Effects of Forest Fragmentation on the Demography of Ovenbirds (*Seiurus aurocapillus*) in the Boreal Forest

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ABSTRACT

The demography of Ovenbirds (*Seiurus aurocapillus*) was compared in landscapes highly fragmented by agriculture, moderately fragmented by forest harvesting, and in contiguous boreal forest of central Saskatchewan. Ovenbirds were less abundant in small, isolated forest patches in fragmented landscapes relative to contiguous forest, although the degree of area-sensitivity depended on the technique used to assess abundance. Males in farm fragments defended larger territories (0.83 ha ± 0.23) than males in contiguous forest (0.62 ha ± 0.14) or forestry fragments (0.61 ha ± 0.16: $P <$ 0.001). The percentage of males that attracted a female was lower in farm (86% ± 3) and forestry fragments (87% ± 3) than in contiguous forest (97% ± 3: $P = 0.05$). Removal experiments demonstrated non-territorial males or "floaters" were more common in contiguous forest than farm fragments. Daily nest survival of forest birds tended to be lower in farm fragments (0.960 ± 0.007) than in contiguous forest (0.977 ± 0.006) or forestry fragments (0.979 ± 0.008: $P = 0.08$). Apparent annual survival of adult males was lower (0.34 ± 0.05) in farm fragments < 20 ha than in large farm fragments > 20 ha (0.58 ± 0.08), forestry fragments (0.56 ± 0.06), or contiguous forest (0.62 ± 0.06: $P = 0.002$). Differences in male survival among landscapes was not caused by increased mortality in small farm fragments, but by increased dispersal of failed breeders (11% unpaired males returned versus 41% of paired males: $P = 0.006$). Small farm fragments were likely population sinks, while large farm fragments, forestry fragments, and contiguous forest were population sources. However, population size in all landscapes was stable over the length of the study suggesting populations in small farm fragments were rescued from local extinction by immigration of Ovenbirds from other landscapes. Populations in farm fragments were more likely to be rescued by first-time breeders (90 ± 5% SY males), while older males were often recruited into contiguous forest (64 ± 4% SY males) and forestry fragments (74 ± 5% SY males: $P = 0.001$). A larger proportion of male Ovenbirds in farm fragments were SY males (59 ± 4%) relative to forestry fragments (47 ± 4%) and contiguous forest (45 ± 4%: $P = 0.02$). Radio-telemetry during the post-breeding period demonstrated males that did not raise young moved more than males that raised young, a pattern consistent in the agricultural landscape and contiguous forest. Together, these results support the hypothesis that Ovenbirds select habitat in an ideal preemptive manner, whereby young Ovenbirds breeding for the first time are excluded from contiguous forest by competition from older Ovenbirds and consequently are forced to use low-quality farm fragments.

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CHAPTER 1 . GENERAL INTRODUCTION

1.1 Habitat selection theory

The ability to distinguish and select different habitats is one of the most important traits possessed by any organism, because it determines the selective environment encountered by individuals within a population (Holt 1987). Most studies of habitat selection have focused on birds, with the majority examining the influence of habitat structure on community or guild organization (reviewed in Cody 1985, Wiens 1989). Less attention has been paid to proximate causes and effects of habitat selection on individual avian species (Holmes et al. 1996, Hunt 1996, Petit and Petit 1996). Detailed quantitative research on factors influencing habitat selection is essential for understanding population processes at local, landscape, and regional scales (Holmes et al. 1979).

Habitat selection in many passerine birds is regulated by density-dependent territoriality, typically in an “ideal free” or “ideal preemptive” manner (Fretwell 1970, Pulliam and Danielson 1991, Rodenhouse et al. 1997). In the ideal free model, birds are capable of settling in all habitats and all birds are equally competitive. As optimal habitats are filled to maximum, newly arriving individuals choose to settle in suboptimal habitat because of crowding effects in the optimal habitat (Rodenhouse et al. 1997). The crowding effect results from density-dependent processes such as increased competition for food or increased risk of predation (Kluyver and Tinbergen 1953). Individuals in optimal and suboptimal habitat have similar fitness because although suboptimal, the less preferred habitat is also less crowded. In contrast, the ideal preemptive model argues individuals differ in competitive ability. Territories in this model are elastic discs (Huxley 1934) that can only be compressed to a certain minimum size. When minimum territory sizes are reached, dominant individuals force subordinates to leave optimal habitats. Exclusion from optimal habitats forces less competitive birds to breed in suboptimal areas. Through density-dependent territoriality, individuals in optimal habitats maintain greater fitness than subordinates in suboptimal habitat by forcing subordinates from optimal habitat before crowding effects occur.

Differential fitness among habitats has important consequences for population dynamics at landscape scales as it affects how different habitats contribute to productivity, survival, and recruitment (Pulliam and Danielson 1991, Holmes et al. 1996, Rodenhouse et al. 1997). Animals that select habitat in an ideal preemptive manner often exhibit a source-sink population structure (Pulliam 1988). Sources are habitats where the number of young produced exceeds the number of adults lost to mortality or emigration (Pulliam 1988). Sinks are habitats where the number of adult birds lost exceeds the number of young produced (Pulliam 1988). Populations persist in sink habitats only if they are "rescued" by immigration of individuals from source habitats (Brown and Kodric-Brown 1977).

Fitness differences among habitats that conform to the ideal preemptive model have been reported for many species, particularly raptors and cavity-nesting passerines (e.g. Krebs 1971, Newton 1986). Most of these studies have compared the demography of birds among habitats that differ in vegetation structure (e.g. Krebs 1971, Andrén 1990, Dhondt et al. 1992). Less is known about habitat factors that influence breeding populations of migratory songbirds that build open-cup nests (Holmes et al. 1996). However, many migratory songbirds are in decline, making such information crucial (Robbins et al. 1989a, Askins et al. 1990). The causes of forest songbird declines are poorly understood, but many researchers agree that loss and fragmentation of remaining breeding habitat may be major factors (Robbins et al. 1989a, Askins et al. 1990, Rappole and McDonald 1994). Habitat-specific demographic information, particularly as it relates to habitat fragmentation, is needed to investigate the nature of habitat selection in forest songbirds and its role in population regulation.

1.2 Habitat fragmentation, source-sink dynamics, and the ideal preemptive model

Habitat fragmentation is a process by which continuous habitats are subdivided into smaller pieces (Hunter 1996). Although fragmentation occurs through natural processes (e.g. windthrow or fire), anthropogenic changes are the dominant cause of fragmentation in most ecosystems (Andrén 1994). Habitat fragmentation has three major effects, namely loss of original habitat, reduction in size of remaining habitat patches, and increasing isolation of habitat patches (Faaborg et al. 1995, Hunter 1996). At a landscape scale, habitat fragmentation by anthropogenic activities occurs in three main stages (Hunter 1996). The first stage is dissection, where linear features such as roads or powerlines create two or more habitat patches. The second stage is perforation, where large openings in contiguous habitat create new habitats that may be less suitable to species that existed in the original habitat. Dissection and perforation create a large amount of edge habitat, which can have positive and negative effects on forest songbirds. The final phase of fragmentation is attrition, which occurs when perforation and dissection reduce the original habitat to the point where the landscape matrix is no longer dominated by the original habitat.

Evidence has accumulated that forest songbirds are negatively impacted by forest fragmentation (reviewed in Walters 1998). Community level studies have demonstrated that many species of forest songbirds avoid small, irregularly shaped, and isolated forest patches (reviewed in Freemark et al. 1995). However, mechanisms causing fragmentation sensitivity in forest songbirds remain poorly understood. Many forest songbirds may be absent from small fragments simply because small populations have greater extinction risk because of environmental and demographic stochasticity (Diamond 1984). Small forest fragments may remain "empty" as isolation reduces the probability birds can disperse to them. In contrast, many bird species have persisted in small forest fragments for decades, but at reduced densities relative to larger forest patches (Ambuel and Temple 1983, Blake and Karr 1987). Lower population density often indicates lower habitat suitability (Holmes et al. 1996, Petit and Petit 1996, but see Van Horne 1983), which suggests forest songbirds avoid small forest fragments.

Demonstrating that preemptive behaviour creates a source-sink population structure in fragmented landscapes requires information on many demographic parameters (Holmes et al. 1996, Petit and Petit 1996). However, most studies of habitat selection and forest fragmentation have focused on abundance and/or breeding productivity (Donovan et al. 1995a, Hoover et al. 1995, Robinson et al. 1995a, but see Porneluzi and Faaborg 1999). If fragmentation creates suboptimal habitat and habitat selection in forest birds occurs in a preemptive way, the following predictions can be made: 1) population density should be greater in contiguous forest than in forest fragments (Fretwell 1970, Fretwell and Lucas 1970); 2) territories in forest fragments should be larger than in contiguous forest (Petit and Petit 1996); 3) nesting success should be lower in forest fragments than contiguous forest because of increased predation or brood parasitism by the brown-headed cowbird (*Molothrus ater*); 4) the probability an individual will return to forest fragments in subsequent years should be lower in fragments than contiguous forest because of greater mortality or increased dispersal (Holmes et al. 1996); 5) unpaired individuals should be more common in forest fragments than in contiguous forest (Petit and Petit 1996); and 6) birds in forest fragments should be younger and in poorer body condition than individuals in contiguous forest (Enoksson 1988, Piper and Wiley 1989, Holmes et al. 1996, Hunt 1996, Petit and Petit 1996).

1.3 Fragmentation in the boreal forest

Studies on habitat fragmentation and its effects on forest songbirds have mainly been conducted in the deciduous forests of the eastern and central United States. Wiens (1995) argued that generalizing the impacts of fragmentation from eastern areas to other regions is inadequate, as the same species may have different life history strategies in areas with different disturbance regimes. Similarly, most research on the effects of forest fragmentation has been conducted in landscapes fragmented by agriculture. Recent evidence suggests landscapes fragmented by forestry may be more suitable for forest songbirds than forest mosaics created by agriculture (Rudnicky and Hunter 1993, Andrén 1995, Hanski et al. 1996, King et al. 1996, Bayne and Hobson 1997). However, few studies have directly compared the effects of landscape fragmentation by different anthropogenic processes in the same geographic region. Differences among studies could simply reflect regional patterns rather than differences between landscapes fragmented by forestry and agriculture.

The southern boreal forest is a fire driven ecosystem, which exists as a natural mosaic of different forest types and seral stages (Eberhart and Woodard 1987). The natural patchiness and high diversity of forest stand types that exist in the boreal forest provide a myriad of different habitats for the diverse avian community. Birds make up 70% of the vertebrate biodiversity in the boreal forest (Schieck et al. 1995), with about 40% of these species being Neotropical migrants (Robbins et al. 1989a). Although the southern boreal forest has one of the most diverse breeding bird communities in North America, little is known about factors influencing community structure or population dynamics of birds in this region (Schieck et al. 1995).

In the past 80 years, the natural disturbance regime in the southern boreal forest has changed dramatically. Human activities such as road creation, forestry, and agriculture have replaced fire as the dominant disturbance in this region. Although animals in the boreal forest may be adapted to a patchy landscape created by fire, it is unclear whether human-induced patchiness mimics the effects of natural processes (Hunter 1996).

1.3.1 *Study area*

The study was conducted in and around the Prince Albert Model Forest (hereafter PAMF) of central Saskatchewan (53° 50' N - 105° 50' W: Fig. 1.1). The PAMF is located in the mixedwood section of the southern boreal forest (Bouman et al. 1996). Three distinct land-uses occur within the PAMF. Prince Albert National Park (hereafter contiguous forest) is a 387,500 ha area of protected contiguous forest, with over 60% of

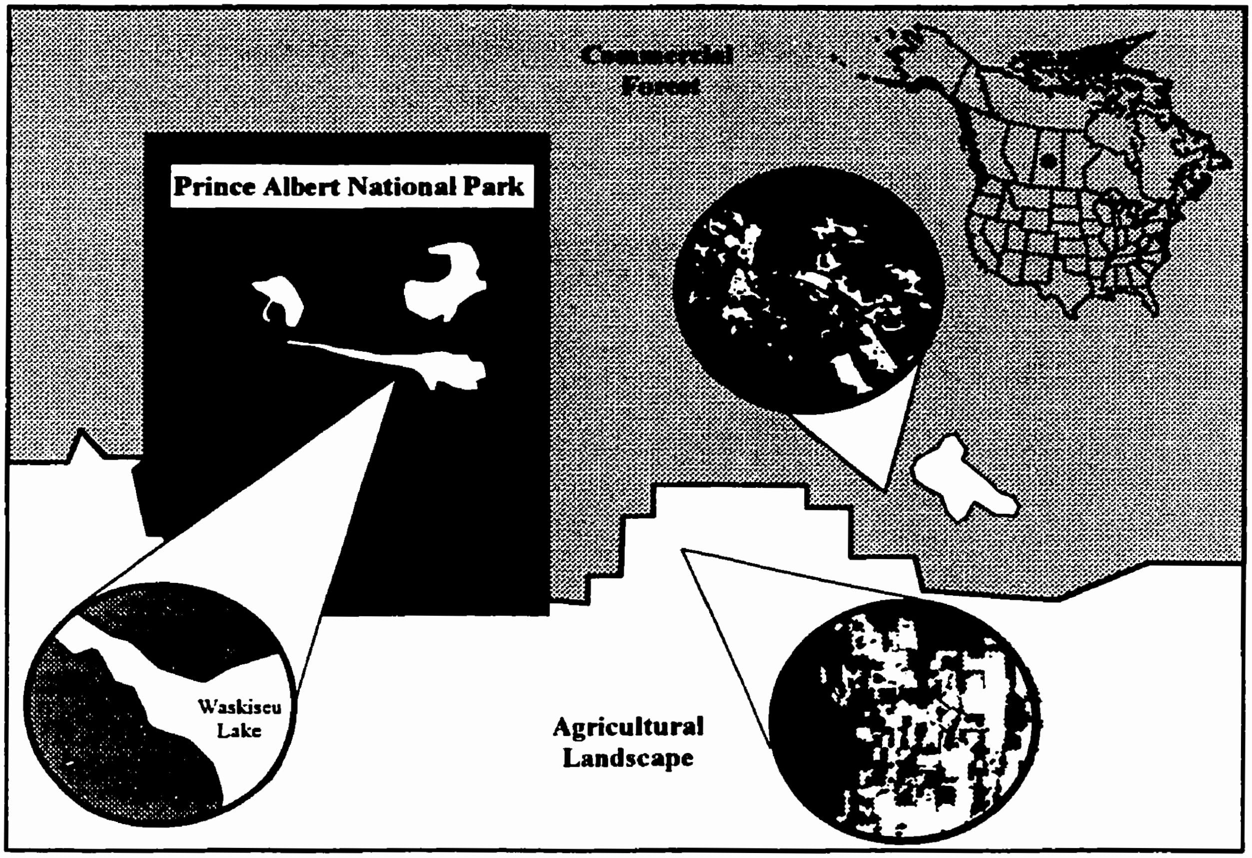

Figure 1.1 – Location of study area. The dark area within circles represents the amount of forested land within a 5 km radius of one site in each landscape. Light areas represent waterbodies in the contiguous forest, clearcuts made since 1980 in the commercial forest, and hay or crop land in the agricultural landscape. Scale is approximately 1 to 625,000.

the forest habitat greater than 60 years of age. Small perforations caused by recreational activity exist in a few areas and several roads dissect the park. Weyerhaeuser Forest Management Area (hereafter forestry fragments) is an 84,000 ha area of crown land, east of PANP, where ≈25% has been harvested since 1969. Harvesting in the area follows a two-pass clearcut system, where series of forest blocks of 40 ha are interspersed with large clearcuts about the same size. The road network in this area is highly developed. Although fragmented, the landscape matrix in this area is still dominated by forest. Finally, the rural municipality (RM) of Paddockwood (hereafter farm fragments) is an agricultural region directly south of PANP, where most of the land is privately owned. The forested area in this landscape has undergone attrition, as agricultural land dominates the landscape and forest habitat exists only as small remnants. About 70% of the 135,000 ha of this RM has been converted to pasture, grain, oilseed, or hay fields since 1911 (van Wilgenburg unpublished data). Wheat (*Triticum* spp.) and canola (*Brassica* spp.) are the dominant crops. About 23% of the RM is comprised of forest remnants (Van Wilgenburg unpublished data). Forest loss in and around the RM of Paddockwood is occurring at about 1.3% per year (Fitzsimmons unpublished data).

Sites were mature (60+ yrs) to old (100+ yrs) mixedwood forest. The overstory was dominated by trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*), with some black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and balsam poplar (*Populus balsamifera*). The shrub layer was variable in density and composition but included beaked hazelnut (*Corylus cornuta*), green alder (*Alnus crispa*), rose (*Rosa* spp.), red-osier dogwood (*Cornus stolonifera*), saskatoon (*Amelanchier alnifolia*), and white spruce saplings.

1.4 Study species

The Ovenbird (*Seiurus aurocapillus*) was chosen as the model species for this study because: 1) they are a "forest interior" species and seem to be sensitive to fragmentation in other areas of their range (Van Horn and Donovan 1994); 2) they are a Neotropical migrant and like many migratory songbirds are in decline in some areas of their range; 3) they are relatively abundant in undisturbed forests, reaching densities around 10 males per 10 ha, making mark-recapture studies feasible (Van Horn and Donovan 1994); 4) numerous studies have examined the effects of forest fragmentation on Ovenbird ecology, allowing for regional comparisons; 5) they have a large geographic range that covers most forested areas of North America, making the results broadly applicable; 6) they forage and nest on the ground, so they may be susceptible to changes in micro-habitat conditions and/or changes in predator communities associated with forest fragmentation; and 7) they have been selected as an "indicator" species by the Saskatchewan forestry industry, yet virtually no information on their breeding ecology is available for the western boreal forest.

Male Ovenbirds vigorously defend an all-purpose territory that is used for mating, nesting, and feeding young. Arrival date in the boreal forest is variable and depends on weather conditions, but typically is the third week of May. Most relationships of Ovenbirds are monogamous, although polygyny and polyandry have been reported (Hann 1940). Nesting usually begins the first week of June. Female Ovenbirds are responsible for nest construction, maintenance, and incubation of the "dome-shaped" nest, which is always on the ground. In most areas of its range Ovenbirds are single-brooded, laying 3 to 6 eggs in each clutch. Females lay one egg per day. Incubation lasts about 12 days, and young leave the nest 8 to 10 days after hatching. In the boreal forest, fledging usually occurs the last week of June. Little is known about renesting behaviour, but females are thought to build a second nest if the first one fails (Porneluzi and Faaborg 1999). Ovenbirds typically feed on the ground, where they probe for insects in the leaf litter. Territory size is negatively correlated with food abundance (Smith and Shugart 1987). Males help raise fledglings, usually feeding half the brood. Juveniles become independent of adults about 30 days after leaving the nest (Van Horn and Donovan 1994). Adult Ovenbirds undergo a prebasic molt in August before leaving for migration. Little is know about migratory patterns. Ovenbirds overwinter in tropical wintering grounds that range from southern Mexico to northwestern Venezuela, although they seem to be most abundant in Central America during this period (Van Horn and Donovan 1994).

1.5 Thesis outline

The objective of this thesis was to evaluate the consequences to Ovenbirds of selecting territories in a landscape highly fragmented by agriculture, a landscape moderately fragmented by forestry, and in contiguous forest. In chapter 2, the abundance of Ovenbirds was compared among forest fragments that ranged in size from 0.5 to 120 ha in size in landscapes fragmented by agriculture and forestry. These data were compared to Ovenbird abundance estimates from contiguous forest. Different methods of data collection were compared. In chapter 3, the proportion of territorial males attracting females to their territories was compared among landscapes. Removal experiments were used to determine if the number of floaters was different in contiguous forest than in farm fragments. Chapter 4 examined the effects of forest fragmentation on adult survival and dispersal. The effect of adult dispersal on the age structure of

Ovenbird populations was also examined. Nest survival data were used to determine whether forest fragments were population sinks and contiguous forest a population source. In chapter 5, the movement patterns of male Ovenbirds that raised young versus those that failed to breed were compared in contiguous forest and farm fragments. In chapter 6, a source-sink model with density-dependent juvenile dispersal was created to demonstrate how Ovenbird populations might persist in fragmented sink habitat. The baseline model was modified to determine if female-biased mortality and density-independent dispersal by adult Ovenbirds influenced population persistence and population structure. Finally, Chapter 7 provided a summary of the thesis that discussed the effects of forest fragmentation on Ovenbirds in the context of the ideal preemptive model and source-sink population dynamics.

CHAPTER 2 . FOREST FRAGMENTATION AND OVENBIRD ABUNDANCE

2.1 Introduction

The Ovenbird is often used as a model species for studying the effects of forest fragmentation on forest birds (Villard et al. 1993, Donovan et al. 1995a, Burke and Nol 1998, Ortega and Capen 1999). Although it is widely accepted that Ovenbirds are sensitive to forest fragmentation, the relative importance of area and isolation of forest fragments as predictors of Ovenbird abundance differs among studies (Van Horn and Donovan 1994). In hardwood forests of southern Ontario, Burke and Nol (1998) used point-counts and spot-mapping; Ovenbird abundance was significantly correlated with area (12 to 2,353 ha) but not isolation. In Maryland and Virginia, Robbins et al. (1989b) used point-counts; forest fragment area (0.1 to 3,000 ha) was an important predictor of Ovenbird presence but only when fragments were isolated. In central Saskatchewan, Johns (1988) used point-counts in small aspen fragments (0.04 to 36.7 ha); Ovenbird abundance was not correlated with area but was negatively correlated with isolation. Clearly, studies differ in their assessment of Ovenbird sensitivity to area and isolation of forest fragments.

Although Ovenbirds may respond to fragmentation differently among regions (Villard et al. 1993), it is difficult to assess regional variation in fragmentation effects because abundance is often determined in different ways. Most studies have relied on transect or point-count surveys, which may not be accurate ways of determining fragmentation sensitivity (Verner 1985, Haila et al. 1993, Drapeau et al. 1999). Point-count sampling assumes the number of individuals detected per station is proportional to density. Haila et al. (1993) argued the assumption of proportionality is problematic when point-counts are conducted in fragments of variable size because the observation radius is difficult to control (i.e. birds can be detected at greater distances in larger patches). Transect surveys or spot-mapping can reduce biases associated with variable detection distance, as observers often survey entire fragments (Verner 1985). However, transect surveys become logistically difficult in large fragments requiring subsets of fragments to be sampled. When sampling subsets, the territorial boundaries of individuals are often unknown, making it difficult to determine the proportion of an individual's territory that overlaps the survey area (Best 1975, Verner 1985).

Another problem in comparing the effects of fragmentation on bird densities among regions, is some studies use probability of occurrence whereas others use density. Probability of occurrence of many forest songbirds increases with fragment area (Opdam et al. 1985, Robbins et al. 1989b). Although biological explanations (i.e. edge effects) are typically given as explanations for increased probability of occurrence in large fragments, few studies have accounted for the possibility that individuals are randomly distributed in the landscape, making probability of occurrence a weak statistic for demonstrating area-sensitivity (Møller 1987). A positive correlation between density and fragment area/isolation provides stronger evidence for fragmentation sensitivity. However, many studies demonstrating reduced densities of forest birds in small fragments include sites with no birds (Blake and Karr 1987, Johns 1993). Although "empty" fragments are biologically important, they tend to have a disproportionate influence on the slope of linear regression models.

The objective of this chapter was to determine if Ovenbirds in the boreal forest were sensitive to forest fragmentation and whether fragmentation sensitivity occurred because: 1) probability of occurrence was influenced by fragment area/isolation; 2) density of occupied fragments was influenced by area/isolation; or 3) point-counts and transect surveys provide biased estimates of density relative to detailed mapping. Radio-telemetry and data from detailed mapping were used to determine whether differences in territory size between fragments and contiguous forest might explain area-sensitivity of Ovenbirds. It was hypothesized that the probability of Ovenbird occurrence would be positively correlated with forest fragment area because they require a minimum-sized area in which a territory will fit. If fragmentation had no effect on Ovenbird abundance, I predicted occupied fragments would have similar densities to contiguous forest and territory sizes would be similar between landscapes. Point-counts and transect surveys were hypothesized to overestimate density in larger fragments relative to detailed mapping.

2.2 Methods

2.2.1 *Site selection*

Sites were selected from 1:12,500 air photo and forest inventory maps, based on tree composition, age, isolation, shape, lack of disturbance (e.g. cattle grazing or selective timber harvest), and area. All sites were pure aspen or aspen-spruce mixedwoods and were > 50 years old. Farm fragments were completely isolated from other fragments by a field or pasture, with a mean (± 1 SD) minimum distance among neighbouring patches of 54 ± 30 m. The distance among sampled patches was at least 500 m. Forestry fragments were isolated on at least three sides by a clearcut less than 20 years of age or a major haul-road. Control sites were chosen from forest inventory maps for PANP and were located in upland forests similar to those surveyed in the fragmented landscapes.

2.2.2 *Ovenbird surveys*

Ovenbirds were surveyed along transects during the breeding season (June 1 to July 7) from sunrise to 12:00 CST. Density of male Ovenbirds was determined by recording the number of singing individuals responding to playback of Ovenbird song (Porneluzi and Faaborg 1999). Playback elicited responses from males not previously singing (Van Horn et al. 1995). Each site was systematically surveyed by walking parallel transects spaced 100 m apart. All sites < 30 ha were surveyed completely. For sites larger than 30 ha, a 16 ha subsection was surveyed. Each subsection was adjacent to two edges. In 1995 and 1996, 16 and 56 farm fragments, 16 and 19 forestry fragments, and 9 and 10 contiguous forest plots were surveyed, respectively. Each site was visited once.

