

Golden-winged Warbler (*Vermivora chrysoptera*) habitat selection, mating behaviour, and  
population viability in a fragmented landscape at the northern range limit

by

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**Dedication**

This thesis is dedicated to my grandfather (Dr. William Glenn Stokes), who passed away during the second year of my research and who always encouraged me to pursue a PhD.

## Abstract

The Golden-winged Warbler (*Vermivora chrysoptera*) is an early-successional specialist and one of the fastest declining songbird species in North America. This decline is related in part to habitat loss and degradation of contemporary forests; however, the consequences of anthropogenic disturbance on the species need further evaluation. Thus, I assessed occupancy, population growth, mating behaviors, and hybrid habitat use by Golden-winged Warblers across a range of disturbance levels within southeast Manitoba, Canada. Golden-winged Warblers consistently responded most strongly to disturbance at the 1-km scale. Forest patches with greater agricultural matrix cover at a 1-km scale were less likely to be occupied by Golden-winged Warblers. However, warblers did select for early-successional habitat created via resource extraction and other anthropogenic disturbances at this scale. Despite higher densities, productivity declined in landscapes with greater edge density because of Brown-headed Cowbird (*Molothrus ater*) brood parasitism. Additionally, pairing success was reduced in patches with lower forest cover at a 1-km scale, although extra-pair paternity rates were not impacted by patch or landscape characteristics. These results suggest that proximate habitat cues used to select nesting sites may be decoupled from realized fitness in this system. Of the sub-populations I monitored, all showed negative population growth suggesting that anthropogenically disturbed forests may act as ecological traps for Golden-winged Warblers. The most productive habitat for Golden-winged Warbler will have high forest cover and minimal anthropogenic edges. Hybridization with Blue-winged Warblers (*Vermivora cyanoptera*) has also been suggested as a reason for population declines range-wide and I found that hybridization is now occurring in low levels in the Manitoba population. I found no difference in the habitat used by Golden-winged Warblers compared with hybrids at either a territory or landscape scale. The low proportion of

hybrids found in Manitoba and the lack of a distinguishable difference in habitat use by Golden-winged Warblers and hybrids indicates that management efforts to encourage habitat use by Golden-winged Warblers while discouraging habitat use by Blue-winged Warbler are unlikely to be a successful conservation strategy. Instead, management efforts should focus on maintaining or creating early-successional habitats with minimal anthropogenic edges.

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## **Chapter 1: Introduction**

### **Habitat selection**

As ecologists, one of the primary questions we attempt to answer is whether habitats have the capacity to support viable populations of species. Habitat varies in quality, affecting the individual fitness of animals (Fretwell and Lucas 1970, Pulliam 2000) and exerting strong selection pressure for habitat selection (Wiens 1976, Rosenzweig 1981, Cody 1985). By definition, habitat quality is the suite of resources and environmental conditions that determine the presence, survival, and reproduction of an individual or population (Hall et al. 1997). Both low- and high-quality habitats may be occupied by species throughout their range and the distribution of individuals relative to habitat quality can determine population persistence. As habitats worldwide become converted or modified by humans, low-quality habitats have become a more dominant component of the landscape for some species (Vitousek et al. 1997). Migratory birds are particularly vulnerable to landscape change because they require a broad range of habitats across multiple landscapes throughout their life cycle. Understanding how habitat selection decisions impact individual fitness and ultimately, population persistence, can help ecologists determine what habitat components are important for predicting species presence and population viability.

Habitat can be defined as the unique set of physical environmental factors used by a species for survival and/or reproduction (Block and Brennan 1993). Habitat selection is a hierarchical process in space and time (Johnson 1980) that will result in the disproportionate use of some habitats over others (Hutto 1985). The four nested scales include the overall geographic range of the species, the home range/territory within the geographic range, the habitat components used within the territory such as a nesting site, and the specific foraging locations

within those habitat components. The habitat occupied by a particular species can range from low to high quality, resulting in consequences or benefits to survival and productivity of an individual depending upon the particular grade of habitat being occupied. A high-quality habitat is one that increases an individual's fitness or contribution to future generations (Fretwell and Lucas 1970, Van Horne 1983). Therefore, birds have evolved to select habitat in a way that maximizes their fitness and the choices made are the result of natural selection (Hildén 1965).

The ultimate factors that influence avian survival and reproduction include food availability and protection from predation or weather (Hildén 1965, Zanette et al. 2000, Nagy and Holmes 2005). There are also structural and functional requirements unique to each species and based on body structure and innate activities (Hildén 1965), for example the need for a place that males can display to females to attract a mate. These ultimate factors are related to a series of proximate factors with which birds are associated. The proximate factors can be classified as: 1) landscape, 2) terrain, 3) nest-, song-, and feeding sites, and 4) other animals (Hildén 1965). While not all of these elements need to be present to trigger a settling response, some of the elements must combine and reach a certain threshold to elicit an individual to settle. There may even be one primary stimulus that outweighs the others and whose presence will elicit an individual to settle even in a suboptimal habitat (Hildén 1965).

Studies of bird-habitat relationships have formerly been limited by the relatively small spatial scales at which they have traditionally been studied (Cody 1985, Wiens et al. 1986). However, the development of the field of landscape ecology and the simultaneous application of hierarchy theory to ecological systems has changed the way ecologists are able to study and perceive the operation of ecological processes.

### **Habitat selection as a hierarchical process**

Hierarchy theory provides a framework to understand complex ecological systems that operate across multiple scales (O'Neill et al. 1986). According to the theory, the components of a system are organized into levels of functional scale, each level having a triadic structure (O'Neill 1989, Bissonette 1997, King 1997). First, the focal level of observation interest is chosen (L). The next higher level in the hierarchy (L+1) constrains the components and processes of the focal level. The lower level component(s) (L-1) may provide mechanistic explanations for patterns at the focal level. The levels of the hierarchy can be applied to both temporal and spatial scales, with higher levels taking place over longer periods of time or over larger areas than lower levels. In this way, hierarchy theory can be used to simplify complex interactions within a system and help to understand the various processes impacting a specific focal level. To fully understand a system, there must be an examination of the processes that occur at larger spatial (or temporal) scales. Hierarchy theory provides a useful framework for simplifying, organizing, and understanding the process of habitat selection.

It is well accepted that birds select territories at multiple spatial scales in a hierarchical process. Initially, they key in on patterns at large spatial scales and then continue to make decisions at progressively smaller scales (Hildén 1965, Johnson 1980). The decisions made at larger spatial scales constrain the decisions that can be made at smaller spatial scales (Hutto 1985). As ecology develops as a discipline, it has become increasingly apparent that ecological processes (dispersal, migration, reproductive success, foraging, etc.) occur at different scales (Addicott *et al.* 1987, Fahrig 1998); therefore, the disruption of these processes is also scale-dependent.

### **Habitat selection within a landscape ecology paradigm**



Traditionally, ecologists focused on examining ecological processes at local spatial scales partly because that was what was logistically possible for field studies (O'Neill et al. 1986, Wiens et al. 1986, Wiens 1989). However, technological advances such as GIS have afforded the ability to examine ecological processes at much broader spatial scales. Ecologists have come to recognize that ecological processes need to be examined at a scale relevant to both the organism and process being studied (Wiens 1989, Forman 1995, Saab 1999). As a result, the field of landscape ecology was developed to provide a way to examine the effects of spatial and temporal scales in ecological systems (Forman and Godron 1986). A landscape can be defined as a spatially heterogeneous area composed of habitat patches where individuals live and disperse (Turner 1989, Dunning et al. 1992). The type and amount of different habitat patches present in the landscape are known as landscape composition while the spatial positions of each habitat patch in relation to each other define the landscape configuration (Forman 1995). Landscape ecology is the study of how landscape composition and configuration affect ecological patterns and processes (Forman and Godron 1986, Turner 1989).

Landscape ecology provides a useful framework for exploring habitat selection in birds because of their mobility and ability to assess habitat patterns at multiple spatial scales before selecting a place to breed, forage, or winter (Hildén 1965). Examining only local habitat variables may not be adequate to understand bird distribution, abundance, or population dynamics. Birds can be associated with vegetation structure at relatively fine scales (MacArthur and MacArthur 1961, Wiens and Rotenberry 1981, Klaus and Buehler 2001, Confer et al. 2003), but habitat preference and population dynamics can also be associated with broad landscape patterns (Pearson 1993, Driscoll et al. 2005, Thogmartin 2010). Landscape patterns may also serve as proximate cues that birds respond to when selecting habitats. The proximate cues of

landscape pattern are generally expected to represent ultimate factors such as food or nesting site availability, risk of brood parasitism or predation, or avoidance of intra- or inter-specific competition.

Much emphasis has been placed on distinguishing the difference between habitat loss and habitat fragmentation (Fahrig 2003, Collinge 2009) because the two can have independent effects on individual fitness and population persistence and thus, biodiversity. In the natural world, habitat loss almost always occurs as a consequence of habitat fragmentation, resulting in collinearity between the two that can be difficult to tease apart and often this correlation is simply ignored. This problem was brought to the forefront in the 1990s when two key papers addressed the importance of examining the effects of habitat loss and habitat fragmentation independently (Andr  n 1994, Fahrig 1997). The purpose of distinguishing between the two is to determine the relative importance of habitat amount versus habitat configuration, as well as the degree of independence between the multiple causal factors that may be affecting a population (Fahrig 1997, Fahrig 2003). Although the concept of habitat fragmentation as an independent process is now widely accepted in landscape ecology, both empirical studies (Fahrig 2003) and statistical methods (Koper *et al.* 2007, Smith *et al.* 2009) often remain unable to disentangle the collinearity.

A primary focus of landscape ecology research has been on whether habitat amount or configuration matters more for species persistence. Habitat amount has overwhelmingly been found to be the most important determinant of demographic parameters for most populations inhabiting patchy landscapes (Donovan *et al.* 1995, Robinson *et al.* 1995, Tewksbury *et al.* 1998, Debinski and Holt 2000, Fahrig 2001). Fahrig (1997, 1998) found that the effects of habitat amount outweigh the effects of habitat configuration and that habitat placement can rarely

mitigate extinction risks induced by habitat loss. Flather and Bevers (2002) demonstrated that, over a broad range of habitat amounts and arrangements, population size was largely determined by habitat amount. However, habitat configuration became important in landscapes with low amounts of habitat because species persistence became uncertain due to dispersal mortality. These findings have important conservation implications because they suggest that habitat fragmentation may not show negative impacts on populations until reaching a critical threshold of habitat loss. As such, species persistence depends on both habitat amount and configuration.

While habitat loss consistently results in negative impacts to nearly all organisms studied (Fahrig 2003, Ewers and Didham 2006), habitat fragmentation can have positive, negative, or neutral effects (McGarigal and McComb 1995, Fahrig 2003, Smith *et al.* 2011). Negative effects of habitat fragmentation can be due to edge effects (Gates and Gysel 1978, Chalfoun *et al.* 2002, Fletcher *et al.* 2007), reduced connectivity among patches (Dale 2001, Frankham *et al.* 2002), or changes in the spatial distribution of resources (Saunders *et al.* 1991, Andr  n 1994). Positive effects of fragmentation can be due to increased landscape complementarity (Law and Dickman 1998, Ethier and Fahrig 2011), increased number of patches resulting in a buffer against the occurrence of a stochastic event (den Boer 1981), or decreased interpatch distance (Fahrig 2003). Consequently, fragmentation could have both positive and negative effects on a single individual or population.

