) for a given individual, because in the Ovenbird, flight feathers are typically grown in the nest while tail feathers are grown once the young have fledged, altering the microclimate and energetic regime under which the different feathers are grown (Betini et al. 2009). Therefore, we predicted that δ^2H_f from primaries will have a lower δ^2H_f than rectrices. Adults moult in August and September (Pyle 1997) whereas nestlings grow their feathers in June and July. Hence, if age-specific differences in δ^2H_f are correlated with within breeding season variation in precipitation amount, we predicted that δ^2H_f would decrease with increasing amount of rainfall, as expected from continental patterns (Clark & Fritz 1997). Additionally, we compared predictions from the continental model linking δ^2H_f with predicted δ^2H_p (Bowen et al. 2005; Clark et al. 2006) to the observed δ^2H_f from a study area located close to the Atlantic coast. This comparison aimed to determine whether δ^2H_f assignment predictions based on the long-term GNIP average are as accurate for coastal compared to more inland regions (Langin et al. 2007; Coulton et al. 2009; Van Wilgenburg et al. 2012).

4.2 Methods

4.2.1 Study area and experimental design

The study was conducted in the Black Brook District (47° 23' N, 67° 40' W), a 2000 km^2 land base owned by J.D. Irving Ltd. located in northwestern New Brunswick, Canada (ca. 200 km from the Gulf of St. Lawrence). The region is characterised by a mosaic of relatively small management units of spruce plantations (37%) and deciduous (25%), coniferous (20%), and mixedwood (18%) forest stands. Mean patch size per stand type ranges from 16.1-107.0 ha (Etheridge et al. 2005, 2006).

In 2006, an experiment was designed to monitor the demographic response of the Ovenbird to single-tree selection harvesting (Haché & Villard 2010). The treatment removed 30-40% of the basal area (cross-sectional area at breast height [1.35 m] of all trees with a diameter $\geq$ 10 cm) every 20-25 years, 20% of which is associated with the creation of skid trails (5m wide and 20 m apart). The remaining 10-20% is harvested from the residual stand between skid trails. Specifically, five pairs of study plots (25 ha each) located in untreated mature deciduous stands ($\geq$ 30 years since last disturbance) were used in a before-after control-impact paired design (BACIP). One plot of each pair was harvested by single-tree selection harvesting during the winter between the first and second year of the study. The distance between the most distant study plots was 40 km. We marked most territorial males each year and conducted intensive nest searching (Pérot & Villard 2009; Haché & Villard 2010). Some nest searching was also performed in 2005 in control stands. Males banded in the study area in year x that returned in year $x + 1$ were assumed to have moulted in the study area prior to fall migration (Pyle 1997). In 2008 ($n = 7$), 2009 ($n = 21$), 2010 ($n = 23$), and 2011($n = 14$), the two 3rd rectrices were collected from returning males. When nestlings were 6-9 days old, two 6th primaries were plucked from two randomly chosen nestlings per nest. Primaries were collected in both treated plots (i.e. single-tree selection) and controls in 2005 ($n = 5$), 2006 ($n = 10$), 2008 ($n = 7$), 2009 ($n = 19$), 2010 ($n = 26$), and 2011 ($n = 21$).

In nestlings, rectrices do not grow significantly until they have fledged. To determine whether variation in δ^2H_f reflects the different feather types taken from nestlings and returning males, both primaries (p1) and rectrices (r3) were collected from 49 hatch-year birds captured during the 2010 fall migration at the Lesser Slave Lake Bird Observatory (LSLBO), Alberta, Canada (55° 20' N, 114° 40' W). Prior to fall migration (pre-basic moult), hatch-year birds replace their coverts, body feathers, and rarely tertials while the flight feathers and rectrices are only replaced after their first breeding season (Pyle 1997).

4.2.2 Stable isotope analysis

All feathers were cleaned using 2:1 chloroform:methanol solution to remove surface oils. Samples were prepared according to Wassenaar (2008) and analysed at the Stable Isotope Hydrology and Ecology Laboratory of Environment Canada (2005-2010) and the Colorado Plateau Stable Isotope Laboratory (2011). An H_2 pulse generated from high-temperature (1350°C) flash pyrolysis for each sample (350 ± 20 µg) was used to obtain stable-hydrogen measurements by continuous-flow isotope-ratio mass spectrometry (CFIRMS). In order to account for exchangeable hydrogen in keratins, we used comparative equilibration with in-house keratin working standards, BWB (-108‰), CFS (-147.7‰), CHS (-187‰), for which the δ^2H value of non-exchangeable H had been previously established (Wassenaar & Hobson 2003). Both labs used the same standards and analyzed samples the same way. All results are expressed as nonexchangeable deuterium isotopic ratio (δ^2H_f) in units of per mil (‰) and normalized according to the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale. Based on within run analyses of keratin standards, we assume measurement error to be ca. ±2‰.

4.2.3 Statistical Analyses

Interpolated amount-weighted mean δ^2H_p for the growing season for our study area estimated by the GNIP model (Bowen et al. 2005; http:www.waterisotopes.org) were converted to a predicted range of δ^2H_f using the calibration equation for songbirds suggested by Clark et al. (2006, 2009). To test for age, year, and age × year interaction effects on δ^2H_f, we used a two-way ANOVA. A generalized linear mixed model was used to determine whether δ^2H_f from nestlings was significantly influenced by year, treatment, and year × treatment interaction (fixed effects) while controlling for the nested experimental design (i.e. nest[plot] and plot[pair of plots]; random effects). This analysis only included values for nestling samples collected in 2009-2011, owing to low sample sizes in treated plots during previous years. Returning males could not be assigned to a given study plot as they often move substantially during the post-fledging period (Haché et al., unpublished data). Hence, because individuals may grow their feathers in different habitat types than those where they held a territory, the effect of harvest treatment on δ^2H_f from returning males could not be tested and all individuals were considered as a random sample from our study area to test for a year effect (one-way ANOVA). We tested for a within individual difference in δ^2H_f by comparing mean values from primaries and rectrices collected from hatch-year birds using a paired t-test. An ANCOVA was used to determine whether δ^2H_f was influenced by the Julian date at which nestling primaries were collected, and whether the observed pattern changed among breeding seasons (2009-2011). A similar analysis could not be performed for returning males because their moulting dates could not be determined. Lastly, linear regressions were performed to investigate potential causal relationships between δ^2H_f in nestlings and returning individuals and the amount of precipitation in months prior to feather growth/moult. Hence, different combinations of the total amount of precipitation (mm) in May and June were considered for nestlings (3 models), whereas combinations of monthly precipitation values during the breeding season (May-July; 6 models) in the previous year (hereafter, year *x*-1) were considered for returning individuals. Precipitation data for our study area (St-Leonard weather station) were obtained online from Environment Canada (http://www.climate.weatheroffice .gc.ca).

4.3 Results

In our study area, the estimated growing season mean δ^2H_p ranged from -62.4 to -64.8‰ (Bowen et al. 2005; note that three 20' x 20'grids were included in our study area, each with a δ^2H_p value). These values calibrated in δ^2H_f corresponded to a range of -80.8 to -82.9‰, close to the mean δ^2H_f of -86.2 ± 12.6‰ SD ($n = 153$; range: -45.5‰ to -111.9‰) measured from the feather samples. Age significantly influenced δ^2H_f as shown by a significant age × year interaction ($F_{3,143} = 7.51$, $p < 0.001$; Figure 4.1). The most important departures from the predicted long-term average δ^2H_f were observed in 2005 for nestlings (-65.5‰) and in 2010 for returning males (-67.0‰; Figure 4.1b). When analyses were conducted by age class, a significant year effect was observed in δ^2H_f for both returning males ($F_{3,61} = 61.68$, $p < 0.001$) and nestlings ($F_{2,52} = 46.56$, $p < 0.001$; Figure 4.1). Furthermore, there was no significant difference between the δ^2H_f of nestlings in treated plots (-94.6 ± 7.0‰) and controls (-93.3 ± 8.8‰; $F_{2,52} = 2.35$, $p = 0.132$). Note that the latter analysis was performed using only data from 2009, 2010, and 2011. There was a significant variation in δ^2H_f within breeding season for nestlings ($F_{1,65} = 4.20$; $p = 0.045$). However, only 10% (R^2)

of this variation was explained by Julian date (Figure 4.2). Finally, mean δ^2H_f varied slightly with feather type (rectrices: -134.0 ± 7.6‰; primaries: -135.9 ± 8.3‰) plucked from the same hatch-year birds captured in Alberta during fall migration ($t_{1,48}$ = - 2.42, df = 48, p = 0.020). A linear model including the annual variation in the total amount of precipitation in May and June was the best predictor of the negative relationship between yearly variation of δ^2H_f in nestlings ($F_{1,5}$= 5.80, R^2 = 0.59, p = 0.074; Figure. 4.3a). The second-best model (total amount of precipitation in June) explained 19% less of the observed variation. For returning birds, the amount of precipitation in June in year x-1 was the only model showing the predicted negative relationship ($F_{1,3}$= 2.90, R^2 = 0.59, p = 0.231; Figure. 4.3b).

4.4 Discussion

We found an age effect on δ^2H_f in the Ovenbird that varied significantly among years (age × year interaction), while only a small fraction of the overall variation was explained by habitat type, feather type, and Julian date. Most years, δ^2H_f values from nestlings were lower than those from returning males (19.0, 15.9, and 10‰ lower for 2009, 2010, and 2011, respectively). In 2008, δ^2H_f was similar for both age classes, though it should be noted that sample sizes were small that year. Hence, researchers should account not only for age class but also for a year-specific age effect when using δ^2H_f to assign the origin of individuals. This finding has especially important implications for studies assigning geographic origins of birds using mean δ^2H_p from long-term databases.

Several non-exclusive hypotheses related to evaporative water loss in individuals can be proposed to explain the observed age-specific differences in δ^2H_f. Body water lost through evaporation is depleted in deuterium relative to basal body water and this can result in progressive enrichment of the body H pool (Wolf & Walsberg 1996; McKechnie et al. 2004). Adults may have a greater metabolic rate during feather growth than juveniles and this may result in higher δ^2H_f in adults due to increased evaporative water loss. This hypothesis would be consistent with the observed difference between songbirds and raptor species. In raptors, moult and breeding activities coincide, which would result in a disproportionately high metabolic rate during feather growth due to increased work during that period (Langin et al. 2007). Within songbirds, differences in nestling-adult δ^2H_f values among species could be due to the different levels of heat stress to which each age group are typically exposed (McKechnie et al. 2004). The American Redstart is an open-cup nester and the conditions experienced by nestlings and adults may be closer than in the Ovenbird, which builds a ground domed nest that may provide a more stable microclimate than that experienced by adults. Feather growth rate can also differ among individuals of different ages (Bortolotti 1984), which might result in different δ^2H_f irrespective of levels of physical activity or microenvironment because isotopic compositions are dictated by rate-limiting processes. The observed discrepancy in δ^2H_f between adults and nestlings may also reflect differences in hydrogen budgets of individuals. Langin et al. (2007) attributed the differences in δ^2H_f they found between adult and nestling American Redstart to the fact that adults ingest drinking water whereas nestlings acquire water through soft food items (e.g. Lepidoptera larvae in insectivorous birds; Omland & Sherry 1994; O'Neil et al. 1996; Stodola et al. 2010). Lastly, differences in δ^2H_f between feathers from juveniles and adults might be expected in species using a capital breeding strategy, whereby stored nutrients that differ isotopically from those available in the local environment are transferred to offspring and incorporated into their feathers (Klaassen 2003). This explanation is unlikely to apply here, given that songbirds are income breeders (Langin et al. 2006).

On average, nestlings that grew their primaries in study plots treated by single-tree selection harvesting had slightly lower δ^2H_f (2.5‰) than those hatched in control plots. However, given that the measurement error of δ^2H_f analyses is of the order of 2‰, we cannot make strong inferences from this result. The dome-shaped nest of the Ovenbird may have reduced some of the effects of abiotic factors such as heat stress, resulting in a substantially lower effect on δ^2H_f than that observed in an experimental manipulation of nest box temperature on nestling Tree Swallows (Betini et al. 2009). Experimental manipulations of ambient temperature may be required to determine the causes of differences between adult and nestling δ^2H_f values in open-cup nesting species.

The difference in δ^2H_f between the 3rd rectrix and 1st primary of hatch-year birds captured during fall migration (1.9‰) also fell within measurement error. This suggests that all flight feathers were grown at the same location and could be used to assign birds to geographic regions. This result contrasts with the extensive within feather variation in δ^2H_f reported in some raptors (Smith et al. 2009).

Most of the variation in δ^2H_f in New Brunswick Ovenbirds reflected year and age effects. By generating mean δ^2H_f values for both age classes in different years with relatively small variations, we were able to account for the large range in the observed values (66.5‰). Interestingly, the maximum departure from calibrated δ^2H_p values predicted from the GNIP dataset for both age classes reported in this study occurred in different years. Nestlings grow most of their feathers in July whereas adults are thought to undergo a pre-basic moult in August or September (Pyle 1997). This time lag in feather growth and variable year effects between age classes challenged our understanding of how year-specific weather patterns influence δ^2H_f (Smith et al. 1979; Hobson 2011). It is also interesting to note that the annual variation in the amount of precipitation in May and June was correlated with variations in δ^2H_f of nestlings. A similar pattern was observed between the amount of precipitation in June in year x-1 and δ^2H_f from returning males. These correlations are consistent with an effect of amount of precipitation within and among breeding seasons on δ^2H_f, as well as with the observed age × year interaction. However, the limited number of years available prevented us from making strong inferences regarding a potential causal relationship, especially for returning males.

This study, along with that of Langin et al. (2007), suggests that much of the variation in δ^2H_f in songbirds of known origin and, potentially, in other species groups having a similar moulting pattern (e.g. waterfowl; Coulton et al.

2009), can be accounted for by modeling year- and age-specific isoscapes (e.g. Van Wilgenburg et al. 2012). Year-specific isoscapes will soon become available through a new web-based tool, IsoMap (http://isomap.stanford.edu/). Extensions of such work could also allow accounting explicitly for other factors (e.g. age or feather type) that would reduce the number of assumptions that are currently underlying the use of stable hydrogen isotopes to estimate animal movements, presumably increasing assignment accuracy.

Future work should focus on investigating the cause of the year × age interaction in this study to determine the generality of our findings and to account for the remaining unexplained variation in δ^2H_f. Without such information, this year × age interaction cannot be included in predictive models. We would be hesitant, for example, to generalize our results away from coastal regions. Our findings suggest that coastal effects on δ^2H_f can be modeled for our focal species based on rainfall amount. Similar studies simultaneously testing the assumptions underlying the stable isotope approach (δ^2H_f) for "problematic species" (e.g. shorebirds and raptors) are important to shed some light on the relevance of this method for these species (Hobson 2011). Other authors have called for laboratory experiments to better understand the physiological ecology of focal species and to identify proximate causes of variation in δ^2H_f (Hobson et al. 1999; Martínez del Rio et al. 2009; Hobson 2011). This would likely further improve the spatial resolution of δ^2H_f and increase our ability to assign geographical origins.

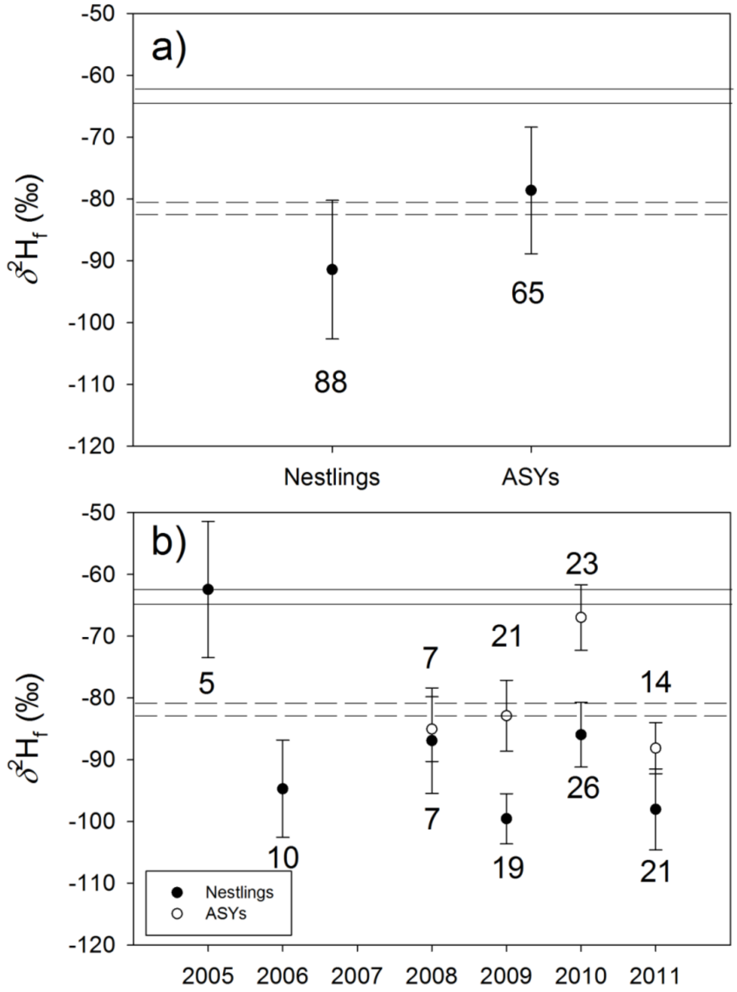

Figure 4.1. Differences in δ^2H_f (‰; mean ± SD and sample size) between after-second year returning males (ASYs) and nestling Ovenbirds (a) and between after-second year males and nestlings in different years (b). In each figure, solid horizontal lines represent the range of amount-weighted mean δ^2H_p for the growing season of the study area and the dash lines correspond to δ^2H_f values corrected using the calibration equation suggested by Clark et al. (2006). All feathers were collected in the Black Brook District, New Brunswick, Canada. Note that the mean values from (a) are not from a normal distribution.