In 1997, Ovenbirds were surveyed using point-counts in eight contiguous forest plots and 53 farm fragments. The distance at which birds were heard was not estimated. However, the location of individuals was mapped to ensure birds were in the site and were not counted at previous stations (Blondel et al. 1970). Each site had one to five point-count stations. Except for the smallest fragments, all stations were 75 m from an edge and were 250 m apart. Stations were selected apriori from air photos, with the goal of maximizing the number of stations per site. At each station, all Ovenbirds heard singing in a 10 minute observation period were recorded. Stations were visited twice during June. Two observers conducted point-counts and alternated visits. Point-count surveys were done from sunrise to 09:00 CST.

In 1997 and 1998, detailed mapping was used to determine the absolute density of Ovenbirds at four sites in contiguous forest (12.25 ha), three sites in forestry fragments (12.25 ha), and 14 sites in farm fragments (5 to 42 ha). At each site, all male Ovenbirds were captured and uniquely colour-banded. Each male's territory was mapped in the first two weeks of the breeding season. Playback of Ovenbird song instigated territory defense by males and was used to draw individuals to the edge of their territory (Falls 1981). Once an individual responded, the speaker was moved away from the bird until the individual no longer approached the speaker. The playback methodology was repeated in the four cardinal directions. The procedure took about 30 to 45 minutes per male. Flagged grids (50 x 50 m cells) facilitated location. Playback observations were augmented with visual and acoustic observations made during subsequent visits to establish pairing status (Chapter 3).

2.2.3 *Vegetation and landscape attributes*

For sites surveyed in 1995 and 1996, vegetation structure was estimated at the mid-point of every second transect. The canopy and shrub layer were classified as open (<25% closure), mostly open (25 to 50% closure), mostly closed (50 to 75%), or closed (>75%) following the Saskatchewan forest inventory classification (Kabzems et al. 1986). The proportion of the canopy and shrub layer composed of coniferous species was estimated to the nearest 25 %. The height of the canopy was estimated to the nearest 5 m, while the height of the shrub layer was estimated to the nearest 1 m. The same methodology was used in 1997 except estimates were made around the point-count stations.

Landscape attributes in the agricultural landscape were determined from LANDSAT Thematic Mapper satellite imagery taken in 1995 by the Prairie Farm Rehabilitation Agency. Isolation was defined as the percentage of non-forested cover within 5 km of a site. For sites in the harvested landscape, digitized forest inventory maps created at a 1:12,500 scale were used to determine fragment area and isolation. Most forestry fragments were connected to larger tracts of forest on the fourth side. The fourth edge of the connected forestry fragments was defined as the boundary between the observed fragment and the adjacent forest stand, given the adjacent stand was unsuitable Ovenbird habitat. Unsuitable Ovenbird habitat was defined as any stand < 20 years or stands with < 25% deciduous trees (Hobson and Bayne 2000a,b). Isolation was the amount of young forest cover (< 20 years) and non-forested land within 5 km of a site. All forest stand types were included when estimating isolation in the harvested landscape, as the LANDSAT imagery from the agricultural landscapes did not distinguish among forest types.

2.2.4 *Radio-telemetry*

In 1999, the territory size of breeding male Ovenbirds was determined using radio telemetry. Twelve Ovenbirds in five farm fragments (10 to 42 ha in size) and five Ovenbirds in two contiguous forest plots were fitted with radio-transmitters. These sites were used in previous years for detailed mapping and contained a flagged grid. Two to three males in each plot were fitted with a Holohil Ltd. (112 John Cavanaugh Road, Carp, ON) Bd2A transmitter that weighed about 0.62 grams. Transmitters were attached to Ovenbirds by gluing the transmitter to feather stubs (Chapter 5), following the method of Warnock and Warnock (1993). Beginning the day following transmitter attachment, each bird was located two to four times per day from 04:00 and 19:00 CST, for an average of 10 days (range of 9 to 21 days). Ovenbirds were located on foot and careful attention was made not to flush the bird. The direction by which territories were approached was randomized each visit.

2.2.5 *Statistical analysis*

For transect data, density was calculated as the number of males detected divided by the area sampled. For point-count data, the abundance of Ovenbirds was the maximum value of the two visits, averaged for all stations in a site. It was assumed Ovenbirds could be heard for 100 m from a point-count station, so abundance per station was divided by 3.14 to obtain the density estimate (males per ha). Density was estimated in two ways with the detailed mapping data. First, Ovenbirds whose entire territory fit within the boundaries of the grid were included. In a subsequent analysis, Ovenbirds whose territories partially overlapped the boundaries of the contiguous forest grid were also included in the density estimate. For each individual, the proportion of the territory overlapping the grid was determined using the geographic information system Arcview. All density estimates are reported as males per 10 ha.

Linear and logistic regression modeling were used to determine which factors within landscapes influenced Ovenbird density and probability of occurrence. Each analysis began with a global model that included fragment area, isolation, landscape configuration, and the six vegetation variables. Year and date of survey were included for the transect data. Landscape configuration was measured as the mean nearest-neighbour distance (MNN) and was calculated using the program FRAGSTATS (McGarigal and Marks 1995). MNN was positively correlated with isolation ($R^2 = 0.63$, $P < 0.001$), so a linear model was fit to the MNN-isolation relationship and the residuals used as the independent variable in subsequent analyses. To determine whether sites without Ovenbirds drove the area-density relationship, models were created for only those sites occupied by Ovenbirds. In each analysis, several curves were fit to the area-abundance relationship (linear, logarithmic, quadratic, log-log, and a non-linear Michaelis-Menten function). The curve that maximized the R^2 value was selected. Model selection was done in blocks, with all possible combinations of vegetation variables examined first. Once the most parsimonious model for vegetation structure was determined, all possible combinations of landscape variables were examined. The model with the lowest Akaike Information Criterion value (AICc) corrected for small sample size was selected as the model with the best fit (Burnham and Anderson 1998). If two or more models had similar AICc values (<2), the model with the fewest parameters was chosen.

Density of Ovenbirds was compared among landscapes using an ANCOVA with landscape, year, and the vegetation variables as independent variables. Separate models were created for the point-count, transect, and detailed mapping data. These analyses were done for sites occupied by Ovenbirds. Model selection is described above. To determine if sampling methodology influenced density estimates among landscapes, a two-way ANOVA was used, with survey method (point-count, transect, and detailed mapping) and landscape (farm fragments and contiguous forest) as the independent variables.

To compare territory size among landscapes, a nested ANOVA with site nested within landscape was used. These analyses were done separately for the radio-telemetry and detailed mapping data. Territory size for each radio-tagged individual was estimated using a 95% minimum convex polygon in Arcview using the extension Animal Movement 2.0 (Hooge and Eichenlaub 1997).

Data are reported as means ± 1 SD unless otherwise reported.

2.3 Results

Ovenbirds were common in the study area and were detected in 74% of farm fragments, 69% of forestry fragments, and all contiguous forest plots. The average size of farm fragments where Ovenbirds were absent was 2.9 ± 2.6 ha (range 1.1. to 7.4 ha). The average size of forestry fragments where no Ovenbirds were found was 3.6 ± 2.1 ha (range 1.7 to 8.8 ha).

2.3.1 *Agricultural landscape*

For transect data, Ovenbird occurrence was positively correlated with farm fragment area ($\chi^2 = 11.7$, $P < 0.001$) and negatively correlated with shrub height ($\chi^2 = 4.3$, $P = 0.04$: $R^2 = 0.49$). Ovenbird density was positively correlated with farm fragment area ($t= 7.6$, $P < 0.001$) and canopy closure ($t = 2.1$, $P = 0.04$), and negatively correlated with Julian date ($t = -2.0$, $P = 0.05$) and shrub height ($t = -2.5$, $P = 0.02$: $R^2 = 0.51$). The curve that best fit the area-density relationship was a log-log function. (Fig. 2.1A). Using a partial correlation coefficient controlling for the other variables in the model, area explained 45% of the variation in the data. For occupied sites, Ovenbird density was positively correlated with area ($t = 3.5$, $P = 0.001$) and canopy closure ($t = 2.1$, $P = 0.05$), and negatively correlated with canopy height ($t = -1.8$, $P = 0.09$), %

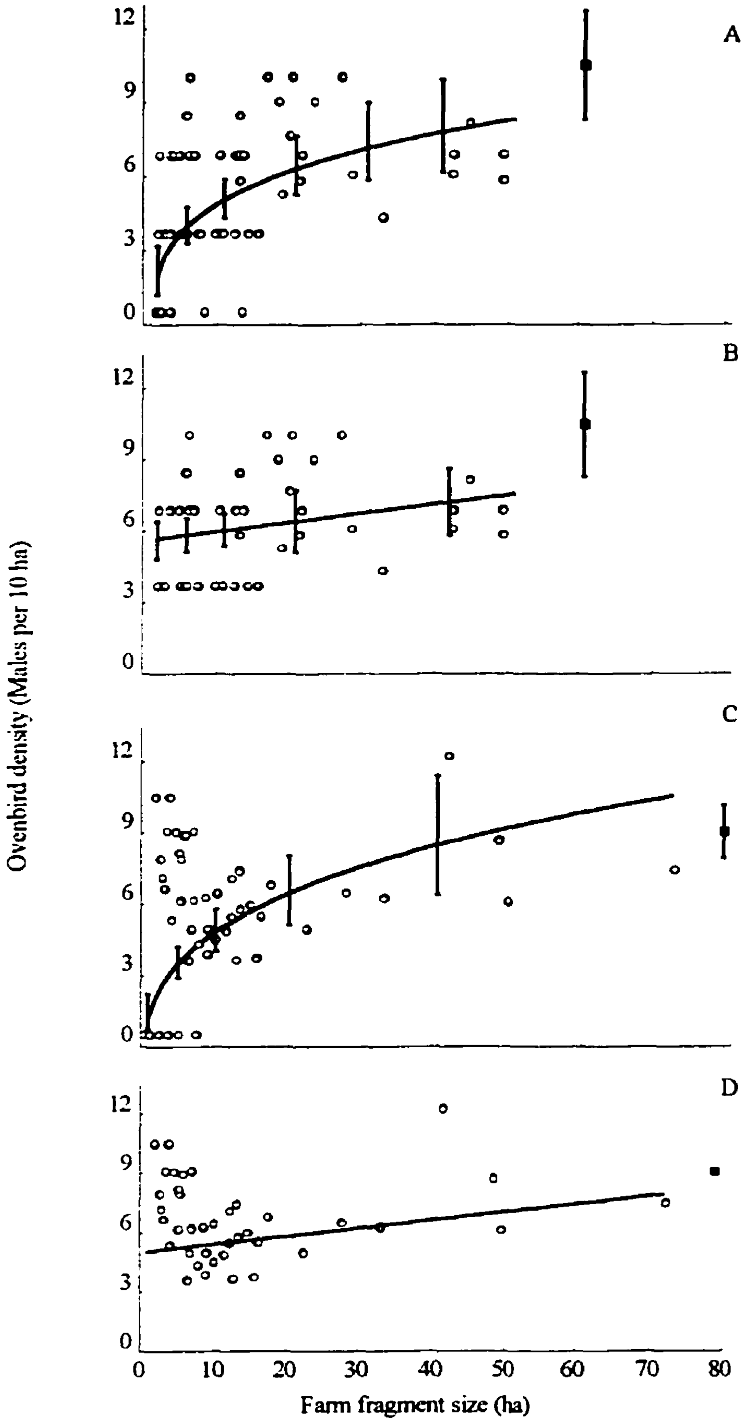

Figure 2.1 - Scatterplots showing the relationship between Ovenbird density and farm fragment size for: A) transect surveys for all sites; B) transect surveys for sites containing Ovenbirds; C) point-count surveys for all sites; D) point-count surveys for sites containing Ovenbirds. Bars indicate 95% confidence intervals for mean estimated density at that farm fragment size. The solid square symbol shows the mean density of Ovenbirds in contiguous forest.

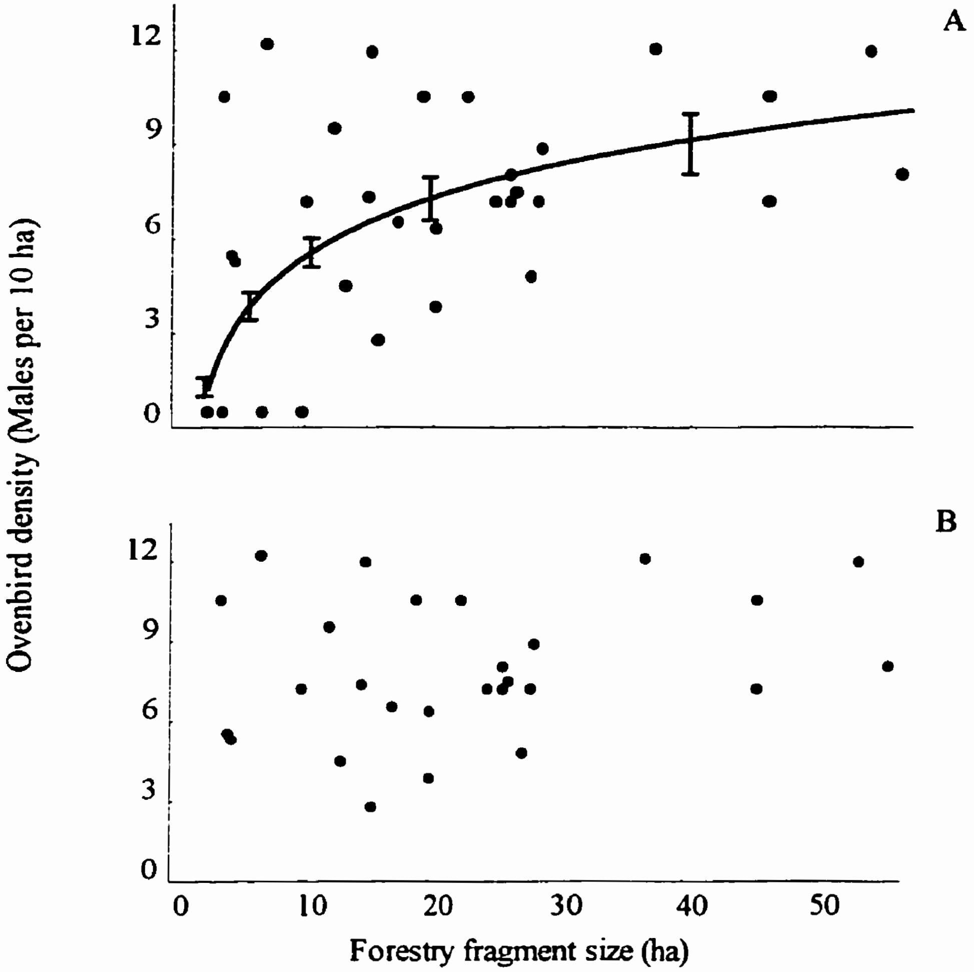

Figure 2.2 - Scatterplots showing the relationship between Ovenbird density and forestry fragment size for transect surveys for all sites; B) transect surveys for only sites containing Ovenbirds. Bars indicate 95% confidence intervals for mean estimated density at that forestry fragment size.

coniferous trees ($t = -1.8$, $P = 0.09$), and Julian date ($t = -2.0$, $P = 0.05$: $R^2 = 0.34$). Area explained 22% of the variation in this data set. The curve that best fit the area-density relationship was a linear function (Fig. 2.1B).

For point-count data, Ovenbird occurrence was positively correlated with farm fragment area ($\chi^2 = 6.2$, $P = 0.01$) and negatively correlated with isolation ($\chi^2 = 4.5$, $P = 0.03$: $R^2 = 0.30$). Ovenbird density was positively correlated with farm fragment area ($t = 6.2$, $P < 0.001$) and negatively correlated with isolation ($t = -4.0$, $P < 0.001$) and MNN ($t = -1.8$, $P = 0.08$: $R^2 = 0.51$). The curve that best fit the area-density relationship was a log-log function (Fig. 2.1C). Controlling for other variables in the model, area explained 44% of the variation in the data. At occupied sites, Ovenbird density was positively correlated with farm fragment area ($t = 2.7$, $P = 0.01$) and negatively correlated with isolation ($t = -2,7$, $P = 0.01$), MNN ($t = -1.8$, $P = 0.08$), conifer cover ($t = -1.9$, $P = 0.07$), and shrub height ($t = -2.3$, $P = 0.03$: $R^2 = 0.42$). The curve that best fit these data was a simple linear function (Fig. 2.1D). Area explained 16% of the variation in this data set.

2.3.2 *Harvested landscape*

Based on transect data, the occurrence of Ovenbirds was positively correlated with forestry fragment area ($\chi^2 = 6.2$, $P = 0.01$: $R^2 = 0.31$). Ovenbird density was positively correlated with area ($t = 3.6$, $P = 0.001$) and canopy closure ($t = 2.8$, $P = 0.01$: $R^2 = 0.38$). The curve that best fit these data was a log-log function (Fig. 2.2A). Area explained 31% of the variation in the data set. At occupied sites, density was negatively correlated with % coniferous shrubs ($t = -1.9$, $P = 0.07$) and positively correlated with year (t = 4.0, $P = 0.001$: $R^2 = 0.42$). Area was not an important predictor of Ovenbird density in the harvested landscape when unoccupied sites were removed from the analysis (Fig. 2.2B).

2.3.3 *Comparisons among landscapes*

For sites with Ovenbirds, transect data indicated the density of male Ovenbirds was different among landscapes ($F_{2,86} = 19.7$, $P < 0.001$), controlling for canopy closure ($F_{1,86} = 4.6$, $P = 0.03$) and % coniferous trees ($F_{1,86} = 3.2$, $P = 0.08$: $R^2 = 0.38$). Based on Bonferroni-corrected multiple comparisons, the density of Ovenbirds was lower in farm fragments than contiguous forest or forestry fragments (Table 2.1). For point-counts, Ovenbird density was greater in contiguous forest than farm fragments ($F_{1,49} = 31.0$, $P < 0.001$: Table 2.1), controlling for shrub height ($F_{1,49} = 3.9$, $P = 0.05$) and conifer cover ($F_{1,49} = 8.7$, $P = 0.005$). Detailed mapping data demonstrated Ovenbird density was different among landscapes, using whole territories to estimate density ($F_{2,18} = 6.8$, $P = 0.006$) and when partial territories were included in density estimates ($F_{2,18} = 32.7$, $P < 0.001$). Again, density in farm fragments was lower than in contiguous forest and forestry fragments, while forestry fragments and contiguous forest had similar densities of Ovenbirds (Table 2.1).

2.3.4 *Comparisons among sampling methods*

Regardless of whether whole or partial territories were used to determine density, contiguous forest had higher Ovenbird density than farm fragments ($F_{1,132} = 62.7$, $P < 0.001$ and $F_{1,132} = 34.5$, $P < 0.001$, respectively). Using whole territories, differences among survey methods were detected ($F_{2,132} = 5.0$, $P = 0.008$). Bonferroni-corrected multiple comparisons indicated density estimates from detailed mapping were lower than point-counts, whereas transect surveys were intermediate (Table 2.1). Including partial territories in the estimates of density, there was only weak evidence of a difference among methods ($F_{2,132} = 2.3$, $P = 0.10$). The interacting effect of method and landscape was never a significant predictor of Ovenbird density.

2.3.5 *Territory size*

Ovenbird males in farm fragments had larger territories (0.83 ± 0.23: $n = 49$) than males in contiguous forest (0.62 ± 0.14: $n = 47$) or forestry fragments (0.61 ± 0.16: $n = 35$: $F_{2,119} = 25.6$, $P < 0.001$). Mean territory size was different among sites within landscapes ($F_{9,119} = 5.32$, $P < 0.001$). The variance in territory size was greater in farm fragments than in contiguous forest or forestry fragments (Levene test $_{df=2,128} = 5.99$, $P < 0.001$). However, a single-factor Kruskal-Wallis test indicated median territory size was also larger in farm fragments than the other landscapes ($\chi^2 = 28.3$, $P < 0.001$). Based on a Pearson correlation coefficient, the mean territory size per site was negatively correlated with the density of male Ovenbirds, whether whole territories ($r = -0.61$, $P = 0.03$) or partial territories ($r = -0.68$, $P = 0.01$) were used to estimate density. The variance in territory size was not significantly correlated with the density of male Ovenbirds regardless of whether whole ($r = -0.23$, $P = 0.46$) or partial territories ($r = -0.45$, $P = 0.13$) were used to estimate density.

Based on the radio-telemetry data, territory sizes were not significantly different among landscapes ($F_{1,10} = 2.4$, $P = 0.15$), although the trend was towards larger territories in farm fragments (1.75 ± 0.81) than in contiguous forest (1.55 ± 0.41). Again, mean territory size among sites within landscapes was significantly different

Table 2.1 - Mean number (least squares means controlling for other variables in model) of male Ovenbirds per 10 ha in farm fragments, forestry fragments, and contiguous forest as estimated by different sampling techniques. Density estimates based on sites where Ovenbirds occurred. 95% confidence intervals around the mean are provided for each landscape.

Survey method	Farm Fragments	Forestry Fragments	Contiguous Forest
Point counts	4.8 (4.0 – 5.6)		10.1 (8.5 – 13.0)
Transect surveys	5.1 (4.4 – 5.7)	7.9 (7.0 – 8.8)	8.3 (7.2 – 9.3)
Detailed mapping (Whole territories)	4.6 (3.9 – 5.4)	7.1 (5.5 – 8.6)	6.5 (5.2 – 7.9)
Detailed mapping (Partial territories)	4.6 (3.9 – 5.4)	8.9 (7.3 – 10.1)	9.9 (8.5 – 11.2)

($F_{5,10} = 4.6$, $P = 0.02$). The variance in territory size was not different between landscapes (Levene test $_{df=1,15} = 1.2$, $P = 0.28$).

2.4 Discussion

2.4.1 *Fragmentation effects on Ovenbirds*

Ovenbirds were influenced by fragmentation of their habitat in the boreal forest. However, area-sensitivity of Ovenbirds within fragmented landscapes was mostly a function of requiring fragments above a minimum size rather than a strong increase in density with fragment area. Ovenbirds were unlikely to be present in farm and forestry fragments less than 3 ha, particularly when fragments were isolated. Based on radio-telemetry observations, Ovenbird home ranges were around 1.7 ha, with a range from 0.7 to 3.7 ha. Thus, fragments < 3 ha may not be large enough for an Ovenbird home range.

The density of Ovenbirds also increased with farm fragment area for sites containing Ovenbirds, although the relationship was weak. Overall, the best fitting model explained a relatively small proportion of the variance. Several factors likely explain this poor fit. First, the vegetation estimates used in this study were relatively coarse and focused on canopy level attributes. Ovenbird abundance may be more strongly correlated with ground cover attributes such as grass or herb cover. Second, the presence of a single individual in a small fragment can create an extreme density estimate that is an artifact of the small size of the fragment. Finally, the nature of the landscape matrix around forest fragments may influence how Ovenbirds perceive fragments. For example, Ovenbirds may identify the edge interface between forest and roads as different than the interface between forest and fields.

Ovenbird density was considerably higher in contiguous forest and forestry fragments than in farm fragments. Typically, lower density of forest birds in farm fragments has been attributed to individuals avoiding edges (Villard 1998). The dogma that Ovenbirds avoid edges is questionable for several reasons. First, individuals were observed in small farm fragments, which had little core area (area > 50 m from edge). Second, Ovenbirds were equally dense in forestry fragments and contiguous forest, although the former had a substantial amount of edge habitat. Finally, radio-telemetry observations of male Ovenbirds during the nesting and post-fledging period in the study area indicate no pattern of edge avoidance (Mazerolle unpublished data, Chapter 5).

Several studies have shown male Ovenbirds in areas with low abundance of ground-dwelling arthropods have larger territories than Ovenbirds in areas where arthropod abundance is high (Stenger 1958, Zach and Falls 1975, Smith and Shugart 1987). Although many factors influence the abundance of ground-dwelling insects, soil moisture is thought to be a major factor (Burke and Nol 1998). Small farm fragments often have higher temperatures, increased wind-speed, and greater evapotranspiration, which can reduce the water content of the leaf litter relative to larger blocks of forest, and concomitantly reduce the abundance of ground-dwelling arthropods in farm fragments (Burke and Nol 1998). The larger size of Ovenbird territories in farm fragments suggests individuals may expand their territories in these habitats to acquire sufficient food resources. However, Ovenbirds in farm fragments may have larger territories than individuals in contiguous forest because reduced densities allow all individuals to utilize more space.

Isolation of forest fragments was an important predictor of Ovenbird density in the agricultural landscape for the point-count data. Isolated sites may be less likely to be colonized and may remain empty for longer periods than less isolated sites (Gutzwiller and Anderson 1992, Dunning et al. 1995, Villard et al. 1995). Ovenbirds may also avoid isolated areas, as breeding success can be lower in isolated fragments (Donovan et al. 1997). Generalist predators in fragmented landscapes are more strongly influenced by landscape composition than local patch characteristics such as fragment area (Oehler and Litvaitis 1996, Donovan et al. 1997). Landscape configuration was also an important predictor of Ovenbird density, indicating Ovenbirds tend to use fragments that are close to other fragments, even in areas with high forest cover. Why isolation and landscape configuration were not important predictors of Ovenbird density for transect data is unclear. However, when the 1996 transect data was analyzed separately, isolation was a significant predictor of Ovenbird density.