Habitat configuration such as forest edge density and isolation could serve as proximate cues for birds during the habitat selection process. The quality of forest habitat is often degraded in forest fragments compared to intact habitats of the same size, primarily due to edge effects (Temple and Cary 1988, Fahrig and Merriam 1994, Friesen *et al.* 1995). Many studies show increased nest predation and nest parasitism rates with increasing proximity to edges (Gates and

Gysel 1978, Andren and Angelstam 1988, Yahner 1988, Chalfoun et al. 2002) because of the changes in predator species assemblages and increases in density of predators near edges (Bayne and Hobson 1997). Food availability may also decline in edge habitats (Zanette et al. 2000). Thus, for many bird species, it is likely that forest edge serves as a proximate cue for the ultimate factors of predation and parasitism risk, food availability, and potential nest sites. The magnitude of these effects has been found to vary in relation to distance from an edge. They can also vary among species, habitat types, and geographic areas (Paton 1994, Andr  n 1994, Donovan et al. 1997, Sisk and Battin 2002, Peak et al. 2004). The degree of isolation of habitat patches has been found to be an important predictor of species occurrence and population abundance (B  lisle et al. 2001, Harris and Reed 2001). Further, isolation may result in lower pairing success if individuals are unable to disperse to locate a mate (Dale 2001, Cooper and Walters 2002).

### **Landscape influences on mating systems**

A mating system is the way that an individual achieves reproductive success and has evolved to maximize the fitness of the individual (Darwin 1871, Emlen and Oring 1977). A mating system includes the number of mates acquired, the behavioral strategies employed to gain those mates, as well as patterns of parental care (Emlen and Oring 1977). The type of mating system that can evolve in a population is constrained by two primary environmental conditions: the spatial and temporal distribution of resources (Emlen and Oring 1977, Clutton-Brock and Harvey 1978). The distribution of resources, such as food and shelter, determine how individuals are spaced in the environment (Emlen and Oring 1977, Clutton-Brock and Harvey 1978, Clutton-Brock 1989). In vertebrates, females usually make a higher investment in the production of offspring, so her reproductive success is dependent upon the resources available to raise young (Orians 1969, Trivers 1972, Clutton-Brock and Vincent 1991). A male's reproductive success is

often strongly influenced by the number of females he can fertilize, so the distribution and spacing of females may dictate the distribution and spacing of males (Trivers 1972, Emlen and Oring 1978, Clutton-Brock 1989). Anthropogenic changes to the landscape can directly impact the spatial and temporal distribution of resources (Banks et al. 2007). Thus, it has the potential to strongly impact mating systems, as well as behavior associated with mating.

In 1990, Gibbs and Faaborg reported a significantly lower pairing success of male Ovenbirds in isolated forest patches than those in continuous forest tracts. At the time, they speculated that this could be due to a female preference for larger tracts with more resources and higher nesting success, or to higher predation on females in fragments. Several other studies on Ovenbird pairing success in fragmented habitat soon followed (Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998, Rodewald and Yahner 2000). Although all studies confounded fragmentation with patch size, Rodewald and Yahner (2000) did find that pairing and nesting success were unrelated indicating that low reproductive success in fragments could not explain the inability of males to find mates.

These findings have particularly important implications for the conservation of species that display reduced pairing success in fragmented patches. Most conservation efforts focus on increasing survival and reproductive success, but this would be an unsuccessful strategy if low productivity was a result of low pairing success. Birds with female-biased dispersal may be particularly susceptible to population declines owing to a loss of connectivity (Dale 2001). Therefore, if decreased pairing success is found in populations living in fragmented patches, conservation efforts should address the causal mechanisms.

Extensive genetic evidence reveals that extrapair copulation (EPC) and extrapair fertilization (EPF) is widespread in socially monogamous songbirds (Griffith et al. 2002,

Westneat and Stewart 2003). EPF provides direct benefits for the lifetime fitness of males, as well as direct benefits to females in the form of increased resources provided by an extra-pair male or indirect benefit in the form of increased genetic quality of offspring (Griffith et al. 2002, Foerster et al. 2003).

EPC rates are influenced by factors such as density and breeding synchrony (Westneat and Sherman 1997, Yezerinac et al. 1999). Habitat fragmentation is capable of either increasing or decreasing density (Debinski and Holt 2000, Banks et al. 2007), as well as altering breeding synchrony among isolated fragments (Johannesen et al. 2000), so it follows that fragmentation could alter EPC rates. Females may experience decreased movement in fragments so not only does this limit access to EPC opportunities but may also influence their decision to settle in an isolated patch. The high rates of unpaired males found in isolated fragments may, therefore, be influenced by female avoidance of such patches due to decreased opportunities for EPC. Only a handful of studies have examined the influence of fragmentation on EPC, but those that have provide results that imply significant impacts to the way that an individual is able to achieve reproductive success in a fragmented environment (Evans et al. 2009, Kasumovic et al. 2009, MacIntosh et al. 2011). Changes in mating behavior can have consequences for the long-term persistence of a population. While a behavioral response may be adaptive in the short term or in a single patch, it may not be adaptive at a broader spatial or temporal scale.

### **Focal species: Golden-winged Warbler**

#### *The Golden-winged Warbler – a declining early-successional specialist*

My research focuses on one of the most rapidly declining early-successional avian species in North America (Sauer *et al.* 2017): the Golden-winged Warbler (*Vermivora chrysoptera*, Figure 1). The Golden-winged Warbler is a Neotropical migratory songbird; its

current range extends from Tennessee westward to Minnesota and northward to Ontario and Manitoba. This species is one of the most rapidly declining songbirds in North America, with average overall declines of 2.3% per year (Sauer et al. 2017). In Canada, the species declined by 79% from 1993 to 2002 (SARA 2006), and in 2006 was listed as ‘threatened’ under the Species at Risk Act (SARA) registry. There are multiple factors implicated in the decline of this songbird, the most cited being habitat loss and genetic swamping by Blue-winged Warblers (*Vermivora cyanoptera*) (Gill 1980, Gill 1997, Buehler et al. 2006). Like other early-successional species, Golden-winged Warblers are experiencing habitat loss because of forest regrowth and the suppression of natural disturbances (e.g., fire, flood) (Askins 2001, Trani et al. 2001). Much of the early-successional habitat presently available is heavily anthropogenically influenced. While Golden-winged Warblers will occupy these habitat types, they may not be suitable for successful breeding. For example, Kubel and Yahner (2008) found only a 15% nest success rate within utility rights-of-way. Simultaneously, the remaining habitat is being fragmented into smaller patches, creating more edges that may be exposed to low-quality matrix habitat such as agriculture. The effects of such a matrix on Golden-winged Warbler habitat selection and productivity remain unknown. However, Golden-winged Warblers exhibit area-sensitivity and generally avoid patches of less than two hectares while increasing occupancy and density of patches that are greater than 12 hectares (Hunter et al. 2001).

Figure 1. Golden-winged Warbler male.



Another consequence of habitat fragmentation and conversion of forest to agriculture has been the expansion of Brown-headed Cowbird (*Molothrus ater*) populations, allowing them to encounter avian species that historically had not evolved with nest parasitism (Brittingham and Temple 1983). The combination of habitat loss and cowbird parasitism could be another important contributing factor to the decline of Golden-winged Warblers. Confer et al. (2003) suggest that cowbird parasitism may decrease the production of fledglings by 17% in northern New York. Because much of the remaining early-successional habitat is now found along agricultural edges, preferred habitat may act as an 'ecological trap' since cowbirds are also more abundant in agricultural settings (Donovan and Thompson 2001, Gates and Gysel 1978).



Hybridization with Blue-Winged Warblers has resulted in genetic swamping of the Golden-winged Warbler phenotype (Buehler et al. 2006, Vallender et al. 2009). Geographic isolation is thought to have resulted in separate evolutionary trajectories and speciation of the Golden-winged and Blue-winged Warbler about 3 million years ago (Gill 1980). While both species prefer early-successional habitat in the breeding range, Golden-winged Warblers were found at more northern latitudes and higher altitudes than Blue-winged Warblers and large patches of contiguous forest prevented contact (Gill 1980). Over the last 150 years, humans have cleared large expanses of forest for agriculture, which has resulted in increased sympatry between the two species. Genetic swamping has occurred where previously allopatric populations of Golden-winged Warbler and Blue-winged Warbler become sympatric and the Blue-winged Warbler genotype and phenotype is able to replace that of the Golden-winged Warbler (Gill 1980).

In most observed cases, sympatry results in hybridization and follows a predictable pattern of complete loss of the Golden-winged Warbler phenotype within 50 years or less (Gill 1997, but see Confer et al. 2010 for exception). Active hybridization is known to have taken place in the Northeastern US for at least 150 years and possibly even longer (Toews et al. 2016), and the rate of occurrence is increasing as the range of Blue-winged Warbler continues to expand northward into areas previously dominated by Golden-winged Warbler (Gill 1980). The range expansions seen in both Golden- and Blue-winged Warblers have been attributed to changes in habitat but climate change may also be a factor (SARA 2006). If current trends of Blue-winged Warbler range expansion continue, and allopatric populations of Golden-winged Warbler continue to decline, the future survival of the Golden-winged Warbler is uncertain (Gill 2004, Buehler et al. 2006, Vallender et al. 2009).

The mechanism that allows for the predictable replacement of Golden-winged by Blue-winged Warblers remains unclear (Vallender et al. 2007a, Vallender et al. 2009). However, uni-directional gene flow from Blue-winged Warbler to Golden-winged Warbler has been ruled out as a mechanism (Shapiro et al. 2004, Dabrowski et al. 2005, Vallender et al. 2007a), as has reduced mating success of Golden-winged Warbler or hybrids that phenotypically resemble Golden-winged Warbler (Vallender et al. 2007b). While mitochondrial DNA (mtDNA) shows a 3-4.5% genetic divergence between the two species (Shapiro et al. 2004, Dabrowski et al. 2005), recent mapping of the nuclear genome reveals that they may be more closely related than previously thought based on mtDNA (Toews et al. 2016). Toews et al. (2016) found only a handful of genes that had diverged between the two species and most of those were related to plumage.

Further, although Gill (1980) suggested a pattern of Golden-winged Warbler replacement by Blue-winged Warblers within 50 years of initial contact, this pattern has not been followed in a few populations. In a New York population located in Sterling Forest State Park, Golden- and Blue-winged Warblers have coexisted for over 100 years (Confer et al. 2010, Confer and Tupper 2000) with very little hybridization and stable population sizes (Confer and Knapp 1981, Confer et al. 2010). This successful coexistence appears to be related to differences in habitat selection, with Blue-winged Warbler exclusion from swamp forests that were used by Golden-winged Warblers (Confer et al. 2010). In addition, Golden-winged Warbler nest success was 75% higher in swamp forests than in surrounding upland (Confer et al. 2010). These results suggest that potential refugia for Golden-winged Warbler occur where Blue-winged Warbler do not breed.