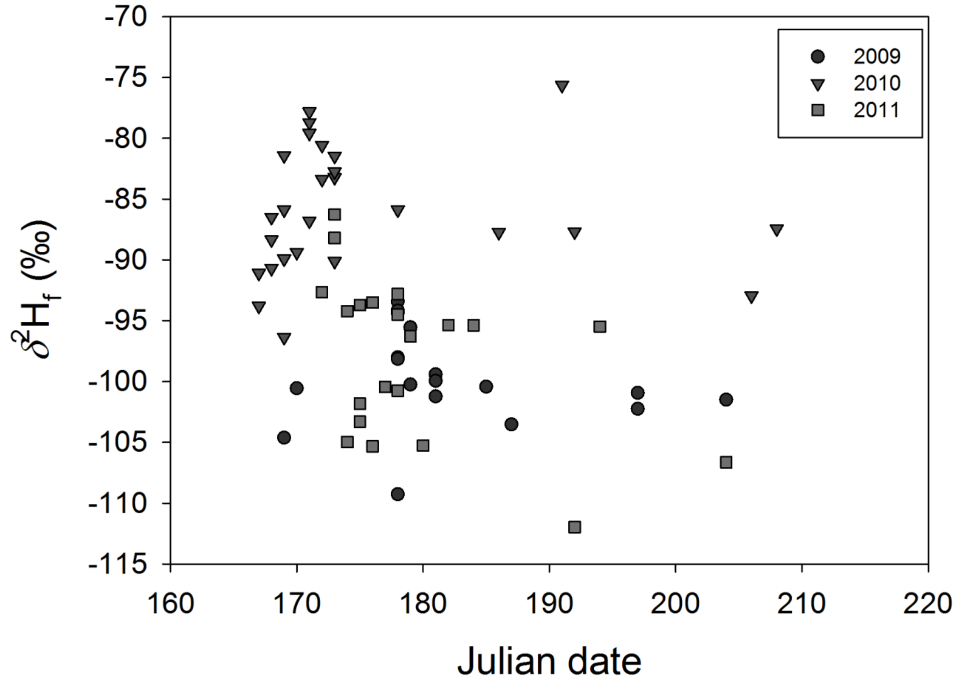

Figure 4.2. Relationship between δ^2H_f in primaries from nestling Ovenbirds and Julian date at which feathers were collected for two breeding seasons. All feathers were collected in the Black Brook District, New Brunswick, Canada.

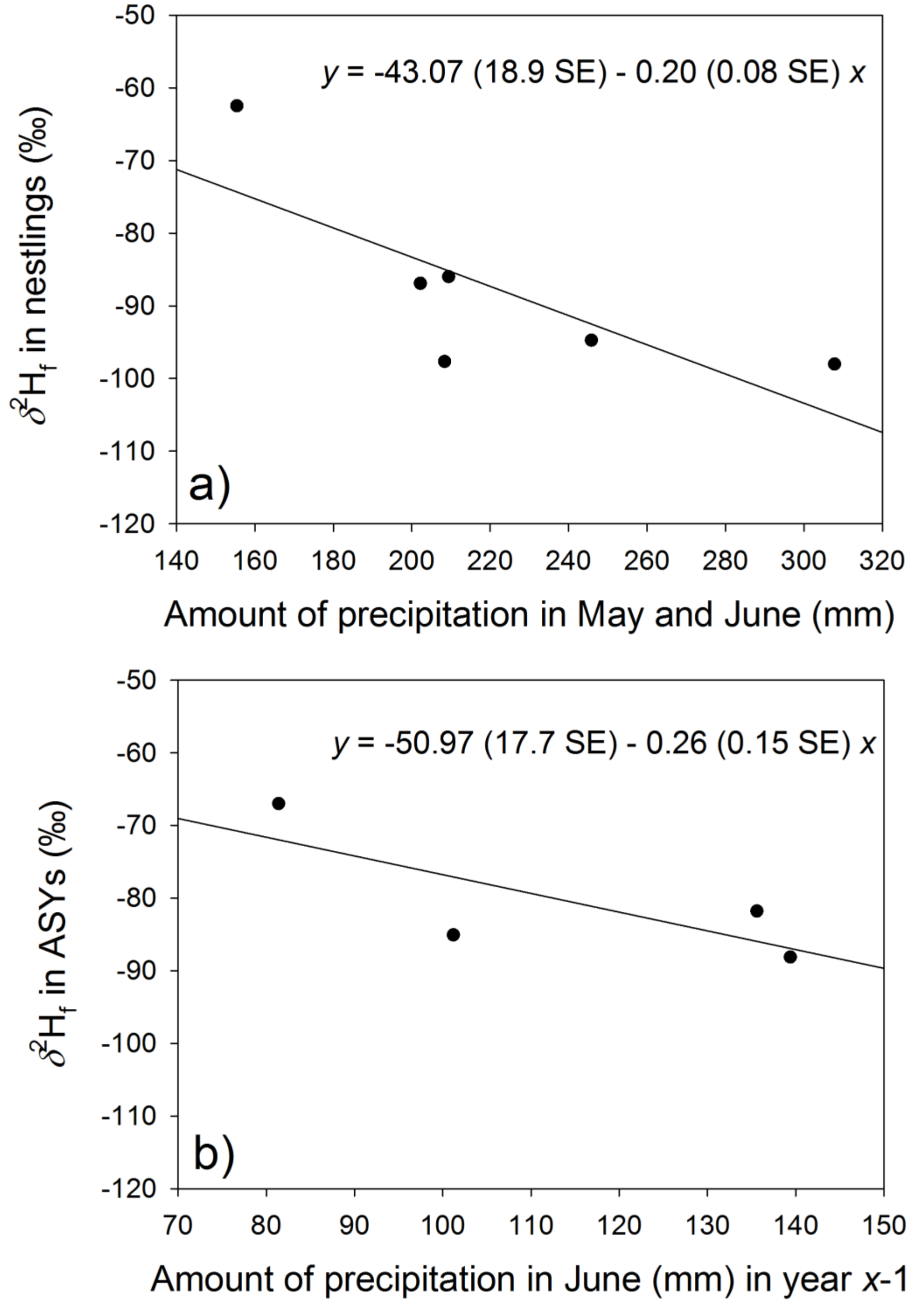

Figure 4.3. Linear relationships between the annual variation of δ^2H_f in nestling and the amount of precipitation in our study area (a) and between the annual variation of δ^2H_f in after second year males (ASYs) and the amount of precipitation in our study area during the previous year (b).

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CHAPTER 5: TRACKING NATAL DISPERSAL IN A COASTAL POPULATION OF A MIGRATORY SONGBIRD USING FEATHER STABLE ISOTOPE (δ^2H, δ^{34}S) TRACERS

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5.1 Introduction

Dispersal is a key component of animal demography because it controls rates of immigration and emigration among populations (Colbert et al. 2001; Bullock et al. 2002; Hanski & Gaggiotti 2004). Most songbirds are characterized by low natal philopatry (but see Dale et al. 2005) and the rare data available suggest that first-year breeders may disperse over tens (Winkler et al. 2005; Tittler et al. 2009; McKim-Louder et al. 2013) or even hundreds of kilometres (Paradis et al. 1998; Hobson et al. 2004; Studds et al. 2012) prior to establishing their first breeding territory. Conversely, experienced breeders show high site fidelity (Greenwood & Harvey 1982; Holmes & Sherry 1992; Haché & Villard 2010). Hence, gene flow and connectivity among avian populations should mainly reflect natal dispersal (Tittler et al. 2006), which is commonly estimated as the straight-line distance moved by an individual from its natal area to its first breeding site (Greenwood & Harvey 1982). Empirical estimates of natal dispersal distances are required to determine the spatial scale over which breeding populations of widely-distributed species interact and, thus, to define relevant conservation units. Unfortunately, traditional mark-recapture approaches are generally inefficient for measuring dispersal (Hobson 2008, but see McKim-Louder et al. 2013). Recently, intrinsic markers such as stable isotopes, trace elements, genetic signatures, species assemblages of parasites, and diseases have been suggested as potential means by which dispersal movements can be tracked without marking individuals (Hobson & Norris 2008). In particular, stable-hydrogen isotope ratios in feathers (δ^2H_f) have proven to be useful for detecting bird movements at continental scales (Hobson & Wassenaar 2008).

Using δ^2H_f, Hobson et al. (2004) obtained some of the first estimates of dispersal in the Ovenbird (*Seiurus aurocapilla*) and American Redstart (*Setophaga ruticilla*) in western Canada based on the number of first-year birds that were “isotopic outliers” relative to expected baseline isotopic values for six study sites. Studds et al. (2012) used this marker to generate a species-specific isoscape for Bicknell’s Thrush (*Catharus bicknelli*) and assignment tests to determine the area of likely origin of first-year breeders (i.e. second-year individuals; hereafter SY). That study provided minimum natal dispersal distances and evidence for spatio-temporal discrepancy in demographic connectivity. Although univariate approaches provide important insights into natal dispersal, it is generally recognized that multiple isotopes or combinations of techniques improves the spatial resolution for assigning individuals to their natal area (e.g. Donovan et al. 2006; Szép et al. 2009; Coulton et al. 2010; Van

Wilgenburg & Hobson, in prep.). Stable isotope measurements of sulfur ($\delta^{34}S$) may be particularly useful in distinguishing individuals growing feathers in coastal regions vs. inland since marine-derived sulfates are generally more enriched in ^{34}S than terrestrial sources and volatilized sulfates from ocean spray can be deposited inland over considerable distances directly or through precipitation (Jamieson & Wadleigh 2000; Kelly et al. 2005; Zazzo et al. 2011).

We investigated the use of stable isotope tracers to estimate natal dispersal distances in the Ovenbird. Given that our study area is located within 160 km of a significant body of seawater (Gulf of St Lawrence), we jointly used δ^2H_f and $\delta^{34}S_f$ to obtain a finer-scale assignment than using δ^2H_f alone. We anticipated significant longitudinal structure in $\delta^{34}S_f$ based on distance from the coast and prevailing weather. We first created species-, age-, and year-specific feather isoscapes (West et al. 2010) for our study region and then assigned first-year breeders to their natal origin using these isoscapes and likelihood-based assignment tests based upon bivariate probability density functions. Our specific objectives were to estimate the proportion of local vs. immigrant SY breeders recruited into our local breeding population and to determine the minimum distance moved by immigrants. Based on the typically low natal philopatry reported in songbirds, we predicted that most SY breeders would be immigrants. However, we had no *a priori* expectations regarding the spatial extent of natal dispersal movements by Ovenbirds as they have never been precisely quantified.

5.2 Methods

5.2.1 Study area

Since 2006, an individually-marked subpopulation of male Ovenbirds have been monitored in northwestern New Brunswick, Canada (47°23' N67°40'W; Black Brook District; Figure 5.1) to quantify the effects of an experimental harvest treatment on population dynamics (Haché & Villard 2010; Haché et al. 2013). Black Brook is a 2 000 km^2 managed forest district owned by J.D. Irving Ltd. The landscape is a mosaic of spruce plantations and deciduous, mixedwood, and coniferous stands at the interface of the northern hardwoods and Acadian forest regions (Mosseler et al. 2003).

5.2.2 Feather samples, benchmark values, and isoscapes

In 2010, most territorial males in the 250-ha area monitored in Black Brook (10 × 25 ha study plots; see Haché & Villard 2010 for details) that were not marked in previous breeding seasons (i.e. recruits) were captured (89%; 55/62) using mist-nets and playbacks of conspecific songs and marked with three color bands and a numbered aluminium band. Territorial individuals were also captured and marked in two additional 25-ha plots as part of a translocation experiment (see Villard & Haché 2012 for details; n = 12 and 16). Two 3rd rectrices were plucked from each captured individual for aging and isotope analyses. Males were aged as second-year (SY; i.e. first-year breeder) or after second-year (ASY) individuals following the criteria of Donovan & Stanley (1995) adapted by Bayne & Hobson (2001). In 2010-2012, we also collected feather samples from 48 returning ASY males banded in the previous year (hereafter "returning ASY"; n = 23, 14, and 11 for 2010, 2011, and 2012, respectively). During the same period, an additional 225 territorial males were captured within ca. 5 km of 22 additional locations outside Black Brook (10.2 ± 1.4, mean ± SD, individuals per location; 16, 3, and 3 sampling locations in 2010, 2011, and 2012, respectively). The total sampling area covered ca. 180 000 km^2 (340 × 530 km; mean distance between closest sampling locations was 64.6 km, range = 28.9 - 134.0 km; Figure 5.1). Only feather samples from ASY males captured at these sampling locations were used to generate the feather isoscapes because they were believed to provide local values of $\delta^{34}S_f$ and δ^2H_f based on the assumption that ASY individuals have high breeding site fidelity (Bayne & Hobson 2002; Porneluzi 2003; Haché & Villard 2010) and moulting occurs in the vicinity of the breeding territory (Pyle 1997; but see Hallworth et al. 2013). In total, we measured δ^2H_f for all SY (2010) and returning ASY males from Black Brook (2010-2012), and for all ASY males from the 22 additional sampling locations (2010-2012). Values of $\delta^{34}S_f$ were also measured for all SY males (2010) from Black Brook, but only for returning ASY males from 2010 and 2012, owing to logistical constraints. For the same reason, only three individuals per additional sampling location were analyzed for $\delta^{34}S_f$ (n = 66).

Stable-hydrogen isotope ratios from feathers collected in the same breeding area can vary among years (Langin et al. 2007; Haché et al. 2012). As our goal was to assign SY males captured in 2010 (feathers grown in 2009) to their natal area the previous year, we had to control for a potential yearly variation in isotope values by creating a year-specific δ^2H_f isoscape reflecting expected values for feathers grown in 2009. Thus, we only used δ^2H_f values from returning ASY males (Black Brook) captured in 2010 (feathers grown in 2009) as the benchmark values for the year-specific δ^2H_f isoscape. We could not visit our entire study region in a single year to create this isoscape and had to apply a correction factor for δ^2H_f values from samples collected at locations surrounding Black Brook in 2011 (feathers grown in 2010; n = 3) and 2012 (feathers grown in 2011; n = 3) based on the yearly variation we saw in ASY males at Black Brook. Specifically, we measured the difference in δ^2H_f values between returning ASY males (Black Brook) captured in 2010 vs. 2011 and 2010 vs. 2012. We then used these differences to adjust δ^2H_f from ASY males captured at sampling locations outside Black Brook in 2011 and 2012. Only δ^2H_f values from six sampling locations had to be calibrated as the ASY males from the remaining 16 locations were all captured in 2010. This approach assumes that year-to-year variation in δ^2H from growing-season precipitation is similar across the total sampling area. Values of $\delta^{34}S_f$ were not calibrated to account for annual variation as there was no *a priori* reason to expect annual variation in this isotope. However, we still tested for a year effect using a *t*-test.

Mean $\delta^{34}S_f$ and δ^2H_f from individuals captured at the 12 study sites in Black Brook were pooled in 4 locations (3 sites per location) covering the extent of the study area (Figure 5.1). Mean values from these and the additional locations surrounding Black Brook were assigned a centroid and used to generate the isoscapes. Spatial autocorrelation among mean values from each sampling location (n = 26) was modelled for both isotopes using semivariance analyses and kriging interpolations. We investigated several semivariogram models (ordinary spherical, circular, exponential, Gaussian, or linear), and selected the model that minimized the root-mean-square error. Isoscapes were created in ArcGIS 10 using the Geostatistical Analyst extension (ESRI, Redlands, CA).

5.2.3 Stable isotope analyses

Surface oils were removed from feathers using a 2:1 chloroform:methanol solution. Samples were prepared according to Wassenaar (2008) and analyses were conducted at the Stable Isotope Hydrology and Ecology Laboratory of Environment Canada ($\delta^{34}S_f$ in 2010-2012 and $\delta^{2}H_f$ in 2010 and 2012) and the Colorado Plateau Stable Isotope Laboratory ($\delta^{2}H_f$ in 2011). High-temperature (1350°C) flash pyrolysis generating an H_2 pulse for each sample (350 ± 20 µg) was used to obtain $\delta^{2}H_f$ measurements by continuous-flow isotope-ratio mass spectrometry (CF-IRMS). To account for exchangeable hydrogen in keratins, comparative equilibration was done using in-house keratin working standards (BWB = -108 ‰, CFS = -147.7 ‰, and CHS = -187 ‰; Wassenaar & Hobson 2003). The two laboratories used the same protocol and standards for $\delta^{2}H_f$ measurements. Values of $\delta^{34}S_f$ were also measured by CF-IRMS (3500 ± 100 µg of tissue per sample). All results are expressed as nonexchangeable deuterium ($\delta^{2}H_f$) and sulphur ($\delta^{34}S_f$) isotopic ratios in units of per mil (‰) and normalized to Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) and Canyon Diablo Triolite, respectively. Based on within-run analyses of keratin standards, we assumed measurement error to be ca. ±2‰ for both δ^2H_f and $\delta^{34}S_f$.

5.2.4 Assignment test

Previous studies have reported differences in δ^2H_f between juveniles (i.e. nestlings, hatch-year, or SY birds) and ASY individuals ranging between 6 - 32.6‰ (Gow et al 2012; Haché et al. 2012; Studds et al. 2012). Our goal was to assign SY males assumed to have grown their rectrices mostly during the first few weeks postfledging (i.e. rectrices only start emerging from feather sheaths a few days prior to fledging; S. Haché, M.-A. Villard, & E.M. Bayne, pers. observ.). Thus, to link SY results to an ASY feather isoscape, we had to apply a correction factor to account for the documented effect of age. The most parsimonious approach was to use the value from a long-term study that measured age-specific variation in δ^2H_f among populations of Bicknell's Thrush (Studds et al. 2012). Studds et al. (2012) reported that δ^2H_f was on average ~6‰ lower in first-year breeders/fledglings than in adults at the northern edge of the Bicknell's Thrush breeding range. This portion of its range corresponded to the extent of our isoscapes and this comparison based on values from first-year breeders/fledglings (i.e. inert tissue) is more appropriate than values from growing feathers of nestling Ovenbirds obtained by Haché et al. (2012). Hence, we added 6‰ to δ^2H_f of all SY males ($\delta^2H_{f6‰}$) prior to assigning their origin to the ASY feather isoscapes. To examine how sensitive the results of assignment tests were to this correction factor, we generated similar analyses for SY males after using 50% higher and lower correction factors (i.e. $\delta^2H_{f3‰}$ and $\delta^2H_{f9‰}$).