Ovenbird density was higher in forestry fragments than farm fragments. Several factors make fragmentation by harvesting less severe than fragmentation by agriculture. First, the forestry fragments surveyed were often connected on the fourth side to larger tracts of forest, which may have increased the density estimate. Second, the landscape matrix around forestry fragments was dominated by regenerating forest (< 20 years). Although unsuitable habitat for breeding, regenerating forest may be more permeable to movement than agricultural fields and could be used for foraging. Third, predator communities in harvested landscapes are often similar to those in contiguous forest, suggesting reproductive success of Ovenbirds may be similar in forestry fragments and contiguous forest (Rudnicky and Hunter 1993, Bayne and Hobson 1997). In contrast, predator abundance and composition often change in fragmented agricultural landscapes, resulting in lower nest success for most forest birds (Bayne and Hobson 1997, Donovan et al. 1997). Consequently, Ovenbirds may avoid farm fragments because of reduced reproductive success in this habitat (Chapter 4). Finally, farm fragments in the RM of Paddockwood often contain trails and grain bins that may be avoided by Ovenbirds.

2.4.2 *The importance of survey method*

Point-count and transect surveys are common ways of assessing area-sensitivity in forest songbirds. However, the validity of point-counts and transect surveys as means of determining area-sensitivity has been challenged (Verner 1985, Haila et al. 1993, Drapeau et al. 1999). When only Ovenbird territories located within boundaries of contiguous forest and forestry fragment grids were included, point-count and transect data provided higher estimates of density than detailed mapping. When partial territories from the detailed mapping data were incorporated, no difference in the density estimate was observed among sampling methods. Although temporal and spatial variation may have influenced these results, the data indicate the three methods provide similar estimates of Ovenbird density.

Although the three survey methods provided similar estimates of Ovenbird density, point-counts and transect surveys include individuals whose territories only partially overlap the boundaries of the sampling area. Whether males whose territories only partially overlap the borders of contiguous forest plots should be included in density estimates is debatable, although most studies have included them (Villard et al. 1993, Burke and Nol 1998). In contiguous forest, males generally have neighbours surrounding them on all sides, increasing the number of partial territories that are counted. In contrast, males near the edges of farm fragments can not have an adjacent neighbour and thus, partial territories can not be included in any estimate of density. Regardless, when those territories that were entirely within the contiguous forest sampling grids were used to determine density, the density of Ovenbirds was lower in farm fragments than contiguous forest or forestry fragments. These results suggest some mechanism other than sampling bias is influencing Ovenbird density among landscapes in the boreal forest. Possibly, males in farm fragments require larger territories than in contiguous forest, resulting in lower densities in fragmented landscapes.

2.4.3 *Summary*

As hypothesized, the probability of Ovenbird occurrence was strongly correlated with forest fragment size. Based on radio-telemetry observations fragments < 3 ha tend to be too small for an Ovenbird home range. The density of Ovenbirds also increased with farm fragment size, although the relationship was weak. More importantly, Ovenbirds were more abundant in contiguous forest and forestry fragments than farm fragments, indicating Ovenbird density is negatively affected by fragmentation. In part, the higher density of Ovenbirds in contiguous forest arose from biases inherent in standard sampling methods. However, accounting for survey biases, Ovenbirds were still more abundant in contiguous forest. Possibly, Ovenbirds in farm fragments require larger territories to obtain sufficient resources relative to individuals in contiguous forest. As in other areas of the Ovenbird's range, these results indicate conservation efforts in the boreal forest should focus on preserving large tracts of suitable habitat in forest-dominated landscapes rather than groups of smaller fragments in agriculturally-dominated areas.

CHAPTER 3 . FOREST FRAGMENTATION AND PAIRING SUCCESS OF OVENBIRDS

3.1 Introduction

Within populations of passerine birds, many males may be unsuccessful in acquiring a mate during the breeding season (Breitwisch 1989, Newton 1992). Many factors influence pairing success of males, including age, body condition, and territory quality (Breitwisch 1989, Muller et al. 1997). Pairing success is typically lower in habitats with few individuals and/or where birds have reduced foraging or nesting success (Probst and Hayes 1987, Holmes et al. 1996, Hunt 1996). Interactions between territory quality and male age can also occur, as older males can force younger males into suboptimal breeding habitat, where the probability of attracting a female is lower (Ficken and Ficken 1966, Sherry and Holmes 1989, Hunt 1996, Holmes et al. 1996, Petit and Petit 1996).

Previous studies have compared how the age of males influences pairing success in different vegetation types (e.g. Krebs 1971, Holmes et al. 1996, Petit and Petit 1996). Less is known about whether habitat selection at landscape scales influences pairing success. For example, Ovenbirds select mature deciduous or mixed forests with a closed canopy and relatively sparse understory (Smith and Shugart 1987, Van Horn and Donovan 1994). However, equally important to Ovenbirds are the relative amounts of edge and interior habitat, proportion of forest cover in an area, sizes of forest patches, and proximity to roads (Wenny et al. 1993, Burke and Nol 1998, Ortega and Capen 1999). In particular, pairing success of male Ovenbirds is lower near edges and in small forest fragments than in the interior of large blocks of forest (Wander 1985, Gibbs and Faaborg 1990, Porneluzi et al. 1993, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998).

Four hypotheses have been proposed to explain reduced pairing success of Ovenbird males in forest fragments relative to contiguous forest. The female-biased mortality hypothesis suggests high predation on females by generalist predators characteristic of fragmented landscapes, creates a surplus of males in forest fragments (Gibbs and Faaborg 1990). In the conspecific-attraction hypothesis, females actively select dense populations of territorial males, so males in small fragments or in areas with few conspecifics are less likely to be paired (Smith and Peacock 1990). The habitat-selection hypothesis argues females avoid breeding near edges and in small or isolated forest fragments because of greater nest predation and brood parasitism, or lower food availability (Van Horn et al. 1995, Burke and Nol 1998). Finally, the mate-selection hypothesis suggests females prefer older and/or larger males that tend to obtain better quality territories in larger forest fragments (Villard et al. 1993).

All of the above hypotheses assume unpaired males are territorial. However, unpaired Ovenbird males could also exist in contiguous forest, but might be "floaters" that do not defend a territory (Hensley and Cope 1951, Sherry and Holmes 1989, Meek and Robertson 1991, Newton 1992, Kokko and Sutherland 1998). In contrast, risks involved in floating among fragments in fragmented landscapes could be greater than in contiguous forest. Male Ovenbirds might defend poor quality territories in forest fragments where the probability of attracting a female is low, rather than increase mortality risk by being a floater. If this is the case, differences in pairing success of Ovenbirds between fragmented landscapes and contiguous forest may have more to do with differences in behaviour and movement patterns of unpaired males, than actual differences in the ratio of breeding to non-breeding males.

The objective of this chapter was to determine if the pairing success of territorial male Ovenbirds was different in farm fragments, forestry fragments, and contiguous forest. I hypothesized males in small farm fragments would be less likely to attract females than individuals in contiguous forest because females avoid poor quality habitats where reproductive success is low. Low-density populations were expected to have lower pairing success than high-density populations, so published data were used to make regional comparisons of pairing success from areas with different densities of males. Finally, removal experiments were conducted to determine if unpaired males in contiguous forest were more likely to be floaters than in the fragmented agricultural landscape.

3.2 Methods

3.2.1 *Pairing success of territorial males*

In fragments within each landscape (Table 3.1), grids marked with flagging tape at 50 m intervals were created. In the contiguous forest, there were three 12.25 ha grids (two in 1997 and one in 1998). Each grid was at least 100 m from any trail, road or waterbody. In forestry fragments, three 12.25 ha grids (two in 1997 and one in 1998) were created. All forestry fragments were surrounded by clearcuts created since 1990, or permanent roads. However, grids in forestry fragments bordered only two edges and did not cover the entire fragment. Ten grids were established in the agricultural

Table 3.1 - The ratio of paired to unpaired Ovenbird males observed each year at each site.

Site	Area (ha)	1996	1997	1998
	Farm Fragments			
Bossemaier	5	0:1		1:1
Cabin	5			2:1
Triangle 1	5		2:1	
Connolly	7	2:0	2:1	
Hulit	10			3:1
Dinius	11		3:0	
Dump	12		7:0	
Dean	15		8:0	8:1
Bader	20	6:3	10:1	9:2
McConnell[a]	42			7:1
	Forestry Fragments			
Bear			11:1	
Clarine Lake				10:2
Snowfield			11:2	
	Contiguous Forest			
Namekus Lake				11:0
Mud Creek			12:1	
Powerline			14:0	

[a] 12.25 ha subsection surveyed

landscape. All farm fragments were completely isolated by agricultural fields or roads. Grids in farm fragments covered the entire fragment and ranged in size from 5 to 42 ha (Table 3.1). The exception was the 42 ha farm fragment where a 12.25 ha portion was surveyed. All contiguous forest and fragments created by forestry were surveyed in one year only. Six farm fragments were surveyed in one year, whereas the other four were surveyed for at least two years (Table 3.1).

On each grid, all males were captured using song playback to draw Ovenbirds into mist-nets. Once captured, Ovenbirds received a United States Fish and Wildlife Service aluminum band and three leg bands made of coloured plastic to form a unique band combination. Most Ovenbirds were captured within two weeks of arrival. Upon capture, measurements of right wing chord (mm) and mass (g) were taken, and the third right rectrix plucked for aging Ovenbirds (see below). Mass was measured using a 30 g Pesola scale. Each male's territory was mapped in the first two weeks of the breeding season (Chapter 2). Each bird was followed for a cumulative period of 90 min or until evidence of pairing was observed. Ovenbirds were followed for a maximum of 30 min per day. Evidence of pairing included: 1) male seen in vicinity of female; 2) male carrying food; 3) male or female seen with young; or 4) an active nest found within territory. As Ovenbirds are monomorphic, a non-singing individual tolerated by a male within a 5 m radius or emitting "tsip" notes was considered its female mate (Lein 1980).

Age was determined using the wear pattern of the third rectrix. Ovenbirds were classified as either second-year, breeding for the first time (hereafter SY), after second-year (hereafter ASY), or unknown. Individuals with a rectrix tip angle $\leq 78°$ were classified as SY, whereas all Ovenbirds with feather tip angles $\geq 90°$ were classified as

ASY (Donovan and Stanley 1995). Individuals with feather tip angles that were intermediate were classified as unknown age. One person, with no knowledge of where feathers were collected, measured all feathers. To maximize precision, all feathers were measured in the laboratory by scanning each feather into a computer and expanding the image 700 times. Images were printed and the angle of the feather tip measured using grid paper and a protractor.

3.2.2 *Removal experiments*

To determine if colonization by floaters was more likely to occur in contiguous forest than in farm fragments, removal experiments were conducted in one farm fragment and one contiguous forest site in 1997 and 1998. For four to five days before removal, Ovenbirds were surveyed on each grid, using detailed mapping. Evidence of pairing success was determined at this time. Before removal, males in territories adjacent to the removal zone were colour-banded. This ensured colonization by floaters was by new individuals and not resident individuals expanding their territories into the removal area (Newton 1992). To avoid encountering migrant Ovenbirds, removals took place when females were incubating eggs (June 12 in farm fragments for both years and June 15 in 1997 and June 13 in 1998 for the contiguous forest plots). For two weeks following removal, each site was visited daily for the first three days and every second or third day after that to determine when or if floaters colonized areas where males were removed. A floater was defined as a bird observed singing in an area where an individual had been removed but was not banded. At days 12 through 14, detailed mapping was conducted to determine which territories had been filled.

3.2.3 *Statistical analysis*

To determine if the pairing success of male Ovenbirds differed among landscapes, a weighted least squares (WLS) ANOVA was used (Neter et al. 1985). In this analysis, the dependent variable was the percentage of male Ovenbirds paired per site, while the independent variable was landscape. The weighting variable was the number of individuals recorded per site. A WLS approach was used because the variance in the percentage of male Ovenbirds paired was inherently higher in small fragments, simply because fewer males were present in these sites (i.e. estimates of pairing success were less precise in small fragments than in larger fragments). Each data point was weighted by the term:

$$w_i = \frac{1}{X_i^2} \tag{3.1}$$

where w_i was the weighting term applied to each data point and X was the number of individuals per site (Neter et al. 1985). By weighting each data point by the number of individuals per site, the importance of small farm fragments with only one or two individuals was reduced (Neter et al. 1985). In addition, a logistic regression model was created to determine if landscape effects were influenced by age, distance of territory centre from edge (log-transformed), body condition, edge *landscape, and age*condition. Body condition was measured as mass corrected for wing length, time of day captured, and Julian date captured (Chapter 4). To create the most parsimonious models that explained the greatest amount of variation in the data, all possible combinations of variables were examined (Kleinbaum et al. 1988). The model with the lowest Akaike Information Criterion value (AICc) corrected for small sample size (Burnham and Anderson 1998) was selected as the model with the best fit. If two or more models had similar AICc values (<2), the model with the fewest parameters was chosen.

To determine if pairing success of Ovenbirds was dependent on population density, an analysis using the results of published studies was conducted. To be included in this analysis, a study needed to report pairing success and Ovenbird density for fragments surrounded by agricultural land or fragments surrounded by clearcuts relative to contiguous forest. To determine if the proportion of paired male Ovenbirds was influenced by landscape, density of territorial males (males per 10 ha), or the interaction between landscape and density, a logistic regression model was created. All data are reported as means ± 1 SE unless otherwise stated.

3.3 Results

3.3.1 *Pairing success of territorial males*

Pairing success was determined for 162 males (Table 3.1). Seven males that could not be captured were given average body condition values for pairing success analyses. The percentage of males paired per site was significantly lower in farm (86 ± 3) and forestry fragments (87 ± 3) than in contiguous forest (97 ± 3: $F_{2,21} = 3.7$, $P = 0.05$). Although there was a difference in pairing success among landscapes at the site level, the logistic regression model that best fit the data included the distance from edge ($\chi^2 = 9.1$, df = 1, $P = 0.003$). Territories of unpaired Ovenbirds were closer to the edge (median 55 m, range - 20 to 140m) than paired Ovenbirds (median 80 m, range 20 - 500 m). The effect of edge on pairing success occurred equally across landscapes, as the interaction of edge and landscape was not a significant predictor of pairing success ($\chi^2 = 1.5$, df = 1, $P = 0.48$). Age was a weak predictor of pairing success ($\chi^2 = 4.2$, df = 2, $P =$

0.12), as many birds had intermediate tip angles and were classified as unknown age (30%). The model was rerun using the less stringent age classification provided in Donovan and Stanley (1995), where birds with rectrix tips ≤ 84° were SY and all others were ASY (i.e. all individuals of known age). With this age classification, the best fitting model included distance from edge ($\chi^2 = 8.2$, df = 1, $P = 0.004$) and age ($\chi^2 = 4.2$, df = 1, $P = 0.02$). SY males had a lower probability (82% of 83 males) of being paired than ASY males (94% of 79 males).

3.3.2 *Comparisons with other studies*

For all studies combined (Table 3.2), the model that best predicted pairing success included landscape ($\chi^2 = 21.3$, df = 2, $P < 0.001$) and the interaction between landscape and density ($\chi^2 = 20.1$, df = 2, $P < 0.001$). Farm fragments and forestry fragments had a lower proportion of paired males (63% of 246 males and 67% of 122 males, respectively) than contiguous forest (82% of 236 males: Table 3.2). The proportion of paired males was positively correlated with density of males in farm fragments ($\chi^2 = 18.2$, $r = 0.22$, $P = 0.001$), negatively correlated with density of males in forestry fragments ($\chi^2 = 3.8$, $r = -0.11$, $P = 0.05$), and not influenced by density of males in contiguous forest ($\chi^2 = 0.02$, $P = 0.89$).

3.3.3 *Removal experiments*

In 1997, six males were removed from the contiguous forest plot (Fig. 3.1A). Within one day, two new males were observed. On day two, a third individual was observed on the plot. By day 10, five new males were present and remained until the

Table 3.2 - Density estimates (males per 10 ha) and percentage of males paired in contiguous forest and forest fragments across North America. Numbers in parentheses are the number of Ovenbirds in each treatment for which pairing success was determined.

State/Province	Fragmented By	Density in Forest	Density in Fragment	% Paired in Forest	% Paired in Fragment	Reference
New Jersey	Agriculture	7.6	1.4	85 (46)	53 (73)	Wander 1985
Missouri	Agriculture	2.2	1.4	75 (20)	24 (17)	Gibbs and Faaborg 1990
Pennsylvania	Agriculture	6.9	3.0	67 (27)	47 (17)	Porneluzi et al. 1990
Ontario	Agriculture	4.5	2.3	82 (46)	63 (38)	Villard et al. 1993
Saskatchewan	Agriculture	8.7	5.2	97 (38)	84 (87)	This paper
New Brunswick	Forestry	1.9	1.1	91 (23)	82 (22)	Sabine et al. 1996
Maine	Forestry	6.1	8.4	80 (40)	52 (61)	Hagan et al. 1996
Saskatchewan	Forestry	8.7	7.5	97 (38)	86 (37)	This paper

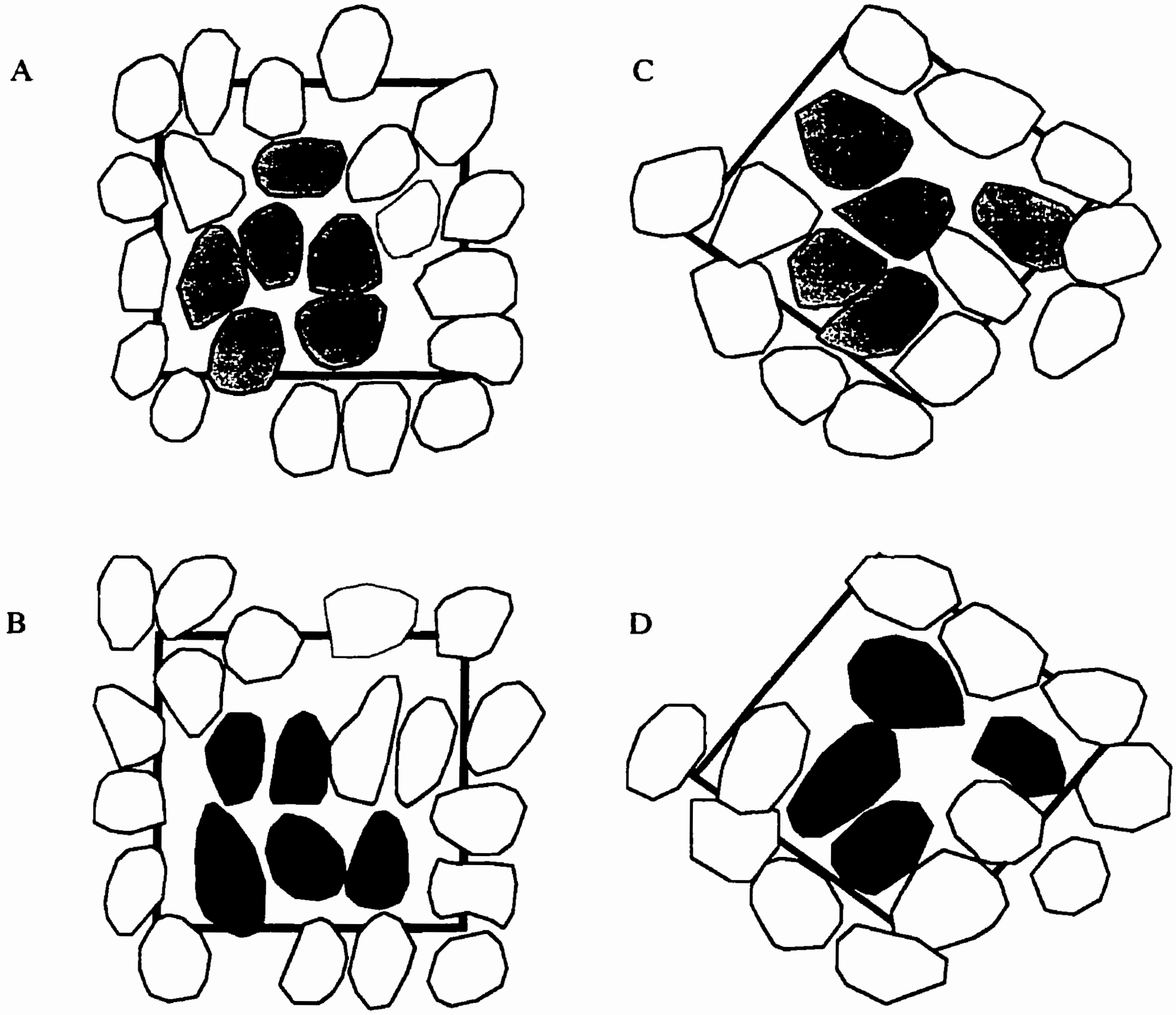

Figure 3.1 - Territory locations of male Ovenbirds on removal grids in contiguous forest: A) prior to removal of six males in 1997; B) two weeks after removal in 1997 with colonization by five floaters; C) prior to removal of five males in 1998; and D) two weeks after removal in 1998 with colonization by four males. Individuals with: 1) hatched pattern were removed; 2) solid white pattern were colour-banded and remained on the site; and 3) solid black were floaters that recolonised vacant territories. The square represents the boundary of a 9 ha removal grid, which was bordered on all sides by forest of similar composition. Scale is approximately 1 to 6,000.

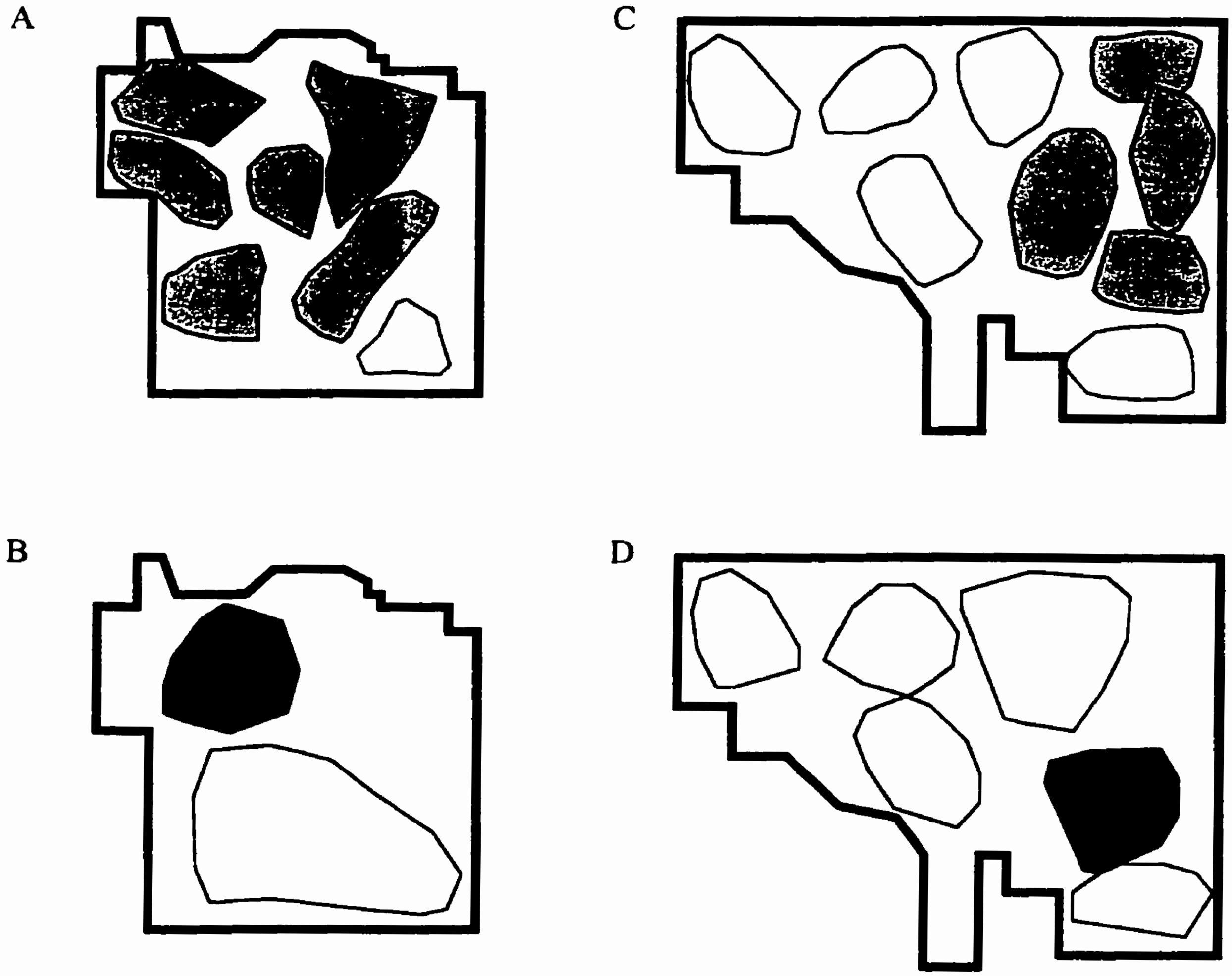

Figure 3.2 - Territory locations of male Ovenbirds on removal grids in the agricultural landscape: A) prior to removal of six males in 1997; B) two weeks after removal in 1997 with colonization by one floater; C) prior to removal of four males in 1998; and D) two weeks after removal in 1998 with colonization by one floater. Individuals with: 1) hatched pattern were removed; 2) solid white pattern were colour-banded and remained on the site; and 3) solid black were floaters that recolonised vacant territories. The boundaries of these grids were adjacent to grain fields. The 1997 grid was 11 ha and the 1998 grid was 15 ha. Scale is approximately 1 to 6,000.

end of the experiment (Fig. 3.1B). Of the five floaters observed, four were seen with females. Two territorial males on the plot before removals occurred, shifted territories (Fig. 3.1B). During 1998 in the contiguous forest, five males were removed (Fig. 3.1C). Within one day, two males had colonized the empty territories. Another two males were observed on day 10 (Fig. 3.1D). All floater males were observed with females by the end of the experiment.