While there is still much to understand about this hybridization complex, both species are in decline and Golden-winged Warblers appear to be declining faster than Blue-winged Warblers

(Sauer et al. 2017). Presently, the only Golden-winged Warbler populations that remain allopatric to Blue-winged Warbler are found in Manitoba, northern Minnesota, and the highest altitudes of the Appalachian Mountains. Extensive research and monitoring has occurred in the Appalachian region for the last 20 years (Buehler et al. 2007), but little is known about the presumed genetically pure population within Manitoba, including total population size or rates of productivity. Thus, Manitoba provides a unique opportunity to study the Golden-winged Warbler in one of the only remaining locations that remain allopatric to Blue-winged Warblers. While it may be too late for populations that have already been genetically introgressed, the remaining allopatric Golden-winged Warbler populations could potentially be managed in a way that allows them to avoid hybridization or remain highly productive, thus playing a critical role in conserving the species.

#### *Golden-winged Warbler Breeding Ecology*

The Golden-winged Warbler is a socially monogamous, territorial, and sexually dimorphic passerine in the wood warbler family (Parulidae). Like other passerines, they will produce mixed-paternity broods through extra-pair fertilization (Reed et al. 2007, Vallender et al. 2007b). In addition, Golden-winged Warbler also produce hybrids via interbreeding with Blue-winged Warbler. The hybrid offspring are fertile with no known differences in breeding success when compared with Golden-winged Warbler of Blue-winged Warbler genotypes (Vallender et al. 2007).

In Manitoba, males arrive in mid-May, with females arriving about a week later. Breeding begins in late May and lasts until mid-July (see Chapter 3). Golden-winged Warbler territories average 1-2 hectares in size and generally contain a dense herb and shrub layer, scattered trees, and a forested edge (Frech and Confer 1987, Klaus and Buehler 2001) in a patchy

and structurally complex distribution (Rossell et al. 2003). Golden-winged Warblers nest on or near the ground and the nest is often placed at a micro-edge where dense vegetation transitions into a more open area (Confer et al. 2011). Nests may be placed in a variety of substrates but generally will feature a taller, sturdier stem among the supporting vegetation that is grasped by the adult when accessing the nest (Confer et al. 2011). Golden-winged Warbler lay 3-6 eggs and the female incubates for 10-12 days (Canterbury 1990, Confer et al. 2011). Nestlings remain in the nest for 9-10 days while both the male and female deliver food (Canterbury 1990). Post-fledging, the young remain in dense vegetation within the nesting territory while the parents continue to deliver food (Canterbury 1990). Within 3-5 days, the brood is split between the male and female and all move from the nesting territory into denser forest (Peterson 2014). Double-brooding has never been documented in Golden-winged Warbler, but if a clutch is lost early during the breeding cycle, a second breeding attempt may occur (Confer et al. 2011).

Nest success rates vary across the Golden-winged Warbler range and habitat type (Demmons 2000, Kubel and Yahner 2008, Bulluck et al. 2013, Aldinger et al. 2015). Differences in predator numbers and/or communities as well as Brown-headed Cowbird parasitism are two potential mechanisms behind the observed differences in nest success rates (Klaus and Buehler 2001, Confer et al. 2003, Confer et al. 2011). Several studies have attempted to quantify the characteristics of successful Golden-winged Warbler nests, although all have focused solely on the patch or local scale (Confer et al. 2003; Demmons 2000; Klaus and Buehler 2001, Bulluck and Buehler 2008). The common feature that repeatedly emerged was that Golden-winged Warbler require structurally complex and patchy vegetation (Bulluck and Buehler 2008, Confer et al. 2003, Confer et al. 2011) with high herbaceous cover, few large canopy trees, and many shrubs (Klaus and Buehler 2001, Confer *et al.* 2003). Spatial complexity is needed to facilitate

all the requirements of breeding, such as tall song perches (Rossell 2001), transitional edges for nests (Demmons 2000, Confer et al. 2011), forest edges (Ficken and Ficken 1968, Frech and Confer 1987) that may be used post-fledging (Peterson 2014), and shrubs and trees for foraging (Ficken and Ficken 1968, Confer 1992). However, characteristics of nests and territories also vary depending upon the specific habitat or region in which the Golden-winged Warblers are found (Demmons 2000, Klaus and Buehler 2001, Confer et al. 2003). Because Golden-winged Warblers occupy a wide range of early-successional habitat types with different plant species, it is a difficult task to identify universal characteristics of successful nests by examining only locally influential attributes. While these studies may be applicable to specific locations or habitat types, they cannot be applied range-wide and there is a need to determine broader-scale characteristics of successful nests and highly productive habitat.

#### *Golden-winged Warbler Habitat Selection*

Confer and Knapp (1981) suggest that Golden-winged Warblers are habitat specialists that require early stages of plant succession to breed and will not persist in areas that exceed a specific successional stage (10-30 years). Numerous studies have confirmed this requirement; Golden-winged Warblers often inhabit brushy fields, overgrown pastures, deciduous forest openings, woodland edges, dry hillside thickets, wetland edges, recently logged areas, and utility rights-of-way (Canterbury 1990, Confer and Knapp 1981, Frech and Confer 1987, Kubel and Yahner 2007, Martin et al. 2007). Reproductive success appears to be affected by successional stage, with higher clutch sizes found in earlier succession habitat with greater herb cover than in later succession habitat with more tree cover (Confer et al. 2003). Recent research indicates that Golden-winged Warbler fledglings require intact mature forest to survive post-fledging (Peterson 2014), which impacts the full-season breeding habitat requirements for this species.

Little was known of the population size and habitat preferences of the Golden-winged Warbler in Manitoba until recently when extensive surveys were conducted by C. Artuso of Bird Studies Canada. Artuso (2009) has documented several thousand breeding birds within three years of surveys, a population size much higher than previously assumed (Buehler et al. 2007). Artuso (2009) found the Golden-winged Warbler range in Manitoba follows the prairie to boreal forest transition zone, known as the aspen parkland transition zone. Despite the new information about population size and habitat use, information is still lacking about the populations' demographics and what represents highly productive habitat. This has created a challenge for the identification of critical habitat necessary to maintain stable population sizes, and so additional research is needed.

### **Knowledge gaps**

Data collected during standardized surveys often becomes the primary source of information on a species' habitat needs. Based on the results of these surveys, researchers infer habitat selection and preference according to the theory that individuals should reproduce and survive better in preferred habitats (Hildén 1965). As a result, avian conservation strategies and management plans often assume that estimates of population presence or abundance are positively correlated with habitat quality (Vickery et al. 1992). While sometimes true, Van Horne (1983) reported that density could be a misleading indicator of habitat quality if negatively correlated with critical population parameters that determine population viability (ie. pairing success, nest success, fledgling survival). Without demographic information on survival and annual fecundity, assumptions should not be made about the quality of any given habitat (Van Horne 1983). Mismatches between habitat selection and individual fitness have been identified in many taxa, particularly those inhabiting contemporary anthropogenic landscapes where

ecological processes have been recently altered (Boal and Mannan 1999, Battin 2004, Weldon and Haddad 2005). The ability for a species to adapt to abrupt environmental conditions that have not been part of its evolutionary history is likely to be limited (Pigliucci 2001, Sultan and Spencer 2002, Auld et al. 2010). Habitats where maladaptive preferences exist have been termed ‘ecological traps’ (Schlaepfer et al. 2002) and can become population sinks where a population cannot sustain itself without immigration (Brown and Kodric-Brown 1977, Pulliam 1998). However, the environmental circumstances that result in a disconnect between habitat preference and population viability remains unknown in many taxa. While many studies have documented numerical responses of avian populations (i.e., abundance or density) to various types of disturbance, fewer have addressed the impacts of habitat selection in anthropogenically disturbed landscapes on multiple aspects of population viability (i.e., survival, productivity, changes in mating systems, and genetic status) simultaneously (Banks et al. 2007, Stutchbury 2007).

In this study, I explored the impacts of anthropogenic disturbance on demographic parameters, population dynamics, and behavior of a disturbance-adapted forest species, the Golden-winged Warbler. To do so, I established seven study sites across the extent of the Golden-winged Warbler range in southeast Manitoba. The levels of anthropogenic disturbance and habitat fragmentation spanned the range of what occurs naturally in this region. In Chapter 2, I examined how patch context and matrix type impacted habitat selection and occupancy. In Chapter 3, I calculated the population growth rate,  $\lambda$ , by measuring survival and seasonal productivity across seven sites in southeast Manitoba as a function of habitat composition and configuration at two spatial extents. In Chapter 4, I examined the impacts of both ecological and social factors on male pairing success and extrapair paternity rates. In Chapter 5, I determined the current rate of hybridization in the southeast Manitoba population of Golden-winged

Warblers and assessed multi-scale differences in habitat selection by hybrids and genetically pure warblers.

### **Organization of Thesis**

My dissertation is organized as a sandwich thesis with four data chapters that are intended to be/have been submitted to separate journals. For the sake of consistency, all chapters are formatting per the guidelines of the Journal of Avian Biology.

Chapter 1- Introduction

Chapter 2 – “Matrix type impacts habitat use by the Golden-winged Warbler” has been submitted to the journal ‘Landscape Ecology’.

Chapter 3 - “Source-sink dynamics of the Golden-winged Warbler in a fragmented landscape at the northern range limit” will be submitted to the journal ‘Journal of Avian Biology’.

Chapter 4 - “Pairing success and extrapair paternity rates are impacted by male age and percent forest cover in an early successional songbird.” will be submitted to the journal ‘Behavioral Ecology and Sociobiology’.

Chapter 5 - “The final frontier: Early-stage genetic introgression and hybrid habitat use at the northwestern extent of the Golden-winged Warbler breeding range” was published in the journal ‘Conservation Genetics’ in June 2017.

Chapter 6 – Conservation and Management Implications



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## **Chapter Two. Matrix type impacts habitat use by the Golden-winged Warbler.**

### **Abstract**

Habitat suitability of the landscape in which a habitat patch is embedded may be as important to wildlife as the habitat quality within a patch. Therefore, matrix type is a critical element of landscape context. The Golden-winged Warbler is a declining species that requires early-successional habitat for nesting but is often found within a broader landscape dominated by either late-successional forest or agriculture and other anthropic land uses. My objective was to determine the impacts of matrix composition and configuration on probability of occupancy across the northwestern extent of the Golden-winged Warbler range, and to understand the spatial extent at which the matrix is influential. I used data from presence/absence surveys of Golden-winged Warblers that took place in Manitoba, Canada in 2008-2010 to model probability of occurrence across Manitoba, Canada. Golden-winged Warblers are rare across Manitoba with a maximum probability of occurrence of only 0.21. Golden-winged Warblers responded most strongly to landscape elements at a 1-km scale. The probability of presence declined as agricultural cover increased, and increased as bare ground cover increased at this scale. No other land use types, including grassland, coniferous forest, or other anthropogenic land uses, impacted the presence or absence of Golden-winged Warblers. These findings provide evidence that matrix type matters and the fragmentation of forest by agricultural land uses will reduce suitable habitat to a greater extent than the amount of forest lost to habitat conversion.