We generated spatially-explicit assignment tests using bivariate normal probability density functions (BNPDF; Royle & Rubenstein 2004; Hobson et al., in review) to determine the likely origin of SY males. The likelihood that a given raster cell (*j*; 2 km × 2 km cell size) within the feather isoscapes was a potential origin was estimated based on the following equation:

$$f\left(x^i y^i \middle| \mu_j \Sigma\right) = \frac{1}{2\pi\sigma_x\sigma_y\sqrt{1-\rho^2}} \exp\left(-\frac{1}{2(1-\rho^2)}\left[\frac{\left(x^i-\mu_x\right)}{\sigma_x^2} + \frac{\left(y^i-\mu_y\right)}{\sigma_y^2} - \frac{2\rho(x - \mu_x)\left(y-\mu_y\right)}{\sigma_x\sigma_y}\right]\right)$$

Where $f(x^i y^i|\mu_j\Sigma)$ is the likelihood that an individual (*i*) with given δ^2H_f (x^i) and $\delta^{34}S_f$ (y^i) values originated from a raster cell *j*, while μ is the mean, σ is the standard deviation, and ρ is the correlation between δ^2H_f (*x*) and $\delta^{34}S_f$ (*y*) predicted for each raster cell (*j*) within the feather isoscapes. Predicted mean isotopic composition for each raster cell (*j*) was generated from the calibrated isoscapes (δ^2H_f and $\delta^{34}S_f$). The parameter μ_j is therefore a vector of means for each raster cell (*j*) within the feather isoscapes presented as:

$$\mu = \left[\mu_{\delta^2H_f}, \mu_{\delta^{34}S_f}\right]_j$$

Each BNPDF was parameterized using both δ^2H_f and $\delta^{34}S_f$ isoscapes and the following variance-covariance matrix:

$$\Sigma = \begin{bmatrix} \sigma^2_{\delta^2H_f} & \sigma_{\delta^2H_f,\,\delta^{34}S_f} \\ \sigma_{\delta^2H_f,\,\delta^{34}S_f} & \sigma^2_{\delta^{34}S_f} \end{bmatrix}$$

where $\sigma^2\delta^2H_f$ and $\sigma^2\delta^{34}S_f$ are the expected variance for each isotope ratio and $\sigma_{\delta^2H_f}$, $\sigma_{\delta^{34}S_f}$ is the covariance between the pair of isotope ratios. The variance-covariance matrix had to be validated to define the likelihood a cell within the extent of our isoscape corresponded to a potential origin. This was achieved by using a subset of samples from ASY males (i.e. assumed known origin; n = 66, 36% of all ASY in the dataset). We assumed a spatial stationarity of variance-covariance across our study area (Royle & Rubenstein 2004; Hobson et al. in review). For all SY males (2010), we generated a binary raster layer to classify each cell as a likely (1) or unlikely (0) origin based on a 2:1 odds ratio. Odds ratios between 2:1 and 4:1 would provide the best depiction of the geographic distribution of assigned versus true origins for samples from multiple individuals (Van Wilgenburg et al. in prep). Given results based on 4:1 odd ratios were qualitatively similar to those from 2:1 odd ratios (Haché et al. unpublished data), only results from the latter is provided. We estimated the likely origin of all SY males by summing the binary surfaces. We conducted similar analyses to assign the 23 returning ASY males captured in 2010 (Black Brook) to the isoscapes to determine the spatial resolution and classification accuracy (i.e. percent of returning ASY with an assigned area that overlapped their known origin) provided by this approach. Assignment tests were generated using scripts employing the raster (Hijmans & Van Etten 2012) package in R v 2.15.2. For each SY male assigned as an immigrant (i.e. assigned origin did not overlap the sampling location where it was captured; as opposed to a resident), we calculated the minimum linear distance between breeding location and natal area (Studds et al. 2012) using ArcGIS v 10.

Research was approved by the University of Moncton Animal Care and Use Committee (Permit Numbers: 10-06, 11-04, and 12-02), Canadian Wildlife Service (Permit Numbers: SC2710 and SC2751), and the U.S. Fish and Wildlife Service (Permit Number: MB11009A-0).

5.3 Results

Of the 10.2 male Ovenbirds captured on average (± 1.4, SD; n = 225) at each of the 22 sampling locations outside Black Brook, 6.5 were ASY (± 2.1; range of 3 - 10 individuals per location; n = 142). When added to the 23 ASY males captured in Black Brook in 2009 and subsequently recaptured in 2010, samples from a total of 165 and 89 ASY males were used to produce the δ^2H_f and $\delta^{34}S_f$ isoscapes, respectively (Figures 1- 2). In Black Brook, we also recaptured 14 returning ASY males in 2011 and 11 in 2012. There was year-to-year variation in δ^2H_f from returning ASY males (2010 = -67.0 ± 5.3‰, 2011 = -88.1 ± 4.1‰, and 2012 = -78.9 ± 5.1‰). Thus, to correct for this year effect in δ^2H_f, we added 21.1‰ to the δ^2H_f of 20 ASY males captured at sampling locations (n = 3) outside Black Brook in 2011 and 11.9 ‰ to those of the 25 ASY males captured at the three other sampling locations in 2012. Mean $\delta^{34}S_f$ values differed significantly between years (2010 = 6.79 ± 0.58‰ and 2012 = 6.30 ± 0.29‰; t_{32} = -2.6, p = 0.014), but this difference was negligible when considering the 2‰

measurement error. In 2010, we captured 35 SY males breeding in Black Brook (δ^2H_f = -68.0 ± 10.2‰ and $\delta^{34}S_f$ = 7.06 ± 0.86‰; Figure 5.2).

The δ^2H_f isoscape was generated using ordinary kriging based upon a Gaussian semivariogram model (root-square-mean error = 4.59). The model-estimated parameters were a major range of 120.7 km, nugget of 0.81, and sill of 31.8. Data for $\delta^{34}S_f$ were kriged to create an isoscape based upon a spherical semivariogram model (root-square-mean error = 1.03). The semivariogram model parameters for the $\delta^{34}S_f$ isoscape included a major range of 120.7 km, nugget of 0, and sill of 11.8. The δ^2H_f isoscape showed generally more enriched values in southeastern portion of the isoscape with gradual depletion along a southeastern-northwestern gradient, whereas the $\delta^{34}S_f$ isoscape corresponded to the anticipated coastal effect with more enriched values mostly along the coast creating an east-west gradient (Figure 5.1).

The assigned origin of 22 of the 23 ASY males of known origin overlapped their sampling location (classification accuracy of 95.6%; Figure 5.3A). Similarly, based on $\delta^2H_{f6‰}$ values, 94.2% of the SY males (33/35) were classified as residents (Figure 5.3B). The two individuals classified as an immigrants had minimum dispersal distances of 39 km and 237 km. Using a correction factor with a 50% higher or lower δ^2H_f value had negligible consequences on assigned areas (Figure 5.3C-D). Based on $\delta^2H_{f9‰}$, only the same two individuals were classified as immigrants (minimum dispersal distances of 32 km and 240 km). Using $\delta^2H_{f3‰}$, 88.6% of the SY males were considered as residents (31/35 individuals). Once again, the same individuals were classified as immigrants (minimum dispersal distances of 44 km and 234 km), while two additional individuals classified as immigrants had minimum dispersal distances of only 6 km and 13 km.

The distance between where SY males were captured and the farthest likely natal origin (i.e. maximum distance of dispersal) could not be estimated because in all cases, it reached the edge of the isoscape, suggesting that they could have originated from an area beyond the study area. However, the population-level assigned origin (i.e. sum of the binary surfaces for each SY male; Figure 5.3B) indicated that likely origins of SY males only reached edges of the isoscapes in small areas in the southeast and northeast, suggesting that the majority of SY males had a maximum natal dispersal distance < 200 km from Black Brook. The assigned area of returning ASY males (Figure 5.3A) was similar to that of SY males, suggesting that the maximum natal dispersal distance is a conservative estimate as it corresponds to the maximum spatial resolution provided by this approach.

5.4 Discussion

By combining age- and year-specific $\delta^{34}S_f$ and $\delta^{2}H_f$ Ovenbird isoscapes and bivariate assignments tests, we showed that most SY males (94%) recruited in our coastal-breeding population likely originated locally (i.e. hatched in Black Brook; residents). This finding was surprising based on the low natal philopatry generally reported in songbirds (Greenwood & Harvey 1982). When summing the assigned areas of all SY males (Figure 5.3B), our estimates of maximum distances of natal dispersal still suggested that movements generally occurred over a short distance (< 200 km). This information on natal dispersal movements offers insights about the area over which many population processes are taking place and, ultimately, how populations are structured. Most importantly, we argue that results from this study identify the spatial scale at which conservation plans for the Ovenbird and ecologically-similar songbirds should be implemented (see also Tittler et al. 2006, 2009).

Estimates of minimum natal dispersal distances suggest that most SY males can be considered as residents and in the rare instances where individuals were classified as immigrants (n = 2), natal dispersal would have occurred from within 240 km of our study site. The Black Brook District covers 2 000 km^2 (ca. 80 km × 25 km), suggesting that a high proportion of males recruited into the district's Ovenbird population likely hatched "locally". Based on δ^2H_f outliers, Hobson et al. (2004) considered 9.5% (± 8.1%; n = 6) of SY male Ovenbirds breeding in western Canada as long-distance dispersers which is consistent with the percentage of immigrants (5.7%) in our study. However, they could not separate short-distance dispersers from residents. A band-recovery study from Europe (Paradis et al. 1998) and a North American study using one-year time-lagged correlations in point-count data (Tittler et al. 2009) both estimated mean natal dispersal distances < 100 km in several landbird species. Alternatively, Studds et al. (2012) showed that natal dispersal movements in Bicknell's Thrush reached 700 km, but that most individuals likely originated from within 200 km of their breeding territory. Unlike the Ovenbird, the Bicknell's Thrush occurs at low abundance, population sizes are declining (Rich et al. 2004), and they have a small, highly-patchy breeding range (Rimmer et al. 2001). Paradis et al. (1998) showed that interspecific variation in natal dispersal distance was negatively correlated with population size and the spatial extent of the breeding range, consistent with the observed differences between Ovenbird and Bicknell's Thrush populations. In contrast, the Prothonotary Warbler (*Protonotaria citrea*) and Tree Swallow (*Tachycineta bicolor*) also have different population sizes and breeding ranges (Petit 1999; Winkler et al. 2011), yet show a similar pattern in natal dispersal distances. Median natal dispersal in Tree Swallows is 2.3 km (1.3% of individuals dispersed 50-210 km; Winkler et al. 2005), as opposed to 1.4 km (maximum of 17 km) in the Prothonotary Warbler (McKim-Louder et al. 2013). However, those results are from nestbox studies and there are concerns about whether inferences from such studies can be made to populations breeding in natural nest sites (Lambrechts et al. 2010; Wesolowski 2011).

The assigned origin of most SY males reached the edge of our isoscape, limiting our ability to generate accurate estimates of maximum natal dispersal distances. However, in most cases, the likely origin only reached small areas at the edge of the isoscape (ca. 190 km from Black Brook; Figure 5.3B), suggesting that we likely captured most of the area that would have been assigned had we examined isoscapes of larger spatial extent. This is based on the assumption that similar isotopic composition is unlikely to occur over large areas beyond the extent of our isoscape as a result of the latitudinal and longitudinal gradients reported for $\delta^{34}S_f$ and $\delta^{2}H_f$, respectively. Similar coastal conditions at the same latitude also do not occur elsewhere in the Ovenbird's breeding range as the North American Rocky Mountains being the western limit (Porneluzi et al. 2011). Also, the assigned likely natal origin of the SY males monitored in this study (Figure 5.3B) covers an area similar to the assigned origin of the returning ASY males from Black Brook (known origin; Figure 5.3A) suggesting that our estimates of maximum distance of natal dispersal are constrained by the spatial resolution (i.e. uncertainty) provided by this approach and might even be shorter. Nevertheless, we recognize that dual isotopic mapping over the entire range of the species would be required to consider all possible isotopic origins of birds arriving in our study area.

We minimized sources of error in our δ^2H_f isoscape by controlling for interspecific, age, and year effects which are all known to influence δ^2H_f (Gow et al. 2012; Haché et al. 2102; Hobson et al. 2012). Elevation is another factor influencing δ^2H_f (Poage & Chamberlain 2001; Hobson et al. 2003). Most of the area covered by our isoscapes varied from 0-600 m in elevation (NASA Land Processes Distributed Active Archive Center, 2012), but we are confident that our sampling design integrated the majority of this variation within our δ^2H_f isoscape. Other potential factors explaining spatial variation in the δ^2H_f isoscape are fine-scale variation in temperature, moisture level, and amount of precipitation (Dansgaard 1964) which might be especially important near coastlines (see also Hallworth et al. 2013).

Unlike δ^2H_f, we had no *a priori* reason to expect inter-annual variation in $\delta^{34}S_f$. Similarly, $\delta^{34}S_f$ is unlikely to be influenced by the age of an individual because little diet-tissue isotopic discrimination occurs in these isotopes as a result of metabolic activity (Krouse et al. 1991; Hobson 2008). Overall, the spatial variation observed in the $\delta^{34}S_f$ isoscape corresponds to the anticipated coastal effect (deposition of volatilized marine sulfates) previously observed (Jamieson & Wadleigh 2000; Lott et al. 2003; Kelly et al. 2005; Valenzuela et al. 2011; Zazzo et al. 2011). However, in some instances, the overall gradient in $\delta^{34}S_f$ across our isoscape as a function of distance to the ocean seems to have been altered by local processes that we do not fully understand (reviewed by Krouse et al. 1991; Chambers & Trudinger 1979; Jamieson & Wadleigh 2000).

We calibrated δ^2H_f of SY males using data from reported age related variation in δ^2H_f from a 10-year study on Bicknell's Thrush (Studds et al. 2012). The assumption that this correction factor (6‰) is consistent among songbird species and breeding seasons needs to be validated as it could have important implications when assigning origin of SY males to ASY feather isoscapes. However, there were only subtle differences between the assigned origin of SY males based on this correction factor ($\delta^2H_{f6‰}$) and those with 50% higher and lower ($\delta^2H_{f9‰}$ and $\delta^2H_{f3‰}$) values suggesting that our approach remains relatively robust.

Low recapture rates often prevent the use of extrinsic markers to evaluate natal dispersal. The main advantage of the isotope approach is that it allows tracking natal dispersal of a completely random sample of a population of first-year breeders, whereas mark-recapture studies require an initial marked population that can be biased. Multivariate assignment tests have been used to assign the geographic origin of numerous taxa (e.g. birds [Wunder et al. 2005; Evans Ogden et al. 2006], invertebrates [Miller et al. 2010; Flockhart et al. 2013], and mammals [Henaux et al. 2011]), but most studies documented migratory patterns and fewer explored age-specific dispersal movements. Our results are consistent with those from other studies suggesting that although philopatry is low in songbirds, natal dispersal typically occurs over relatively short distances. Findings from this study could be used to test predictions about effects of landscape fragmentation on immigration rates and dispersal movements (e.g. Garrard et al. 2012). However, future studies should consider: 1) using larger isoscapes, i.e. whole breeding range, to provide estimates of both minimum and maximum dispersal distances; 2) investigating natal dispersal in females; and 3) including additional chemical markers (e.g. $\delta^{13}C$, $\delta^{15}N$, $^{87}Sr/^{86}Sr$, and trace elements; Kosciuch et al. 2008; Poesel et al. 2008; Sellick et al. 2009) to determine the maximum spatial resolution available to investigate biologically relevant spatial scales for management planning to conserve bird populations. Nonetheless, we recommend that to maintain Ovenbird and ecologically-similar songbird populations, management units within a few hundred kilometers should be implemented to provide sources populations for potential recruits (see also Ward 2005; Schaub et al. 2013). Effective management strategies should also facilitate movements among breeding populations to minimize the cost of natal dispersal (Mitchell et al. 2009; Trainor et al. 2013; but see Cox & Kesler 2012).

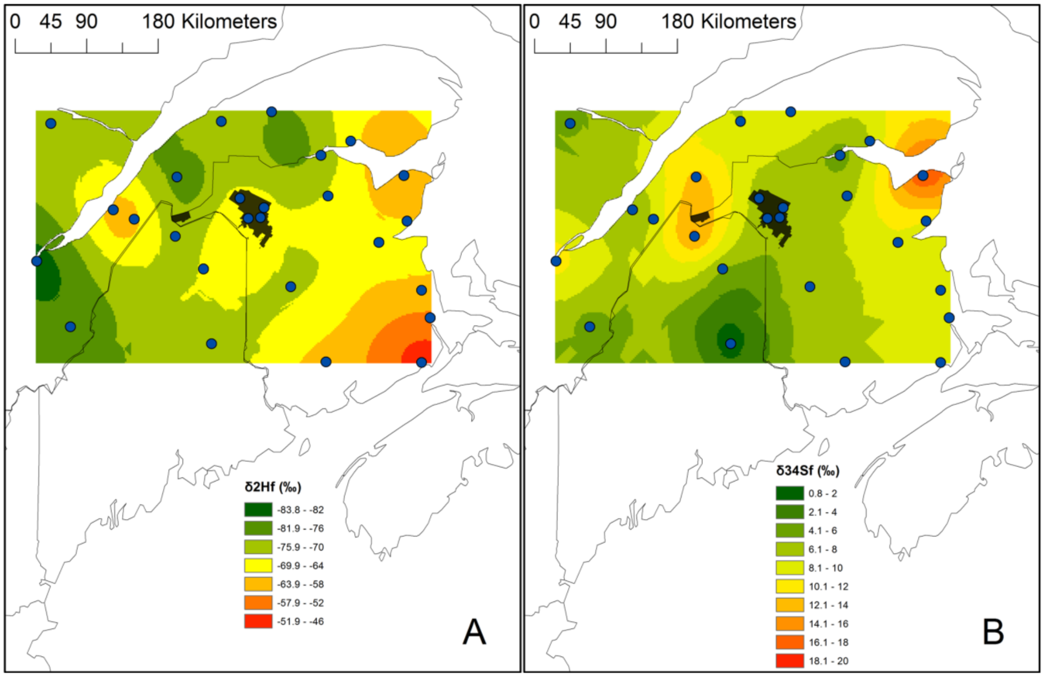

Figure 5.1. $\delta^{2}H_{f}$ (A) and $\delta^{34}S_{f}$ (B) Ovenbird isoscapes based on samples from ASY males collected in 2010 and calibrated 2011 and 2012 data. Isoscapes were based on ordinary Gaussian and ordinary spherical semivariogram models, respectively. Blue points are the 26 sampling locations and in black is the Black Brook District.