In 1997, six of seven paired males were removed from an 11 ha farm fragment (Fig. 3.2A). On day nine, a new male was observed at the north end of the plot (Fig. 3.2B). The individual present before removal moved throughout the farm fragment. In 1998, four males from a possible nine were removed from a 15 ha farm fragment (Fig. 3.2C). Of the territory holders removed, three were paired and one was unpaired. The only new male observed in the 1998 farm fragment, was observed first on day six and was present until the end of the experiment (Figure 3.2D). The floater males were not observed with females in the farm fragments. Only three of the floaters could be captured; two were SY males and one was of unknown age.

3.4 Discussion

3.4.1 *Pairing success of territorial males*

Landscape factors such as fragment size, distance of territory from edge, and the amount of local forest cover surrounding fragments influence pairing success of territorial Ovenbirds (Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998). In this study, males with territories farther from edges had a greater probability of attracting a mate. This apparent edge avoidance by females is similar to Van Horn et al. (1995) who found in an agricultural landscape in Missouri that 22% of males within 300 m of an edge were paired, whereas 76% of males with territories greater than 300 m from an edge were paired. Similarly, the proportion of paired Ovenbirds was greater in patches with more core area in southern Ontario, an effect attributed to the reluctance of females to nest near edges (Burke and Nol 1998).

Avoidance of edges by female Ovenbirds has been attributed to increased nest predation and brood parasitism near edges (Van Horn et al. 1995, Burke and Nol 1998). Nest survival of Ovenbirds in the boreal forest was lower in farm fragments relative to contiguous forest (Chapter 4). A study using artificial nests in my study area also found ground nests at edges of farm fragments were 25% more likely to be destroyed than nests at edges of forestry fragments or in contiguous forest (Bayne and Hobson 1997). These results imply the type of edge and the landscape in which it occurs may be important factors influencing nesting success (Bayne and Hobson 1997, Donovan et al. 1997). However, the interacting effect of landscape and edge did not affect pairing success, suggesting that type of edge had little effect on pairing success.

Younger male Ovenbirds seemed to have a lower probability of attracting females than older males, although this depended on the method used to age birds. Numerous studies have shown older birds to have greater pairing success than younger birds (reviewed by Saether 1990). Although many factors limit breeding success of younger males, territorial behaviour of older males may force younger males into suboptimal habitats where they are less likely to attract mates (Van Horne 1983, Breitwisch 1989, Sherry and Holmes 1989). The proportion of SY males was greater in farm fragments than in forestry fragments or contiguous forest (Chapter 4). A skewed age-ratio among landscapes suggests older males in forested habitats may preempt younger males and force them to breed in suboptimal habitats in farm fragments. At a regional scale, the proportion of SY Black-throated Blue Warblers (*Dendroica caerulescens*) was greatest at the edge of the range of this species (Graves 1997). Graves (1997) argued peripheral populations exist in sink habitats and are filled by SY birds that are forced to leave source habitats at the centre of the range because of competition from older birds.

Another factor influencing pairing success in Ovenbirds is adult survival. That Ovenbirds are monogamous, not all males are paired, and unpaired females are rarely observed (Hensley and Cope 1951, Stewart and Aldrich 1951, Villard et al. 1993, Marra and Holmes 1997 but see Saether and Fonstad 1981), suggests female survival is lower than male survival. Gibbs and Faaborg (1990) argued the difference in pairing success of Ovenbirds between fragments and contiguous forest was likely caused by greater female mortality in fragments. However, survival of females need not be different among landscapes for differences to exist in pairing success among landscapes. Female Ovenbirds may preferentially choose territories in contiguous forest and use lower quality fragments only when territories in contiguous forest are filled. If females preferentially select contiguous forest, then small differences in survival between males and females at a regional level would also cause a greater male sex bias in fragments, because a smaller proportion of the females would be forced to settle in fragments (Chapter 6).

The density of male Ovenbirds in different regions of North America did not influence pairing success in contiguous forest. Thus, females do not avoid areas with low densities of males per se, suggesting conspecific-attraction has little effect on pairing success. In fact, pairing success was negatively correlated with population density in landscapes managed for forestry. This result was caused by low pairing success in high-density Ovenbird populations in Maine, where immediately after clearcutting, Ovenbirds from harvested areas forced themselves into remaining forest (Hagan et al. 1996). Hagan et al. (1996) argued increased intraspecific competition caused by high Ovenbird densities made it difficult for male Ovenbirds to maintain pair bonds. In contrast, the forestry fragments examined in this study and those of Sabine et al. (1996) existed in a matrix of regenerating forest stands cut within the last decade. High pairing success in stands surrounded by regenerating forest relative to those found immediately after clearcutting suggests "normal" conditions within intact forestry fragments may become reestablished relatively quickly after disturbance to the surrounding forest, although they still may not reach those observed in contiguous forest. In contrast, regional density of Ovenbirds was positively correlated with pairing success in agricultural landscapes. Why density of male Ovenbirds influences pairing success in agricultural landscapes at a regional scale, but not in contiguous forest is unclear. Regardless, these data indicate that in regions where the density of male Ovenbirds is lower, the effect of fragmentation by agriculture on pairing success is most severe (Villard et al. 1993).

3.4.2 *Removal experiments and floaters*

Removal experiments demonstrated some unpaired Ovenbirds were floaters. Floaters are typically late-arriving males that fail to acquire territories and, as a result, spend their time wandering among territory holders (Newton 1992). Assuming floaters are looking for a territory vacancy, these data suggest habitat in contiguous forest is saturated and that preemptive behaviour limits the number of breeding males that obtain territories (Newton 1992). However, Marra and Holmes (1997) argued removal experiments do not necessarily demonstrate habitat saturation. When male and female Black-throated Blue Warblers from the same territory were removed, colonization by other males was rare (Marra and Holmes 1997). In contrast, when males were removed and females were present, most territories were colonized by a new male or an adjacent territory holder (Marra and Holmes). Thus, Marra and Holmes (1997) argued removal experiments test for the relative availability of females rather than the availability of habitat per se.

The notion that fragments have a lower proportion of paired males relative to contiguous forest has been based exclusively on observation of males that are territorial (Villard et al. 1993). However, unpaired floaters were more likely to fill territory vacancies in contiguous forest than in farm fragments, suggesting the ratio of paired to unpaired males may be similar in contiguous forest and farm fragments, but the strategies employed by unpaired males among landscapes are different. Potentially, floating in an open landscape matrix with fields or clearcuts may increase predation risk relative to contiguous forest (Wesolowski 1981). Alternatively, the greater density of males in contiguous forest plots may create more intraspecific competition relative to farm fragments (Newton 1992). With increased competition, males in contiguous forest may be more prone to float relative to males in forest fragments. In fragments, where the density of males is lower, Ovenbird males may be better able to maintain territories (Smith and Arcese 1989, Newton 1992), although they may not attract a mate.

Like most removal experiments, the origin of our floaters was not known (Newton 1992, Marra and Holmes 1997). Banding nearby territory holders demonstrated that replacement individuals were not residents expanding their territory. However, whether the floaters came from a true non-territorial population or were territorial individuals that had already suffered breeding failure and were attempting to locate a new territory is unknown. During the study, 12 banded males that demonstrated territorial behaviour disappeared before the end of the breeding season, suggesting some of the Ovenbirds observed as floaters may have dispersed into the removal area from a previously held territory. Porneluzi and Faaborg (1999) found that paired Ovenbird males that failed to raise young almost never returned to the territory they held in a previous year, which they attributed to increased dispersal of failed breeders between breeding seasons. However, most direct evidence for within-season breeding dispersal by passerines following breeding failure indicates females are more likely to move than territorial males (Jackson et al. 1989).

3.4.3 *Summary*

This study and others suggest pairing success of Ovenbirds is influenced by habitat fragmentation. Differential pairing success among landscapes in the boreal forest seems to be the result of female mate selection and to a lesser extent, female selection for habitats where breeding success is high. Differences in survival of male and female Ovenbirds undoubtedly exist, but whether these are related to landscape type is unknown. Density of conspecifics does not seem to influence pairing success of territorial Ovenbirds, but the presence of floaters could result from the extremely high density of Ovenbirds that characterizes the boreal forest. It remains unclear whether limited habitat or the number of females in the population regulates the ratio of territorial to floater males. Regardless, unpaired males seem to use different strategies in different landscapes.

CHAPTER 4. FOREST FRAGMENTATION, ADULT DISPERSAL, AND BREEDING SUCCESS OF OVENBIRDS

4.1 Introduction

For some forest songbirds, reproductive success is greater in large tracts of forest than in smaller, more fragmented forest patches (Wilcove 1985, Robinson et al. 1995a, Donovan et al. 1995a, but see Friesen et al. 1999). Low reproductive success in fragmented landscapes can be caused by several factors, including increased nest predation (Wilcove 1985, Paton 1994, Bayne and Hobson 1997), increased brood parasitism by brown-headed cowbirds (Brittingham 1983, Robinson et al. 1995b), and decreased pairing success (Villard et al. 1993, Chapter 3). The decline in breeding productivity caused by fragmentation often creates population sinks (Pulliam 1988, Donovan et al. 1995a, Trine 1998, Porneluzi and Faaborg 1999). In contrast, large forest stands often function as population sources (Pulliam 1988, Dias 1996). Long-term persistence of forest songbirds in fragmented landscapes suggests populations in small forest fragments are maintained by dispersal, presumably from source habitats in less fragmented areas (Donovan et al. 1995a, Robinson et al. 1995a, Villard et al. 1995).

Theoretical and empirical research on the effects of forest fragmentation on source-sink dynamics have focused mainly on the consequences of differential reproductive success among landscapes (Donovan et al. 1995a,b, Robinson et al. 1995a). Less is known about how habitat fragmentation influences adult survival or dispersal and in turn how adult dispersal or survival affects source-sink dynamics (Porneluzi and Faaborg 1999). However, many adult forest songbirds have a high degree of breeding site fidelity, returning year after year to same breeding territory (for reviews see Greenwood and Harvey 1982, Holmes and Sherry 1992). Previous reproductive success is a good predictor of site fidelity, as birds unsuccessful at breeding are less likely to return to sites than birds that raise young (Drilling and Thompson 1988, Payne and Payne 1993, Roth and Johnson 1993, Murphy 1996, Haas 1998). That birds in forest fragments typically have lower reproductive success than birds in contiguous forest suggests return rates to fragmented areas may be lower, which in turn could influence landscape-level population dynamics. Alternatively, increased nest predation in forest fragments is typically caused by increased abundance of nest predators and changes in composition of predator communities (Morrell and Yahner 1995, Oehler and Litvaitis 1996, Bayne and Hobson 1997, Kurki et al. 1998). If nest predators common in agricultural landscapes also kill adult songbirds, then adults may suffer greater mortality in small fragments relative to contiguous forest.

Previous demographic comparisons of passerine populations in different vegetation types have shown sink habitats are maintained through immigration of young birds breeding for the first time (Brown and Kodric-Brown 1977, Alatalo et al. 1985, Holmes et al. 1996, Petit and Petit 1996). Young birds are assumed to colonize sink habitat because they are preempted from breeding in source habitat by older birds (Sherry and Holmes 1989, Pulliam 1996). However, whether preemptive territory behaviour functions at large landscape scales and can alter the age structure of populations among landscapes is poorly understood (but see Graves 1997, Huhta et al. 1998).

The objective of this chapter was to compare Ovenbird survival and nest success among landscapes fragmented by agriculture and forestry to sites in contiguous boreal mixedwood forest of central Saskatchewan. It was hypothesized reproductive success would be lower in landscapes fragmented by agriculture than in landscapes fragmented by forestry or in contiguous forest. It was expected that male Ovenbirds in the fragmented agricultural landscape would have lower apparent annual survival than in contiguous forest, likely because of increased dispersal from sites where reproductive success was low. I also hypothesized farm fragments would have a larger proportion of SY males because of increased immigration by young males with no prior breeding experience and greater emigration of failed breeders. Finally, a simple demographic model based on the estimates of adult and nest survival was created to determine whether populations in each landscape were sources or sinks.

4.2 Methods

4.2.1 *Capture methodology*

In forest stands within each landscape, grids marked with flagging tape at 50 m intervals were created. In the contiguous forest, two-25 ha grids were surveyed from 1996 through 1999, with an additional 12.5 ha grid added in 1998. Each grid was at least 100 m from any hiking trail, road, or waterbody. In fragments surrounded by clearcuts, a 32 ha and a 20 ha grid were surveyed every year, with an additional 12.5 ha grid added in 1998. Fourteen grids were established in forest fragments in the agricultural landscape and were completely isolated by agricultural fields. In the agricultural landscape, grids covered the entire patch and ranged in size from 5 to 42 ha.

Seven grids in the agricultural landscape were surveyed in all years, with the remainder added in the second and third years of study (Table 4.1).

On each grid, song playback was used to attract males into mist-nets. Once captured, all Ovenbirds received a United States Fish and Wildlife Service aluminum band and three leg bands made of coloured plastic to form a unique band combination. Most Ovenbirds were captured within two or three weeks after arrival. Upon capture, right wing chord (mm) and mass (g) were measured, while the third right rectrix was plucked to determine age (see Chapter 3). Each grid was visited at least 3 times per season to determine which Ovenbirds had returned.

4.2.2 *Statistical analysis*

To determine if apparent annual survival or recapture probability of male Ovenbirds varied within and among landscapes, Cormack-Jolly-Seber models were fit to the mark-recapture data. A maximum likelihood estimate of each parameter was calculated using the computer program MARK (White and Burnham 1999). Using MARK, I determined if sites within each landscape had similar survival and recapture estimates and could be pooled to derive more precise survival estimates. For each landscape, I began with a fully parameterized global model that included site, year, and site x year. One of the forestry fragments and one of the contiguous forest sites were examined for only a two year period (1998-1999), so I was unable to generate a recapture probability for these sites (White and Burnham 1999). Initially, these sites were excluded from analysis. For the global model in the agricultural landscape, site was replaced with fragment size (ha), as many sites had too few individuals to generate precise site-specific survival estimates. To create the most parsimonious model that

Table 4.1 – Landscape attributes and period of time each site was surveyed for mark-recapture study.

Site	Area (ha)	Forest Cover[a]	Time Period
	Farm Fragments		
Bossemaier	5	25	1996-99
Cabin	5	64	1998-99
Triangle 1	5	18	1997-99
Triangle 2	5	19	1997-99
Carruthers	7	33	1996-99
Connolly	7	26	1996-99
Horvath	10	22	1996-99
Hulit	10	63	1998-99
Church	11	16	1997-99
Dinius	11	21	1996-99
Dump	12	44	1998-99
Dean	15	30	1997-99
Bader	20	45	1996-99
McConnell	42	22	1996-99
	Forestry Fragments		
Bear	35	49	1996-99
Clarine Lake	25	62	1998-99
Snowfield	25	50	1996-99
	Contiguous Forest		
Namekus Lake	-	100	1998-99
Mud Creek	-	100	1996-99
Powerline	-	100	1996-99

[a] Percentage of land area within one km radius of each site that was forested.

explained the most variation in the data, all possible combinations of independent variables were examined (Kleinbaum et al. 1988). Based on the Akaike Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 1998), the model that required the fewest parameters to explain the most variance was selected (i.e. had the lowest AICc). When two or more models had similar AICc values (<2), the model with the fewest parameters was chosen. Statistical significance of each variable was determined by individually removing each variable and comparing the results of the reduced model to the optimal model using modified likelihood ratio tests (Lebreton et al. 1992).

For each landscape, nest success was calculated using the Mayfield method (Hensler and Nichols 1981). Mayfield estimates weight the importance of each nest, based on the stage the nest was discovered and the number of days the nest was observed. Daily survival probability was estimated using the 50% mid-way assumption, where a nest was assumed to have fledged or been destroyed midway between subsequent visits. Insufficient data was available to generate precise Mayfield estimates for each site. Therefore, data were pooled among sites within landscapes. The Mayfield estimates for each landscape were compared using the program CONTRAST (Sauer and Williams 1989).

To determine if the age structure of Ovenbird populations differed among landscapes, a weighted least squares (WLS) ANOVA was used (Neter et al. 1985). In this analysis, the dependent variable was the percentage of SY males per site in each year, while the independent variables were landscape and year. The weighting variable was the number of individuals recorded per site. Each data point was weighted by the term:

$$w_i = \frac{1}{X_i} \tag{4.1}$$

where w_i was the weighting term applied to each data point and X was the number of individuals per site (Neter et al. 1985). A similar analysis was done to determine if the age of new recruits differed among landscapes. Recruits were defined as Ovenbirds not previously captured at sites where banding had taken place in previous years.

To determine if mass or right wing length of male Ovenbirds was different among landscapes, ANCOVA were conducted. Independent variables included in these analyses were landscape, year, age, and all two-way interactions. Time and Julian date were also included in models for predicting mass. As many of the returning Ovenbirds were resighted rather than recaptured (79%), only mass and right wing length at first capture were used. For all generalized linear models, all possible combinations of independent variables were examined and the model with the lowest AICc presented.

A two-factor Kruskal-Wallis test was used to determine if the distance moved between subsequent capture locations was different among landscapes and for males that returned in successive years versus males that "skipped" a year (i.e. males absent from sites in the year following banding but detected in a future year). For males that returned to a site more than once, the distance between first capture and first return were used in analyses. A Kruskal-Wallis test was also used to determine if distance moved between successive capture locations was different between males whose nests were destroyed relative to those that fledged young.

All results are reported as means ± 1 SE unless otherwise reported.

4.2.3 *Source-sink models*

To determine whether populations in each landscape were sources or sinks, estimates of male survival and nest success were used to create a simple demographic model (e.g. Porneluzi and Faaborg 1999). The finite rate of change for Ovenbird populations (λ) was calculated for each landscape. When λ is >1 it indicates a source population, while λ <1 indicates a sink population. Calculations of λ were modified from Pulliam (1988):

$$\lambda = \phi_A + \phi_J\beta + \phi_J\alpha\beta \qquad (4.2)$$

where ϕ_A was survival of adult females from one breeding season to the next, ϕ_J was survival of juvenile females from fledging to the following breeding season, α was the probability a female would renest following failure, and β was the number of female young produced per adult female per nesting attempt, where:

$$\alpha = 1\text{-}DSR^I \qquad (4.3)$$

$$\beta = DSR^I * C_F \qquad (4.4)$$

with DSR being daily nest survival probability, I the incubation period of 25 days, and C_F the average number of juvenile females produced per successful nest (see Results). I assumed equal number of juvenile males and females fledged from each clutch and that clutch size and nest failure were constant over the length of the breeding season. Direct estimates of female or juvenile survival were not available. Instead, I assumed apparent annual survival of males represents a maximum survival estimate for females, as female songbirds often have lower return rates than males (Greenwood and Harvey 1982). Annual survival of juvenile Ovenbirds, like many passerines, is poorly understood because most individuals disperse far away from the natal site (Greenwood and Harvey 1982). Thus, juvenile survival was modeled over a range of possible values.

4.3 Results

4.3.1 *Apparent survival and recapture probability*

Overall, 398 males were captured over the four years of study and 163 returned to the same site at least once (Table 4.2). In contiguous forest, 151 males were captured and 67 returned to the same site at least once. For the two contiguous forest sites surveyed from 1996 to 1999, there was no evidence that survival or recapture differed among sites ($\chi^2 = 1.9$, df = 1, $P = 0.17$ and $\chi^2 = 0.8$, df = 1, $P = 0.39$, respectively) or years ($\chi^2 = 0.1$, df = 1, $P = 0.76$ and $\chi^2 = 0.1$, df = 1, $P = 0.88$). Pooling data from the three contiguous forest sites, apparent annual survival of male Ovenbirds was 0.62 ± 0.06 with a recapture probability of 0.58 ± 0.08. In forestry fragments, 116 males were captured and 50 returned to the same site at least once. For the two forestry fragments surveyed from 1996 to 1999, there was little evidence that survival or recapture differed among sites ($\chi^2 = 0.5$, df = 1, $P = 0.48$ and $\chi^2 = 1.6$, df = 1, $P = 0.21$) or years ($\chi^2 = 2.6$, df = 1, $P = 0.11$ and $\chi^2 = 4.3$, df = 1, $P = 0.12$). Pooling data from all three forestry fragments, apparent annual survival of male Ovenbirds was 0.56 ± 0.06 with a recapture probability of 0.70 ± 0.09. In farm fragments, 131 males were captured and 46 returned to the same site at least once. The most parsimonious model indicated that fragment size was positively correlated with apparent annual survival ($\beta = 0.8$, $\chi^2 = 5.4$, df = 1, $P = 0.02$) and negatively related to recapture probability ($\beta = -1.8$, $\chi^2 = 8.3$, df = 1, $P = 0.004$).

Table 4.2 - Reduced *m*-array of male Ovenbirds marked and recaptured in each landscape. Numbers are pooled over all sites within each landscape.

Landscape	Year	R_I	1997	1998	1999	r_i
Farm Fragments	1996	42	12	2	1	15
	1997	60		24	2	26
	1998	67			23	23
	m_j		12	26	26	
Forestry Fragments	1996	47	23	2	0	25
	1997	46		14	5	19
	1998	62			23	23
	m_j		23	16	28	
Contiguous Forest	1996	52	20	4	1	25
	1997	79		27	7	34
	1998	71			27	27
	m_j		20	31	36	
All Sites	1996	141	55	8	2	65
	1997	185		65	14	79
	1998	200			73	73
	m_j		55	73	89	

R_i = number of marked individuals released in year (i), including newly marked and previously marked individuals. For example, in 1997, 185 male Ovenbirds were released from all sites with 130 individuals newly marked in that year along with birds that were recaptured from 1996. Annual values are the number of individuals from a given release cohort that were first recaptured in that year. r_i = the total number of individuals from a release cohort captured at least once. m_j = the total number of recaptures in a given year.

As farm fragment size was an important predictor of apparent annual survival and recapture probability, the sites in the agricultural landscape were split into small farm fragments (< 15 ha) and large farm fragments (>20 ha). Although this split was somewhat arbitrary, it provided two groups with approximately equal numbers of males in each category. Apparent annual survival for male Ovenbirds was significantly higher in large farm fragments (0.58 ± 0.08) than in small farm fragments (0.34 ± 0.05: $\chi^2 = 6.0$, df = 1, $P = 0.01$). The recapture probability in small farm fragments was 100% while a number of males in large fragments were alive in any given year but not captured or seen (0.61 ± 0.12: $\chi^2 = 4.7$, df = 1, $P = 0.01$). Overall, apparent annual survival was significantly lower in small farm fragments than all other landscapes ($\chi^2 = 8.6$, df = 2, $P = 0.01$: Fig. 4.1). The recapture probability was significantly higher in small farm fragments than all other landscapes ($\chi^2 = 6.2$, df = 2, $P = 0.05$).

4.3.2 *Breeding success and return rate*

Over four years, 121 nests from 12 species were located. Of these, 64 (nine species) were located in farm fragments, 21 (three species) in forestry fragments, and 36 in contiguous forest (seven species). All were open-cup nesting species that nested on the ground (84% of nests) or had shrub nests less than 2 m high. Daily nest survival probability was greater in contiguous forest (0.977 ± 0.006) and forestry fragments (0.979 ± 0.008) than in farm fragments (0.960 ± 0.007) for all species combined ($\chi^2 = 4.9$, df = 2, $P = 0.08$: Table 4.3). Brood parasitism by brown-headed cowbirds did not occur in the contiguous forest or forestry fragments. In farm fragments, brood parasitism occurred in 23% of nests, but most of these nests ($n = 9$) were parasitized in 1997.