## Introduction

Habitat loss is the single biggest threat to global biodiversity (Hanski 2005, Newbold et al. 2015), and the conversion of much of the world's land area to anthropogenic land uses will only continue as the human population grows (Ellis and Ramankutty 2008, Foley et al. 2011). While the effects of habitat loss on biodiversity are generally large and negative (Fahrig 2003), the magnitude of these effects may be dependent upon the anthropogenic matrix land uses within which remaining habitat patches are embedded (Ricketts 2001, Haila 2002, Rodewald 2003, Ewers and Didham 2006, Kupfer et al. 2006, Laurance 2008). Landscapes are composed of heterogeneous land cover types that vary in the extent to which they provide substitute resources, impede dispersal, and create 'high-contrast' edge zones (Donald and Evans 2006, Kupfer et al. 2006, Mendenhall et al. 2014). It follows that the matrix will influence the extent to which a given amount of habitat loss translates into negative impacts on a population (Kupfer et al. 2006). Recent meta-analyses have confirmed that the composition of the matrix plays a central role in determining biodiversity in fragmented landscapes (Prevedello and Vieira 2010, Watling et al. 2011). The inclusion of matrix type can significantly improve the explanatory power of models evaluating effects of landscape context on species richness, occupancy, and abundance (Gustafson and Gardner 1996, Denöel and Lehmann 2006, Sozio et al. 2013).

Despite an acknowledgment of the importance of the matrix, its effects are still not fully understood and empirical data are limited in regard to the ecological importance of specific matrix types (Kupfer et al. 2006). The matrix can affect both within- and among-patch processes in heterogeneous landscapes by increasing or decreasing predation and/or parasitism rates (Rodewald and Yahner 2001, Borgmann and Rodewald 2004, Patten et al. 2006, Williams et al. 2006), by enhancing or impeding dispersal (Haas 1995, Schooley and Wiens 2004, Haynes and

Cronin 2006), or by providing or limiting availability of secondary habitat and food resources (Johnson 2000, Harvey et al. 2006, Umetsu and Pardini 2006). A comprehensive review across taxa concluded that matrix type effects were strongly species-specific (Prevedello and Vieira 2010), which is not unexpected as different organisms perceive the same landscape in different ways depending on ecological requirements and behavior (Gustafson and Gardner 1996, Andr  n et al. 1997, Tischendorf et al. 2003, Eycott et al. 2012). Many species-specific differences are related to the ability to use the matrix as secondary habitat (Bender and Fahrig 2005, Umetsu and Pardini 2006, Hodgson et al. 2007), and some studies suggested that matrix quality increases as the structural similarity with the habitat patch increases, in turn increasing occupancy by the focal species (Forman 1995, Renjifo 2001, Perfecto and Vandermeer 2002, Anderson et al. 2007). However, species-specific responses to the matrix make broad generalizations difficult among and even within species (Prevedello and Vieira 2010, Kennedy et al. 2011), indicating a need for examination in threatened populations.

Neotropical migrants that require disturbance-dependent habitats have become a conservation concern due to the suppression of natural disturbance in human-dominated landscapes (Brawn et al. 2001, Thompson and Degraaf 2001). Much of the North American landscape is now dominated by human land uses, including agriculture, urban and exurban development, mining, and resource extraction. Thus, there is less available open land subject to natural disturbance regimes, and the small remnant patches of early-seral forest embedded in this landscape may not provide suitable habitat for many of these declining bird species (Litvaitis 2001). Presently, most remaining early-successional habitat patches are either powerline corridors, rights of way (ROW), forest clearcuts, or abandoned pastures (Askins 2001). Imbeau et al. (2003) suggest that the correlations found between early-successional species and ‘edge’

habitat exist because most of the remaining early-successional habitat happens to be the exposed edges of mature forest fragments.

One such early-successional species is the Golden-winged Warbler (*Vermivora chrysoptera*), which has been experiencing sharp population declines over the last 45 years and is of high conservation concern (Roth et al. 2012; Sauer et al. 2017). The Golden-winged Warbler (hereafter Golden-winged Warbler) is a Neotropical passerine in the wood warbler family (Parulidae). The species' breeding range extends from Georgia to Massachusetts, westward to Minnesota, and northward into Quebec, Ontario, and Manitoba. The wintering range spans across Nicaragua southward to Venezuela, Colombia, and northern Ecuador (Confer 1992). Over the past 40 years, the range has expanded northward and westward, while contracting in the southern Midwest and New England states, as well as in the lower elevations of the Appalachian Mountains (Buehler et al. 2007; Confer 1992). Global populations of Golden-winged Warbler have been declining for almost 50 years, with annual average declines of 2.28%, although recent declines have exceeded 5% per year in the core of the breeding range (Sauer et al. 2017). The US Fish and Wildlife Service considers the Golden-winged Warbler to be a species of concern and has recommended protection under the Endangered Species Act (U.S. Fish and Wildlife Service 2011). In Canada, the Golden-winged Warbler is listed as 'threatened' by the Species at Risk Act (COSEWIC 2006). An ongoing conservation plan, the Golden-winged Warbler Conservation Initiative, aims to stabilize and manage global populations of Golden-winged Warbler (Buehler et al. 2007) and a recovery strategy has now been developed for Canada (Environment Canada 2014).

While numerous studies have addressed Golden-winged Warbler habitat use, nearly all have focused on the patch level (Canterbury 1990; Confer et al. 2010; Klaus and Buehler 2001;



Kubel and Yahner 2008; Patton et al. 2010). Many studies mention the Golden-winged Warbler preference for a forested edge or nearby mature forest patch without going into further detail (Frech and Confer 1987; Confer 1992; Klaus and Buehler 2001). Thogmartin (2010) was the first to complete a cross-scale analysis of Golden-winged Warbler habitat selection; he used Breeding Bird Survey data from the upper midwest prairie hardwood transition zone and discovered that Golden-winged Warbler respond to habitat variables at multiple scales but that occupancy was best predicted by coarser scales. He recommended that Golden-winged Warbler conservation could be addressed most effectively at larger landscape scales (8000 – 80000 ha) (Thogmartin 2010). This is likely to be true throughout the Golden-winged Warbler range, but we lack information about the impacts of matrix elements at a landscape scale.

In this study, I investigated Golden-winged Warbler occurrence across the Manitoba range extent. I used presence-absence surveys conducted by Bird Studies Canada in 2008-2010 to examine the impacts of aggregate landscape and individual matrix composition and configuration on Golden-winged Warbler habitat use at landscape scales of 1-, 2-, and 4-km. Migratory bird species use a hierarchical approach to choose breeding habitat, with landscape-level habitat characteristics being chosen initially (Hildén 1965, Johnson 1980), and I predicted an avoidance of anthropogenically disturbed habitats at these landscape scales.

## **Methods**

### *Study Site*

Presence/absence surveys were conducted by Bird Studies Canada across the estimated distributional range of Golden-winged Warbler in Manitoba, Canada (Dunn and Garrett 1997; Edie et al. 2003; Dunn and Alderfelder 2006) from May 27 – July 14 in 2008, 2009, and 2010 (Fig. 2.1). The Golden-winged Warbler uses early-successional habitats with stratified layers of

herbaceous, shrub, and tree cover (Confer 1992). In Manitoba, these conditions are most often found in the aspen parkland transition zone (hereafter APTZ), a transitional habitat between prairie and boreal forest that contains patchy open deciduous and mixed-wood forest in a variety of seral stages. Similar conditions occur along an elevational gradient in Riding Mountain National Park (50.65° N, 99.97°W), the Duck Mountains (51.67°N, 100.92°W), the Porcupine Hills (52.56°N, 101.37°W) and the Arden Ridge (50.34°N, 99.30°W).

### *Bird Surveys*

The surveys were conducted across the southern third of Manitoba, Canada. Three hundred and thirty individual routes were surveyed; each had 10-16 stops (at least 400 m apart) for a total of 4,783 survey points (Figure 2.1). Observers used a GPS to locate survey routes and stops, either walking or driving between points. At each stop, the observer conducted a five-minute survey and all Golden-winged Warbler seen or heard were recorded. I subsequently converted these data to Golden-winged Warbler presence or absence to reduce bias in abundance estimates that could be introduced by observer skill level and detectability (Bart and Earnst 2002, O'Donnell et al. 2015).

The sampling design varied slightly depending upon region. In all regions of Manitoba other than RMNP, survey routes were chosen by simple random sample. Each stop along the route was located at least 400m away from the next stop, but the surveyor increased the distances between points to avoid unsuitable habitat such as open agricultural field (Confer 1992). Kubel and Yahner (2007) found that in mixed-shrubland forests, it was difficult to detect singing Golden-winged Warblers at distances >100m so the placement of stops every 400 m ensured independence. The direction of each route was random unless constrained by factors such as private property, or impassible landscape features such as bogs. In RMNP, a different survey

design was used to coincide with the conditions of Bird Studies Canada's contract with Environment Canada. There, hexagons with 600m long sides were overlaid across RMNP using ArcGIS (ESRI 2013). Each hexagon contained a route with 11 stops that were 300m apart. Hexagons were randomly chosen to be surveyed using a random number table with the constraint that they were no more than 2 km from road or trail.

The Golden-winged Warbler Working Group determined the standardized Golden-winged Warbler survey protocols on April 22, 2008. Surveys were conducted from May 27 through June 28 on all days when weather was suitable (no persistent precipitation, temperature  $>0^{\circ}\text{C}$ , wind  $<25\text{km/hr}$ ). Survey points were not revisited within the same year due to time constraints and decreased Golden-winged Warbler detection rates later in the breeding season. Surveys began 30 minutes before sunrise until 11 AM during the period of May 27-June 14, and until 10:30 AM during the period of June 15-June 27. A 5-minute recording consisting of 16 bouts of type-1 Golden-winged Warbler song each separated by 17 seconds of silence was broadcast at each stop. Mp3 players and Sony SRS-BTM30 6-Watt portable speakers were broadcast at maximum volume (90 - 100 Decibels). In 2008, a 5-minute territorial male playback was used followed by 2 minutes of passive listening at each stop to maximize the likelihood of detecting Golden-winged Warbler (Kubel and Yahner 2007). In 2009 and 2010, after noting in 2008 that males sometimes responded to playback after the passive listening period was over, an additional three minutes of passive listening was added before beginning the five-minute territorial playback to maximize our ability to detect males. We included year in statistical analyses to account for variation among years caused by this sampling change and other interannual differences. All Golden-winged Warbler seen or heard were recorded during the survey period, noting a compass direction and whether they were  $<100\text{m}$  or  $>100\text{m}$  from the

observer. Detections greater than 100m away were not included in further analysis due to a high amount of detectability error for Golden-winged Warbler at this distance (Kubel and Yahner 2007).

### *Landscape Structure and Scale*

I used land cover classification data from GIS layers supplied by the Manitoba Land Initiative that were generated based on data from the years 2000-2002 (MLI 2015). These data include 18 distinct land cover classes. Classes that consist of anthropogenic disturbance include agricultural, grassland/rangeland (hereafter, grassland), forage crops, cultural, forest cutovers, bare ground/rock/gravel/sand (hereafter, bare ground), and roads/trails. In the survey areas, bare ground is generally associated with recently disturbed areas that are being mined for gravel and rock aggregate. The classes that contain habitat suitable for Golden-winged Warbler as determined from published habitat associations of the species (Confer 1992) include deciduous forest, open deciduous forest, mixed-wood forest, burns, and forest cutovers. I excluded land-use types that were not found near the survey points or that were very rare on the landscape within the Golden-winged Warbler range, including cultural, burns, and forest cutovers. I merged agriculture and forage crop into a single agriculture class, and deciduous and open deciduous forest into a single deciduous forest class because they represented variations of the same habitat type.