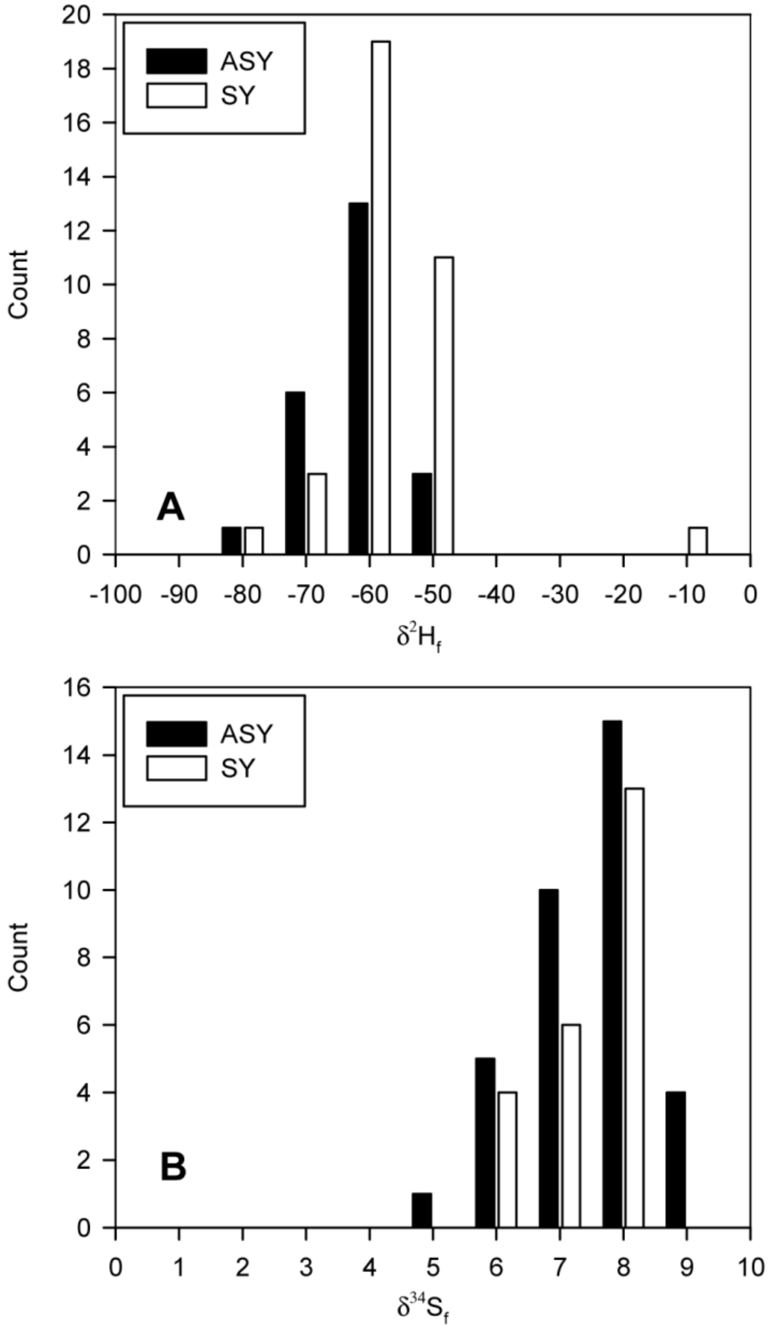

Figure 5.2. Histograms of δ^2H_f (A) and $\delta^{34}S_f$ (B) from returning ASY (n = 23) and SY (n = 35) males breeding in the Black Brook District, New Brunswick, in 2010.

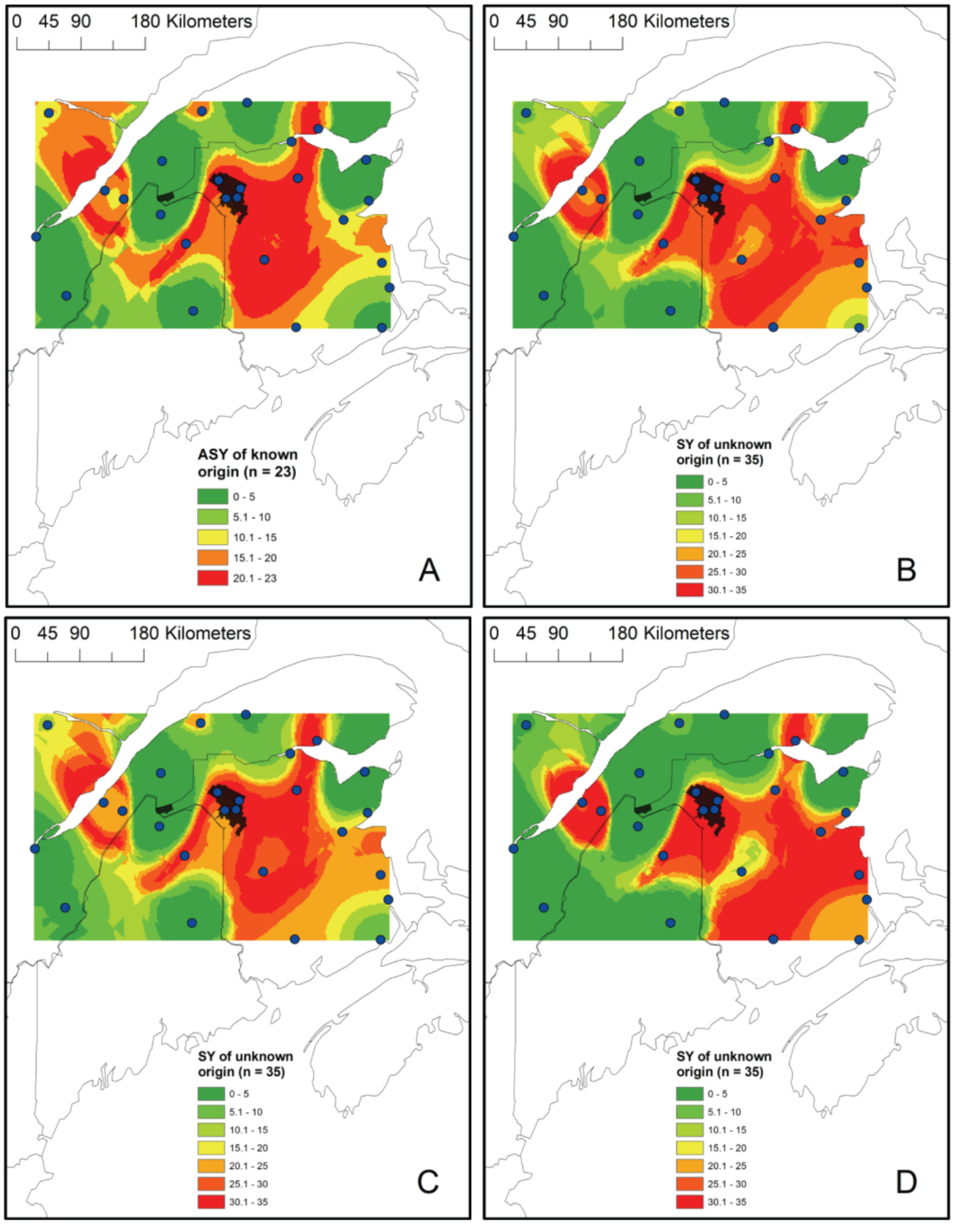

Figure 5.3. Geographic distribution of the assigned origin of 23 returning ASY (A) and 35 SY male Ovenbirds known to have bred in the Black Brook District (in black; B-D), New Brunswick. Assignments of SY males were based on $\delta^{2}H_{f6‰}$ (B), $\delta^{2}H_{f3‰}$ (C) and $\delta^{2}H_{f9‰}$ (D). Maps represent the sum of all binary raster layers of each individual assignment. Blue points are the 26 sampling locations and in black is the Black Brook District.

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CHAPTER 6: DEMOGRAPHIC RESPONSE OF A NEOTROPICAL MIGRANT SONGBIRD TO ALTERNATIVE FOREST MANAGEMENT AND CLIMATE CHANGE SCENARIOS

A version of this chapter is in preparation for publication. Haché S., R. Cameron, M.-A. Villard, E. M. Bayne, and D. A. MacLean. In prep. Demographic response of a neotropical migrant songbird to alternative forest management and climate change scenarios.

6.1 Introduction

Even though the numerical responses of species to intensive management of forest ecosystems have been well documented for many taxa (Fuller & Harrison 2005; Edman et al. 2008; Vanderwel et al. 2009; Work et al. 2010; Haché et al. 2013a), most authors acknowledge the need for long-term demographic studies to model effects of forestry and other anthropogenic disturbances on population dynamics. Long-term mensurative studies can be used to estimate population growth rates (Morris & Doak 2002; MacKenzie et al. 2003), but the underlying demographic processes that have the greatest influence on population growth rate cannot be identified. With the exception of game species, most studies that have modelled the demographic response of wildlife to human land use have focused on species at risk (Morris & Doak 2002; Ralls et al. 2002, but see Ball et al. 2003). These studies provide insights for management, but are often constrained by small sample size and rarely document the mechanisms that are responsible for declines in population size, which may be different from those acting once a species becomes at risk (Beissinger & Westphal 1998; Reed et al. 2002; Gilroy et al. 2012). An alternative to this approach is to model the demographic response of relatively common species that are sensitive to human land use (Lindenmayer et al. 2000, Wintle et al. 2005). Such "focal species" respond to moderate alterations of high-quality habitat (Lambeck 1997) and their relative abundance makes it possible to document changes in vital rates. This "proactive" approach allows the development of adaptive management frameworks (Dzus et al. 2009) aiming to prevent sensitive species from becoming at risk (Abbitt et al. 2000).

In North America, many forestry companies have implemented sustainable forest management plans in an attempt to maintain biodiversity. For example, the extent and configuration of cutblocks and mixed-species plantations are often designed to emulate natural disturbances (Crow & Perera 2004; Long 2009; Kuuluvainen & Grenfell 2012). Nonetheless, economic challenges along with issues expressed by some authors about natural disturbance emulation (e.g. Klenk et al. 2008) have limited the implementation of such an approach (Long 2009). Indeed, harvesting tends to differ from natural disturbances in its occurrence, extent, severity, and synchronicity across the landscape (Bergeron et al. 2002, Angers et al. 2005). Forestry activities tend to benefit species associated with early-seral forest and many of these species are threatened in regions undergoing massive reforestation without active logging (Askins 2001; Schlossberg et al. 2010). However, management of even-aged stands through clearcutting and plantation silviculture reduces the area of suitable habitat for species associated with late seral-stages, whereas partial harvest systems in deciduous stands may degrade habitat degradation for many taxa (Edman et al. 2008; Vanderwel et al. 2009; Work et al. 2010; MacKay et al., in press) owing to the gradual loss of old forest characteristics and simplification of the vertical structure (Angers et al. 2005).

The Ovenbird (*Seiurus aurocapilla*) is known as one of the most sensitive vertebrate species to habitat alteration in northern hardwood forests (Vanderwel et al. 2007, 2009). Important reductions in density and even extirpation have been documented following intensive partial harvest treatments such as shelterwood harvesting (50-70% of tree removal; Vanderwel et al. 2009). In less intensive treatments (e.g. 30-40% tree removal through selection harvesting), reductions in density and productivity per unit area tend to be proportional to the wood volume removed (Haché et al. 2013b; but see Morris et al. in press). Nonetheless, this ground-foraging songbird remains locally common (Haché & Villard 2010; Porneluzi et al. 2011), making it a good focal species to develop demographic models and project future trends under alternative forest management scenarios (e.g. Larson et al. 2004).

In addition to pressure from human activities, there is growing concern about the effects of climate change on populations and ecosystems (Rodenhouse et al. 2009; Burrows et al. 2011; Reichert et al. 2012). In the northern hardwood forest, complex interactions among abiotic factors are anticipated to alter species composition and population sizes for many species (Rodenhouse et al. 2008, 2009; Groffman et al. 2012). For example, long-term monitoring at the Hubbard Brook Experimental Forest and recent climatic models suggest that snow cover events (i.e. number of times that the snowpack forms and dissipates during the year) are expected to increase substantially (14-40%) by 2100, with a 20-79 day decrease in the number of snow-covered days owing to warmer temperatures (Campbell et al. 2010). These projections, along with the negative effect of experimental reduction in snow cover on abundance and richness of litter arthropods in the following spring (Templer et al. 2012), suggest that ground-foraging birds feeding on invertebrates such as the Ovenbird may be affected by climate change (Groffman et al. 2012). Depending on the greenhouse gas emission scenario and modelling approach, Rodenhouse et al. (2008) projected that Ovenbird incidence in the Breeding Bird Survey (i.e. proportion of BBS [Sauer et al. 2001] routes detecting the species; measure generally correlated with abundance) would be 7.2% to 45.6% lower by the end of the century. Yet, very small differences in occupancy are expected (0% to -1.5%), suggesting that the species should occupy the same area, but at lower densities. Similar patterns are projected for other ground-foraging species and neotropical migrants (Rodenhouse et al. 2008). Understanding how different land use and climatic scenarios will influence focal populations in intensively managed forest landscapes is critical to determine the relative importance of alternative threats and adjust conservation/management plans accordingly.

In this study, our objective was to evaluate the effects of different forest management projections and climate change scenarios on demographic parameters of a breeding population of Ovenbirds. We combined empirical data on the demographic response of this species to habitat alteration (Haché & Villard 2010; Haché et al. 2013b; Haché et al. 2014; Vernouillet et al. in review), projected timber yields from a forest timber supply model developed by J.D. Irving, Limited (Black Brook District), and anticipated impacts of climate change on our focal species to model number of territorial males and young produced and population growth rate (λ) over a 75-year period (2012-2087). Specifically, we modelled the status of a regional Ovenbird population over the projected period according to the current forest timber supply model and potential reductions (10% and 20%) in the ratio of selection harvesting to shelterwood (i.e. larger areas managed through shelterwood). These projections were combined with three scenarios on climatic change effects on breeding habitat quality: 1) no effect; 2) 10% reduction in habitat quality by 2087; and 3) 50% reduction in habitat quality by 2087 (Rodenhouse et al. 2008). Changes in habitat quality were used as a proxy for changes in Ovenbird density and number of young produced (Haché et al. 2013b).

Source-sink dynamics, where demographic sources ($\lambda > 1$) maintain population levels in demographic sinks ($\lambda < 1$), have been reported in many bird species (Pulliam 1996; Rodenhouse et al. 1997; Murphy 2001; Tittler et al. 2006). Therefore, we modelled Ovenbird abundance: 1) irrespective of habitat-specific population growth rate, assuming that surplus individuals would emigrate, whereas territory vacancies would be supplemented by demographic sources outside the study area; and 2) by considering intrinsic change in population size as a function of population growth rate in the absence of emigration or immigration (i.e. the Black Brook District would support a closed breeding population of Ovenbirds). Support for a closed population comes from stable isotope analyses that have shown that most individuals recruited in individually-marked subpopulations in the study area were probably hatched locally (i.e. within Black Brook; Haché et al. in review).

6.2 Methods

6.2.1 Study area

The study was conducted in the Black Brook District, northwestern New Brunswick, Canada (47°23'N, 67°40'W). The land base covers 2000 km^2 and is privately owned by J.D. Irving, Limited. Black Brook is one of the most intensively-managed forest in eastern North America (Montigny & MacLean 2005). It is composed of deciduous stands (25% of total area; sugar maple [*Acer saccharum*], yellow birch [*Betula alleghaniensis*], and American beech [*Fagus grandifolia*]), conifer stands (20%; black spruce [*Picea mariana*], white spruce [*P. glauca*], jack pine [*Pinus banksiana*]), mixedwood stands (18%), and conifer plantations (37%; see Etheridge et al. 2005 for details).

For 30 years, J.D. Irving Limited, has managed deciduous stands and deciduous-dominated mixedwood stands using partial harvest treatments, selection harvesting being the most widely used (Figure 6.1). This treatment typically removes 30-40% of the basal area (cross-sectional area at breast height [1.35 m] of all stems with a diameter ≥ 10 cm) every 20-25 years. The creation of skid trails (5 m wide) accounts for ca. 20% of the basal area removal, the extra 10-20% being harvested in the residual forest between skid trails. Other treatments of similar intensity resulting in different configurations of residual trees such as strip and patch cuts (i.e. group selection) and pre-commercial thinning occur sporadically. Alternatively, shelterwood harvesting (Figure 6.1) removes 50-70% of the basal area and is applied to improve growing stock and reduce the prevalence of American beech which is severely affected by beech bark disease.

Since 1957, coniferous stands have been managed primarily through plantation silviculture. The species most often planted are white and black spruce and, to a lesser extent, red and Norway spruce (*P. rubens*; *P. abies*) and white pine (*P. strobus*). Conifer plantations are generally harvested when they reach 40-50 years (G. Adams, J.D. Irving Limited, pers. comm.). Naturally-regenerated conifer forests represent 4% of the district and are restricted to riparian buffer strips or reserves (MacLean et al. 2010; see Etheridge et al. 2005 for details).

6.2.2 Ecology and habitat-specific demography of the Ovenbird

The Ovenbird is a neotropical migratory songbird that reaches its highest density and productivity per unit area in mature deciduous and deciduous-dominated mixedwood stands with a relatively closed canopy and sparse understory (Pérot & Villard 2009; Porneluzi et al. 2011). It is a ground-nesting species foraging almost exclusively on litter invertebrates (Holmes & Robinson 1988) and consuming prey proportional to their availability (Stenger 1958).

Annually from 2006-2011, we monitored the demographic response of the Ovenbird to selection harvesting in five pairs of 25-ha study plots, including five treated plots and five controls (Haché & Villard 2010; Haché et al. 2013b; Haché et al. 2014; Vernouillet et al. in review). Specifically, we measured density, productivity per unit area, per capita productivity, recruitment, and apparent survival of juveniles and adults during the first five years post-harvest except juvenile survival (until day 14), which was measured during the fourth and fifth years post-harvest (Table 6.1). Lower density, productivity per unit area, food abundance, and larger territory size have been reported following selection harvesting, but these effects were no longer significant by the fifth year post-harvest (Haché et al. 2013b). Selection harvesting had no significant effect on apparent adult survival rate (Haché & Villard 2010; Vernouillet et al. in review), juvenile survival rate (Haché et al. 2014), or per capita productivity (Haché et al. 2013b; see also Leblanc et al. 2011).