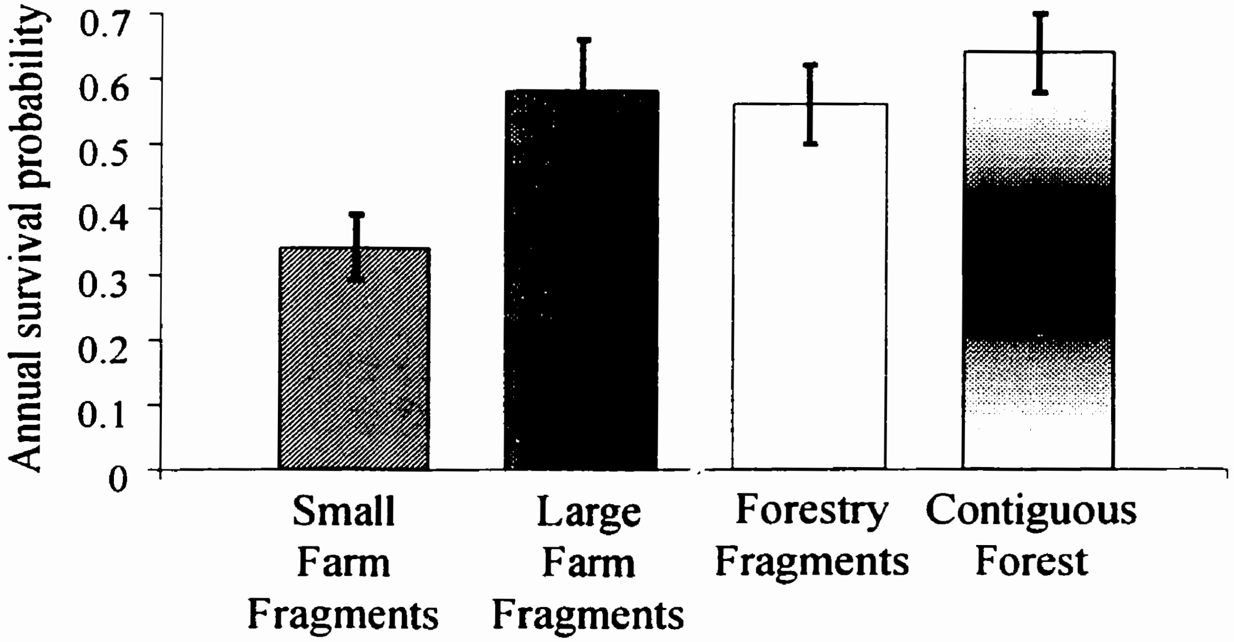

Figure 4.1 - Apparent annual survival probability of male Ovenbirds in each landscape. Error bars represent limits of 95% confidence intervals for each estimate.

Table 4.3 - Number of forest songbird nests located in each landscape and the fate of those nests. Mean daily survival probability (± 1 SE) is based on a Mayfield estimate.

Landscape	Fledged young	Destroyed	Exposure days	Daily survival Probability
Farm fragments	28	36	902	0.960 ± 0.007
Forestry fragments	15	6	289	0.979 ± 0.008
Contiguous forest	23	13	581	0.978 ± 0.006

Using contingency table analysis, the probability a male returned in a subsequent breeding season was dependent on pairing success the previous year ($\chi^2 = 9.4$, df = 1, $P = 0.002$). Unpaired Ovenbirds (11% of 28 males) were less likely to return in a subsequent year than were paired males (41% of 136 males). The probability a male returned in a subsequent breeding season when his nest was destroyed (29% of 21 males) was not significantly different from males observed with young (46% of 50 males: $\chi^2 = 1.9$, df = 1, $P = 0.17$).

4.3.3 *Age structure and body condition*

The proportion of SY male Ovenbirds in the population was different among landscapes ($F_{2,46} = 2.7$, $P = 0.08$). A larger proportion of the population in farm fragments (0.47 ± 0.04) were SY males relative to contiguous forest (0.37 ± 0.04) or forestry fragments (0.33 ± 0.04). This pattern was consistent over the length of the study, as year was not a significant predictor of the population age structure ($F_{2,46} = 0.6$, $P = 0.95$). However, considerable numbers of individuals (23%) had intermediate feather angles and were classified as unknowns. Differences in the age structure among landscapes were stronger when the less stringent age classification was used (i.e. all individuals classified as either SY or ASY males as in Chapter 3). Using the less stringent age classification, farm fragments (0.59 ± 0.04) had significantly greater proportion of SY males than forestry fragments (0.47 ± 0.04) or contiguous forest (0.45 ± 0.04: $F_{2,47} = 4.1$, $P = 0.02$: Fig. 4.2A).

The proportion of SY Ovenbirds recruited into the population was also different among landscapes ($F_{2,25} = 5.9$, $P = 0.009$). More SY males were recruited into farm

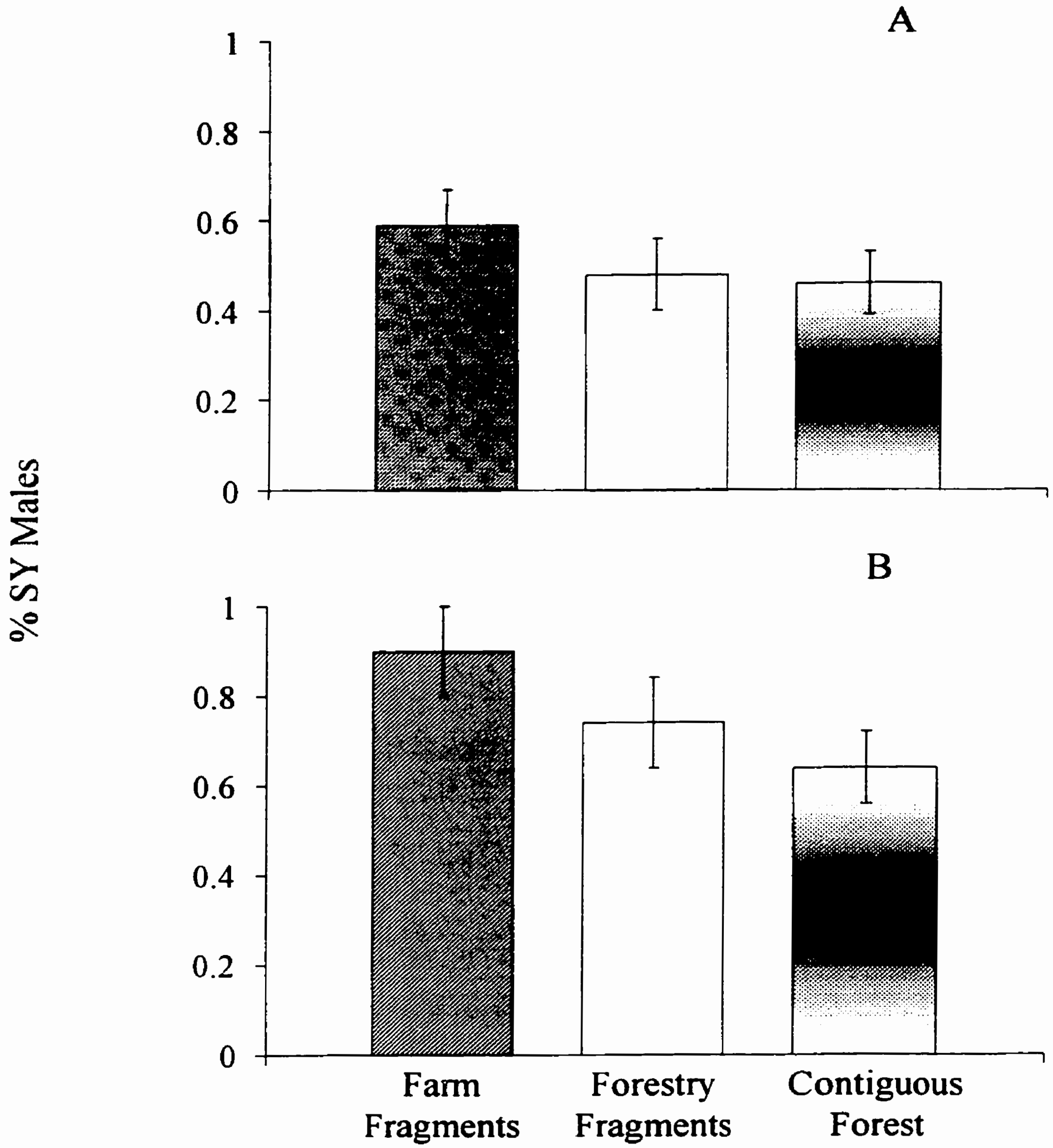

Figure 4.2 –Mean proportion (weighted least squares means) of: A) population that were SY males; B) recruits that were SY males. Recruits were unbanded individuals captured at sites where banding had taken place in previous years. Error bars represent limits of 95% confidence intervals. SY males had a third rectrix with a tip angle of ≤ 84°.

fragments (0.90 ± 0.05) than forestry fragments (0.73 ± 0.05) or contiguous forest (0.70 ± 0.04). This pattern was similar using the less stringent age classification, as farm fragments (0.90 ± 0.05) had a significantly greater proportion of SY recruits than forestry fragments (0.74 ± 0.05) or contiguous forest (0.64 ± 0.04: $F_{2,26} = 9.4$, $P = 0.001$: Fig. 4.2B).

Controlling for the other variables retained in each set of models, no differences in mass ($F_{2,398} = 1.5$, $P = 0.22$) or wing length ($F_{2,398} = 0.1$, $P = 0.92$) of male Ovenbirds in the different landscapes could be detected (Table 4.4). Mass at first capture was different among years ($F_{2,398} = 5.1$, $P = 0.007$). The interacting effect of year and landscape on mass was also significant ($F_{6,398} = 3.0$, $P = 0.007$), although no clear trend existed in the data (Table 4.4). Mass at first capture was positively correlated with time of day ($\beta = 0.24$, $F_{1,398} = 24.5$, $P < 0.001$) and Julian date ($\beta = 0.18$, $F_{1,398} = 11.0$, $P < 0.001$). Age was not related to mass ($F_{1,398} = 0.7$, $P = 0.42$). In contrast, ASY males had slightly longer primary feathers than SY males (76.9 ± 0.1 mm vs. 76.0 ± 0.2 mm, respectively: $F_{1,398} = 5.2$, $P = 0.02$). Correcting mass for structural body size (wing length), time of day, and date measured, no differences in body condition were observed among landscapes ($F_{2,398} = 1.8$, $P = 0.16$), but body condition differed among years ($F_{2,398} = 4.6$, $P = 0.01$). The interacting effect of landscape and year also affected body condition ($F_{6,398} = 2.9$, $P = 0.008$), although no clear pattern existed.

4.3.4 *Distances between subsequent territories*

There was no difference in the median distance moved between subsequent capture locations for males that returned in successive years (50 m: range 10 – 300m: $n = 136$) versus males that skipped a year (60m: range 10-250 m: $n = 24$: $H = 0.55$, $P =$

Table 4.4 - Mean wing length, mass, and body condition (± 1 SE) for second-year (SY) and after-second year (ASY) male Ovenbirds in each landscape.

Landscape and age class	# Males Measured	Wing Length (mm)	Mass (g)	Body Condition[a]
Farm Fragments				
SY	96	76.2 ± 0.20	19.0 ± 0.11	-0.15 ± 0.10
ASY	35	76.9 ± 0.45	19.2 ± 0.19	-0.01 ± 0.16
Forestry Fragments				
SY	74	76.3 ± 0.23	19.1 ± 0.12	-0.09 ± 0.13
ASY	42	76.8 ± 0.39	19.3 ± 0.14	0.02 ± 0.14
Contiguous Forest				
SY	94	76.3 ± 0.19	19.3 ± 0.10	0.09 ± 0.10
ASY	57	76.6 ± 0.29	19.4 ± 0.12	0.19 ± 0.12

[a] Body condition values were the residuals from a linear regression model correcting mass for time when captured, date captured, and wing length.

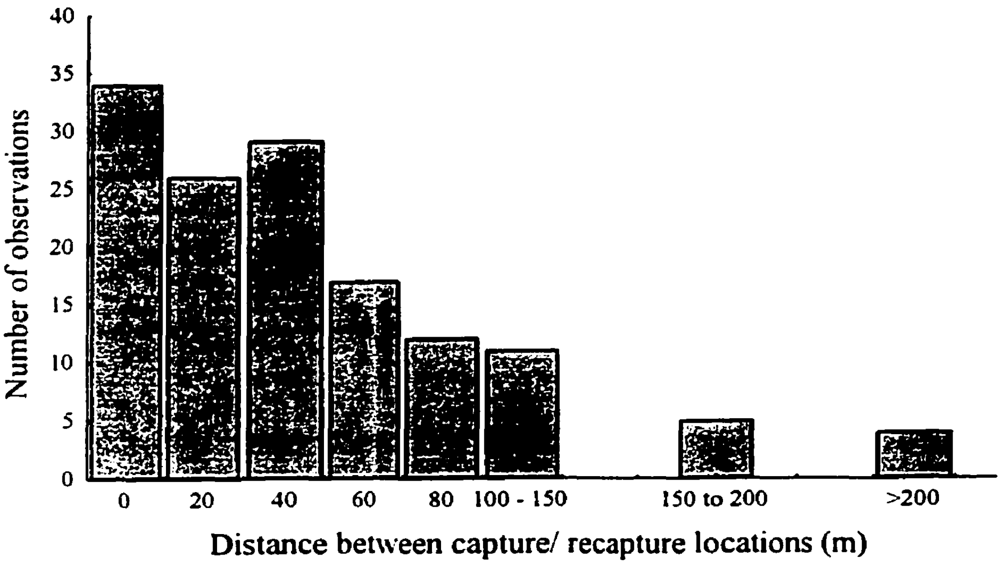

Figure 4.3 - Frequency distribution of distance (m) moved by Ovenbirds between recapture locations in subsequent years.

0.47). Most (88%) returning males were relocated within the same territory (<100 m) as in previous years (Fig. 4.3). There was no difference in the distance moved by returning males among landscapes (H = 0.68, $P = 0.88$). The median distance moved by males whose nests were destroyed (30m: range 10 – 100m: $n = 9$) versus males that fledged young (50 m: range 10-280: $n = 23$) was also not different (H = 2.2, $P = 0.14$).

4.3.5 *Source-sink status*

The average number of Ovenbird females produced per successful nest (assuming an equal sex ratio) was 2.07 ± 0.45 in small farm fragments, 2.25 ± 0.29 in large farm fragments, 2.23 ± 0.41 in forestry fragments, and 2.25 ± 0.52 in contiguous forest. Juvenile survival of about 25% would have been sufficient to allow forestry fragments, large farm fragments, and contiguous forest to be population sources (Fig. 4.4A). However, small farm fragments would have required juvenile survival of at least 45% to allow for a positive finite rate of change in the population. At the apparent annual survival probability I observed, small farm fragments were likely population sinks (Fig. 4.4B). However, if lower apparent survival in small farm fragments was caused exclusively by increased dispersal (i.e. average survival of adults from all landscapes was used in the model), then juvenile survival of 30 to 40% would have been sufficient for small farm fragments to act as population sources (Fig. 4.4B: but see Discussion).

4.4 Discussion

4.4.1 *Survival versus dispersal*

Apparent annual survival of male Ovenbirds was lower in small farm fragments than in large farm fragments, forestry fragments, and contiguous forest. Low

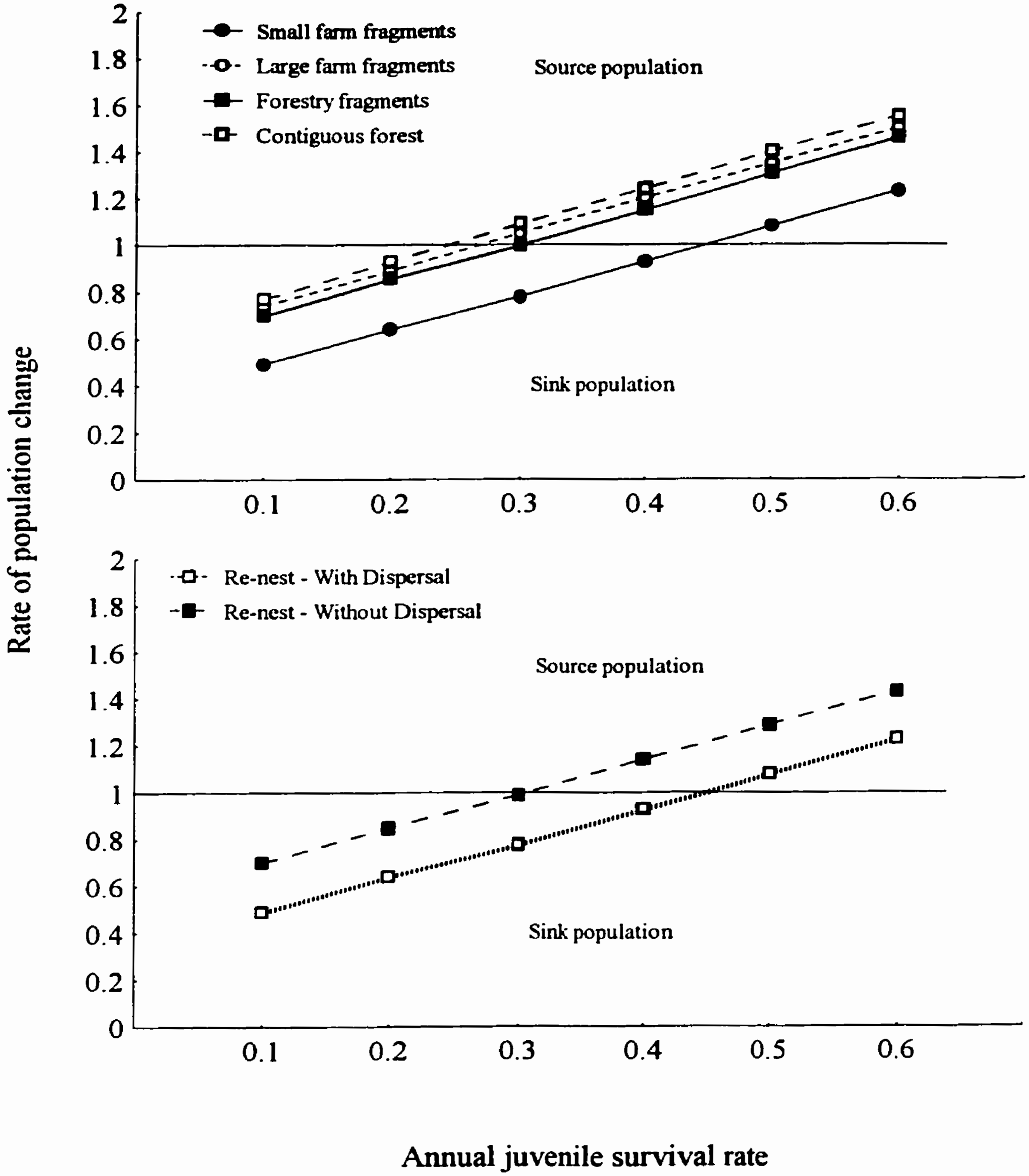

Figure 4.4 - Effects of juvenile survival on source-sink status of Ovenbird populations: A) in each landscape based on mean adult survival and nest success for that landscape; B) in small farm fragments using observed adult survival (including dispersal) versus average apparent survival across landscapes (excluding dispersal).

reproductive success in small farm fragments likely caused increased dispersal from this habitat relative to the other landscapes. That males who raised young were more likely to return in a subsequent year than males that did not raise young supports the dispersal hypothesis. Unpaired males seemed the most likely to disperse, as they had an apparent annual survival probability of only 11%. Males that fledged young were also more likely to return than males whose nests were destroyed, although this difference was not statistically significant. In Missouri, Porneluzi and Faaborg (1999) found that 41% of Ovenbird males observed with fledglings returned the next year, while only 10% of males not observed with fledglings returned. In Saskatchewan, some of the males whose nests were destroyed may have returned in subsequent years because a later nesting attempt was successful.

Ovenbirds with a lower probability of reproducing may also have been in poorer body condition, and therefore more likely to die between breeding seasons (Haas 1998). However, no differences in body condition for paired versus unpaired males (Chapter 3) or among males in the different landscapes were observed. Alternatively, Ovenbirds in small farm fragments may have experienced increased over-winter mortality because of energetic stresses caused by renesting (Haas 1998). However, unpaired males likely expended less energy than breeding males, as they did not have to care for young, yet almost never returned.

Dispersal from sites was not always permanent. The probability of recapturing Ovenbirds in each landscape ranged from ≈60 to 100%. In contiguous forest, males not recaptured every year may have been present, but missed because of small changes in territory location (e.g. they moved just off the grid). However, it unlikely males were missed in large farm or forestry fragments, as changes in territory location among years would not influence the recapture probability for that site as the entire forest patch was searched. In addition, the number of Ovenbirds present on each grid each year was consistent, suggesting all males present were accounted for. That male Ovenbirds did not always have a recapture probability of one suggests some male Ovenbirds dispersed to new breeding sites and then for whatever reason returned to sites where they had previously bred (Lebreton et al. 1993).

4.4.2 *Age structure*

Increased immigration into small farm fragments by young males seemed to compensate for low apparent annual survival. However, high turnover of males in small farm fragments resulted altered the age structure, as young males made up a larger proportion of the population in small farm fragments than in the other landscapes. Possibly, older males in larger forest stands forced young Ovenbirds to breed in small farm fragments by preemptive territory selection in contiguous forest (Holmes et al. 1996). Alternatively, young males with no prior breeding experience may not have recognized the lower suitability of small farm fragments and simply filled vacancies left by males that did not return to sites where breeding success was low (Wilcove 1985).

The low apparent annual survival in small farm fragments suggests that males that breed in small farm fragments were more likely to disperse in subsequent years relative to ovenbirds in contiguous forest. However, whether dispersing ovenbirds sought territories in contiguous forest or whether they simply relocated to other patches within fragmented landscapes is unknown. Ovenbirds with territories in small fragments may have learned small farm fragments were poor quality habitat and may have sought territories in higher quality habitat (i.e. contiguous forest) in subsequent years. Alternatively, ovenbirds may be "hard-wired", automatically dispersing after failed breeding attempts, and simply filling available territory vacancies they encounter (i.e. they do not learn to recognize fragments as poor quality). That males colonizing territories in contiguous forest were likely to be older suggests that males breeding in small forest fragments dispersed to contiguous forest in subsequent years (i.e learned to avoid small fragments). However, the contiguous forest and agricultural landscape examined in this study were relatively close together, such that dispersing individuals from small farm fragments had a relatively high probability of randomly encountering territories in contiguous forest. In more fragmented landscapes, where the distance to contiguous forest is greater, failed breeders that disperse may never encounter good-quality habitat. In addition, non-territorial floaters were more common in contiguous forest than in fragmented landscapes (Chapter 3). The larger proportion of ASY males that were recruited into contiguous forest populations could also result from floaters obtaining territories as they get older, rather than failed breeders dispersing from the small farm fragments to the larger forest blocks (Sherry and Holmes 1989).

4.4.3 *Source-sink dynamics and habitat fragmentation*

Although sample sizes were small, nest success appeared lower in farm fragments. If juvenile survival was around 30% (Donovan 1995b, Porneluzi and Faaborg, 1999), small farm fragments were population sinks. In contrast, large farm fragments, forestry fragments, and contiguous forest, were population sources. However, Porneluzi and Faaborg (1999) argued models using adult survival estimates that include dispersing individuals are more likely to conclude a habitat is a sink. While it is true dispersal will have no effect on λ if dispersing individuals emigrate to another patch of sink habitat, it is not if dispersing individuals emigrate to source habitat. Loss of breeding adults from sink habitat for whatever reason will tend to magnify effects of low reproductive success and further reduce λ (Haas 1998).

Fragmentation by forestry seemed to have little effect on nesting success and survival of adult Ovenbirds relative to contiguous forest. The impact of anthropogenic fragmentation in forested landscapes on Ovenbird abundance and demography seem highly dependent on the type of disturbance and time since disturbance. In New Hampshire, King et al. (1996) found no difference in density, pairing success, or nesting success of Ovenbirds close to 5-year-old clearcut edges relative to forest interiors. Similarly, pairing success of male Ovenbirds did not differ between forest patches in a harvested landscape and in contiguous forest in New Brunswick (Sabine et al. 1996). Ovenbird density and pairing success were lower within 150 m of gravel logging roads relative to forest interiors in Vermont, although fledging success was similar (Ortega and Capen 1999). In recently fragmented areas in Maine, Ovenbirds with territories in forest stands that were clearcut, were forced into remaining forestry fragments resulting in such extremely high densities that males could not defend their territorial boundaries or maintain pair bonds (Hagan et al. 1996). Clearly, forestry activities can affect Ovenbird demography, but whether these effects persist in the long term is not clear. Unlike agricultural landscapes where fragmentation effects are long-lasting and change predator communities, the effects of fragmentation caused by harvesting may be more ephemeral and less likely to increase nest predation (Rudnicky and Hunter 1993, Bayne and Hobson 1997).

4.4.4 *Summary*

Forest fragmentation is having negative impacts on Ovenbird populations in many areas of North America. Increased nest predation and cowbird parasitism have created vast areas of sink habitat where breeding productivity seems to be insufficient to compensate for adult mortality. However, many highly fragmented areas still support high densities of Ovenbirds. My observation of more SY Ovenbirds in small farm fragments than in the other landscapes, suggests Ovenbird populations in small farm fragments are being rescued by immigration of excess juveniles produced in less fragmented areas. The larger number of ASY recruits in contiguous forest also suggests failed breeders from small farm fragments may be dispersing to contiguous forest. Although dispersal by adults from farm fragments to contiguous forest may have negative impacts on populations in small farm fragments, it may benefit the overall population. If ASY Ovenbirds have greater reproductive success than SY Ovenbirds, dispersal from fragments to contiguous forest could increase productivity in contiguous forest more than would be expected if adults returned to fragments (Chapter 6).

CHAPTER 5 . FOREST FRAGMENTATION AND POST-BREEDING MOVEMENT PATTERNS OF ADULT OVENBIRDS

5.1 Introduction

Isolation of forest fragments influences the composition of forest songbird communities (Robbins et al. 1989b, Freemark and Collins 1992). However, the mechanisms determining whether a species is present in isolated forest fragments remain unclear. It is often assumed the open landscape matrix in which forest fragments exist, acts as a barrier to movement that limits the ability of birds to colonize isolated areas (Whitcomb et al. 1981, Lynch and Whigham 1984). Although the ability to move among fragments is key to the persistence of forest songbird metapopulations (Villard et al. 1995), how habitat gaps influence forest songbird movements is poorly understood (Desrochers and Hannon 1997, Grubb and Doherty 1999, Cassady-Saint Clair et al. 1999).