Because Golden-winged Warblers migrate long distances, they must choose a habitat patch to occupy when returning to the breeding grounds. This is a hierarchical process, as birds are influenced by different factors at progressively smaller scales as they narrow their range of movement from large (migration patterns) to small (feeding and nesting sites) (Hildén 1965, Hutto 1985). The result is that final occupancy patterns are influenced by aspects of the

landscape at broader scales. To attempt to capture this effect and to determine the landscape spatial scale that most strongly influenced habitat selection (Fahrig 2001, Holland et al. 2004), I created a 4-km buffer around each survey point. This was the maximum possible extent in my data set, and equivalent to or greater than spatial extents studied in most other avian landscape studies (e.g., Refrew and Ribic 2008, Ribic et al. 2009). Additionally, Thogmartin (2010) found that Golden-winged Warblers responded to forest composition at broad landscape scales. I then subdivided the 4-km landscapes around each survey point using three different buffer extents (1-, 2-, and 4-km) and intersected each buffer with the land-use vector in ArcGIS 10 using Spatial Analyst (ESRI 2013).

To assess the impacts of matrix composition, I calculated the percentage cover for all matrix types (agriculture, bare ground, roads, conifer, grassland) within each buffer. I calculated the configuration of each matrix type within the landscape using edge density (m/ha) in ArcGIS 10 (Table 2.1). To examine whether Golden-winged Warblers were simply responding to “forest” vs “matrix”, I summed the proportion cover of all matrix types into an aggregate matrix cover variable. I did the same with all deciduous forest to create an aggregate forest cover variable. To quantify overall landscape configuration, I calculated the aggregate edge density by summing the values of edge density for all matrix types (Table 2.1). Each survey point had a binary response variable of either presence or absence of Golden-winged Warbler. While survey points were located within forested habitats, a variety of natural and anthropogenic land use types were present within the 1-, 2-, and 4 km landscapes (Table 2.2).

### *Occupancy analyses*

The presence or absence of Golden-winged Warbler during the surveys was the result of two factors; occupancy ( $\psi$ , the probability that a bird is present) and detectability ( $p$ , the

probability that a bird is detected given that it is present). Because of the large amount of area covered by the surveys and limited time, surveys were conducted only once. I thus corrected for potential errors in species detection using the method described in Lele et al. (2012). I included covariates that I expected to affect both the probability of detection and the probability of occupancy (Lele et al. 2012). I expected that the observer (volunteer vs trained technician), year, and day of year could influence the probability of Golden-winged Warbler detection ( $p$ , Kubel and Yahner 2007) so I included these parameters as covariates to explain detection probability. To explain occupancy ( $\psi$ ), I included aggregate landscape variables (deciduous forest cover, total matrix cover, and total edge density) and matrix element variables (total cover and total edge density of each individual matrix type).

I fit occupancy models using generalized linear mixed models (GLMMs) with a logistic distribution and logit link function. Due to the potential for correlation among data points such as those within a single route, the type of GLM appropriate for the data is a generalized linear mixed effect model (GLMM). A GLMM is an extension of the GLM that allows the predictor variables to include both fixed and random effects and was fitted using maximum likelihood (Quinn and Keough 2002). I included the survey route as a random effect within all models. Although the proportion of deciduous forest and agriculture are weakly collinear ( $r = 0.67$ ), Smith et al. (2009) found that including all variables of interest in a model is the least biased way to obtain estimates of the relative effects of each, even if they are highly correlated; thus I included all variables of interest in our models. I evaluated the goodness of fit of each global model by visually examining the residuals using diagnostic plots (McCullagh and Nelder 1989).

Because of the large number of potential explanatory variables involved, I examined aggregate landscape and matrix element variables separately using multi-stage information-

theoretic approach using Akaike's second-order information criterion ( $AIC_c$ ) (Burnham and Anderson 2002). First, for each of the three aggregate landscape variables (total matrix cover, forest cover and total edge density; Table 2.1), I identified the spatial scale(s) with the most statistical support (defined throughout as those with  $\Delta AIC_c < 2$ ) which were retained for the next step. Second, the pool of variables (measured at the most supported scale for each aggregate variable) was combined in a multi-model multiple logistic regression analysis to determine the final set of aggregate landscape variables with the most statistical support (Appendix 2.2). The second branch of the analysis focused on matrix element variables associated with the amount and configuration of individual matrix elements within the landscape (agriculture, roads, bare ground, grassland, coniferous). Like the aggregate landscape variable analysis, the first round identified the most important scale(s) for each variable, which were retained for the next step. Second, I combined variables from the first step in a multi-model multiple logistic regression analysis to identify the matrix elements with the most support (Appendix 2.3). Finally, I incorporated the top variables from the aggregate and matrix element analyses into a single analysis to produce the set of best ( $AIC_c < 2$ ) models including both matrix element and aggregate landscape variables. Although the global and the null models were not competitive, they were included for comparison. I selected the top-ranking model(s) using Akaike's Information Criterion (Burnham and Anderson 2004).

I evaluated the goodness-of-fit of the global model with a Hosmer and Lemeshow (2000) goodness-of-fit test. To assess multicollinearity in the global models, I examined tolerance values for the covariates (Allison 1999) and checked for overdispersion in the data by examining the Pearson ( $X^2$ ) test statistic for the global models divided by degrees of freedom (Burnham and Anderson 2002).

To quantify the model fit, I calculated the area under the curve (AUC) of the receiver operating characteristic (ROC) function, as recommended for rare/threatened species (Fielding and Bell 1997). A receiver–operating characteristic curve plots the true positive cases (sensitivity) against corresponding false positive cases ( $1 - \text{specificity}$ ) across a range of threshold values (Fielding and Bell 1997). Values of AUC can range from 0.5, indicating that the model’s predictions are no better than random, to 1.0, indicating the model discriminates perfectly between presence and absence predictions (Pearce and Ferrier 2000). I used 10-fold cross-validation, which randomly splits the data into ten independent groups, using nine groups of known data as the training set and the 10<sup>th</sup> group of unknown data as the testing set. I repeated the training and testing process ten times to calculate the standard deviation and variance for the AUC of the highest ranked model (Hirzel et al. 2006). I completed all analyses in SAS 9.4 (SAS 2013).

I used the most supported model to create a predictive map of the Golden-winged Warbler occupancy by generating a continuous surface using IDW (inverse distance-weighted) raster interpolation in the geographic information system ArcGIS 10 (ESRI 2013). The map indicates where Golden-winged Warblers have the lowest to highest probability of occurrence across their Manitoba range based on the most-supported model.

## **Results**

### *Golden-winged Warbler survey results*

Golden-winged Warblers were detected at 467 of 4,783 survey points (9.8%). The breeding range extends from southeast Manitoba northwest to RMNP and northwards into the Duck Mountains and Porcupine Hills (Figure 2.1). The highest rate of detection occurred in the aspen parkland transition zone (APTZ) of southeast Manitoba, with detections at 11.9%



(192/1620) of survey points. Golden-winged Warblers were found in a variety of habitat types, but all had sufficient canopy gaps to allow growth of a dense shrub layer. These canopy gaps existed both as a result of human disturbance (powerline, right of way, logging, resource extraction) or natural disturbance (tree fall, fire, natural openings within deciduous or mixedwood forest, and along waterways). The most common canopy tree species associated with singing Golden-winged Warbler males was trembling aspen (*Populus tremuloides*). Golden-winged Warblers were also found within early successional balsam poplar (*Populus balsamifera*) and bur oak (*Quercus macrocarpa*) stands. Golden-winged Warblers were never found in pure coniferous stands despite evidence that this habitat type is widely used elsewhere (Confer 1992).

#### *Habitat occupancy models*

There was no evidence of lack of fit of the global occupancy model based on the Hosmer and Lemeshow (2000) goodness-of-fit test ( $\chi^2_8 = 9.98$ ,  $P = 0.27$ ) and the overdispersion parameter ( $\hat{c} = 1.03$ ). The final model was somewhat useful in predicting Golden-winged Warbler occurrence (AUC = 0.726; Appendix 2.4). The effect of day of year on Golden-winged Warbler detection probability ( $p$ ) was negative, indicating that Golden-winged Warbler detection probability declines as the season progresses (Table 2.4). As the breeding season progressed, the odds of Golden-winged Warbler detection decreased by 3% each day. There was no measurable effect of year or observer on Golden-winged Warbler detection probability. The top-ranking models included only variables at the 1-km scale (Appendix 2.1). The probability of Golden-winged Warbler presence decreased as the amount of agriculture cover increased within 1 km (Table 2.4, Figure 2.2) and increased as the amount of bare ground cover increased within 1 km (Table 2.4, Figure 2.3). I found no support for an effect of edge density on the probability of

Golden-winged Warbler presence. I also found no evidence that a grassland, road, or coniferous forest matrix impacted the probability of Golden-winged Warbler presence.

The Golden-winged Warbler range within Manitoba includes large tracts of deciduous forest, much of which occurs within federally- and provincially-protected parks and forests. However, the predictive map indicates that Golden-winged Warblers have the highest probability of presence in the southeastern portion of the range, the northern border of Riding Mountain National Park, and the border of the Duck Mountains (Figure 2.4). The highest probability of Golden-winged Warbler presence is only 0.21, indicating they are a rare species even in the most optimal habitat in Manitoba. The percentage of deciduous forest habitat with a probability of presence above 0.15 is only 6% across the extent of the Manitoba breeding range.

## **Discussion**

Surprisingly, matrix composition influenced habitat occupancy more than habitat amount for Golden-winged Warblers, adding to the growing literature documenting the importance of matrix type on habitat use in fragmented landscapes (Fahrig and Merriam 1994, Kupfer et al. 2006, Prevedello et al. 2010). Golden-winged Warblers avoided forest patches embedded within an agricultural matrix but not other matrix types, highlighting the importance of distinguishing between matrix types and not simply considering them as a single homogeneous ‘non-habitat’ (Ewers and Didham 2006, Kupfer et al. 2006). The lack of response to forest cover contrasted with habitat selection behaviour documented for this species elsewhere (Thogmartin 2010, Peterson 2014). Manitoba has higher forest cover and lower levels of fragmentation than other studied regions, and perhaps does not reach a threshold of forest cover below which the response to forest cover becomes observable. Another possibility is that they respond to forest cover at scales even larger than those measured here (Thogmartin 2010).

The causal mechanisms that make forest patches surrounded by agricultural land less suitable for some bird species are not well understood and likely to vary by species (Kupfer et al. 2006). Some of the mechanisms that have been suggested are: 1) changes in food availability or other resources (Burke and Nol 1998, Johnson 2000, Harvey et al. 2006, Umetsu and Pardini 2006); 2) increased levels of predation or parasitism (Rodewald and Yahner 2001, Borgmann and Rodewald 2004, Patten et al. 2006, Williams et al. 2006); and 3) altered dispersal abilities (Haas 1995, Schooley and Wiens 2004, Haynes and Cronin 2006). Golden-winged Warbler avoidance of an agriculturally-dominated landscape is likely a result of their full season breeding requirements, including post-fledging survival and dispersal of young. Peterson (2014) followed transmittered Golden-winged Warbler young in Manitoba for up to a month post-fledging and found that newly fledged young required mature forest patches for foraging and protection from predators (Peterson 2014). Golden-winged Warbler territories and nests are often located near a late-successional forest edge (Aldinger et al. 2015; Moulton, pers. obs.) that provides the newly fledged young with a nearby source of cover and food. However, edges such as these are not available in the agricultural landscapes in my study region because agricultural in forest-dominated (non-prairie) areas of Manitoba are used for cattle grazing. Grazing removes the understory – an essential component of Golden-winged Warbler nest site selection – and can reduce habitat suitability well into a forested patch if cattle have access to the habitat edges (Martin and Possingham 2005).