Using the same protocol as Haché et al. (2013b), we also measured in 2010 the density and productivity per unit area of Ovenbirds in recent (first year post-harvest; n = 3) and old shelterwoods (16-20 years post-harvest; n = 3; 25-ha study plots). No individuals were detected during four surveys in recent shelterwoods, while density (based on eight spot mapping visits – see Haché et al. 2013b for details) and productivity per unit area in old shelterwoods were respectively ca. 37%, and 66% lower than in recent selection cuts. Details on protocols used to generate density and productivity estimates can be found in Haché et al. 2013b; Table 6.1). Ovenbirds can also defend territories in mature conifer-dominated mixedwood and conifer stands and plantations (Guénette & Villard 2005; Mackay et al., in press). We reported density estimates generated from point count and spot mapping data for conifer stands in three categories (≤ 10, 11-25, and > 25 year since harvesting; see Appendix 3 for details).

6.3.3 Modeling approach

6.3.3.1 Step 1. Demographic model

We used the demographic information provided by the studies listed above to generate habitat-specific estimates of density, number of young produced, and population growth rate (λ; Table 6.1). Habitat-specific λ was calculated as:

$$\text{Equation 1:}\ \lambda = \phi_A + (\psi \times (\phi_F \times \phi_A))$$

where ϕ_A is the apparent survival rate of adults, ψ is the per capita productivity, and ϕ_F represents postfledging survival rate at day 14. We made the following assumptions: 1) survival rate of juveniles was the same as that of adults after day 14 (little mortality has been reported between day 14 and independence; Streby & Andersen 2012, 2013; but see Dybala et al. 2013); 2) apparent survival of adults defending a territory in plantations and shelterwoods was equal to that observed in recent selection cuts, until post-treatment density and productivity per unit area reached those of untreated deciduous stands; then, apparent adult survival was assumed to be the same as in untreated deciduous stands; and 3) individuals defending territories in conifer stands and spruce plantations do not produce young (see also Porneluzi et al. 2011).

The sex ratio in adult songbirds is generally male-biased (1.14:0.86; Donald 2007; Amrhein et al. 2012). High pairing success has been reported in untreated deciduous stands and recent selection cuts (Haché et al. 2013b; see also Bourque & Villard 2001). However, the male-biased sex ratio would likely result in low female abundance in recent shelterwoods and conifer stands owing to low habitat quality. This, in turn, would result in low or no breeding success for males in these stands (i.e. shelterwoods and conifers stands, respectively) and negligible contributions to population dynamics (Table 6.1).

In post-harvest years for which we did not have empirical data, density and productivity per unit area in deciduous stands were extrapolated assuming a linear increase with years post-harvest, while per capita productivity was assumed to remain constant (e.g. Haché et al. 2013b). Density and productivity per unit area in these stands were assumed to remain constant once they had reached the same values as untreated stands (Table 6.1). Values were averaged over five-year periods to coincide with the temporal resolution provided by the timber supply model used by the forestry company (see Step 2).

6.3.3.2 Step 2. Forest Timber Supply model

J.D. Irving, Limited, generated its timber supply model for the Black Brook District using Woodstock, which is a linear programming optimization software that determines the optimum treatment schedule to maximize a value across a range of management constraints (Remsoft, Inc. 1996). The simulation is based on an area file which is an aspatial representation of the study landbase that has been subdivided into landscape themes relative to management objectives. For example, attributes such as stand type, operability constraints, and eco-region have been integrated. Individual stands were aggregated into strata based on similar age and stand characteristics. Management interventions included were number of years since final harvest, selection harvest, shelterwood harvest, patch harvest, planting, precommercial, and commercial thinning. Operability limits for these actions were based on J.D. Irving, Limited, operation standards, along with the predicted stand response (i.e. which stand type class, age, and growth projection [yield curve] treated areas will regenerate in post-harvest years). Stand growth patterns were simulated using projections from the STAMAN stand growth model (Vanguard Forest Management Services Ltd. 1993) using the New Brunswick permanent sample plot network to calibrate growth projections. The baseline management strategy was set to maximize spruce, fir, pine, and deciduous hardwood harvest, while ensuring that a specified amount of shelterwood and selection harvest provides the deciduous harvest volume. Other management constraints were in place to ensure non-declining harvest levels, non-declining operable growing stock levels, maintaining protected areas for biodiversity, non-declining forest cover types, and specific planting and percent levels. The forest timber supply model used in this study generated projections of the land base every five years over a 75-year period (2012-2087).

Conifer stands (i.e. conifer and conifer-dominated mixedwood stands and plantations) were considered to have the same habitat quality for Ovenbirds, but abundance varies as a function of the number of years post-harvest. Thus, we reported density estimates for conifer stands in three categories 0-10, 11-25, and > 25 years post-harvest. Similarly, deciduous and deciduous-dominated mixedwood stands were considered equivalent for Ovenbirds (hereafter “deciduous”). Patch cuts, strip cuts and pre-commercial thinning were considered to have a similar effect on Ovenbirds as selection harvesting and these treatments were pooled and are hereafter referred to as selection harvesting. For each 5 year period (17 periods; 2012-2087), the area managed through selection harvesting was divided in two post-harvest categories (1-5 and > 5 years post-harvest), whereas the shelterwood area was divided into six periods (1-5, 6-10, 11-15, 16-20, 21-25, > 25 years post-harvest). The difference in the number of post-harvest years monitored for each treatment reflects the time required before reaching values equal to untreated stands or for shelterwood stands to enter a selection harvesting regime.

6.3.3.3 Step 4. Different forest dynamic outcomes

The main natural disturbances occurring in the study area are insect outbreaks and fires, but they are highly controlled and rarely influence the dynamics of deciduous stands (G. Adams, J.D. Irving Limited, pers. comm.). Stand-replacing windthrows tend to occur every thousand years in forests of the Northeast (Seymour et al. 2002) and the dynamics of an old growth forest of northern Maine indicates a canopy disturbance rate of 9.6% per decade (Fraver et al. 2009). However, other disturbance agents such as droughts and pathogens can interact with abiotic and biotic factors and the resulting dieback can create spatial heterogeneity and influence species composition (Hughes 1960; Amos-Binks et al. 2010). Some mixedwood stands might also represent a natural transition following such natural disturbances (Amos-Binks et al. 2010). In the timber supply model, natural disturbance events are not projected, except for natural senescence beyond a specific stand age. However, to some extent, harvest treatments are allocated to mimic natural disturbances in terms of area and volume harvested. Hence, landscape stochastiticy (e.g. Wintle et al. 2005; Chisholm & Wintle 2007) was not integrated into our models.

First, we used the J.D. Irving, Limited, forest timber supply model for the Black Brook freehold management district (i.e. forestry-as-usual; FAU) to model the Ovenbird response (abundance, number of young produced, and population growth rate) for a 75-year period (2012-2087). We explored three additional management scenarios: 1) no harvesting (i.e. assuming the entire area is comprised of mature stands); 2) 10%; and 3) 20% decrease in the selection to shelterwood harvesting ratio relative to one of the FAU scenarios (i.e. converting 10 and 20% of the area managed through selection harvesting into shelterwood). The "no harvesting model" was meant to provide ecological benchmark values, whereas the two other scenarios allowed quantifying the effects of more intensive harvesting scenarios on the Ovenbird population. By not accounting for natural disturbance, the timber supply model might underestimate the area harvested through salvage logging owing to tree mortality (see Meehl & Tebaldi [2004] for anticipated increase in drought events). Salvage logging and stands with high tree mortality that cannot be salvaged are both expected to have similar effects as shelterwood harvesting on Ovenbird populations. Hence, to some extent, the two more intensive harvesting scenarios can be used to mimic potential responses of the forestry company, and, ultimately, Ovenbird populations, to natural disturbances.

6.3.3.4 Step 5. Climate scenarios

The four harvesting scenarios assumed no effect of climate change on our focal species. This is a realistic assumption as litter invertebrates might adapt, or the invertebrate community might change in response to climate change, maintaining similar overall abundance and biomass. Changes in prey community composition might have limited consequences on generalist insectivores such as the Ovenbird (Stenger 1958). Alternatively, potential negative effects might be compensated by a longer growing season providing opportunities for additional breeding attempts or even double brooding, which has been documented for this species at lower latitudes (Podolsky et al. 2007; see also Townsend et al. 2013).

In our study area, mean annual temperature was 4.5 °C ± 1.2 (SD) between 2009 and 2011 (Environment Canada, 2013). Climatic projections using the Delta method (Ramirez-Villegas & Jarvis 2010) and the SRES A2 (Special Report on Emissions Scenarios; Nakicenovic et al. 2000) emission scenario from four climatic models (ukmo hadgem1: Martin et al. 2006; mpi echm5: Roeckner et al. 2003, 2004; gfdl-cm2.1: Delworth et al. 2006; and cccma_cgcm3_1_t47: Canadian Centre for Climate Modelling and Analysis 2013) suggest that mean annual temperature will increase by 3.4 °C (± 0.8) on average between the 2020-2029 and 2080-2089 periods (ca. 86.3% increase; Ramirez & Jarvis 2008).

In New Hampshire, the Hubbard Brook Experimental Forest experienced a mean annual temperature (2009 - 2011; 5.4°C ± 0.8; Campbell & Bailey 2013) that was slightly higher than in our study area. However, the projected increase in temperature by 2089 when using the same emission scenarios and climatic models is expected to be similar to our study area (3.4°C ± 0.8; see Hayhoe et al. 2007 for mean values from a broader range of emission scenarios and models). Hence, the anticipated negative effects of climate change on Ovenbirds and other ground-nesting songbirds in the Hubbard Brook Experiment Forest and northeastern United States (Rodenhouse et al. 2008; Groffman et al. 2012; Templer et al. 2012) are likely to apply to our study area given their similar forest composition. Two additional scenarios considered potential effects of low (-10%) and high (-50%) reductions of litter invertebrates (i.e. lower habitat quality; Groffman et al 2012; Templer et al. 2012). Ovenbird territory size, density, and productivity per unit area have been shown to be correlated with the abundance of litter invertebrates (Haché et al. 2013b). To model negative effects of lower food abundance on Ovenbirds, we decreased habitat-specific density and productivity per unit area by 0.7% (low) and 3.3% (high) every five years for the duration of the simulation period (10% and 50% reductions, respectively, by 2087). In these models, we assumed no effect of reduced food abundance on per capita productivity (Haché et al. 2013b; but see Seagle & Sturtevant 2005). These two scenarios are consistent with projected declines in Ovenbird incidence according to different emission scenarios and climatic models (Rodenhouse et al. 2008).

6.3.3.5 Step 6. Source-sink dynamics

Breeding adults show high site fidelity (Greenwood & Harvey 1982; Haché & Villard 2010. Hence, the spatial scale at which source-sink dynamics would take place should be commensurate with the extent of natal dispersal movements (Tittler et al. 2006). By combining stable isotope analyses and bivariate assignment tests, we showed that most first-year breeding males (94%) likely hatched within our study area (Haché et al. in review). However, the likely area of origin of most individuals extended up to 200 km beyond the limits of Black Brook. Given this uncertainty in the extent of natal dispersal movements, we modelled Ovenbird abundance and number of young produced based on two population dynamics scenarios. Projections were first generated irrespective of population growth rate, assuming that surpluses or deficits of territorial males were compensated through immigration and emigration (i.e. large-scale source-sink dynamics; Tittler et al. 2006, 2009). The second approach assumed that source-sink dynamics occurred over a spatial scale corresponding to the size of the study area and that population dynamics were not influenced by immigration and emigration (i.e. population size and productivity per unit area were influenced by local population growth rate). This scenario does not necessarily imply absolute closure because a few recruits could still be immigrants (hatched outside of Black Brook) and contribute to gene flow, but population dynamics would still largely be regulated through productivity from within Black Brook.

In summary, we compared predictions from 15, 15, and 5 models for abundance, number of young produced, and population growth rate, respectively, to determine the relative importance of different harvesting, climatic, and population dynamic scenarios on the status of the Ovenbird in Black Brook (Table 6.2). Results are presented as mean annual values per 5-year period.

6.4 Results

From 2012 to 2087, the projected area of deciduous stands remained relatively constant and covered 38 - 46% of the total forested area (64,330 - 85,356 ha). The proportion of untreated deciduous stands showed more variation over the projected period, but followed a similar pattern. The area managed by selection harvesting was expected to increase by ca. 8,000 ha by 2022 and remain relatively constant thereafter, while shelterwood harvesting remained at low levels throughout the projected period (0 - 4.8% of the forest land base, respectively). Lastly, the area covered by conifer stands was projected to vary between 56 - 62% of the total area. Areas for each treatment as a function of the number of years post-harvest under the forestry-as-usual (FAU) scenario are reported in Appendix 4.

According to the FAU scenario without the effects of climate change, 46,070 males would be defending a territory each year during the 2012-2016 period and values were expected to stay relatively constant throughout the projected period (46,996 ± 466 males; ± SE). Male abundance was expected to be 38,842 and 21,579 by 2087 under scenarios of low (-10%) and high (-50%) effects of climate change (i.e. lower habitat quality), respectively (Figure 6.2). Under the FAU scenario without the effects of climate change, male abundance in 2012 was 25% lower than expected from the no harvest scenario without effects of climate change (61,869 males; Figure 6.2A). By 2087, male abundance was higher under the FAU scenario without effects of climate change (43,158 males) and with a 10% reduction in habitat quality (38,842 males) than under the no harvest scenario with a 50% reduction in habitat quality (30,935 males). Higher harvesting intensity (i.e. reducing the selection: shelterwood ratio by 10 and 20%) had less of an effect on the abundance of territorial males than the reduction in habitat quality caused by climate change. Indeed compared to the FAU scenario, 1,092 (± 22) fewer males on average per period (- 2.0% - -2.9%) were predicted under the scenario of a 10% increase in harvesting intensity, while this difference was of 2,185 (± 43) males based on a 20% increase in harvesting intensity (Figure 6.2B).

According to the FAU scenario without effects of climate change, the number of young produced also remained relatively constant throughout the projected period, with 59,904 (± 921) young produced on average per period (Figure 6.3). Interestingly, based on this scenario, productivity would currently (2012-2016) be only 6% lower than values projected from the no harvest scenario without effects of climate change (Figure 6.3A). By 2087, the difference between the number of young produced under the FAU with a 10% reduction in habitat quality (climate change) and the high harvesting scenario was only of 102 young (Figure 6.3B). Differences between the number of young produced based on the FAU scenario and a 10% increase in harvesting intensity was on average 2,520 (± 176), whereas this difference was 5,040 (± 352) young on average per period based on a 20% increase in harvesting intensity.

These results were all generated irrespective of population growth rate and assuming that population size was maintained by immigration and emigration. Based on the FAU harvesting scenario without effects of climate change, the study area was a demographic sink throughout the projected period (0.906 ± 0.009; Figure 6.4). Values are expected to be only slightly lower when considering the two alternative harvesting scenarios, whereas $\lambda = 0.901$ (± 0.002) and 0.896 (± 0.003) when considering a 10% and 20% increase in harvesting intensity, respectively. The lowest λ (0.869) was under the no harvest scenario (Appendix 4). If population size was not maintained though immigration, declines in abundance are expected to occur between 2012 and 2037 (- 28%) and it would stay relatively constant thereafter (mean = 34,514 ± 896; Figure 6.2C). These expected changes in abundance would coincide with an increase in population growth rate by 0.081 between 2012 and 2047 and have a mean value of 0.998 (± 0.001) in subsequent periods (Figure 6.4). Under a scenario assuming no immigration and a 50% reduction in habitat quality, 14,840 males are expected to defend a territory in the study area by 2087 which is 31% less than the predicted value under the same conditions without accounting for population growth rate (Figure 6.2C). Interestingly, under the FAU scenario, the predicted number of young produced was identical if population size was maintained by immigration or not.

6.5 Discussion

Because forests host a disproportionate amount of the world's biodiversity, we need to find better ways to mitigate negative effects of human activities (Gibson et al. 2011; Lindenmayer et al. 2012). Here, we used empirical demographic data to model population dynamics of Ovenbirds breeding in an intensively managed forest landscape. Our findings suggest that Black Brook supports ca. 25% fewer male Ovenbirds than expected based on a no harvest scenario. When considering the number of young produced, this difference was only ca. 6%. The projected effects of climate change on population size and productivity may be more important in the long-term than intensive harvesting. Black Brook is expected to be a demographic sink ($\lambda = 0.920$; 2012 period from the FAU scenario) and population size is expected to decrease by 28% if demographic sources from outside the study area cannot maintain recruitment to compensate for adult mortality. These results provide important insights into the relative importance of land use, climate change, and population dynamics on the future status a forest songbird associated with mature deciduous stands.

Although Black Brook as a whole is likely acting as a demographic sink, our models also suggest that source-sink dynamics are taking place within the study area. Untreated deciduous stands and selection cuts > 5 years post-harvest are expected to act as demographic sources, whereas all other stands types would act as demographic sinks (Table 6.1). The high proportion of demographic sinks in Black Brook is mostly due to the large proportion of conifer stands. These stands represent up to 60% of the study area and this proportion is expected to remain stable throughout the projected period (57% - 62%). Although Ovenbirds would be absent or present at low density in these stands, they would still be supporting ca. 24% of the territorial males (24% - 32% over the projected period if immigration rate remains constant). Under the no harvest scenario, where Black Brook would be comprised only of mature stands, an even higher proportion of individuals were expected to defend a territory in conifer stands (40%), which explains that the lowest population growth rate was predicted under this scenario in spite of the fact that all deciduous stands remain untreated (Figure 6.4; Appendix 4). However, in the absence of immigration, the percentage of breeding Ovenbirds in coniferous stands is expected to be < 5% by 2042. This decline would result in a proportional increase in growth rate (i.e. higher proportion of demographic sources) where local recruitment would compensate for adult mortality. Future studies should continue exploring the potential of intrinsic markers and other technologies to determine whether Ovenbirds breeding in Black Brook should be considered an opened or closed demographic unit. In the meantime, it would be important to document the status of the Ovenbird within ca. 200 km from Black Brook to determine whether these stands could act as demographic sources (see also Lloyd et al. 2005, Bonnot et al. 2011).