Between fledging and migration, territoriality in many songbirds breaks down and individuals begin to move widely (Cherry 1985, Vega Rivera et al. 1999). During this post-fledging period, habitat fragmentation may limit the movements of juveniles, family groups, and even adults. The dispersal of juvenile Crested Tits (*Parus cristatus*) out of forest fragments was delayed relative to individuals from contiguous forest, and this was attributed to a reluctance of juveniles to cross open areas (Lens and Dhondt 1994). Juvenile and adult songbirds in a landscape fragmented by forestry moved through forested corridors rather than across open clearcuts (Machtans et al. 1996). Matthysen et al. (1995) found adult European Nuthatches (*Sitta europaea*) in small forest fragments were less likely to disperse to a new territory in a subsequent year than individuals in contiguous forest. Together, these studies suggest forest fragmentation reduces the mobility of forest songbirds following breeding, and may act as a limit to dispersal (Opdam 1991).

I used radio-telemetry to compare the post-fledging movements of adult male Ovenbirds originating from forest fragments in a landscape dominated by agriculture to those of individuals coming from contiguous forest. Movement patterns were also compared between males seen with young versus those not seen with young to determine whether movements of failed and successful breeders were differentially affected by forest fragmentation. I hypothesized that male Ovenbirds would avoid crossing agricultural fields and thus, would have more restricted movements than males in contiguous forest during the post-fledging period.

5.2 Methods

This study was conducted in the agricultural landscape and contiguous forest. In forest patches within each landscape, grids marked with flagging tape at 50 m intervals were created. In the contiguous forest four-16 ha grids were established, while in the agricultural landscape there were seven grids ranging in size from 6 to 15 ha. Canola or wheat fields isolated all farm fragments with at least 50 m separating adjacent farm fragments.

5.2.1 *Radio-telemetry*

At each site, one to six adult male Ovenbirds were captured. Adults were captured beginning July 2, about a week after most fledglings had left the nest. The last bird fitted with a radio-transmitter was captured on July 17. Fall migration peaks the first week of August at banding stations at the latitude of the study area (Machtans et al. 1996). Ovenbirds had not been observed before capture, so information on pairing success, nesting success, or territory location was unavailable at capture. Each bird was fitted with a Holohil Ltd. (112 John Cavanaugh Road, Carp, ON) Bd2-A radio-transmitter, weighing about 0.6g (≅ 3% of adult Ovenbird body mass). Transmitters had a range of just under 1 km. Information provided by the manufacturer suggested battery life for the radio-transmitters was four weeks (but see results). Transmitters were attached to Ovenbirds in two ways. For 40 Ovenbirds, transmitters were attached by clipping feathers on the back down to stubs (about 2 mm) and affixing the transmitter to the stubs with epoxy (i.e. Warnock and Warnock 1983). A backpack harness was used on 18 Ovenbirds to increase retention time. The harness consisted of two loops of elasticized yarn run through tubes in each transmitter. The two loops were brought together in the centre of the chest and held together using a plastic band that was fixed to the yarn using glue (B. Woolfenden, pers. comm.). This technique kept the yarn from chaffing the underside of the wings. Both techniques were employed in each year.

Each radio-tagged bird was located 1 to 2 times daily using a hand-held receiver and a 4-element Yagi antenna. Locations of each bird were pinpointed by approaching each bird until it moved (i.e. signal changed location). Once Ovenbirds were visually located, they were followed for about ½ hour and information on their location (ground, shrub or tree), activity (e.g. foraging, perching), and whether they were with young were recorded. Locations were marked on maps created for each site and entered into the geographic information system Arcview 3.1. When Ovenbirds moved off grids, a Trimble global positioning system was used to determine the geographic coordinates of new locations.

When a signal could not be located, I searched 3 km transects in each of the four cardinal directions from the last known location. Attempts were made to locate Ovenbirds for about four days after their last sighting. In many cases, it could not be determined whether Ovenbirds had left the study area or whether transmitter failure had occurred. Most "signal losses" occurred at around 3 weeks of radio-transmitter use, which seemed to be the average life span of the transmitters.

5.2.2 *Movement patterns*

Using the program Animal Movement 2.0 (Hooge and Eichenlaub 1997), home-range size (95% minimum convex polygon) was calculated for Ovenbirds that were tracked for at least 7 days. Ovenbirds were often relocated more than once per day, so the 95% minimum convex polygon was based on all points (hereafter 95% MCP All). However, the independence of locations within the same day has been questioned (White and Garrott 1990, but see De Solla et al. 1999), so a 95% minimum convex polygon based on the first observation each day was also calculated (hereafter 95% MCP First). For each individual, mobility (mean distance between daily locations), maximum distance moved (distance between two most extreme points), and whether it crossed a gap (non-forested area greater than 25 m wide) was calculated. For Ovenbirds captured in farm fragments, nearest neighbour analysis (Hooge and Eichenlaub 1997) was used to determine if the distribution of observations within farm fragments was clustered or random. For Ovenbirds that left the forest fragment in which they were captured, the site where they spent the most time was used for the analyses. To determine if Ovenbirds avoided the edges of farm fragments, a 25 and 50 m buffer within each fragment was created and the proportion of locations within each buffer zone calculated. Observed patterns of edge avoidance in each farm fragment were compared to five theoretical home ranges generated in each farm fragment. Theoretical home ranges were created by randomly generating 18 locations (average number of locations obtained) within each farm fragment. Most of the dependent variables did not follow a normal distribution, so non-parametric tests were employed in most analyses. All data are reported as medians and ranges unless otherwise stated.

5.3 Results

Overall, 58 male Ovenbirds were captured and fitted with radio-transmitters. Fourteen Ovenbirds lost transmitters in less than a week and were not included in the analyses. Predators killed three individuals. Of the 44 Ovenbirds followed for more than a week, 25 were captured in contiguous forest and 19 were captured in fragments. Transmitter life was shorter than expected. Three transmitters recovered from Ovenbirds lasted 19 to 23 days. Short battery life made it difficult to determine how many individuals left the study area during the period of observation. However, two Ovenbirds went missing well before the average life of transmitters was reached.

Using a Yates corrected chi-square test, males without young were more likely (10 of 12) to cross gaps in the fragmented landscape than males with young (1 of 7: $\chi^2 = 6.1$, df = 1, $P = 0.01$). Of the 19 males in fragments, four permanently left the fragments where they were captured and were relocated in at least two other fragments. The maximum distance moved by these four individuals was 1,056, 1,380, 1,740, and 5,630 m. The minimum-sized gaps crossed by these individuals ranged from 100 to over 300 m. These males were never seen with young. Six males left the fragment where they were captured, crossed an area of cropland of at least 50 m to an adjacent fragment, and returned to their original fragment on a subsequent day. Only one of these males was seen with young. In contiguous forest, gaps were crossed, but gaps were access roads or powerlines about 25 m wide. In contiguous forest, there was no difference in the gap-crossing frequency of males observed with young (5 of 15) versus males not observed with young (3 of 10: $\chi^2 = 0.7$, df = 1, $P > 0.50$).

Spearman-rank correlation tests indicated the number of observations and the number of days tracked were not correlated with the size of the 95% MCP All ($r_s = -0.13$, $P = 0.39$ and $r_s = 0.11$, $P = 0.48$). Two-factor Kruskal-Wallis tests indicated 95% MCP All, 95% MCP First, mobility and maximum distance moved were not different between landscapes (Table 5.1 and Fig. 5.1A). Males seen with young had smaller 95% MCP All, 95% MCP First, shorter maximum distance moved, and less mobility than males not seen with young (Table 5.1 and Fig. 5.1B). The interaction between landscape and the presence of young was not significant for any variables ($P > 0.50$ in all cases).

Using a Yates corrected chi-square test, males with young (6 of 7) were more likely to have clustered patterns of habitat use in fragments than those without young (4 of 12: $\chi^2 = 5.0$, df = 1, $P = 0.03$). Ovenbird males did not avoid edges. Based on a single-factor ANOVA, the proportion of radio-tracked positions within 50 m of an edge

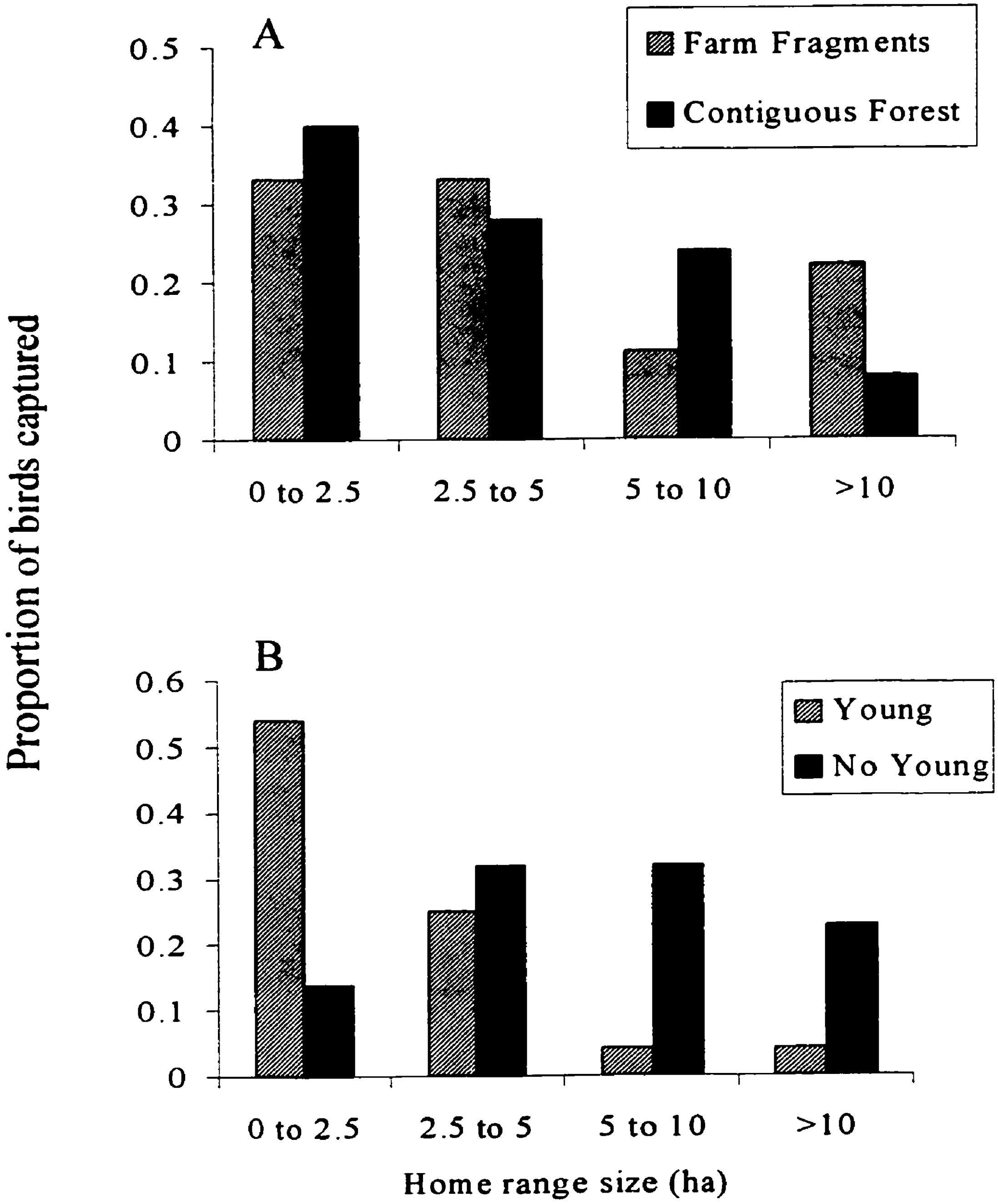

Figure 5.1 - Distribution of male Ovenbird home range sizes (95% MCP): A) in each landscape; B) for males observed with and without young.

Table 5.1 - Median values for movement variables for male Ovenbirds in farm fragments versus contiguous forest and for those seen with young versus those not seen with young. The range is provided in the parentheses.

Movement parameter	Farm Fragments	Contiguous Forest	Seen With Young	Not Seen With Young
95% MCP[a] (All locations) – (ha)	3.3 (0.8 – 238.4)	2.8 (1.1 – 50.4)	1.9 (1.1 – 14.2)	5.7 (0.8 – 238.4)
95% MCP polygon (First location) – (ha)	2.6 (0.4 – 238.4)	1.9 (0.6 – 50.4)	1.6 (0.6 – 11.3)	4.9 (0.4 – 238.4)
Maximum distance (m)	422 (180 – 5630)	290 (185 – 1946)	255 (185 – 750)	503 (180 – 5630)
Mobility (m)	107 (58 –659)	106 (58 – 265)	141 (58 – 199)	159 (68 – 659)
Number of locations	17 (9 – 35)	16 (7 – 52)	19 (7 – 52)	16 (8 – 31)
Number of days	13 (7 – 20)	13 (7 – 23)	14 (7 – 23)	11 (7 – 18)

[a] Minimum convex polygon

(0.75 ± 0.19: mean ± 1 SD) was greater than expected if males randomly used fragments (0.58 ± 0.13: $F_{1,52} = 9.2$, $P < 0.01$). The proportion of radio-tracked positions within 25 m of an edge (0.46 ± 0.27) was also greater than expected if males used fragments randomly (0.30 ± 0.12: $F_{1,52} = 15.1$, $P < 0.001$). For the 50 m buffer, there was weak evidence males without young had a greater proportion of observations near edges (0.80 ± 0.17) than those observed with young (0.65 ± 0.21: $F_{1,17} = 3.1$, $P = 0.09$). Differences were not detected in the proportion of observations near edges using the 25 m buffer for males with and without young ($F_{1,17} = 0.4$, $P > 0.50$)

The method of transmitter attachment did not seem to affect movement patterns. Maximum distance moved ($H = 1.1$, $P = 0.30$), mobility ($H = 0.6$, $P = 0.45$), 95% MCP All ($H = 2.0$, $P = 0.16$), and 95% MCP First ($H = 0.2$, $P > 0.50$) were similar for males that had transmitters attached with epoxy versus those whose transmitters were attached with a harness. Of the four Ovenbirds that permanently left fragments, two had transmitters attached with epoxy and two had harnesses. However, all individuals killed by predators had radio-transmitters attached with harnesses.

5.4 Discussion

5.4.1 *Landscape fragmentation and movement patterns*

Landscape had little influence on the movements of male Ovenbirds. Most individuals remained within a few hundred meters of their capture location for the observation period. In particular, males with young remained clustered in a 2 to 3 ha area around their capture point, suggesting they remained near their breeding territory. Radio-telemetry on male Ovenbirds during the nesting phase suggests average home range size in fragments (1.8 ± 0.8 ha) and contiguous forest (1.6 ± 0.4 ha) are similar to those of Ovenbirds observed with young in the post-fledging period (Chapter 2). In contrast, Ovenbirds observed without young had larger home ranges than males with young, although the movements of these individuals were similar between landscapes.

Ovenbirds crossed gaps frequently, but gap-crossing propensity depended on landscape and the reproductive status of each individual. Individuals that were presumably unsuccessful at breeding crossed gaps in the fragmented landscape more than males with young. Whether males with young were reluctant to move across gaps in the fragmented landscape because of predation risk to young or whether young constrained the movements of adults is unclear. Males with young in contiguous forest had similar movement patterns to those with young in the fragmented landscape. However, males with young in contiguous forest crossed small gaps created by roads and powerlines, whereas males with young in fragments rarely left the fragment, suggesting larger gaps and open fields may be perceived as having greater risk than powerline or road gaps.

Open farmland did not appear to be a barrier to movement for Ovenbirds without young. Long-distance movements by males without young suggest adult dispersal may not be constrained by fragmentation. However, even though Ovenbirds were capable of crossing gaps, they may preferentially move through forested environments when dispersing. Cassady-St. Clair et al. (1999) found Black-capped Chickadees (*Podecile atricapillus*) crossed open spaces of over 200 m if no other choice was available, but were unwilling to cross gaps of less than 50 m when alternate routes through forest were present.

Ovenbirds in fragments did not avoid edges during the post-fledging period. In fact, males seemed to spend more time than expected near the edges of fragments. This pattern of edge-use is in contrast to studies done during the breeding season, which demonstrate the density of male Ovenbirds is lower near edges (Van Horn et al. 1995, Ortega and Capen 1999). Machtans et al. (1996) found the number of dispersing birds captured in mist-nets was greater along the edges of buffer strips, and suggested birds moved laterally along edges rather than cross the edge and into the clearcut. Possibly, greater edge-use by Ovenbirds in fragments can be attributed to such a barrier effect (Opdam 1991).

5.4.2 *Breeding success and movement patterns*

The wider range of movements of male Ovenbirds without young could be caused by several factors. Post-breeding movement may be a strategy for finding areas of high food availability (Cherry 1985, Rappole and Ballard 1987). Alternatively, Ovenbirds may seek out areas with greater vegetation density to reduce predation risk associated with their pre-basic molt. Vega Rivera et al. (1999) argued adult Wood Thrushes (*Hylocichla mustelina*) that left territories during the post-breeding period were searching for "safe havens" where the density of vegetation was greater. Of the Ovenbirds that permanently left fragments in our study, all were last seen in areas of dense deciduous vegetation where the forest canopy was less than 5 m high.

Although evidence is limited, migratory passerines may select future breeding territories before fall migration (Brewer and Harrison 1975, Morton et al. 1991). Thus, Ovenbirds without young may also have been "prospecting" for new territories (*sensu* Morton 1992), while males with young may have been reluctant to leave territories where they were successful. Little is known about adult dispersal in passerine birds, but birds that fail to raise young at a site are less likely to return to that site than birds that raise young (Haas 1998, Chapter 4). Our results are similar to those of Vega Rivera et al. (1999), who found 64% of adult Wood Thrushes that failed to raise young left territories during the post-breeding phase, while only 25% that raised young left territories during the same period. However, the breeding status of radio-tracked individuals in our study was not known before capture. Possibly, individuals not seen with young had separated from their fledglings when captured. All adult Ovenbirds, once young are independent, may move extensively and be willing to cross open gaps.

5.4.3 *Summary*

Adult Ovenbirds moved across gaps of several hundred meters and some individuals moved extensively throughout fragmented and forested landscapes suggesting dispersal is not constrained by forest fragmentation. Thus, Ovenbirds should be able to colonize isolated fragments that have undergone local population extinction. However, point-counts in our fragmented landscape indicate Ovenbirds are often absent from isolated patches (Hobson and Bayne 2000c). Ovenbirds may be more reluctant to cross open space in landscapes where the inter-patch distance is greater. Alternatively, Ovenbirds in isolated fragments may have lower reproductive success than individuals in areas of more contiguous habitat (Donovan et al. 1997). Possibly, Ovenbirds without young were dispersing from small, isolated forest fragments in an effort to avoid areas of low reproductive success. This hypothesis is supported by the fact that male Ovenbirds that fail to raise young have lower site fidelity than birds that raise young (Porneluzi and Faaborg 1999, Bayne 2000). Metapopulation models predicting the occurrence/abundance of birds in fragmented landscapes should account for the possibility that dispersal in forest birds is driven by previous reproductive success. As reproductive success often depends on landscape context, the propensity of many forest songbirds to disperse may be higher in fragmented landscapes than in contiguous forest.

CHAPTER 6 . MODELING THE EFFECTS OF SOURCE-SINK DYNAMICS ON POPULATION STRUCTURE OF OVENBIRDS

6.1 Introduction

Most source-sink models have focused on the effects of density-dependent juvenile dispersal on population persistence (Pulliam 1988, Davis and Howe 1991, Donovan et al. 1995b, Gosselin 1996). Less is known about how source-sink dynamics influences population structure (i.e. age and sex ratios), as previous models have assumed equal sex and age ratios among habitats. However, recent empirical studies suggest sex and age ratios can be quite different in sources and sinks (Villard et al. 1993, Holmes et al. 1996, Chapter 3, and Chapter 4). Adult dispersal and differential survival of the sexes are two major factors that might influence population structure. However, no models have explicitly examined how these life history attributes might influence population structure or size.

The objective of this chapter was to determine how different patterns of adult survival and dispersal might influence the size and structure of Ovenbird populations in fragmented and forested landscapes linked by dispersal. A simple source-sink model similar to Donovan et al. (1995b) was used to test whether unidirectional density-dependent dispersal by juveniles from source to sink habitat could maintain the overall population. The baseline model was modified to determine if population size or structure was influenced by density-independent dispersal by adults from sink to source, or differential survival of males and females.

6.2 Model Outline

6.2.1 *Model structure*

Models were programmed in the computer program Microsoft Excel using the add-in PopTools (Hood 2000). In the model, the landscape consisted of either source or sink habitat. The amount of source habitat in the landscape was limited and was regulated by density-dependent territoriality. The model assumed habitat selection followed an ideal preemptive model (Fretwell and Lucas 1970), and that Ovenbirds competed for the limited number of territories in source habitat. Sink habitat was unlimited and all Ovenbirds seeking territories in this habitat obtained one. The model was not spatially explicit as the distance between source and sink habitat was not considered.

The number of Ovenbirds surviving migration was used to determine how many individuals sought territories in the source habitat. In the baseline model, all SY and ASY Ovenbirds holding territories in year t reacquired the same territory in year $t+1$. In the baseline model, juveniles fledged from the source competed to acquire their first territory in the source. Juveniles fledged from the sink were assumed to have natal habitat fidelity and returned to the sink, where they automatically acquired territories. Competition for territories in the source was density-dependent, so those juveniles not obtaining a territory in the source dispersed to the sink (density-dependent dispersal model). It was assumed no costs were involved in dispersing to sink habitats and no differences in juvenile or adult survival existed among habitats. The probability a juvenile bird obtained a territory in the source was modeled using a decreasing sigmoidal equation:

$$D = \frac{A}{(1 + \exp(((\frac{(x/10)}{B}) - C)} \qquad (6.1)$$

where D was the probability a juvenile seeking a source territory obtained one; A was the value of D at the origin and was set to 1; X was the number of Ovenbirds seeking source territories in the spring; B regulated the strength of the density dependence and was set at 1.5; C was a constant that influenced the range of values of X where the probability of obtaining a territory was only slightly influenced by density and was set at 5. Density of breeding male Ovenbirds is highly variable across their range, but maximum densities typically range from 10 – 12 territories per 10 ha (Van Horn and Donovan 1994). It was assumed that below five territories per 10 ha, the probability of acquiring a new territory was high. Above five territories per 10 ha, the probability of acquiring a new territory was reduced at an increasing rate. At densities of 15 territories per 10 ha the probability of acquiring a new territory was virtually nil (Fig. 6.1). X was modeled as:

$$X = (ASY_S * \phi_A) + (SY_S * \phi_A) + (JUV_S * \phi_J) + (SY_D) \qquad (6.2)$$

where ϕ was the survival estimate for that age class; ASY_S was the number of ASY Ovenbirds returning to a territory in the source; SY_S was the number of SY Ovenbirds returning to a territory in the source; JUV_S was the number of juveniles fledged from the source that sought their first territory in the source; and SY_D was the number of SY Ovenbirds dispersing from the sink and attempting to obtain their next territory in the source. Density dependence functions were separate for males and females.

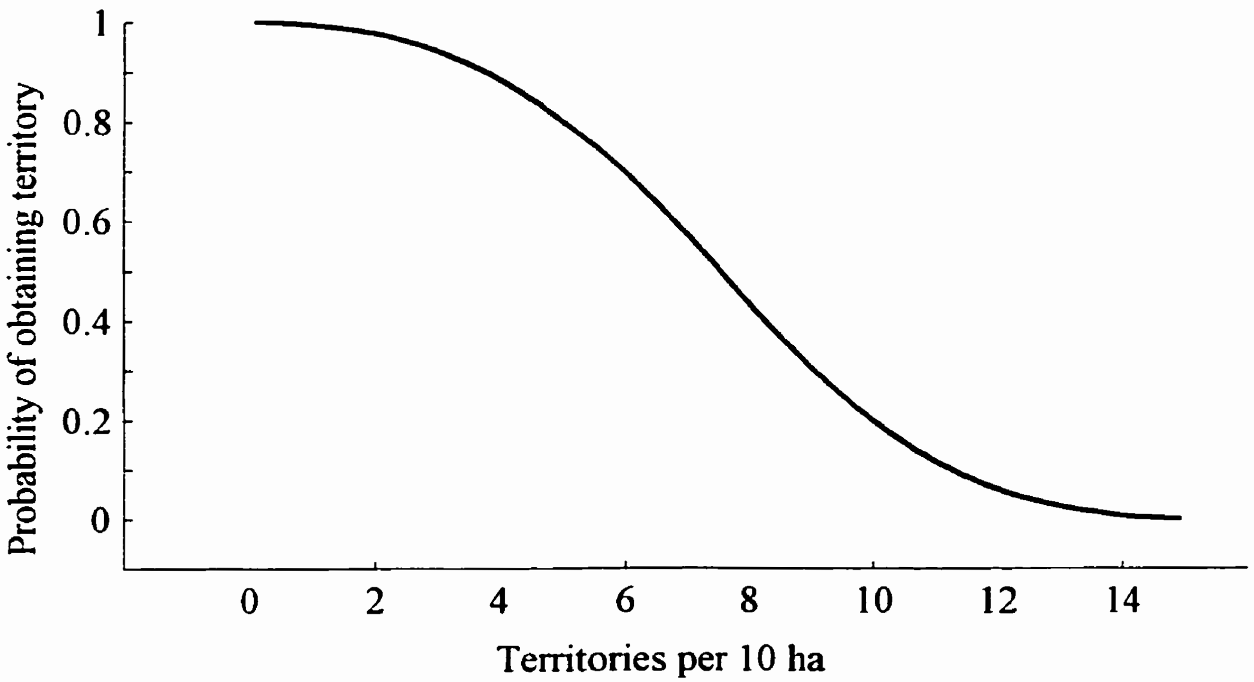

Figure 6.1 - Density dependent function demonstrating relationship between the density of Ovenbirds seeking territories in source habitat each spring and the probability of obtaining that territory.