Habitat suitability in agricultural landscapes might also be compromised by reduced gap-crossing ability by adult birds, which may impact colonization and pairing success. Numerous studies show that forest birds avoid flying across large openings (Desrochers and Hannon 1997,

Tremblay and St. Clair 2011, St-Louis et al. 2014), which impacts pairing success and opportunities for extra-pair mating (Norris and Stutchbury 2001, Banks et al. 2007).

Habitat complementarity (Dunning 1992) appears to be an essential component for the conservation of this species, such that both early and late successional, multi-story habitats must be present within landscapes to fulfil the foraging, nesting, and fledgling needs. Golden-winged Warblers likely use multiple criteria for choosing a breeding territory and must consider potential nest success as well as potential fledgling survival (Peterson 2014). As a result, many areas that appear structurally suitable as breeding territories may remain unoccupied due to inadequate landscape complementarity.

The observed preference for landscapes containing more bare ground was unexpected, but may have occurred due to the availability of early-successional habitat near these sandy or gravelly sites. In Manitoba, the presence of bare ground at a landscape scale usually indicates resource extraction activity, most commonly the removal of gravel and rock aggregate at open gravel pits. Patches of trees are cut within forested landscapes while prospecting for aggregate sources, which results in the creation of early successional habitat suitable for Golden-winged Warblers. Because I studied only occupancy here, not habitat quality, I cannot assess whether this anthropogenically modified habitat confers an advantage to Golden-winged Warblers (e.g., Schlaepfer et al. 2002).

Cumulatively, this highlights the importance of the matrix that surrounds the early-successional habitat patches on which Golden-winged Warblers depend, and demonstrates the need for a whole-landscape approach to the conservation of this species. My results suggest that an appropriate landscape extent at which to focus management action is the 1-km scale. Understanding and predicting the scale(s) at which a species responds to their environment is a

fundamental part of assessing species distributions and habitat use (Wiens 1989, Wiens and Milne 1989, Holland et al. 2004). On the breeding grounds, landscape-scale factors are often better predictors of bird distributions than patch-scale factors (Saab 1999, Mitchell et al. 2001, Lee et al. 2002), perhaps because factors at broader spatial scales often constrain the factors at finer scales (Hostetler 2001). The literature reflects uncertainty regarding the relative importance of specific landscape scales to birds (Saab 1999, Donnelly and Marzluff 2004), but there is a general agreement that different species will respond to factors at different spatial scales (Wiens et al. 1987, Holling 1992, Levin 1992, Saab 1999). Understanding the mechanisms that drive patterns at the 1-km scale will be essential for predicting the effects of anthropogenic activity and environmental change.

While Manitoba is home to a relatively small portion of the global Golden-winged Warbler population (Buehler et al. 2007), my results suggest that previous population estimates for this region are substantially underestimated. The most recent published estimate of the Manitoba Golden-winged Warbler population was 105-270 pairs (COSEWIC 2006), but my study, and additional intensive monitoring of the southeast population, found much higher numbers. There were one or more singing males at 467 independent survey points, which sampled only a fraction of suitable Golden-winged Warbler habitat in Manitoba. Estimates from Artuso (unpublished data) of  $4620 \pm 674$  territorial males in Manitoba suggest that previous approximations have underestimated Manitoba's population size by at least an order of magnitude. Additionally, this region is of high conservation priority to this species. As the loss of early-successional habitat continues to negatively impact Golden-winged Warbler populations elsewhere (Vallender et al. 2009), Manitoba will be an increasingly important population refugia. Currently, the APTZ region of southeast Manitoba faces increased pressure due to resource

extraction, as measured by sharp increases in the number of casual quarry mining permits over the past 12 months related to highway expansion projects (Brian Kiss, 2016, pers. comm). Large portions of habitat have been and will continue to be destroyed, so the future of Golden-winged Warbler and other parkland dependent species in this region is at risk.

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Table 2.1. List of variables used in the logistic regression model sets. All were calculated at three different landscape scales (1 km, 2 km, and 4 km) using ArcGIS.

<sup>a</sup> Each of these variables are calculated for each matrix land cover type found in the survey areas (agriculture, roads, bare ground, grassland, coniferous)

Variable type	Units
Aggregate Landscape variables	
Composition	
Deciduous Forest Cover	%
Total Matrix Cover	%
Configuration	
Total edge density	m/ha
Matrix element variables <sup>a</sup>	
Composition	
Area	%
Configuration	
Edge density	m/ha

Variable type	1000m				2000m				4000m			
	Mean	SE	Min	Max	Mean	SE	Min	Max	Mean	SE	Min	Max
<b>Absent (average values where birds are absent)</b>												
<i>Composition</i>												
Deciduous Forest cover	0.553	0.381	0	0.999	0.534	0.359	0	0.999	0.534	0.321	0.003	0.994
Agriculture cover	0.095	0.190	0	0.926	0.113	0.191	0	0.888	0.121	0.174	0	0.870
Road cover	0.037	0.126	0	0.892	0.042	0.123	0	0.793	0.041	0.107	0	0.596
Bare cover	0.001	0.003	0	0.038	0.001	0.003	0	0.026	0.001	0.002	0	0.020
Grassland cover	0.219	0.272	0	0.983	0.180	0.211	0	0.833	0.170	0.172	0	0.745
Conifer cover	0.017	0.086	0	0.799	0.010	0.060	0	0.531	0.169	0.058	0	0.453
<i>Configuration</i>												
Deciduous Forest edge density	5.695	10.810	0	75.677	21.766	21.706	0.149	128.414	27.142	20.336	0.334	123.269
Agriculture Edge density	3.564	6.349	0	37.971	5.697	8.535	0	34.690	7.713	9.908	0	43.604
Road edge density	3.079	3.979	0	19.590	4.355	4.891	0	24.660	5.771	5.767	0.082	28.616
Bare edge density	3.079	7.361	0	48.681	4.232	7.721	0	52.373	4.892	6.340	0	54.032
Grassland edge density	10.073	11.698	0	48.928	14.172	15.640	0	66.280	18.201	17.157	0	72.231
Conifer edge density	1.251	5.894	0	70.020	1.345	3.535	0	31.348	2.030	3.983	0	24.140
<b>Present (average values where birds are present)</b>												
<i>Composition</i>												
Deciduous Forest cover	0.650	0.326	0.100	0.999	0.659	0.278	0.130	0.998	0.633	0.246	0.200	0.990
Agriculture cover	0.023	0.056	0	0.289	0.040	0.057	0	0.219	0.067	0.098	0	0.445
Road cover	0.016	0.042	0	0.271	0.017	0.040	0	0.255	0.020	0.032	0	0.150
Bare cover	0.003	0.010	0	0.043	0.003	0.009	0	0.050	0.002	0.004	0	0.012
Grassland cover	0.203	0.280	0	0.793	0.171	0.209	0	0.715	0.142	0.145	0	0.483
Conifer cover	0.040	0.120	0	0.675	0.040	0.115	0	0.665	0.037	0.098	0	0.560
<i>Configuration</i>												

Deciduous Forest edge density	3.916	5.836	0	30.601	22.419	20.852	1.230	97.953	26.150	15.499	2.091	77.633
Agriculture Edge density	1.043	2.707	0	14.665	2.413	3.924	0	20.332	4.380	6.466	0	32.558
Road edge density	3.233	3.499	0	10.962	5.066	4.420	0	16.796	6.207	5.175	0.027	20.389
Bare edge density	2.417	4.701	0	26.782	2.893	4.922	0	28.044	3.097	5.092	0.000	28.693
Grassland edge density	7.845	9.058	0	31.245	12.734	12.961	0	39.839	15.204	13.804	0.009	39.871
Conifer edge density	1.158	3.354	0	17.849	1.599	4.023	0	23.981	2.895	5.235	0	22.450

4 Table 2.3. Final model set including most supported models from the aggregate model set and  
 5 the matrix model set. All models included day of year to help explain detection probability, and  
 6 included route as a random effect.

Final Model Set	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Rel. likelihood	ω <sub>i</sub>
<b>Agriculture cover 1km + Bare ground cover 1km</b>	<b>172.98</b>	<b>0</b>	<b>1.00</b>	<b>0.67</b>
Agriculture cover 1km	177.78	4.8	0.09	0.06
Agriculture edge density 1km	177.89	4.91	0.09	0.06
Global	178.57	5.59	0.06	0.04
Total matrix cover 1km + Agriculture edge density 1km	178.61	5.63	0.06	0.04
Total matrix cover 1km + Agriculture cover 1km	178.73	5.75	0.06	0.04
Agriculture cover 1km + Agriculture edge density 1km	178.87	5.89	0.05	0.04
Bare ground cover 1km	179.04	6.06	0.05	0.03
Total matrix cover 1km + Bare ground cover 1km	179.23	6.25	0.04	0.03
Total matrix cover 1km	215.18	41.2	0.00	0.00
Null	224.87	51.89	0.00	0.00

7  
8

9 Table 2.4. Top-ranking model parameter estimates for factors that impact habitat  
 10 occupancy of the Golden-winged Warbler in Manitoba, Canada, 2008-2010.

Parameter	Estimate	SE	LCL	UCL	<i>p</i>
Intercept	4.22	2.78	-1.22	9.67	0.13
Day of year	-0.03	0.02	-0.07	0.00	0.05
Agriculture cover 1 km	-6.44	3.12	-12.55	-0.34	0.04
Bare ground cover 1 km	69.13	29.27	11.76	126.50	0.02

12 Figure 2.1. Location of Golden-winged Warbler (*Vermivora chrysoptera*) survey points in 2008, 2009, and 2010 within the recorded  
13 range in Manitoba ( $n=4,783$  survey points). Red points represent where Golden-winged Warblers were absent and green points where  
14 they were present. Survey data were collected by Bird Studies Canada and used with permission.