It has been estimated that several billions of birds breed in the Canadian boreal forest (Blancher 2002 cited by Calvert et al. 2013). Recent estimates suggest that between 616,000 and 2,090,000 bird nests are lost to industrial forestry operations each year in Canada (Hobson et al. 2013). These estimates would correspond to an annual loss of 564,000 - 1,330,000 potential recruits. Thus, harvesting clearly has important negative effects of forest bird communities. However, separate estimates for even-aged management (clearcuts) and partial harvesting regimes in uneven-aged stands have not been produced. In northern hardwood stands, there is evidence that low intensity (30-40% tree removal) partial harvest treatments could increase species diversity owing to the creation of suitable breeding habitat for early-seral species (Schlossberg et al. 2010; Haché et al. 2013a). Some mature forest specialists have lower abundances in early post-harvest years, but we are unaware of severe declines or local extinctions following such treatment in deciduous stands of North America (e.g. Gram et al. 2003; Vanderwel et al. 2009; Poulin et al. 2010). However, the demographic response of mature forest birds to partial harvesting remains largely unknown (Hobson et al. 2013) and data currently available show contrasted responses among and within species (reviewed by Richmond et al. 2012). For example, the Ovenbird has been referred to as one of the most sensitive bird species to partial harvesting (Vanderwel et al. 2007, 2009), but the numerous lines of evidence presented in this study (see also Leblanc et al. 2011) suggest that it may be more resilient to moderate alteration of the northern hardwood forest than previously reported. The demographic response of the Ovenbird combined with the creation of more suitable habitat for early-seral species would be consistent with predictions from the intermediate disturbance hypothesis which predicts a peak in species richness at intermediate anthropogenic disturbance (e.g. Mayor et al. 2012). Nonetheless, it would be unwise to assume that all mature forest songbirds would be as tolerant to habitat alteration. Snag-dependent species such as the Brown Creeper (*Certhia americana*) and Olive-sided Flycatcher (*Contopus cooperi*) have shown lower reproductive success in recent partial cuts (Robertson & Hutto 2007; Poulin et al. 2010). The status of these and ecologically-similar species breeding in intensively managed forest landscapes should be monitored.

It is believed by many that climate change will have important implications for species abundance and distribution, and, ultimately, species assemblages (e.g. Lawler et al. 2009; Davey et al. 2012; Gallagher et al. 2013). However, the relative contribution of the numerous threats facing bird populations is only starting to be explored (e.g. Calvert et al. 2013). How these factors interact to influence population dynamics is also unknown, but synergistic relationships are anticipated (Coristine & Kerr 2011; Cox et al. 2013). Here, we modelled effects of climate change based using the expected negative impacts on Ovenbird incidence (correlated with abundance) in northeastern North America (Rodenhouse et al. 2008). Rodenhouse et al. (2008) acknowledged the important uncertainty underlying species' response to climate change (see also Kujala et al. 2013). For example, complex interactions among natural disturbances, human land use, invasive species, pests, and pathogens, and climate change are expected and, consequently, changes in stand composition and growth rate are difficult to anticipate (reviewed by Groffman et al. 2012). Although which tree species will dominate deciduous stands in Black Brook by 2087 remains unclear, intensive management should allow maintaining the proportion of conifer vs. deciduous stands. The Ovenbird breeds in a broad range of deciduous ecosystems (Porneluzi et al. 2011), suggesting that it can be resilient to changes in tree species composition. The effects of climate change are therefore more likely to be associated with habitat degradation than habitat loss in our study area (see also Rodenhouse et al. 2008). Even under a low greenhouse gas emission scenario (10% reduction in habitat quality), climate change is expected to have more important effects on the number of male Ovenbirds in Black Brook than the high harvesting scenario (Fig. 6.2b). However, given the uncertainty about species responses to climate change (Rodenhouse et al. 2008), predictions from our scenarios without effects of climate change should also be considered realistic. Nonetheless, predicted differences in the number of territorial males and young produced in 2087 between FAU scenarios and moderate and intensive harvesting scenarios would correspond to a 3-6% (males) and 5-10% (young) degradation in habitat quality as a result of climate change (Fig. 6.2b-6.3b). This suggests that relatively small negative effects of climate change on habitat quality of Ovenbird would be required to have similar effects than the more intensive harvesting scenarios considered in our study area.

The trend analyses reported in this study were based on the assumption that we could model population dynamics with some precision. Studies have provided contrasting estimates of λ for Ovenbird populations. For example, in northern Wisconsin, Flaspohler et al. (2001) reported values of 1.11 and 1.18 for edge and interior habitats, respectively, whereas Leblanc et al. (2011) estimated λ between 0.837- 0.858 among four harvest treatments in deciduous stands from central Ontario (see also Podolsky et al. 2007). Many studies have reported that adult and juvenile survival were the most sensitive parameters used to estimate population growth rate (e.g. Schmutz et al. 1997; Flaspohler et al. 2001). Yet, to our knowledge, this is the first study modelling population dynamics of Ovenbirds based on apparent adult survival estimates specific to a study area. Owing to low return rates of birds banded as nestlings or juveniles, survival during the first calendar year (a.k.a. juvenile survival) remains largely unknown (Sillett & Holmes 2002; Dybala et al. 2013), but we argue that combining data on postfledging and adult survival rates provides the most realistic estimates of juvenile survival currently available for migratory bird species with large breeding ranges (Dybala et al. 2013; McKim-Louder et al. 2013). That being said, we recognize the uncertainty inherent to our modelling approach. For example, female-specific demographic rates (e.g. Podolsky et al. 2007) and a better understanding of population dynamics in conifer stands and shelterwoods would likely generate more precise estimates of population growth rates.

Population dynamics should also be monitored throughout a species' life cycle (Sillett & Holmes 2002; Faaborg et al. 2013). We recognize that habitat loss/alteration and climate change also influence Ovenbirds on the wintering grounds and during migration. In spite of migratory connectivity, population trends associated with conditions experience during the nonbreeding season likely influence population dynamics on the breeding grounds over a spatial scale extending well beyond our study area, irrespective of breeding habitat quality. Hence, although we elected to focus on factors operating during the breeding season, nonbreeding habitat loss/alteration will have an additive effect. Individual-based, spatially-explicit models would allow exploring effects of habitat loss vs. fragmentation (Wintle et al. 2005; Chisholm & Wintle 2007). The Ovenbird can be influenced by landscape composition and structure (Betts et al. 2006, 2007; Wallendorf et al. 2007; Villard & Haché 2012) and, by 2027, the mean patch size of deciduous forest in Black Brook is expected to decrease by ca. 50% (Etheridge et al. 2006). Incorporating landscape history would also provide a better understanding of current and future population status (Schrott et al. 2005). Nonetheless, to our knowledge, we used the most detailed habitat-specific demographic information available for a songbird breeding in an intensively managed forest of North America (see also Morris et al. in press). Our results suggest that climate change will likely have more important effects on songbird populations breeding in the northern hardwood forest than forestry operations. Although these findings should be interpreted with caution, they provide important insight about the future status of bird populations and the opportunity for proactive conservation plans by considering current and future threats known to influence bird populations.

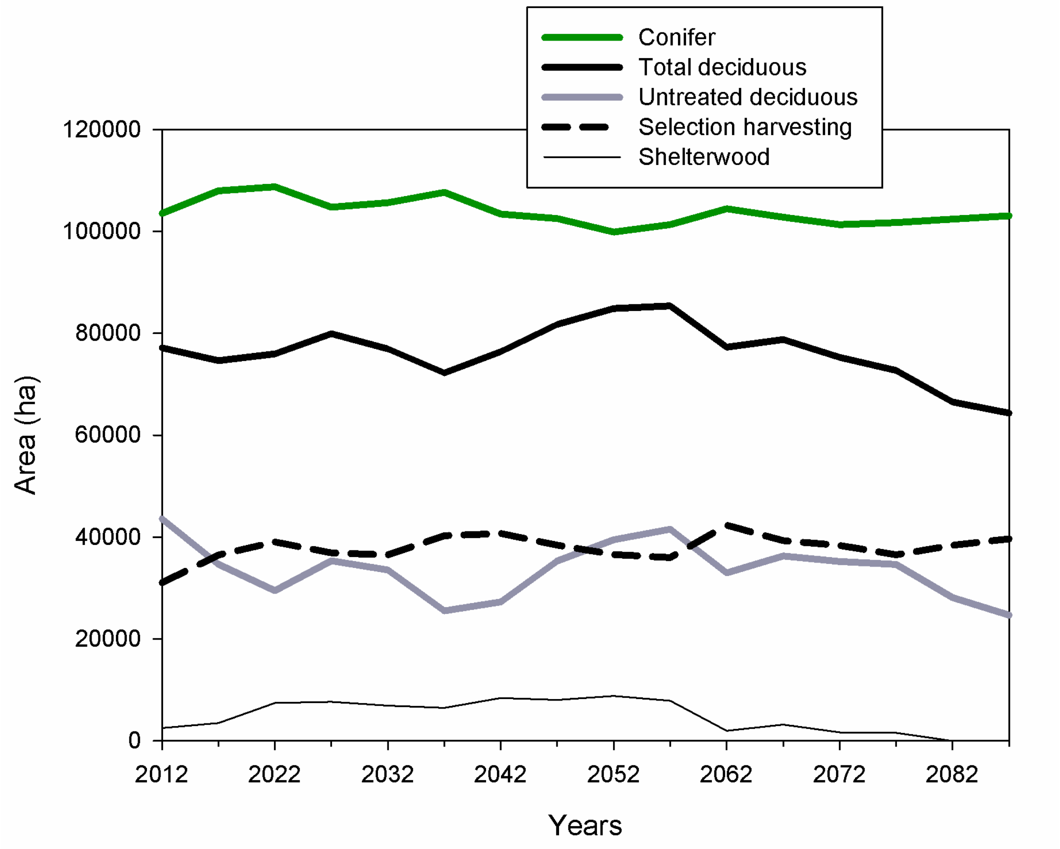

Figure 6.1. Area for each stand category used to model the future status of Ovenbird in Black Brook from 2012-2087. Predictions are based on the forestry-as-usual scenario.

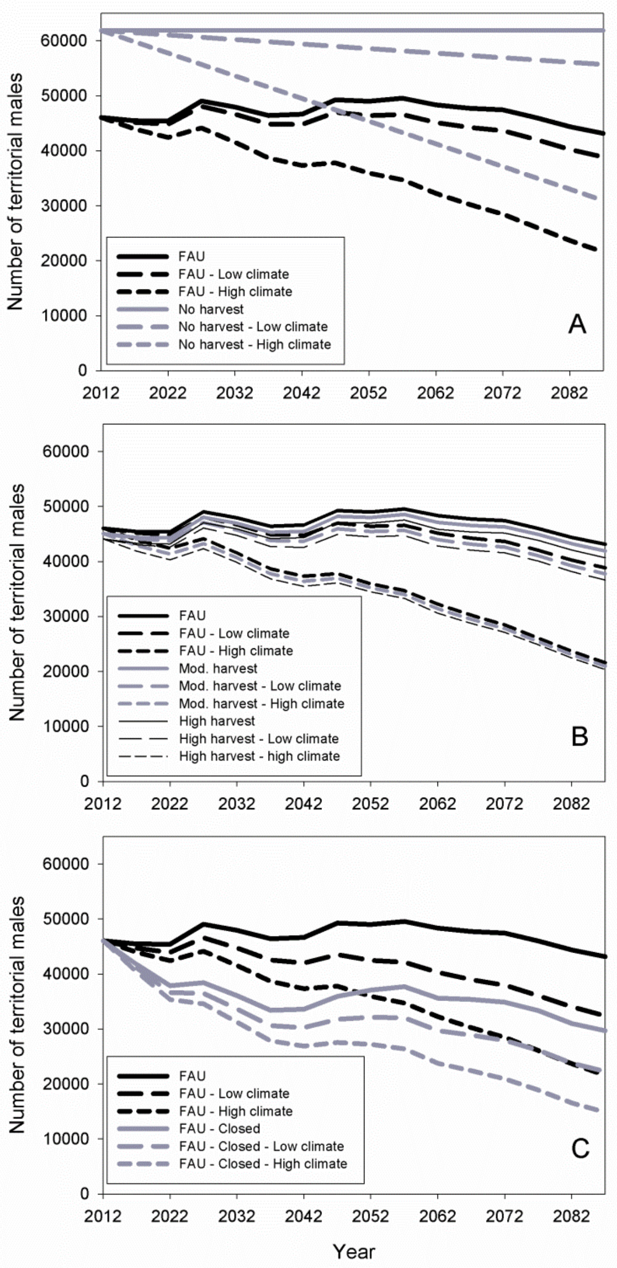

Figure 6.2. Number of males expected to defend a territory in the study area 2012-2087 under the forestry-as-usual scenario and two potential effects of habitat degradation owing to climate change (10 and 50% decrease in habitat quality). Values are compared to the no harvest scenario (A), a 10 and 20% increase in harvesting intensity (B) and assuming that population size is not maintained by immigration (Closed; C).

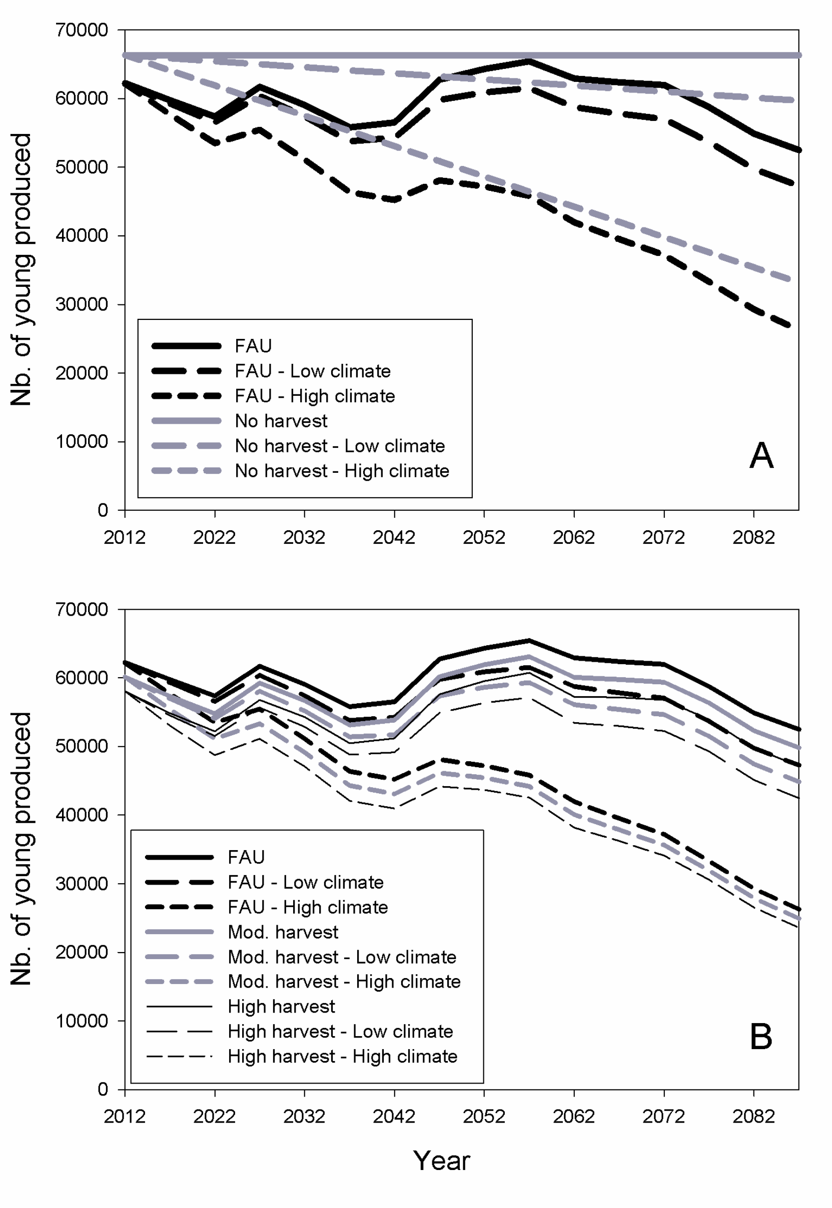

Figure 6.3. Predicted number of young produced in the study area from 2012-2087 under the forestry-as-usual (FAU) scenario and two potential effects of habitat degradation owing to climate change (10 and 50% decrease in habitat quality). Values are compared to the no harvest scenario (A) and a 10 and 20% increase in harvesting intensity (B).

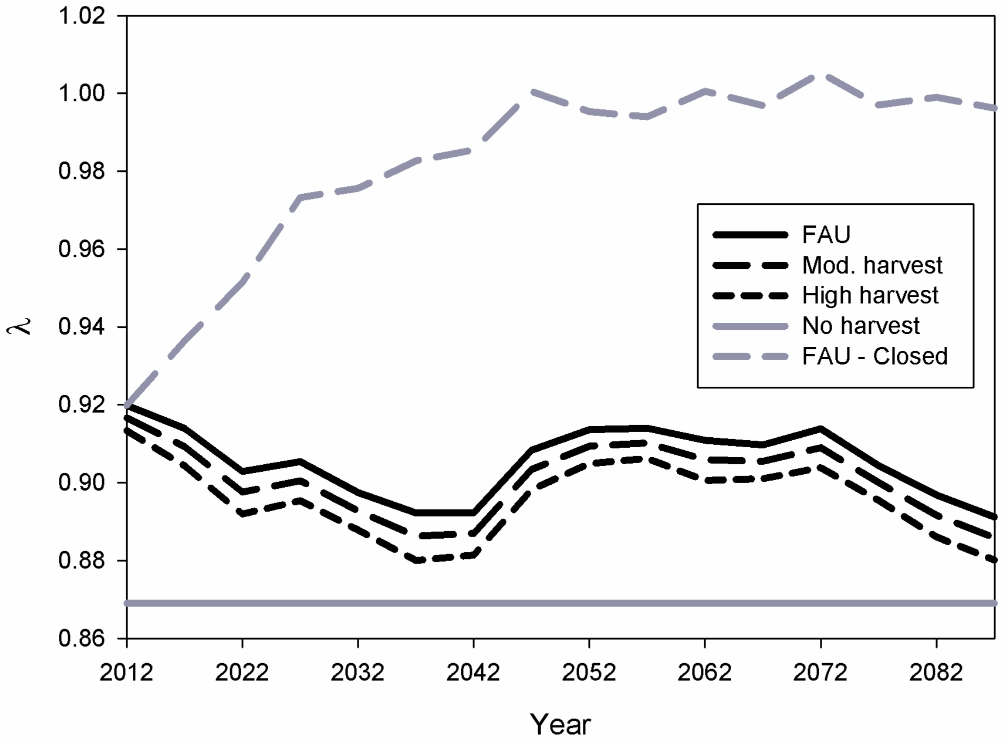

Figure 6.4. Predicted population growth in Ovenbirds breeding in the study area from 2012-2087 under four harvesting scenarios and assuming that population size is not regulated by immigration (Closed).

Table 6.1. Mean values (± SE) used to generate abundance, number of young produced and, population growth rate in Ovenbirds breeding in the Black Brook District, New Brunswick. Empirical data used to generate estimates for the other habitat types are shown in bold.