Once territories were established and juveniles that did not obtain territories in the source had dispersed to the sink, reproduction occurred. The number of juveniles produced was based on the number of female adults alive in that year. The number of juvenile Ovenbirds of each sex that fledged from each nest was assumed to be equal. Once reproduction was finished, the model censused the entire population. The model consisted of 12 distinct age and habitat classes that included: after-second year (ASY_S) adults with territories in the source; second year (SY_S) adults in the source; juveniles fledged from the source (JUV_S); after-second year adults (ASY_K) in the sink, second year (SY_K) adults in the sink, and juveniles fledged from the sink (JUV_K). All groups were modeled separately for males and females. These 12 groups combined, made up the overall population size, with the relative abundance of each group defining the population structure (*sensu* Harrison 1994). The following difference equations (6.3 – 6.9) were used to describe the population size of each age class in each habitat and were calculated separately for males and females:

$$SY_{D\,(t+1)} = (SY_{K\,(t)} * \phi_A * SRa) \tag{6.3}$$

$$ASY_{S\,(t+1)} = (ASY_{S\,(t)} * \phi_A) + (SY_{S\,(t)} * \phi_A) + (SY_{D\,(t)} * D) \tag{6.4}$$

$$SY_{S\,(t+1)} = (JUV_{S\,(t)} * \phi_J * D) \tag{6.5}$$

$$ASY_{K\,(t+1)} = (ASY_{K\,(t)} * \phi_A) + (SY_{K\,(t)} * \phi_A * (1 - SRa)) + (SY_{K\,(t)} * \phi_A * SRa * (1 - D)) \tag{6.6}$$

$$SY_{K\,(t)} = (JUV_{K\,(t)} * \phi_J) + (JUV_{S\,(t)} * \phi_J * (1 - D)) \tag{6.7}$$

$$JUV_{S\,(t+1)} = ((ASY_S\,E_{(t)} + SY_S\,E_{(t)}) * \beta_S) \tag{6.8}$$

$$JUV_{K\,(t+1)} = ((ASY_K\,E_{(t)} + SY_K\,E_{(t)}) * \beta_K) \tag{6.9}$$

The term SRa or adult straying probability was the proportion of SY Ovenbirds that abandoned their territories in the sink and attempted to get territories in the source (density-independent adult dispersal model). It was assumed Ovenbirds that attempted to breed in the sink more than once, always returned to the sink (i.e. ASY males in sink did not disperse). In the baseline model, SRa was set to zero (i.e. all SY Ovenbirds returned to previous breeding sites if they survived). β_S and β_K were fecundity in the source and the sink respectively and were calculated using equation 6.10. D was the probability a bird seeking a source territory obtained one, and was calculated using equation 6.1.

The model began with 25 individuals in each age, sex, and habitat class. Models were run for 200 years to ensure they reached equilibrium values.

6.2.2 *Model parameters*

Fecundity was determined using the results from several studies that reported Mayfield estimates of Ovenbird nest survival and the average number of fledglings produced per successful nest in landscapes fragmented by agriculture relative to contiguous forest or landscapes fragmented by forestry (Table 6.1). Pooled data from all studies used in this estimate, indicated nest success was significantly lower in agricultural landscapes (0.24, 95% CI 0.16 to 0.36) than in forested landscapes (0.48, 95% CI 0.41 – 0.56: $\chi^2 = 9.7$, $P = 0.002$). Fecundity (β) was defined as the mean number of young produced per adult female per year and was calculated as:

$$\beta = (Y * \phi_N) + (Y * \phi_N * (1 - \phi_N)) \qquad (6.10)$$

where Y was the mean number of fledglings produced per successful nest and ϕ_N was the probability a nest survived to fledge young. It was assumed female Ovenbirds fledged a maximum of one brood per year, equal numbers of males and females fledged from successful nests, females renested once if their first nesting attempt failed,

Table 6.1 - Mayfield estimates of Ovenbird nest survival in agricultural and forested landscapes across North America.

Study	Location	Nest survival	Exposure days	Young per successful nesting attempt	Fecundity per adult female per year
		Agricultural Landscapes			
This study	Saskatchewan	0.34	358	4.0	2.26
Brawn and Robinson 1996	Illinois	0.06	77	NA	NA
Donovan et al. 1995b	Missouri	0.27	118	3.2	1.5
Donovan et al. 1995b	Minnesota	0.20	304	3.3	1.19
Porneluzi and Faaborg 1999	Missouri	NA	NA	2.8	1.65
Total		**0.24** **(0.16 – 0.36)**	**857**	**3.3**	**1.39**
		Forested Landscapes			
This study	Saskatchewan	0.52	506	4.2	3.23
Donovan et al. 1995b	Missouri	0.38	365	4.3	2.64
Donovan et al. 1995b	Minnesota	0.42	597	4.0	2.7
Hanski et al. 1996	Minnesota	0.48	240	NA	NA
King et al. 1996	New Hampshire	0.45	1475	NA	NA
Porneluzi and Faaborg 1999	Missouri	NA	NA	4.2	2.1
Total		**0.48** **(0.41 – 0.56)**	**3183**	**4.18**	**3.05**

and nest success and clutch size were constant over the length of the season.

Survival of adult Ovenbirds in the baseline model was 0.62 (e.g. Donovan et al. 1995a). Accurate survival estimates for juveniles are not available for Ovenbirds, so half the average adult survival value (0.31) was used as the estimate of juvenile survival (Temple and Cary 1988, Donovan et al. 1995a).

To determine the sensitivity of the demographic parameters used in the model, a sensitivity analysis was done using average, low (-10%), and high (+10%) estimates for adult, juvenile and nest survival (Table 6.2). Although arbitrary, the high and low values employed were similar to the lower and upper limits of the 95% confidence intervals for these estimates. A two-factor ANOVA was used to test whether changing the survival probability of juveniles, adults, or nests from the low to the high survival estimate had different effects on the finite rate of change (λ) and whether these effects were similar between landscapes (forested versus fragmented). λ was estimated as:

$$\lambda = \phi_A + \phi_J\beta \qquad (6.11)$$

where ϕ_A was survival of adult females from one breeding season to the next, ϕ_J was survival of juvenile females from fledging to the following breeding season, and β was fecundity divided by 2.

6.3 Results

6.3.1 *Source-sink status*

In 85% of the possible combinations of adult survival, juvenile survival, and fecundity examined using parameters from agricultural landscapes, Ovenbird

Table 6.2 - Demographic parameters used in models.

	Low	Average	High
Adult survival	0.52	0.62	0.72
Juvenile Survival	0.21	0.31	0.41
Source Nest Success	0.38	0.48	0.58
Sink Nest Success	0.14	0.24	0.34

populations had a λ <1 (Fig. 6.2A). In contrast, 67% of the possible combinations of demographic information in forested landscapes resulted in λ >1 (Fig. 6.2B).

Sensitivity analyses indicated increasing adult and juvenile survival from low to high caused a larger change in λ (25% and 24%, respectively) than when nest survival was increased by the same amount (17%: $F_{2,54} = 22.0$, $P < 0.001$). There was no difference between source and sink in the percent change for λ when all survival estimates were increased from low to high ($F_{1,54} = 0.1$, $P = 0.75$). However, the interacting effect of treatment and landscape influenced the percent change of λ ($F_{2,54} = 43.1$, $P < 0.001$). In the source, increasing nest success from low to high caused the smallest change in λ (13% increase), while increasing juvenile survival from low to high caused a larger increase in λ than increasing adult survival (32% vs. 21, respectively). In the sink, increasing adult survival from low to high (28%) caused a larger change in λ than when nest success or juvenile survival were increased (21% vs. 18%, respectively).

6.3.2 *Density-dependent natal dispersal*

Since λ was consistently less than 1 using the parameters from agricultural landscapes, Ovenbird populations in this habitat should go extinct. However, Ovenbird populations have persisted in highly fragmented landscapes for decades, indicating they are rescued from extinction by immigration from other populations. Based on average demographic parameters, the density-dependent natal dispersal model resulted in a population of 343 individuals, with 27% existing in sink habitat (Fig. 6.3A). Of the 189 juveniles produced annually in the population, only 20% were produced in the sink

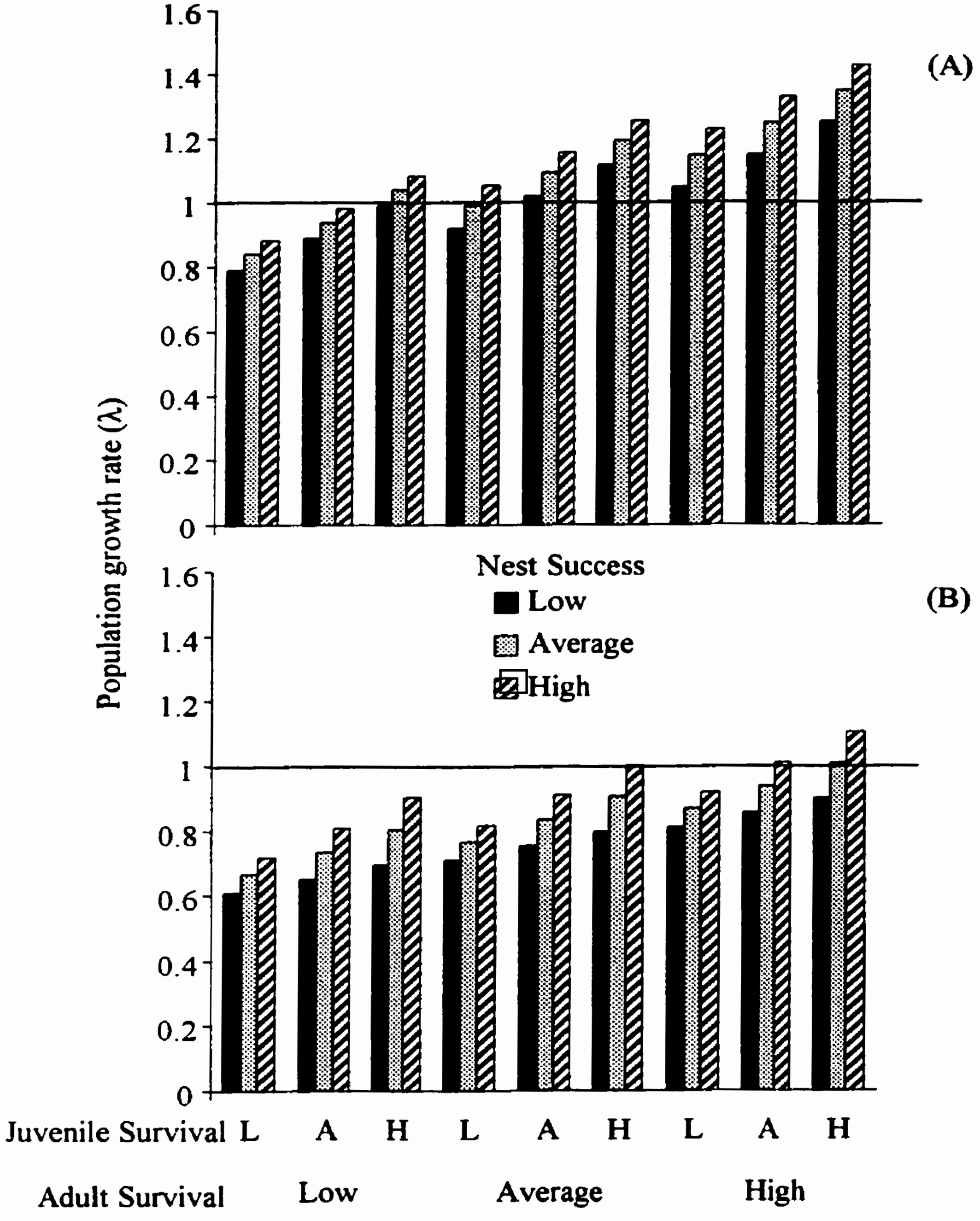

Figure 6.2 - Population growth rate in: A) forested landscapes and B) fragmented landscapes; over the observed range of adult, juvenile, and nest survival values.

(Fig. 6.3a). At average values of adult survival, territory density in the source was 5.4 per 10 ha.

At low (0.52) adult survival, Ovenbirds went extinct (Fig. 6.3B). The sink went extinct much faster (17 years) than the source (267 years). When adult survival was high (0.72), the population increased to 883 individuals, with 67% of the population in the sink and 58% of all juveniles fledged from the sink (Fig. 6.3C). Territory density at high adult survival was 7.0 per 10 ha in the source. The dramatic increase in population size at high adult survival resulted because it was assumed there was unlimited sink habitat and thus, no density dependence in the sink. Low juvenile survival caused extremely rapid population extinction in the sink (10 years) and the source (35 years). High (0.41) juvenile survival also resulted in a very large population, although the population was 14% smaller than that caused by high adult survival.

When nesting success in the source was low, the total population size was 150, but only 8% existed in the sink. Low source productivity caused little competition for territories in the source, so few juvenile Ovenbirds were forced to disperse (< 5%). When nesting success in the source was high, the population reached 457 individuals, which was 48% lower than the increase in population size caused by high adult survival. Reducing nest success in the sink by 10%, caused a 12% drop in population size from the baseline model. This decline was caused by a reduction in the number of juveniles produced in the sink, as the number of Ovenbirds in the source was the same as the baseline model. Increasing sink fecundity resulted in a 22% increase from the baseline model.

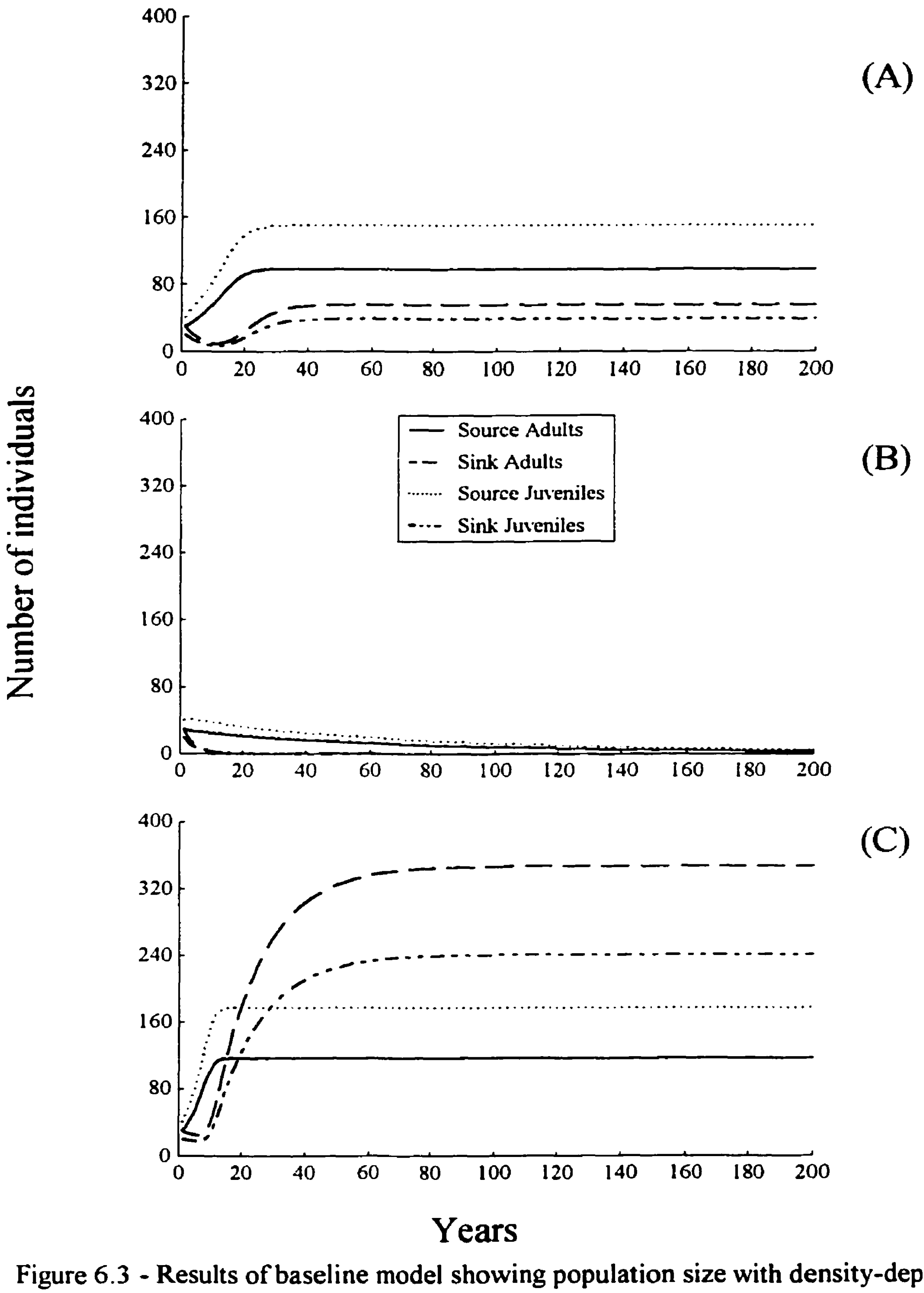

Figure 6.3 - Results of baseline model showing population size with density-dependent dispersal of juveniles from source habitat to sink habitat at: A) average adult survival (0.62); B) low adult survival (0.52); and C) high adult survival (0.72).

6.3.3 *Density-independent breeding dispersal*

Adult dispersal from the sink to the source had a positive effect on population size in the source and sink at average demographic parameters (Fig. 6.4A). Competition with juveniles fledged from the source, forced some adult dispersers to return to the sink (22 to 44%). However, with territory densities ranging from 5.6 and 7.1 territories per 10 ha, many dispersing adults obtained territories in the source. Increased numbers of adults in the source resulted in more juveniles being produced than in the baseline model (Fig. 6.4A). This had a spillover effect on the sink, as the larger number of juveniles produced in the source caused more individuals to disperse to the sink.

When adult survival was high, the opposite effect was observed for population size (Fig. 6.4B). As the adult straying probability (SR_A) increased, the number of individuals seeking territories in the source also increased. By increasing the density in the source, adult dispersers reduced the probability of obtaining a territory in the source so more individuals were forced back to the sink than obtained territories in the source. The decrease in population with size with adult dispersal occurred when the territory density approached 7.5 territories per 10 ha. This density was the point where more than 50% of the Ovenbirds seeking territories in the source had to disperse to the sink. Using high nest survival in the source and high juvenile survival parameters the same pattern was observed, although the straying probability where the population began to decrease in size were different (0.2 and 0.7, respectively).

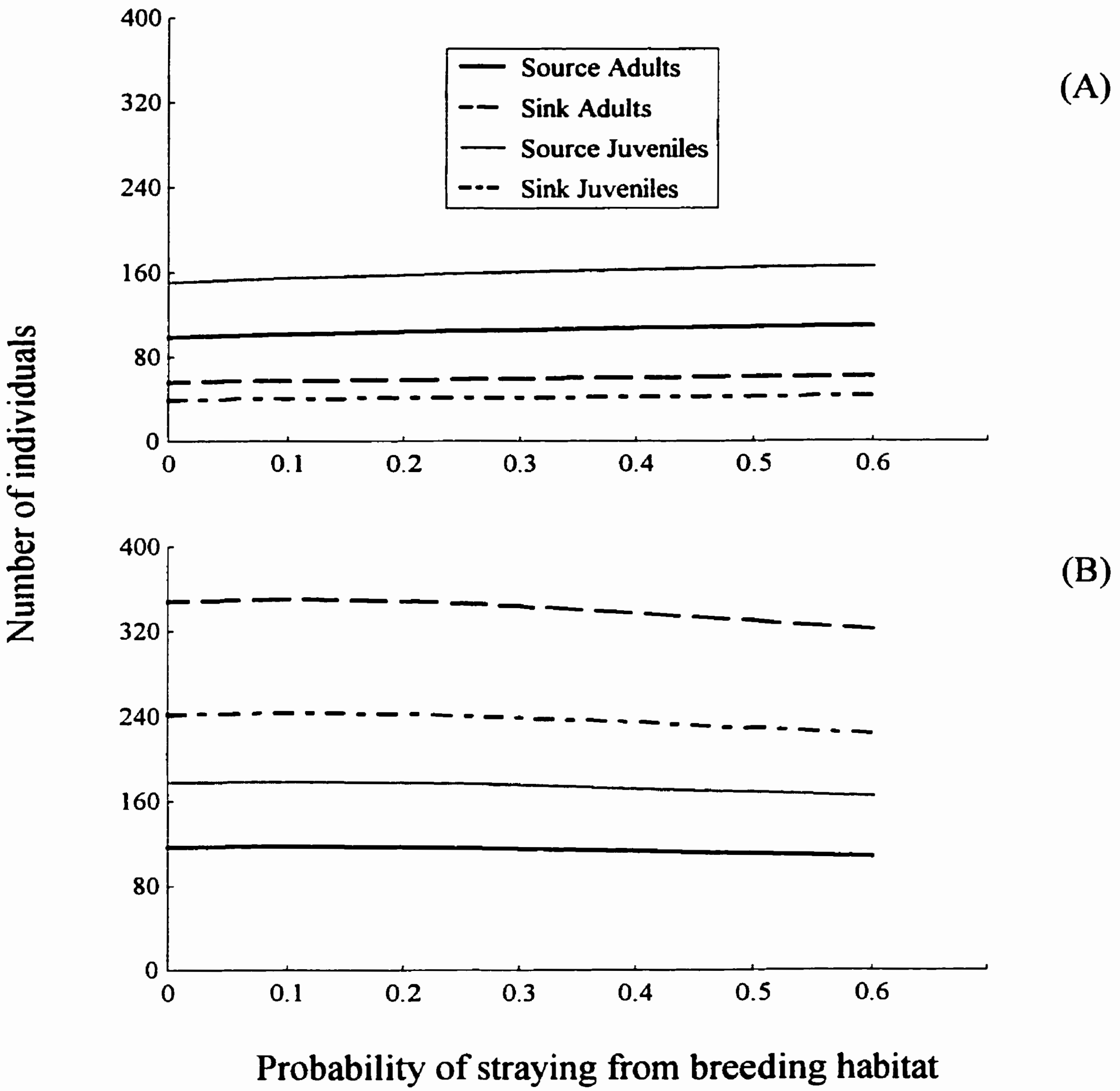

Figure 6.4 - Effects of density-independent dispersal from sink habitat to source habitat on population size at: A) average adult survival (0.62); B) high adult survival (0.72).

Adult dispersal from the sink to the source also affected the age structure of the population. In the baseline model with no adult dispersal, 38% of the adult population were SY Ovenbirds breeding for the first time and 62% were ASY Ovenbirds in at least their second breeding attempt. With increased adult dispersal, adults with territories in the source were less likely to be SY Ovenbirds (31% to 36%: Fig. 6.5). In contrast, SY adults made up a larger portion of adult population in the sink (50 to 61%: Fig. 6.5). Regardless of the demographic parameters used in the model, a larger proportion of ASY adults was in the source.

6.3.4 *Female-biased mortality*

To determine the effects of female-biased mortality on population size and structure, female survival was reduced 5 and 10% relative to male survival. Female biased mortality impacted population size and structure. When female Ovenbird survival was below 0.57, the population always went extinct. When the population persisted, lower female survival resulted in a smaller population at all levels of adult survival. When adult male survival was high, a 10% difference in female survival caused a 79% reduction in population size relative to the model where adult survival of both sexes was high (Fig. 6.6A). Effects of female biased mortality were felt most strongly in the sink, particularly at high levels of adult survival (Fig. 6.6A). When male survival was high (0.72), a 10% difference in female survival caused an 89% reduction in size of the population in the sink but only a 15% reduction in the source (Fig. 6.6A).