15

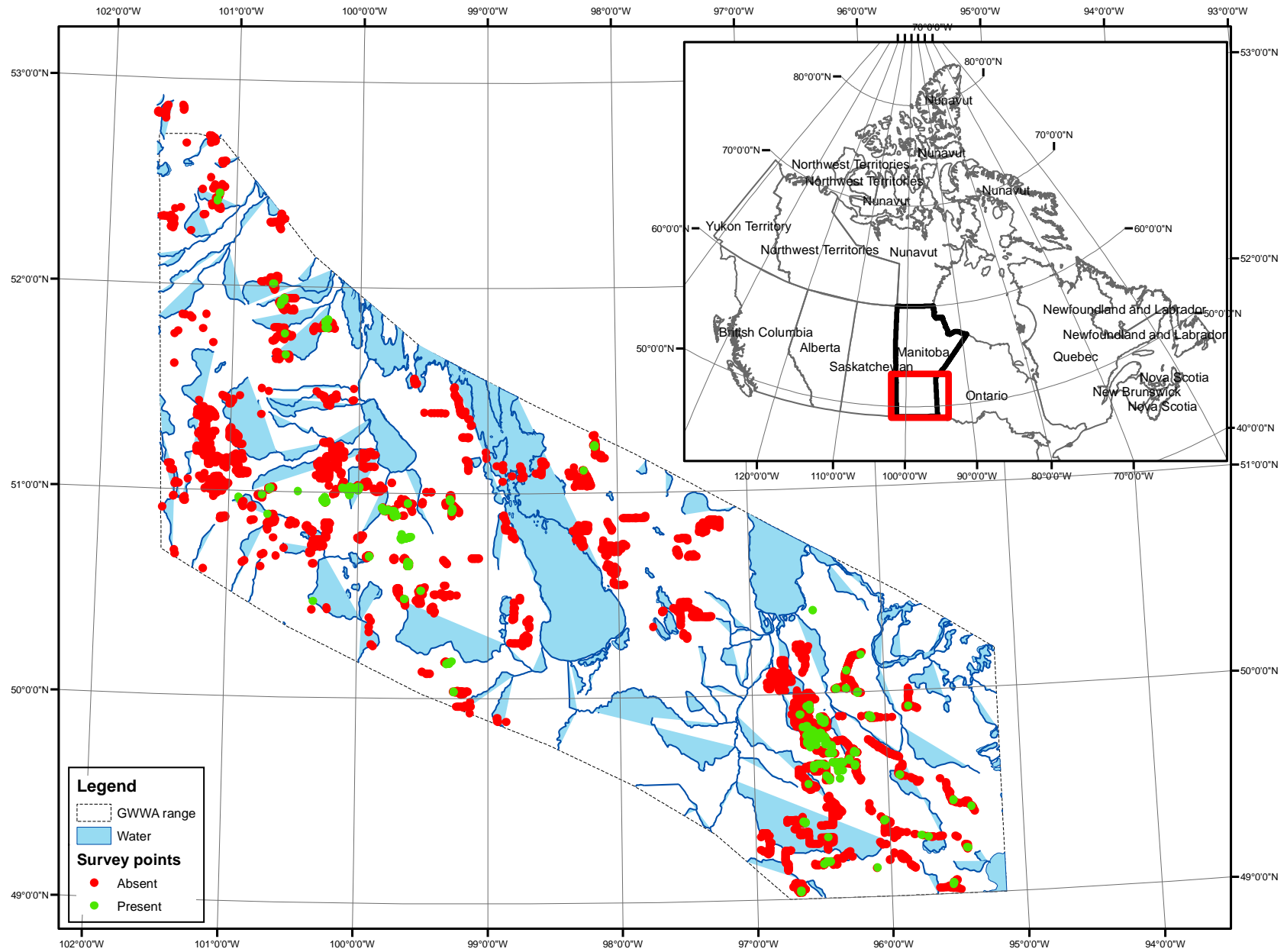






Figure 2.2. Golden-winged Warbler (*Vermivora chrysoptera*) probability of occupancy decreased as the proportion of agriculture increased within a 1-km radius of the survey point in Manitoba, 2008-2010. Standard errors shown as dashed lines. Survey data were collected by Bird Studies Canada and used with permission.

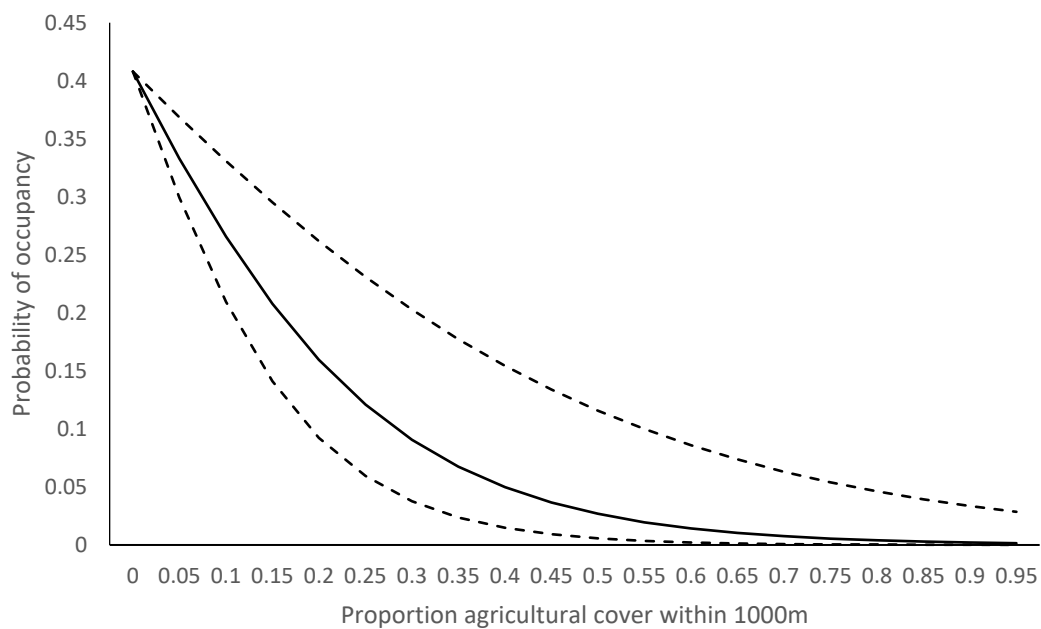


Figure 2.3. Golden-winged Warbler (*Vermivora chrysoptera*) probability of occupancy increased as the proportion of bare ground increased within a 1-km radius of the survey point in Manitoba, 2008-2010. Standard errors shown as dashed lines. Survey data were collected by Bird Studies Canada and used with permission.

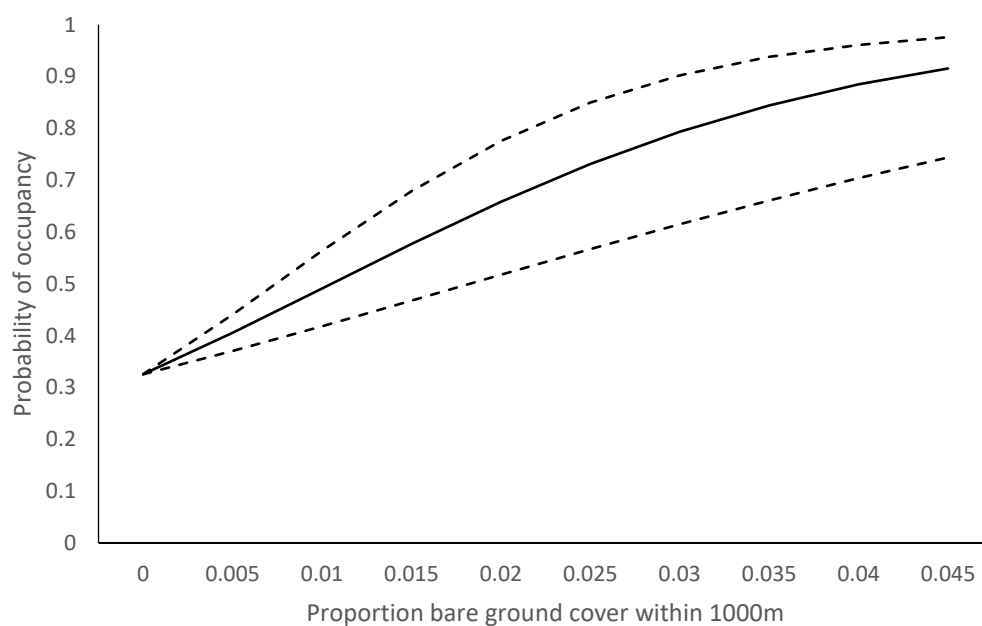
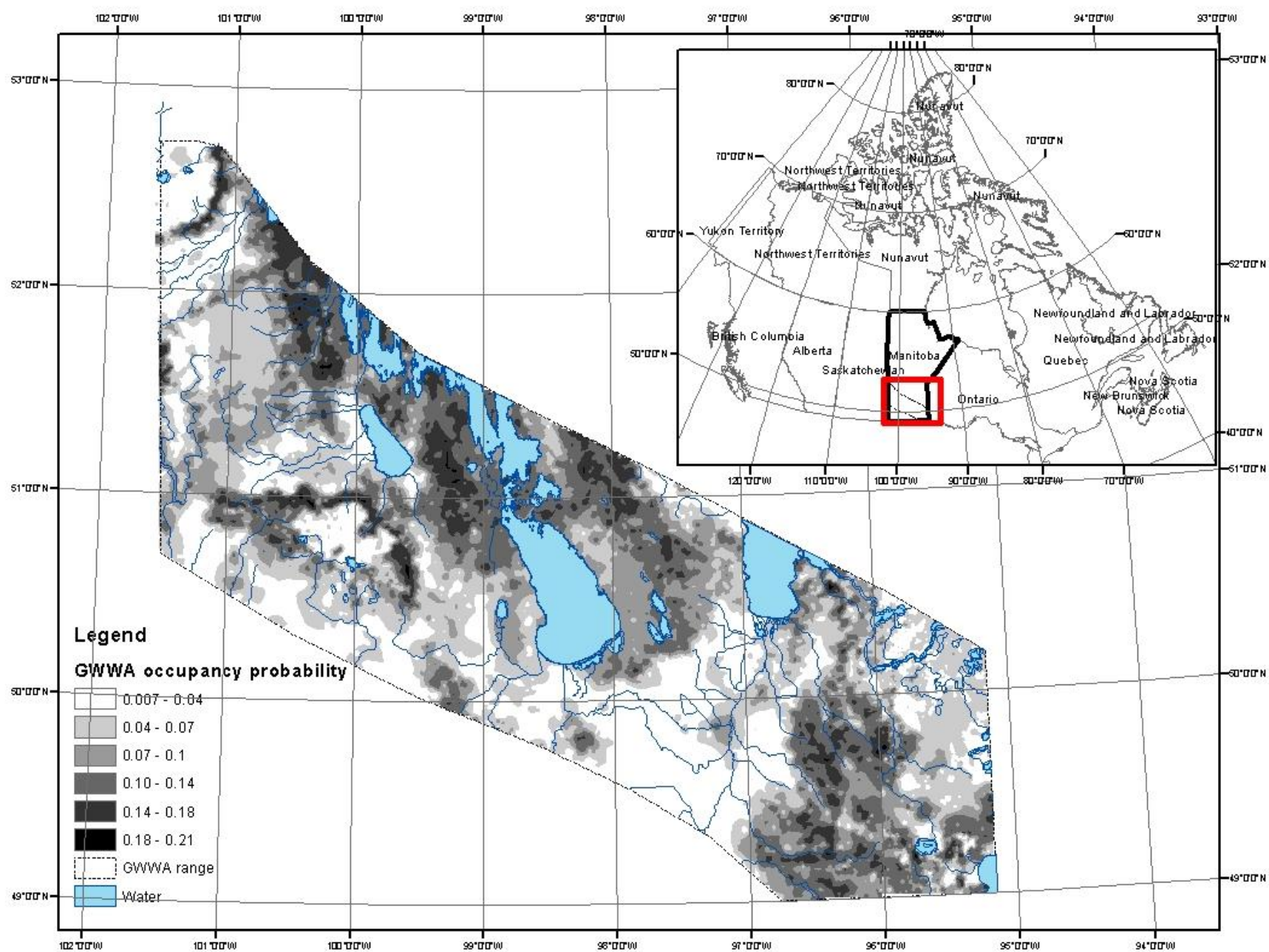


Figure 2.4. Predictive occupancy map of Golden-winged Warbler (*Vermivora chrysoptera*) probability of presence throughout known range in Manitoba, Canada.