	Density (/25 ha)	Productivity (/25 ha)	Per capita productivity	Adult survival	Juvenile survival[1]	λ
Untreated deciduous	**12.0** **(± 0.6)**	**21.5** **(± 1.7)**	**0.86** **(± 0.05)**	**0.73** **(± 0.02)**	**0.33**	1.01
Select. harv. (1 - 5 yrs)	**8.8** **(± 0.4)**	**15.2** **(± 1.5)**	**0.81** **(± 0.06)**	**0.67** **(± 0.03)**	**0.30**	0.92
Select. harv. (> 5 yrs)	12.0	21.5	0.86	0.73	0.33	1.01
Shelt. harv. (1-5 yrs)[2]	**0.7**	**0.6**	**0.46**	0.67	0.30	0.81
Shelt. harv. (6-10 yrs)	2.4	2.1	0.46	0.67	0.30	0.81
Shelt. harv. (11-15 yrs)	4.2	3.6	0.46	0.67	0.30	0.81
Shelt. harv. (16-20 yrs)[2]	**5.9**	**5.1**	**0.46**	0.67	0.30	0.81
Shelt. harv. (21-25 yrs)	7.6	6.6	0.46	0.67	0.30	0.81

Table 6.1. (Continued).

	Density (/25 ha)	Productivity (/25 ha)	Per capita productivity	Adult survival	Juvenile survival[1]	λ
Shelt. harv. (26-30 yrs)	9.4	16.2	0.81	0.67	0.30	0.92
Conifers (0-10)	0	0	0	0	0	0
Conifers (11-25 yr)	**0.7 (± 0.3)**	0	0	0.67	n/a	0.67
Conifers (> 25 yr)[3]	**6.0**	0	0	0.67	n/a	0.67

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[1] We estimated post-fledgling survival as the number of young surviving until day 14 divided by the total number of young monitored per stand category (See Haché et al. (2014) for details).

[2] We only had empirical data from the first and 16th years post-harvest. Values shown represent predicted means for the five year period.

[3] Density estimates from point count data had to be calibrated (see Appendix 4) and we present mean predictions from two datasets (Guénette & Villard; Mackay et al., in press).

Table 6.2. The 15 scenarios used to predict abundance, productivity, and population growth rate in Ovenbirds breeding in Black Brook, New Brunswick. Opened refers to scenarios assuming that population size are maintained (Opened) or not (Closed) by immigration.

Scenario	Response variable
FAU – no climate – Opened	Abundance, productivity, and λ
FAU – 10% climate –Opened	Abundance and productivity
FAU – 50% climate – Opened	Abundance and productivity
No harvest – No climate	Abundance, productivity, and λ
No harvest – 10% climate	Abundance and productivity
No harvest – 50% climate	Abundance and productivity
10% shelterwood – No climate – Opened	Abundance, productivity, and λ
10% shelterwood – 10% climate –Opened	Abundance and productivity
10% shelterwood – 50% climate – Opened	Abundance and productivity
20% shelterwood – No climate – Opened	Abundance, productivity, and λ
20% shelterwood – 10% climate –Opened	Abundance and productivity
20% shelterwood – 50% climate – Opened	Abundance and productivity
FAU – No climate – Closed	Abundance, productivity, and λ
FAU – 10% climate –Closed	Abundance and productivity
FAU – 50% climate – Closed	Abundance and productivity

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CHAPTER 7. SYNTHESIS

7.1 Habitat selection, reproductive success, and source-sink dynamics in the Ovenbird

In this dissertation, I documented the local and regional demography of Ovenbirds in an intensively managed forest landscape (Black Brook district, J.D. Irving, Limited). The Ovenbird is considered to be one of the most sensitive species to the alteration of its habitat (Vanderwel et al. 2007, 2009). Given the current management regimes applied in North America, there are concerns about the status of this species and other species associated with mature forests (Holmes & Pitt 2007; Haché & Villard 2010; Morris et al. in press). I showed that per capita productivity was similar between deciduous stands recently managed through selection harvesting (1-5 years post-harvest) and untreated stands. This pattern, combined with a lower density and productivity per unit area and a larger territory size in harvested than in untreated stands provided strong evidence for an ideal free distribution (IFD; Chapter 2). Furthermore, variation in daily postfledging survival rate was best explained by plot-level abundance of red squirrels and year, irrespective of selection harvesting (Chapter 3). This provided further evidence for an IFD among individuals breeding in stands recently managed through selection harvesting and untreated stands. Thus, variation in productivity per unit area among these two habitat types may not necessarily imply spatial source-sink dynamics.

Natal dispersal is a critical component of population dynamics as it reflects the spatial scale over which demographic processes are taking place in many bird species (Tittler et al. 2006, 2009). In chapter 4, I showed important year and age variation in stable hydrogen isotope ratios from feathers (δ^2H_f) that need to be considered when using this marker to assign birds to geographic origin. Using this information, I generated species-, year-, and age-specific feather isoscapes (δ^2H_f and $\delta^{34}S_f$) to assign the likely natal origin of Ovenbird males breeding in our study area (Chapter 5). Almost all individuals were considered residents (i.e. hatched in the study area; 95.6%), whereas the two individuals considered as immigrants would have originated from within 240 km of Black Brook (Chapter 5). Hence, most individuals recruited in the breeding population of Black Brook would have been produced "locally" and population processes would mainly take place at a spatial scale equivalent to our study area.

Using empirical Ovenbird data available for our study area, I showed that untreated mature deciduous stands along with selection cuts (> 5 years post-harvest) would support demographic sources (Chapter 6), whereas all other stand types considered in this study would seem to be demographic sinks. The study area would currently support an estimated 46,070 males, produce 62,259 young annually, and have a population growth rate of 0.920. When projecting population status of Ovenbirds under alternative harvesting and climatic scenarios over a 75-year period, I showed that harvesting is possibly going to have less of an effect on Ovenbirds than climate change. However, given the uncertainty about species responses to climate change, predictions from our scenarios without effects of climate change should also be considered realistic. Furthermore, if population size is not maintained through immigration, a large decline is expected, but such a pattern is not anticipated for the number of young produced. Interestingly, that untreated mature deciduous stands would support demographic sources as opposed to recent selection cuts provides evidence for an ideal despotic distribution which goes against findings from Chapters 2 and 3. Such a discrepancy can be explained by the use of habitat-specific mean values for each parameter that although they were not significantly different between habitat types (Chapters 2 and 3), they were all slightly lower in recent selected cuts than in untreated mature deciduous stands (Chapter 6). This discrepancy provides an example on how the analytical approach being used can have important implications on the inferences being made.

7.2 Implications for conservation

To conserve biodiversity, it is critical to understand the demographic response of the most sensitive species. This dissertation provided detailed information on population dynamics of one of the vertebrate species most sensitive to partial harvesting in northern hardwood forests. Somewhat surprisingly, based on our detailed demographic information, this species seems more tolerant to selection harvesting than anticipated based on findings from other studies. Individuals tended to adjust the size of their territory to compensate for lower food abundance in selection cuts in the first years post-harvest (Chapter 2). Similar per capita productivity in Ovenbirds among treatments has also been reported in Ontario by Leblanc et al. (2011), suggesting that habitat selection might also follow an IFD in other regions (but see Morris et al. in press). These results raise important questions regarding the relevance of the Ovenbird as a focal species sensitive to habitat alteration in northern hardwood forests. Future studies should determine whether other focal species have similar demographic responses to partial harvesting than the Ovenbird to better understand the impacts of this treatment on mature forest specialists.

Although untreated deciduous stands and old selection cuts (> 5 years post-harvest) acted as demographic sources, there is evidence that recent selection cuts (≤ 5 years post-harvest), shelterwoods, and conifer stands acted as demographic sinks. Individuals defending a territory in shelterwoods and conifer stands likely contribute little to population growth and important annual fluctuations in abundance are expected in these stands if the Ovenbird population is regulated through site dependence (Rodenhouse et al. 1997). These results provide an understanding of the importance of both local habitat quality and landscape context on population dynamics and, ultimately, the status of the Ovenbird in an intensively managed forest landscape.

The demographic model I created can be used by land managers to estimate Ovenbird abundance, number of young produced, and population growth rate and to evaluate additional harvesting scenarios. This model is a particularly useful tool when considering that population dynamics likely occur over a spatial scale corresponding to management units (e.g. Black Brook District; Chapter 5). Thus, by promoting reproductive success, land managers would also favour local recruitment in the subsequent year. On the basis of a few critical assumptions, the demographic model could also be used by the Department of Natural Resources of New Brunswick to determine the status of the Ovenbird in the province.

7.3 Future research and questions

An important objective of this dissertation was to test for effects of selection harvesting on different demographic processes of an individually-marked subpopulation of Ovenbirds. I focused on stand-level dynamics and future studies should test predictions from conceptual models of habitat selection at multiple spatial scales. Different patterns would likely emerge if studies considered a broader spectrum of habitat types (e.g. shelterwood and conifer stands). If my assumption that Ovenbirds cannot breed successfully in conifer stands is correct, then these individuals might be forced to settle in poor habitat owing to despotic behaviour from older and stronger individuals. Also, spatial heterogeneity in habitat quality within stands suggests that source-sink dynamics could occur over small spatial scales (Haché et al. in prep.; see also Flaspohler et al. 2001; Nystrand et al. 2010). Such results would be consistent with predictions from an ideal despotic distribution and combined with those from Chapters 2 and 3 would provide evidence for both spatial and temporal source-sink dynamics acting concurrently.

It is important to continue monitoring Ovenbird demography in Black Brook. The collaboration with J.D. Irving, Limited, provides a unique opportunity for scientists to continue working with the industry on this long-term monitoring and create new experimental designs to address important gaps in avian ecology, while generating inferences relevant to current land use. Additional information is critically needed from Ovenbirds breeding in stands where population size and reproductive success are lower (i.e. shelterwoods and conifer stands; see chapter 6 for a review of the demographic information required to improve the accuracy and precision of the demographic model). New demographic information could be used to regularly update the demographic model and contribute to adaptive management plans (reviewed by Dzus et al. 2009). Of particular interest would be to compare predictions from our aspatial models to those from spatially-explicit models accounting for patch size and configuration, proximity to landscape features, and harvesting history (e.g. 1945-2002; Schrott et al. 2005; Etheridge et al. 2005). Such spatially-explicit models could also be integrated into a program like Marxan (Ball et al. 2009) to generate cost analyses and assist land managers in designing conservation plans maximizing population size and the number of Ovenbirds produced while minimizing costs. Lastly, the Ovenbird is a neotropical migratory songbird and attempts should be made to model population dynamics throughout its annual cycle (e.g. Sillett & Holmes 2002).

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APPENDIX 1. ADDITIONAL DETAILS ON METHODS USED TO DETERMINE BREEDING STATUS OF TERRITORIAL OVENBIRDS, SAMPLE INVERTEBRATES, AND PERFORM STATISTICAL ANALYSES.

A version of this appendix has been published as supplemental material for Haché, S., M.-A. Villard, and E. M. Bayne. 2013. Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. Ecology 94:861–869. Appendix A: Additional details on methods used to determine breeding status of territorial Ovenbirds, invertebrate sampling design, and statistical analyses. Ecological Archives E094-074-A1.

Breeding status

To determine male pairing and breeding status, we plotted curves of cumulative pairing and fledging success, which are based, respectively, on track time (time of direct observation of an individual deemed unpaired) and nest searching time (within a paired male's territory) (after Bourque & Villard 2001; Figure A1.1-A1.2). Sometimes, a male would first be seen with its mate, which represented a case of confirmed pairing success with track time = 0. Similarly, we sometimes found an active nest incidentally, by flushing an incubating or brooding female, which resulted in the confirmation of nesting activity without prior detection of a pair, nor time spent nest searching. In general, however, we had to do track time or nest searching to confirm pairing success or nesting activity, and the cumulative curves were used to determine how much time, on average, was required to reach a certain proportion (e.g. 90%) of all the known cases of pairing or nesting success.

Using the 90% threshold (Figure A1.1), males with an unknown pairing status would have been deemed “unpaired” if total track time conducted within the territory was ≥ 20 min, or “unknown pairing status” if track time was < 20 min. In other words, when we spent at least 20 min. of track time within a territory, pairing status was confirmed in 90% of cases. Using the same approach (Figure A1.1), we considered that paired males with an unknown nesting status had “failed” (nest searching time ≥ 200 min) or an “unknown” breeding status (nest searching time < 200 min).

Using year- and treatment-specific 90% thresholds, we found that 30% of territorial males had an unknown breeding status (i.e. unknown pairing or nesting status). On average, we conducted 104 min (± 58.4 SD; $n = 174$) of nest searching or 12 min (± 10.2 SD; $n = 62$) of track time in the corresponding territories. In this study, we considered males with an unknown pairing status to have failed to breed, since no female was detected. Track time value does not necessarily reflect the actual time that an observer spent in a territory as it required the observation of the territorial male (dispersal or mortality likely explain some of the low track time values). Actually, those territories received particular attention because we wanted to relocate those males to ascertain their status.

The proportion of paired males with an unknown breeding status did not vary according to treatment (23.8 versus 25.8% for treated plots and controls, respectively). Because low values of nest searching time mainly reflected nesting failures late in the breeding season (after a long period of exposure), or confirmation of pairing success late in the breeding season (likely also resulting from nest predation late in the breeding season, i.e. adults not caring for young), we are confident that a high proportion of these males have indeed failed to breed successfully and they were also considered as such in our analyses.

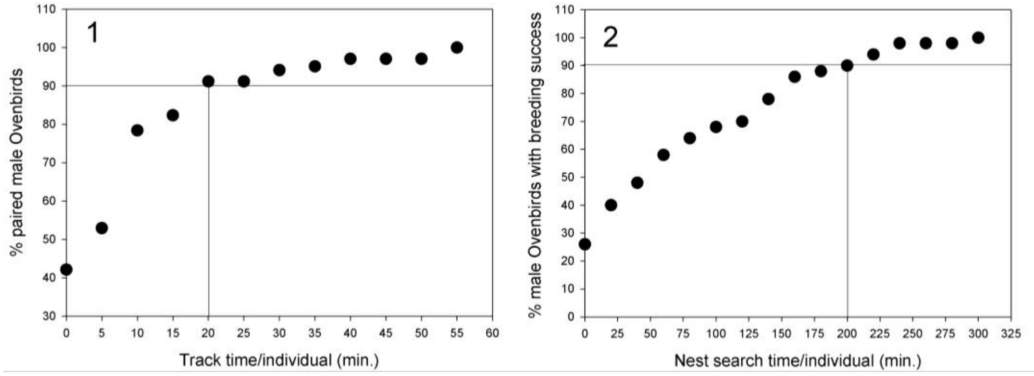

Figure A1.1. Examples of cumulative curves and 90% thresholds that can be used to assigned failure to male territorial songbirds for which pairing (1) or breeding success (2) are considered unknown.

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Invertebrate sampling design and protocol

All study plots were delineated by transects marked every 25 m and each transect was spaced by 50 m, resulting in 231 grid locations. In 2006, 30 locations were randomly chosen from all the locations outside Ovenbird territories and 30 others among locations within territories. We sampled the same 60 locations in subsequent years to allow testing for year effects on food abundance. Sampling was performed 5 m from each grid point in a predetermined direction and all sampling was conducted by the same observer (SH) to avoid potential observer bias.

We removed slugs (*Gastropoda* without shell) from our total biomass estimates as they accounted for a large proportion of the total biomass (~ 45%), but it is unclear whether they are consumed by Ovenbirds (Stenger 1958, but see Zach & Falls 1979). Depending on whether they were brittle, shells > 1 cm^2 were considered as unpalatable to Ovenbirds and they were also removed from biomass estimates. Samples from all locations were preserved in a 70% ethanol solution. Samples were dried at 65°C for 48 hours and the biomass of each group of invertebrates for each study plots was weighed to the nearest 0.1 mg.

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Statistical analyses

To test for effects of treatment, year, and treatment × year interaction on the different response variables, we used variations from of the following linear mixed model (LMM):

$$y = \mu + b_{\tau} + b_{\omega} + b_{\tau \times \omega} + b_{l} + b_{s(l)} + b_{\theta(s)} + b_{\Omega(s)} + \varepsilon$$

Where *y* is the response variable (density, productivity per unit area, productivity per capita, territory size, abundance and biomass for each group of invertebrates), μ is the intercept, b_i is a parameter estimate, τ is the treatment (treated vs. control plots; fixed effects), ω is the year (5 or 6 years; fixed effect), $\tau \times \omega$ is the treatment × year interaction, *l* is the landscape context for each pair of study plots (1-5; random effect), *s*(*l*) is study plots nested in landscape context (1-10; random effect), $\theta(s)$ is territory nested in study plots (random effect), $\Omega(s)$ is quadrat nested in study plots (60; random effect), and ε is the error term. The effect of landscape context was included in our model to account for our paired study plots. Biomass of *Gastropoda* had to be natural-log transformed to meet the conditions of the analysis. Generalized linear mixed models (GLMM) with a Poisson distribution were used when the response variables were from count data (i.e. total abundance of invertebrates, abundance of *Coleoptera* and abundance of *Gastropoda*). Lastly, a GLMM with a negative binomial distribution was used to test the effect of the same predictors on per capita productivity. LMMs and GLMMs were conducted using the MIXED and GLIMMIX procedures, respectively, in SAS 9.2 (SAS Institute Inc, Cary, NC).

APPENDIX 2. RESULTS FROM THE MULTIPLE COMPARISON ANALYSES TESTING FOR YEAR-SPECIFIC TREATMENT EFFECTS AND FIGURES PRESENTING MEAN ABUNDANCE AND BIOMASS OF *COLEOPTERA* AND *GASTROPODA* FOR EACH YEAR AND HABITAT TYPE, AS WELL AS ABUNDANCE BETWEEN SKID TRAILS AND INTER-TRAIL FOREST WITHIN TREATED PLOTS.

A version of this appendix has been published as supplemental material for Haché, S., M.-A. Villard, and E. M. Bayne. 2013. Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. Ecology 94:861–869. Appendix B: Results from the multiple comparison analyses testing for year-specific treatment effects and figures presenting mean abundance and biomass of *Coleoptera* and *Gastropoda* for each year and habitat type and abundance between skid trails and inter-trail forest within treated plots. Ecological Archives E094-074-A2.

Table A2.1. Results from a multiple comparison analysis testing for differences in *densities* between habitat types for each year of the study.