Greater male survival resulted in more males existing in the population and generated a biased sex ratio in the source and sink (Fig. 6.6B). The sex ratio was

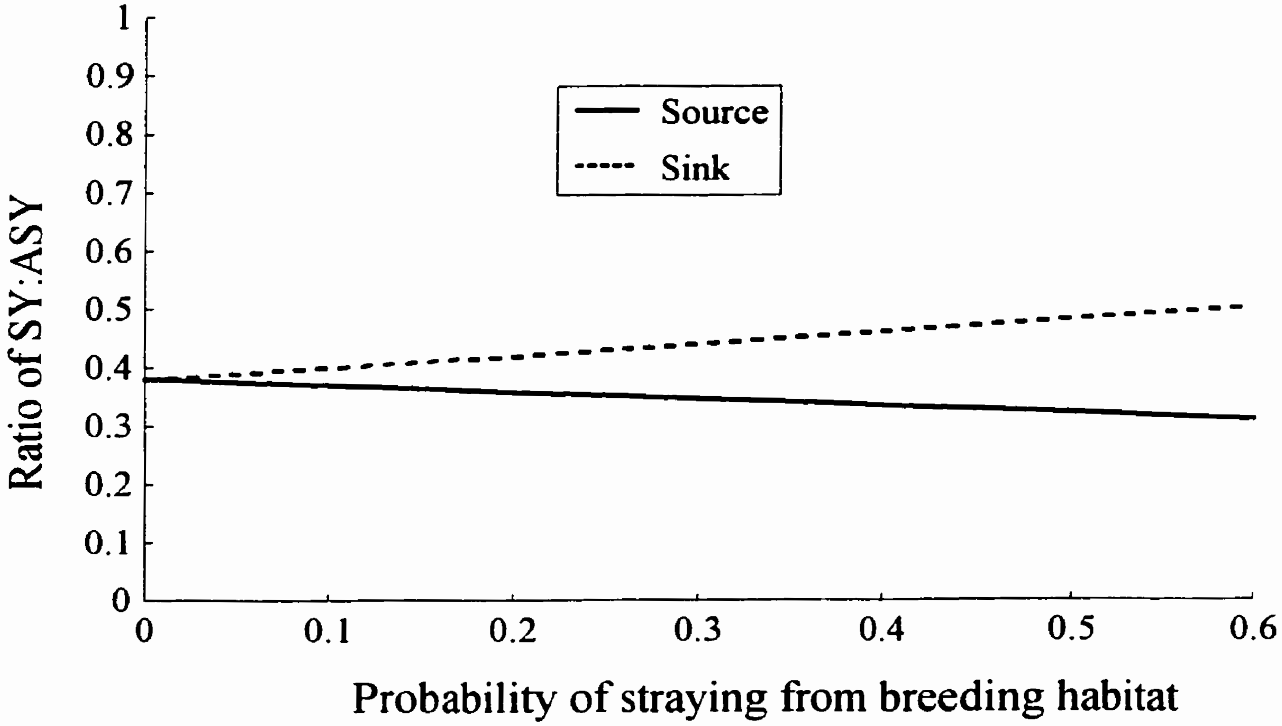

Figure 6.5 - Ratio of SY to ASY adults in source and sink habitat at various values of density-independent adult dispersal.

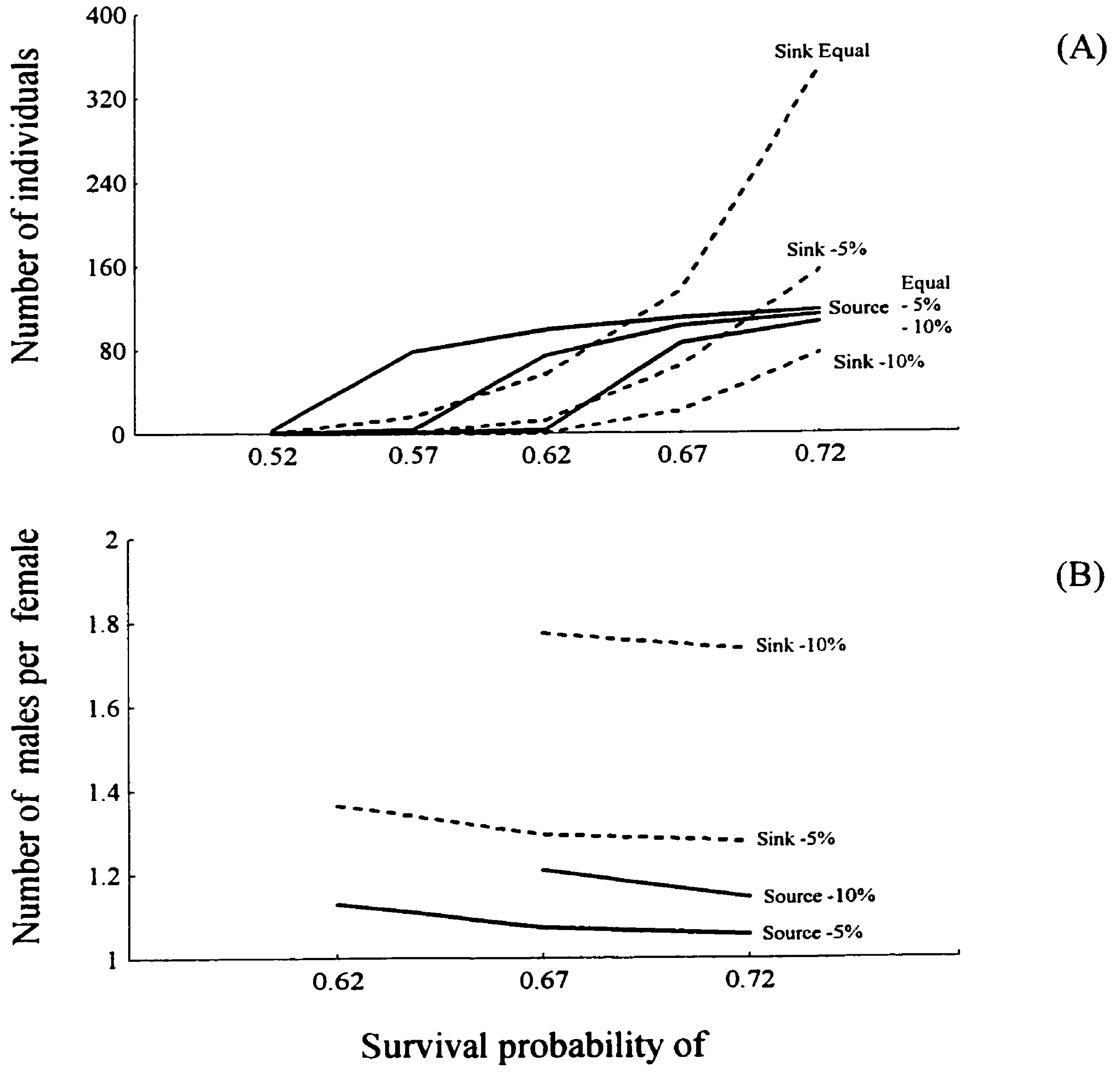

Figure 6.6 - Effects of reducing female survival by 5 and 10% relative to male survival on: A) population size; B) ratio of males to females in sources and sinks.

more strongly male biased in the sink than the source. When male survival was 0.62 and female survival 0.56, there were 113 males per 100 females in source habitat and 136 males per 100 females in sink habitat (Fig. 6.6B). Fewer juvenile females dispersing to the sink caused the greater ratio of males to females in sink habitats. By increasing adult survival, the sex ratio became slightly closer to 1:1 in the source and sink. However, the pattern of a more biased sex ratio between source and sink did not change by altering any of the other demographic parameters.

6.4 Discussion

6.4.1 *Density-dependent natal dispersal*

Using average demographic parameters from a number of studies, forest fragments in highly fragmented agricultural landscapes were population sinks, while larger sites in contiguous forest were population sources. The persistence of Ovenbird populations in highly fragmented areas suggests population processes in sink habitats may be linked to those occurring in the source. Density-dependent dispersal by juveniles from sources to sinks may be one way Ovenbird populations in fragmented areas are rescued from extinction. At average demographic parameters, Ovenbirds in the forested landscape produced enough young to rescue populations in fragments from local extinction and, in some cases, maintained relatively large populations in the suboptimal habitat. In contrast, when demographic parameters were low, most simulations indicated populations declined or went extinct. Importantly, the initial declines of Ovenbird populations in the source-sink system were more rapid in the sink. Programs designed to monitor forest songbird trends should recognize population changes in population size in a given area may be strongly influenced by demographic processes occurring in other locations.

Trend monitoring and habitat suitability indices often use population density as an indicator of habitat quality (Vickery et al. 1992). Lower population density often indicates lower habitat suitability (Petit and Petit 1996). By extension, it has been argued high density will result in greater productivity (Vickery et al. 1992). However, the number of birds within a habitat may be a poor indicator of the quality of that habitat for breeding (Van Horne 1983, Vickery et al. 1992). When Ovenbird survival and fecundity were high, the majority of Ovenbirds in the baseline model existed in the sink and the majority of juveniles produced came from the sink, even though λ in this habitat was less than one. Clearly, evaluating the quality of breeding habitat requires more than simple estimates of abundance.

Habitat fragmentation is detrimental for species with limited dispersal capabilities (Gilpin 1987). In such species, forest fragmentation may lead to a decrease in population size that can increase the chance of extinction because of environmental stochasticity. Birds are assumed to be less affected by habitat fragmentation because movements of individuals between source and sink can rescue subpopulations from local extinction and thus compensate for stochastic effects (Brown and Kodric-Brown 1977). Results of my models support this notion, as Ovenbird populations in forest fragments were maintained when source fecundity and/or adult survival were high enough to force individuals to disperse from the source to the sink. However, dispersal can come at a cost to the overall population. Donovan et al. (1995a) found when juvenile dispersal was not regulated by density-dependent processes, sink populations drained breeding individuals from the source and caused an overall decline in the population.

6.4.2 *Density-independent breeding dispersal*

Dispersal in source-sink models is often modeled as a unidirectional process whereby birds move from source to sinks but not vice versa. However, adult Ovenbirds that do not raise young often disperse from previous breeding sites, presumably in an effort to find a more suitable territory where the probability of success is greater (Roth and Johnson 1993, Murphy 1996, Haas 1998). Dispersal of adults from sink to source had a positive effect on the population. With adult Ovenbirds dispersing from sink to source, the number of juveniles produced by the source increased. The greater number of juveniles produced by the source created a spillover effect into the sink, as a larger number of excess juveniles from the source were forced to disperse to the sink. Dispersal of adults from the sink to the source also resulted in a different age structure, with a greater proportion of SY Ovenbirds existing in the sink than in the source. In this model, it was assumed SY Ovenbirds have the same reproductive success as ASY Ovenbirds. However, if inexperienced breeders have a lower probability of raising a brood, then productivity in the sink would be weakened by adult dispersal while productivity in the source would increase. With a greater proportion of ASY adults in the source, relatively more juveniles would be produced than if the age structure were the same in the source and sink.

6.4.3 *Female-biased mortality*

Many Ovenbird populations in North America appear to have a male-biased sex ratio (Gibbs and Faaborg 1990, Porneluzi et al. 1993, Villard et al. 1993, Van Horn et al.

1995, Burke and Nol 1998), suggesting female survival is lower than male survival. In addition, the male biased sex ratio tends to be more pronounced in forest fragments than in contiguous forest, implying habitat specific differences in survival of males and females (Gibbs and Faaborg, 1990). In a review of 5 studies examining sex ratios of Ovenbird in forest fragments and contiguous forest (Chapter 3), the average number of males per female was greater in forest fragments than in contiguous forest (1.37 and 1.18 males, respectively). For differences in survival between fragmented and contiguous forest to be the only cause of such a difference would require female survival to be at least 20% lower than male survival. Although female survival is poorly known, this large a difference seems unlikely (Greenwood and Harvey 1982, Holmes and Sherry 1992). Differences in sex ratios between forest fragments and contiguous forest are undoubtedly the result of female-biased mortality. However, female survival does not have to be lower in forest fragments than in contiguous forest for the sex ratio to be more biased towards males in forest fragments. In the female biased mortality model, a 5% difference in survival between the sexes caused a sex ratio of 1.36 males per female in the sink and 1.13 males per female in the source. The lower abundance of females meant more females seeking territories in the source obtained them resulting in fewer females dispersing to the sink. Thus, differences in sex ratios between forest fragments and contiguous forest may have little to do with survival differences going on at the patch level. Instead, as the model shows, biased sex ratios in forest fragments may have more to do with population-wide differences in female and male survival and the subsequent effects on female habitat selection.

6.4.4 *Summary*

Population dynamics of forest songbirds like the Ovenbird may be regulated at large scales by source-sink dynamics, particularly in highly fragmented landscapes. Unfortunately, most management practices continue to focus on local-scale demography and ignore the interaction between source and sink habitats at the landscape level. Given the importance of dispersal on population size, persistence, and structure, effective conservation strategies will require information at spatial scales large enough to encompass various subpopulations existing in different landscapes varying in their suitability for reproduction (Donovan et al. 1995a , Villard et al. 1995). The sensitivity of these models to the survival estimates used suggests further work examining the effects of forest fragmentation on forest songbird demography is required.

CHAPTER 7 . SYNTHESIS

7.1 Forest fragmentation and ideal preemptive habitat selection

Small forest fragments in the agricultural landscape were suboptimal habitat for Ovenbirds. Ovenbirds in small farm fragments had larger territories, reduced pairing success, lower nesting success, greater dispersal, a larger proportion of first time breeders, and lower densities than in contiguous forest. Together, these results support the hypothesis that habitat selection by Ovenbirds at a landscape scale occurs in an ideal preemptive manner (Holmes et al. 1996, Petit and Petit 1996).

Ovenbirds were less abundant in farm fragments than in contiguous forest. The lower density of Ovenbirds in small farm fragments may have occurred because Ovenbirds required larger territories in these habitats to acquire sufficient food resources (Smith and Shugart 1987). Alternatively, Ovenbirds may have recognized the lower suitability of fragmented habitat and avoided small farm fragments because of lower reproductive success in this habitat. Consequently, Ovenbirds in farm fragments may have had larger territories than Ovenbirds in contiguous forest simply because more space was available because the density of conspecifics was lower. Regardless of the mechanism, the lower density and larger territory size of Ovenbirds in farm fragments suggests this habitat was suboptimal (Petit and Petit 1996).

The presence of floaters indicated territorial behaviour may have limited the number of individuals that bred, supporting the ideal preemptive hypothesis (Fretwell and Lucas 1970, Petit and Petit 1996, Newton 1992). However, existence of unpaired territorial males also suggests some individuals chose to be floaters (Smith 1978, Smith and Arcese 1989), rather than accept the costs of establishing a territory in marginal habitat. More floaters were observed in contiguous forest than in farm fragments, suggesting the benefits of floating may be landscape-specific. Floaters likely were more common in contiguous forest because the reward of obtaining a territory in this habitat was greater than in farm fragments. Moving through a fragmented agricultural landscape may also have increased predation risk, making floating a less appropriate strategy in this landscape.

Ovenbird populations in the boreal forest seem to have a source-sink structure. Low fecundity in small farm fragments was insufficient to compensate for adult mortality and emigration, creating a demographic sink. The factor that ultimately caused small farm fragments to be demographic sinks was low nesting success, although this was amplified by the interaction between breeding dispersal and individual reproductive success. Ovenbird abundance was relatively constant in all landscapes over the duration of the study suggesting Ovenbird populations in small farm fragments in the boreal forest were rescued from local extinction by immigration. Density, survival, and fecundity were such that more juveniles were produced in contiguous forest than likely could establish territories. The rescue effect in small farm fragments may have resulted from older Ovenbirds forcing younger Ovenbirds to disperse from contiguous forest into small farm fragments (Donovan et al. 1995b, Holmes et al. 1996, Petit and Petit 1996, Hunt 1996).

Although older birds are often dominant over younger birds (Enoksson 1988, Piper and Wiley 1989), the mechanism by which older birds outcompete younger birds is unclear. In migratory species, older birds often arrive on the breeding grounds earlier than younger birds, and settle in preferred habitats first (Holmes et al. 1996, Lemon et al. 1996, Marra et al. 1999). When young birds arrive, prime sites may no longer be available, passively forcing them to settle in lower quality habitats. However, in resident species that maintain year-round territories, younger birds are also found in less preferred areas (Krebs 1971). Variation in habitat selection between different-aged birds likely reflects differences in arrival times, and to some extent active exclusion of young birds from prime breeding locations by dominant older birds.

Young Ovenbirds with no prior breeding experience may not have recognized forest fragments as less suitable than contiguous forest (Pulliam 1996). Although farm fragments were smaller, more isolated, and had more edge habitat than forest stands in contiguous forest, the vegetation structure was similar among landscapes. On the basis of vegetation structure, farm fragments may have looked suitable to naïve Ovenbirds, but could have acted as "ecological traps" because of the greater number of predators in the surrounding agricultural landscape (Pulliam 1996). In contrast, older Ovenbirds seemed to avoid small farm fragments, as almost all Ovenbirds recruited into this habitat were first time breeders. In addition, Ovenbird males that previously bred in small farm fragments were less likely to return to these sites than males in contiguous forest. Together, these results suggest older Ovenbirds "learned" to avoid small forest fragments in the agricultural landscape and they dispersed to more suitable habitats in subsequent years (e.g. Switzer 1993).

When birds disperse and the timing of habitat selection in migratory birds remains unclear. Most models of habitat selection assume habitat and sites are selected more or less continuous with territorial establishment in the spring (Hildén 1965, Wiens 1969).

However, for many migratory species, arrival on the northern breeding grounds occurs well before environmental features essential for survival and reproduction (i.e. leaf out) are available as cues for habitat selection (Hildén 1965). Alternatively, birds may select habitats and sites in late summer/early fall before winter migration (Brewer and Harrison 1974, Adams and Brewer 1981). In this study, male Ovenbirds that failed to raise young moved more widely in late summer than successful breeders, suggesting they were searching for alternative breeding habitats for use in future years.

Most of the patterns observed in this study relied on observations of male Ovenbirds. Whether similar dispersal patterns and the subsequent effects on age structure exist for female Ovenbirds is unknown. In many passerine species, return rates of females are lower than for males (Holmes and Sherry 1992, Marra et al. 1999). Lower site fidelity of females may reflect increased dispersal to find the most suitable territory (Greenwood and Harvey 1982, Holmes and Sherry 1992). However, females were less abundant than males in all landscapes studied, also suggesting differential survival of the sexes. Lower female survival across all habitats may cause less competition among females for territories in contiguous forest. That the sex ratio of Ovenbirds was more male-biased in farm fragments supports this idea, and provides further support for the hypothesis that the ideal preemptive model is applicable at the landscape scale.

7.2 Why are harvested and agricultural landscapes different?

The southern boreal forest of central Canada is crucial habitat for Ovenbirds. The extent of this biome, the high density of Ovenbirds, and their relatively high productivity in this part of the breeding range, suggest a large part of the continental Ovenbird population is produced in this region (Maurer and Heywood 1993, Villard and Maurer 1996). As in most areas of North America, fragmentation by agriculture reduced survival of Ovenbird nests in the boreal forest. Lower reproductive success in fragmented landscapes was likely caused by an increase in the abundance of generalist predators (reviewed in Andrén 1995). Previous studies conducted in the boreal forest demonstrate an increase in abundance and a change in species composition of the corvid community (Bayne and Hobson 1997). Photographs taken at artificial nests also suggest more species of generalist mammalian predators occur at edges of small farm fragments than in contiguous forest (Bayne and Hobson 1997). The red squirrel (*Tamiasciurus hudsonicus*), a major nest predator, was also more abundant in farm fragments than contiguous forest (Bayne and Hobson 1998, Bayne and Hobson 2000), likely due to a "meso-predator" release (Crooks and Soulé 1999). Changes in predator communities associated with agriculture seem to be the major factor reducing habitat quality for forest songbirds in fragmented landscapes in the boreal forest.

Fragmentation by forestry had less impact on Ovenbirds than fragmentation by agriculture. Unlike land clearing in agricultural landscapes, clearcutting creates landscape mosaics that to some extent mimic natural disturbance (Hunter 1996). Harvested landscapes often have larger tracts of mature forest patches than agricultural landscapes. More importantly, gaps created by forestry are usually temporary, and therefore may have less effect on avian communities and nest predators in the long term. Similarly, harvested landscapes retain a forested matrix that prevents the invasion of generalist predators that are adapted to human-dominated landscapes (Andrén 1995). However, this situation may be relevant primarily to the boreal forest, where there is a high degree of natural fragmentation due to fire. In systems where stand-replacing disturbances are less frequent, fragmentation by forestry may have impacts that are more significant. Furthermore, the harvested landscape examined in this study is in the first phase of a two-pass clearcut system. As harvesting continues and fragmentation increases, this landscape may become less suitable for forest songbirds. Loss of specific seral stages in harvested landscapes is of considerable concern. Many bird species in the boreal forest use old mixedwood stands exclusively, and these habitats are predicted to decline in landscapes managed for harvesting (Schieck et al. 1995, Hobson and Bayne 2000a,b).

7.3 Recommendations for future research

Ovenbirds seemed to select habitats in an ideal preemptive manner at the landscape scale. However, determining how preemption occurs requires more information. In particular, settlement patterns in spring need to be examined to determine if Ovenbirds settle earlier in contiguous forest than in small farm fragments (Holmes et al. 1996, Petit and Petit 1996, Huhta et al. 1998). Similarly, more information is required on arrival times of different age classes in different habitats.

Habitat quality was assessed at a landscape scale in this thesis. However, spatial variation in habitat suitability exists at many scales. It is widely assumed that long-distance migrants like Ovenbirds avoid edges of forest fragments (Villard 1998). However, edge-avoidance may not be the case in all regions. Critical evaluations of edge avoidance/preference at small spatial scales are required (e.g. Ortega and Capen 1999). The use of radio-telemetry may be a particularly useful way of assessing habitat use by songbirds at microhabitat scales. More information on factors regulating territory size at the microhabitat level, particularly as it pertains to food abundance, is needed.

Information is also required on the difference in demographic parameters caused by variation in vegetation suitability. Ovenbirds use a variety of stand types in the boreal forest. Potentially, smaller scale source-sink dynamics occur among different forest types within the same landscape. Evaluating source-sink processes could be particularly important in harvested landscapes, where forestry practices are changing the availability of certain stand types and seral stages. In particular, information is required on whether Ovenbirds use young forests that have regenerated after harvesting.

As the literature review in this thesis demonstrates, the effects of forest fragmentation on Ovenbird demography are often different among regions. Possibly, areas where Ovenbird density is low are being rescued by emigration from more productive regions like the boreal forest (Graves 1997). The use of stable-isotope and genetic markers may be helpful in determining whether young birds recruited into a region are showing natal fidelity to that region, or whether dispersal is occurring at regional scales (Hobson and Wassenaar 1997).

Replication of the removal experiments in other areas of the Ovenbirds range would validate whether unpaired males use different strategies in different landscapes. Removing just males, just females, and both males and females from territories would help determine if the existence of floaters is due to limited space, or if the number of females in the population regulates the ratio of territorial to floater males (Marra et al. 1997). It is also unclear whether floaters in boreal forest landscapes are Ovenbirds that held territories and dispersed because of breeding failure or whether they are Ovenbirds that never obtained a territory.

The presence of unpaired males in all landscapes suggests female survival of Ovenbirds is lower than for males. Although differences in male and female survival are predicted for many passerines, little evidence exists to support this claim (Greenwood and Harvey 1982). Future studies examining the effects of forest fragmentation on Ovenbirds should make an effort to gather information on female habitat use and survival. If females experience lower survival in fragmented landscapes than in contiguous forest, estimates of population growth rate may be overestimated.

Although adult survival may be influenced by fragmentation, forest fragmentation seems to have a greater effect on dispersal. However, the scale at which dispersal occurs remains unclear. Use of radio-telemetry is one way of assessing dispersal range of Ovenbirds. With longer transmitter life and better retention methods, it may be possible to track birds to multiple post-breeding sites. By revisiting areas of post-breeding activity the following spring, observers should be able to record movements of adult Ovenbirds between subsequent breeding sites. To effectively document the factors influencing post-breeding movements by Ovenbirds, future research should attempt to determine breeding status before transmitters are attached.

Over the duration of this study, Ovenbird density was relatively constant, and seemed to be at a maximum in contiguous forest. However, Ovenbird numbers likely fluctuate over time. Assuming the ideal preemptive model regulates population dynamics, temporal fluctuations in abundance should be more pronounced in farm fragments than in contiguous forest (Donovan et al. 1995b, Holmes et al. 1996, Chapter 6). Long-term monitoring programs designed to record trends in avian abundance, should examine multiple habitats over the same time period, as declines are likely to occur in suboptimal habitat first.

7.4 Summary

Forest fragmentation by agriculture had deleterious effects on Ovenbirds in the boreal forest. Increased nest predation in small farm fragments relative to other landscapes, created a source-sink population structure. In response to a high probability of predation, male Ovenbirds dispersed from small farm fragments, presumably to find a more suitable territory. Preemptive behaviour by older males in contiguous forest may have excluded young Ovenbirds from obtaining territories in this habitat. Consequently, young Ovenbirds may have been forced to breed in small farm fragments. Whether first-time breeders recognized small farm fragments as suboptimal habitat is unclear, but experienced breeders definitely avoided small fragments. More unpaired males in small farm fragments suggests females preferentially selected territories in contiguous forest. However, unpaired males also existed in contiguous forest, but were more likely to adopt a floater strategy in this habitat. Although dispersal patterns of Ovenbirds remain unclear, failed breeders moved more widely during the post-fledging period, possibly in an effort to find suitable breeding sites for use in subsequent years.

The information collected in this thesis corroborates the myriad of studies that argue conservation efforts designed to manage habitat for forest songbirds should focus on preserving large forest tracts of suitable habitat rather than groups of smaller fragments. However, small fragments should not be ignored in management plans. Small farm fragments in the boreal forest have relatively high densities of Ovenbirds compared to other regions. Even if a small portion of the individuals in farm fragments raise young, the vast size of this landscape may provide a substantial component of the overall population at a regional level. In addition, these small fragments may provide a refuge for younger or less competitive individuals and serve as buffer that stabilizes populations in contiguous forest during poor years (Davis and Howe 1991, Holmes et al. 1996).

The dramatic changes in boreal forest landscapes caused by agriculture and the resulting changes in biodiversity are alarming. Changes in land-use policy that limit the rapid growth of agriculture in this region are required. Given the history of agriculture in the boreal forest, such changes will be hard to implement. Integration of current landowners into the planning phase of conservation strategies for the boreal region is necessary if any management plan is to succeed.

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