Test	DF	*t*-value	*P*-value
Pre-harvest controls vs. treated plots	40	0.64	0.526
Post-harvest (1) controls vs. treated plots	40	5.48	< 0.001
Post-harvest (2) controls vs. treated plots	40	4.51	< 0.001
Post-harvest (3) controls vs. treated plots	40	4.09	< 0.001
Post-harvest (4) controls vs. treated plots	40	3.67	< 0.001
Post-harvest (5) controls vs. treated plots	40	1.28	0.207

Table A2.2. Results from a multiple comparison analysis testing for differences in *territory size* between habitat types for each year of the study.

Test	DF	*t*-value	*P*-value
Pre-harvest controls vs. treated plots	760	0.87	0.385
Post-harvest (1) controls vs. treated plots	760	- 4.34	< 0.001
Post-harvest (2) controls vs. treated plots	760	- 9.01	< 0.001
Post-harvest (3) controls vs. treated plots	760	- 8.61	< 0.001
Post-harvest (4) controls vs. treated plots	760	- 8.25	< 0.001
Post-harvest (5) controls vs. treated plots	760	- 2.11	0.035

Table A2.3. Results from a multiple comparison analysis testing for differences in *productivity per unit area* between habitat types for each year of the study.

Test	DF	*t*-value	*P*-value
Pre-harvest controls vs. treated plots	40	0.95	0.345
Post-harvest (1) controls vs. treated plots	40	2.54	0.015
Post-harvest (2) controls vs. treated plots	40	2.85	0.007
Post-harvest (3) controls vs. treated plots	40	2.48	0.018
Post-harvest (4) controls vs. treated plots	40	2.82	0.007
Post-harvest (5) controls vs. treated plots	40	1.25	0.218

Table A2.4. Results from a multiple comparison analysis testing for differences in *per capita productivity* between habitat types for each year of the study.

Test	DF	*t*-value	*P*-value
Pre-harvest controls vs. treated plots	342	0.03	0.979
Post-harvest (1) controls vs. treated plots	342	0.05	0.961
Post-harvest (2) controls vs. treated plots	342	- 0.30	0.763
Post-harvest (3) controls vs. treated plots	342	0.61	0.545
Post-harvest (4) controls vs. treated plots	342	0.56	0.578
Post-harvest (5) controls vs. treated plots	342	0.56	0.575

Table A2.5. Results from a multiple comparison analysis testing for differences in *total abundance on invertebrates* between habitat types for the first five years of the study.

Test	DF	*t*-value	*P*-value
Pre-harvest controls vs. treated plots	1912	1.04	0.296
Post-harvest (1) controls vs. treated plots	1912	9.88	< 0.001
Post-harvest (2) controls vs. treated plots	1912	7.91	< 0.001
Post-harvest (3) controls vs. treated plots	1912	5.62	< 0.001
Post-harvest (4) controls vs. treated plots	1912	3.82	< 0.001

Table A2.6. Results from a multiple comparison analysis testing for differences in *abundance of Coleoptera* between habitat types for the first five years of the study.

Test	DF	*t*-value	*P*-value
Pre-harvest controls vs. treated plots	1912	1.81	0.070
Post-harvest (1) controls vs. treated plots	1912	6.23	< 0.001
Post-harvest (2) controls vs. treated plots	1912	7.13	< 0.001
Post-harvest (3) controls vs. treated plots	1912	6.81	< 0.001
Post-harvest (4) controls vs. treated plots	1912	4.06	< 0.001

Table A2.7. Results from a multiple comparison analysis testing for differences in *abundance of Gastropoda* between habitat types for the first five years of the study.

Test	DF	*t*-value	*P*-value
Pre-harvest controls vs. treated plots	1912	1.38	0.169
Post-harvest (1) controls vs. treated plots	1912	4.99	< 0.001
Post-harvest (2) controls vs. treated plots	1912	4.78	< 0.001
Post-harvest (3) controls vs. treated plots	1912	3.17	0.002
Post-harvest (4) controls vs. treated plots	1912	4.46	< 0.001

Table A2.8. Results from a multiple comparison analysis testing for differences in *total biomass of invertebrates* between habitat types for the first five years of the study.

Test	DF	*t*-value	*P*-value
Pre-harvest controls vs. treated plots	24	2.50	0.020
Post-harvest (1) controls vs. treated plots	24	2.27	0.032
Post-harvest (2) controls vs. treated plots	24	1.90	0.070
Post-harvest (3) controls vs. treated plots	24	2.50	0.020
Post-harvest (4) controls vs. treated plots	24	0.90	0.376

Table A2.9. Results from a multiple comparison analysis testing for differences in *biomass of Coleoptera* between habitat types for the first five years of the study.

Test	DF	*t*-value	*P*-value
Pre-harvest controls vs. treated plots	24	1.87	0.074
Post-harvest (1) controls vs. treated plots	24	3.00	0.006
Post-harvest (2) controls vs. treated plots	24	3.37	0.003
Post-harvest (3) controls vs. treated plots	24	3.31	0.003
Post-harvest (4) controls vs. treated plots	24	1.96	0.061

Table A2.10. Results from a multiple comparison analysis testing for differences in *biomass of Gastropoda* between habitat types for the first five years of the study.

Test	DF	*t*-value	*P*-value
Pre-harvest controls vs. treated plots	24	1.86	0.075
Post-harvest (1) controls vs. treated plots	24	1.39	0.178
Post-harvest (2) controls vs. treated plots	24	1.64	0.114
Post-harvest (3) controls vs. treated plots	24	0.93	0.363
Post-harvest (4) controls vs. treated plots	24	0.97	0.342

Table A2.11. Results from a multiple comparison analysis testing for differences in *total abundance of invertebrates* between skid trails and inter-trail forest in treated plots for the first four years post-harvest.

Test	DF	*t*-value	*P*-value
Post-harvest (1) residual forest vs. skid trails	994	8.92	< 0.001
Post-harvest (2) residual forest vs. skid trails	994	5.41	< 0.001
Post-harvest (3) residual forest vs. skid trails	994	1.42	0.155
Post-harvest (4) residual forest vs. skid trails	994	- 0.84	0.400

Table A2.12. Results from a multiple comparison analysis testing for differences *in abundance of Coleoptera* between skid trails and inter-trail forest in treated plots for the first four years post-harvest.

Test	DF	*t*-value	*P*-value
Post-harvest (1) residual forest vs. skid trails	994	5.30	< 0.001
Post-harvest (2) residual forest vs. skid trails	994	3.50	< 0.001
Post-harvest (3) residual forest vs. skid trails	994	1.40	0.163
Post-harvest (4) residual forest vs. skid trails	994	3.71	< 0.001

Table A2.13. Results from a multiple comparison analysis testing for differences in *abundance of Gastropoda* between skid trails and inter-trail forest in treated plots for the first four years post-harvest.

Test	DF	*t*-value	*P*-value
Post-harvest (1) residual forest vs. skid trails	994	4.41	< 0.001
Post-harvest (2) residual forest vs. skid trails	994	2.82	0.005
Post-harvest (3) residual forest vs. skid trails	994	1.89	0.059
Post-harvest (4) residual forest vs. skid trails	994	1.30	0.194

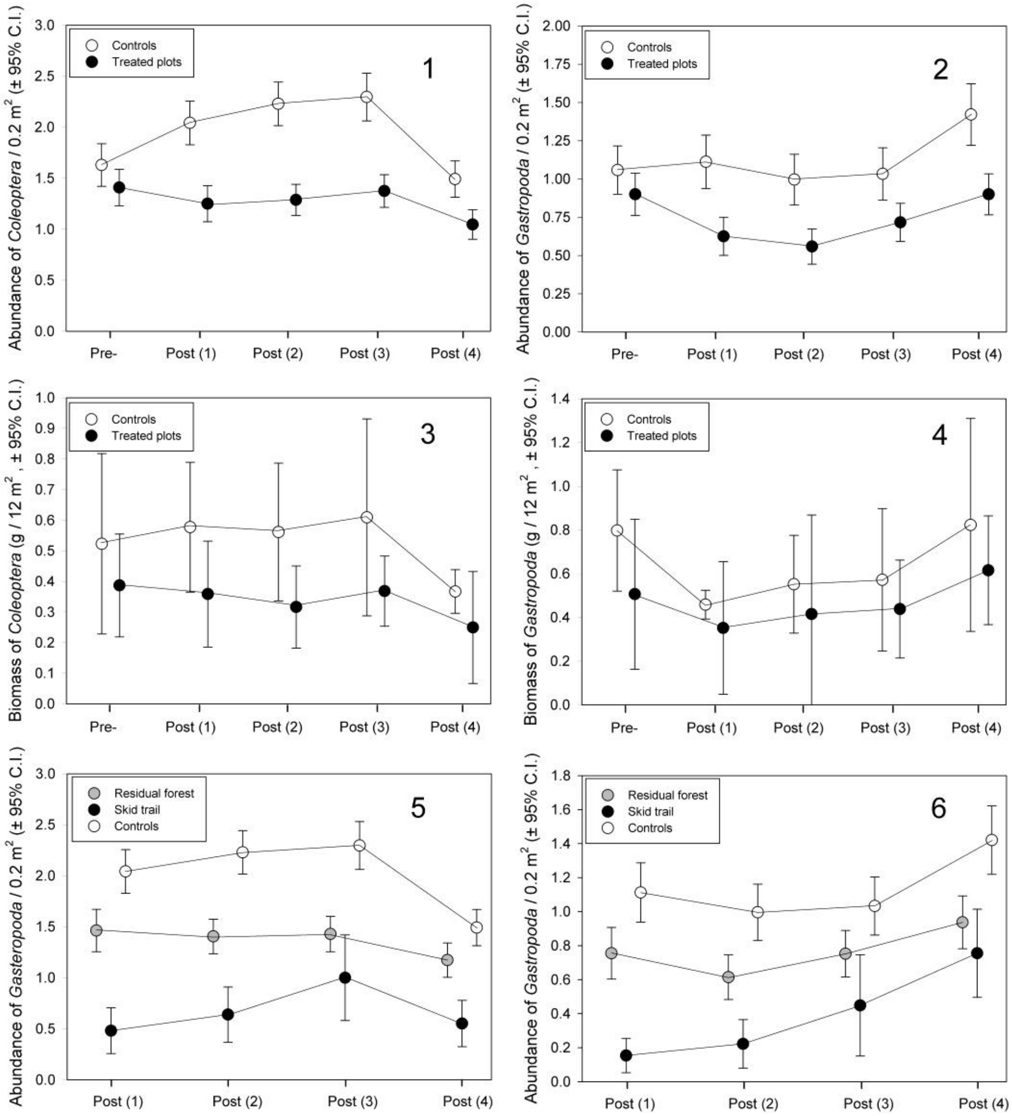

Figure A2.1. Mean (± 95% C.I.) abundance of *Coleoptera* (1) and abundance of *Gastropoda* (2) per sampling point, biomass of *Coleoptera* (3) and biomass *Gastropoda* (4) per study plot, and the abundance of *Coleoptera* (5), and abundance of *Gastropoda* (6) per sampling point in skid trails vs. inter-trail forest in treated plots and controls.

APPENDIX 3. DENSITY ESTIMATES FOR OVENBIRDS DEFENDING TERRITORIES IN CONIFER STANDS.

Based on spot mapping data collected in 2011, Mackay & Villard (unpublished data) have shown that territorial males in young plantations (< 25 year old) are almost exclusively located within 100 m of deciduous stands and there is no evidence of pairing success (see also Porneluzi et al. 2011). There is also no evidence that Ovenbirds defend territories in young conifer stands (≤ 10 year old). Hence, results from spot mapping in eight 25-ha study plots were assigned to young spruce plantations (11-25 years old).

Ovenbird abundance in old plantations and conifer stands (> 35 year old) have been determined using point count surveys (Guénette & Villard 2005; Mackay et al., in press). Guénette & Villard (2005) used mobbing calls of Black-capped Chickadee (*Poecile atricapillus*; 2000-2002; 15 stations) whereas Mackay et al. (in press) used playbacks including calls of 7 focal bird species (2010-2011; 62 stations). Point count data were compiled on the basis of two or three visits per station (100 m radius). Abundance data were converted into density estimates following Sólymos et al. (in press) which accounts for species-specific singing rates and effective detection radius. Predictions were first generated from point count data from untreated deciduous stands and recent selection cuts. These predictions were compared to those from spot mapping data and our results suggest that approach used by Sólymos et al. (in press) would over estimate Ovenbird density in our study area by 25% (Haché et al. unpublished data; see also Hunt et al. 2012). Thus, we applied this correction factor to our density estimates generated from the two data sets (Guénette & Villard 2005; Mackay et al., in press). We report the mean value from both studies as our density estimate for old conifer stands and these values were assigned to all conifer stands > 25 year old.

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APPENDIX 4. PREDICTED AREA, PROPORTION OF TERRITORIAL MALES, AND POPULATION GROWTH RATE PER STAND CATEGORY AND POST-HARVEST YEARS IN BLACK BROOK FROM 2012-2087.

Table A4.1. Predicted area for each stand category by post-harvest years in Black Brook from 2012-2087. Values are based on the forestry-as-usual (for each period) and no harvest scenario (same irrespective of period) scenarios. Untreat. decid. = Untreated deciduous, Select. = Selection, Shelt. = Shelterwood, Conif. = Conifer, and No harv. = No harvest.

Year	Untreat. decid.	Select. 1-5	Select. > 5	Shelt. 1-5	Shelt. 6-10	Shelt. 11-15	Shelt. 16-20	Shelt. 21-25	Shelt. > 25	Conif. 1-10	Conif. 11-25	Conif. > 25	Total area
2012	43,568	8,800	22,251	627	627	627	314	314	0	21,220	39,674	42,641	180,662
2017	34,670	6,870	29,593	1611	627	627	314	314	0	22,182	39,849	45,923	182,577
2022	29,480	7,947	31,100	5035	1144	627	314	314	0	19,617	38,014	51,116	184,706
2027	35,358	3,578	33,295	5209	736	1109	314	314	0	15,070	32,971	56,687	184,640
2032	33,531	7,275	29,226	1332	4187	351	729	314	0	17,481	30,295	57,842	182,563
2037	25,509	6,017	34,241	1456	1332	3009	0	678	0	20,614	28,003	59,041	179,900
2042	27,267	9,853	30,837	6310	374	753	316	0	678	18,187	26,459	58,755	179,790
2047	35,297	3,818	34,584	6468	1082	314	0	197	0	18,311	28,255	55,947	184,272

Table A.4.1 (Continued).

Year	Untreat. decid.	Select. 1-5	Select. > 5	Shelt. 1-5	Shelt. 6-10	Shelt. 11-15	Shelt. 16-20	Shelt. 21-25	Shelt. > 25	Conif. 1-10	Conif. 11-25	Conif. > 25	Total area
2052	39,464	6,897	29,658	1920	5901	1011	0	0	0	21,342	28,378	50,160	184,731
2057	41,525	8,467	27,497	1244	721	5901	0	0	0	23,351	28,826	49,149	186,682
2062	32,984	8,136	34,196	143	1101	721	0	0	0	23,364	29,311	51,755	181,712
2067	36,291	11,188	28,076	1955	143	1101	0	0	0	18,651	34,302	49,831	181,538
2072	35,216	5,364	33,000	1564	0	129	0	0	0	16,878	34,194	50,242	176,587
2077	34,645	10,091	26,388	0	1564	0	0	0	0	18,813	31,305	51,616	174,422
2082	28,114	9,196	29,195	0	0	0	0	0	0	19,599	28,288	54,515	168,907
2087	24,670	11,196	28,464	0	0	0	0	0	0	20,580	27,623	54,833	167,366
No harv.	77,126											103,535	180,662

Table A4.2. Proportion of male Ovenbirds defending a territory and population growth rate in Black Brook from 2012-2087 for each stand category and post-harvest years. Values are based on the forestry-as-usual (for each period) and no harvest scenario (same irrespective of period). Untreat. decid. = Untreated deciduous, Select. = Selection, Shelt. = Shelterwood, Conif. = Conifer, and No harv. = No harvest.

Year	Untreat. decid.	Select. 1-5	Select. > 5	Shelt. 1-5	Shelt. 6-10	Shelt. 11-15	Shelt. 16-20	Shelt. 21-25	Shelt. > 25	Conif. 1-10	Conif. 11-25	Conif. > 25	λ
2012	0.454	0.067	0.232	0.000	0.001	0.002	0.002	0.002	0.000	0.000	0.017	0.222	0.921
2017	0.366	0.053	0.312	0.001	0.001	0.002	0.002	0.002	0.000	0.000	0.018	0.242	0.915
2022	0.311	0.062	0.329	0.003	0.002	0.002	0.002	0.002	0.000	0.000	0.017	0.270	0.904
2027	0.346	0.026	0.326	0.003	0.001	0.004	0.002	0.002	0.000	0.000	0.013	0.277	0.906
2032	0.336	0.053	0.293	0.001	0.008	0.001	0.004	0.002	0.000	0.000	0.013	0.290	0.898
2037	0.264	0.046	0.354	0.001	0.003	0.011	0.000	0.004	0.000	0.000	0.012	0.305	0.893
2042	0.278	0.074	0.314	0.004	0.001	0.003	0.002	0.000	0.014	0.000	0.011	0.300	0.894
2047	0.344	0.027	0.337	0.004	0.002	0.001	0.000	0.001	0.000	0.000	0.011	0.272	0.909
2052	0.387	0.050	0.290	0.001	0.012	0.003	0.000	0.000	0.000	0.000	0.012	0.246	0.915
2057	0.402	0.060	0.266	0.001	0.001	0.020	0.000	0.000	0.000	0.000	0.012	0.238	0.915

Table A.4.2 (Continued).

Year	Untreat. decid.	Select. 1-5	Select. > 5	Shelt. 1-5	Shelt. 6-10	Shelt. 11-15	Shelt. 16-20	Shelt. 21-25	Shelt. > 25	Conif. 1-10	Conif. 11-25	Conif. > 25	λ
2062	0.327	0.059	0.339	0.000	0.002	0.002	0.000	0.000	0.000	0.000	0.012	0.257	0.912
2067	0.365	0.083	0.282	0.001	0.000	0.004	0.000	0.000	0.000	0.000	0.014	0.251	0.911
2072	0.356	0.040	0.334	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.254	0.914
2077	0.361	0.077	0.275	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.014	0.269	0.906
2082	0.304	0.073	0.316	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.295	0.898
2087	0.274	0.091	0.317	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.305	0.893
No harv.	0.598											0.402	0.869