Appendix 2.1. Preliminary model selection of aggregate and matrix variables to determine which scale received the most support using Akaike's Second Order Information Criterion. ED = edge density.

Aggregate variables		Matrix variables	
Parameter	AIC <sub>c</sub>	Parameter	AIC <sub>c</sub>
Total ED 1000	<b>231.1</b>	Ag cover 1000	<b>126.26</b>
Total ED 2000	<b>232</b>	Ag cover 2000	163.8
Total ED 4000	<b>233</b>	Ag cover 4000	187.84
Forest cover 1000	<b>231.02</b>	Ag edge 1000	<b>126.22</b>
Forest cover 2000	<b>232</b>	Ag edge 2000	163.74
Forest cover 4000	<b>233.01</b>	Ag edge 4000	187.84
Matrix cover 1000	<b>215.18</b>	Rd cover 1000	<b>206.31</b>
Matrix cover 2000	229.08	Rd cover 2000	227.58
Matrix cover 4000	233.05	Rd cover 4000	233.05
		Rd edge 1000	<b>206.27</b>
		Rd edge 2000	227.51
		Rd edge 4000	233.03
		Bare cover 1000	<b>179.04</b>
		Bare cover 2000	204.05
		Bare cover 4000	221.07
		Bare edge 1000	<b>187.41</b>
		Bare edge 2000	221.19
		Bare edge 4000	243.66
		Grass cover 1000	<b>198.87</b>
		Grass cover 2000	220
		Grass cover 4000	226.05
		Grass edge 1000	<b>198.9</b>
		Grass edge 2000	220
		Grass edge 4000	226.88
		Conif cover 1000	<b>183.34</b>
		Conif cover 2000	198.67
		Conif cover 4000	214.31
		Conif edge 1000	<b>184.46</b>
		Conif edge 2000	200.16
		Conif edge 4000	212.31

Appendix 2.2. Secondary model selection of aggregate landscape variables. Models with  $AIC_c < 2$  were retained for the final model set.

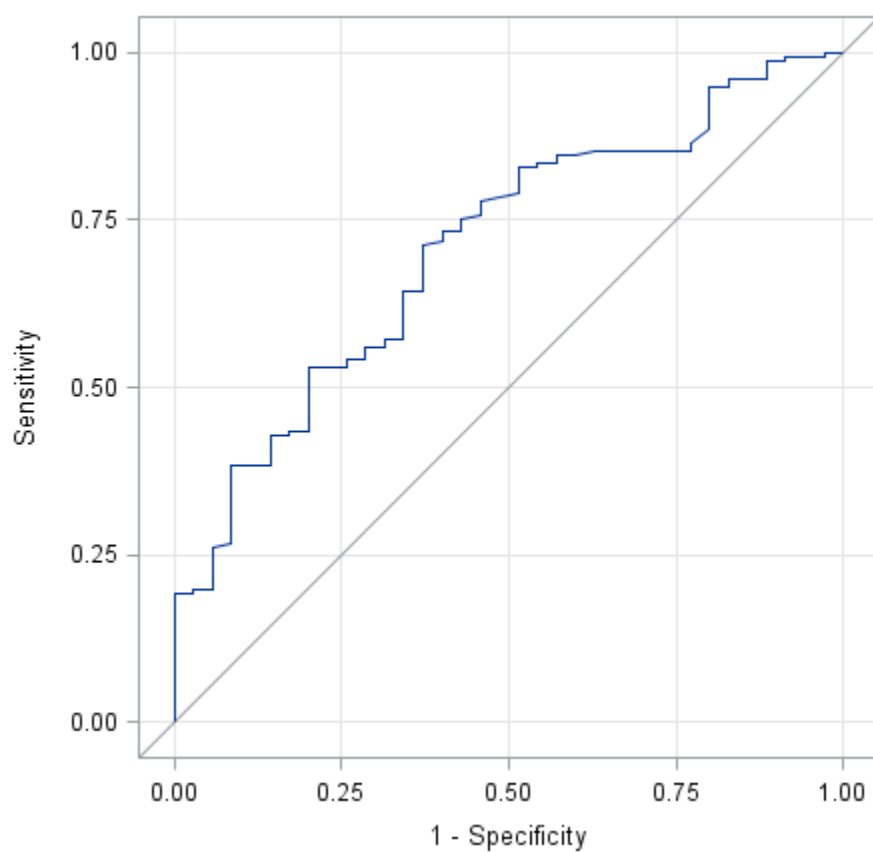
Aggregate Model Set	$AIC_c$
<b>Total Matrix Cover 1km</b>	<b>215.18</b>
Forest cover 1km	231.02
Total edge density 1km	231.1
Total edge density 2km	232
Total forest cover 2km	232
Total matrix cover 4km + Total edge density 4km	232.07
Total matrix cover 2km + Total edge density 2km	232.08
Total matrix Cover 1km+ Total edge density 1km	232.11
Forest cover 1km + Total edge density 1km	232.11
Total edge density 4km	233
Total forest cover 4km	233.01
Total forest cover 2km + Total edge density 2km	233.82
Total forest cover 4km + Total edge density 4km	235



Appendix 2.3. Secondary model selection of matrix element variables associated with composition and configuration of individual matrix elements within the landscape. Models with  $AIC_c < 2$  were retained for the final model set.

Matrix element model set	$AIC_c$
<b>Agriculture cover 1km</b>	<b>177.78</b>
<b>Agriculture edge density 1km</b>	<b>177.89</b>
<b>Bare ground cover 1km</b>	<b>179.04</b>
Coniferous cover 1km	183.34
Coniferous edge density 1km	184.46
Bare ground edge density 1km	187.41
Grassland cover 1km	198.87
Grassland edge density 1km	198.9
Road edge density 1km	206.27
Road cover 1km	206.31

Appendix 2.4. Model validation using 10-fold cross validation to calculate the area under the curve (AUC) for the top-ranking Golden-winged Warbler (*Vermivora chrysoptera*) occupancy model, AUC = 0.72.



**Chapter Three.** Source-sink dynamics of the Golden-winged Warbler in a fragmented landscape at the northern limit of its range.

**Abstract**

An understanding of how spatial and temporal variability may drive changes in population demographics is essential to evaluate source-sink dynamics and long-term metapopulation viability, and to develop effective management strategies. The Golden-winged Warbler (*Vermivora chrysoptera*) is a rapidly declining neotropical migrant facing range-wide habitat loss and fragmentation. This threatened species has been well-studied elsewhere in the range, but population dynamics has not yet been examined at its northern limit, the only portion of the range that remains allopatric to Blue-winged Warblers and where hybrid individuals are rare. From 2011 to 2015, I intensively monitored Golden-winged Warblers at seven study sites with varying levels of fragmentation across southeast Manitoba, Canada. I examined whether nest survival was impacted by fragmentation at a landscape or territory scale, by matrix habitat type, and by temporal factors. I also examined the impact of fragmentation on brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) and the consequences to fecundity. Using data on survival and fecundity, I calculated population growth rates for the southeast Manitoba metapopulation and determined whether subpopulations functioned as sources or sinks. I also calculated the sensitivity and elasticity of population growth to demographic parameters. Adult survival did not vary by sex, year, or study site. Nest survival was only influenced by day of year; it was independent of habitat fragmentation and other habitat variables at all scales. However, brood parasitism increased with greater fragmentation, and reduced the number of young fledged per nest. I was unable to identify any source subpopulations in southeast Manitoba; all sites were consistently sinks that could only persist with immigration. Population growth was driven most by adult survival rates, which is challenging to manage. To improve

fecundity, management efforts should focus on reducing Brown-headed Cowbird brood parasitism by encouraging the creation and maintenance of suitable habitat in patches with greater forest cover and less edge.

## Introduction

Species with a broad range are typically distributed across a heterogeneous landscape in subpopulations that are linked via dispersal (Harrison 1994), and thus subpopulations may have variable rates of intrinsic growth (Harris 1992, Robinson 1992, Donovan et al. 1995, Robinson et al. 1995). Source-sink dynamics may result from this pattern if survival and/or productivity are spatially variable and where the dispersal of individuals from source subpopulations can sustain (at least temporarily) sink subpopulations (Brown and Kodric-Brown 1977, Pulliam 1998). Source-sink dynamics have been used to explain local population persistence in low quality habitats (Dias 1996, Foppen et al. 2000, Murphy 2001) and to argue for the identification and conservation of source habitats (Robinson et al. 1995, Dias 1996). For rare or threatened species, in particular, distinguishing whether subpopulations are sources or sinks can help to predict long-term population viability and contribute to conservation and recovery efforts. A comprehensive understanding of population dynamics requires knowledge of habitat-specific subpopulation demography, the life-history stages that limit population growth, and the habitat or environmental conditions that are responsible for variations among subpopulations.

Human-caused habitat conversion and resulting fragmentation is a major driver of spatial heterogeneity and results in fewer, more isolated habitat patches with greater amounts of edge. Habitat fragmentation can impact individual species positively, negatively, or not at all depending upon how ecological processes are altered (Andrén 1994, Fahrig 1997, Schmiegelow and Monkkonen 2002, Fahrig 2003, Ewers and Didham 2006, Smith et al. 2011). Reduced forest cover, edge effects, and/or increased isolation of habitat patches can change or reduce availability of resources such as nest sites or prey (Saunders et al. 1991, Andrén 1994, Debinski and Holt 2000, O'Donnell 2000) and can alter competition for those resources with hetero- and

conspecifics (Fagan et al. 1999, Piper and Caterall 2003). Reduced nest success may also result from an increase in predators or brood parasites that preferentially use edges or access patches via the matrix (Gates and Gysel 1978, Brittingham and Temple 1983, Andr  n et al. 1985, Wilcove 1985, Crooks and Soul   1999, Chalfoun et al. 2002a, Chalfoun et al. 2002b). Further, adult and juvenile survival can be reduced by increased isolation of habitat patches that impact the ability to disperse across a hostile matrix (Ewers and Didham 2006). If survival and productivity remain reduced below what is necessary for the population to remain sustainable without immigration, the result is a habitat sink. While numerous studies have examined nest success in fragmented landscapes (Villard et al. 1992, Chalfoun et al. 2002), our knowledge of habitat-specific survival and productivity is still lacking for most species (Faaborg et al. 2010) and is necessary to determine population growth rate and viability.

Patches may be embedded within a hostile matrix that can impact the ecological processes within (Saunders et al. 1991, Fahrig 2003). The type and the quality of land cover surrounding isolated patches of primary habitat can determine species occupancy and behavioral and community responses to fragmentation (Kupfer et al. 2006). Matrix land cover has been hypothesized to influence the response of birds to habitat fragmentation via several mechanisms, including: 1) inter-patch movement (dispersal hypothesis): matrix type mediates species' ability to move between primary habitat patches; 2) supplemental or complementary resources (habitat compensation hypothesis): different matrix types provide additional or alternative food sources or nest sites, supporting greater abundances than expected if a species were limited to primary habitat patches alone; 3) vegetation structure of edges (edge effects hypothesis): matrix types that are dissimilar to primary habitat increase the negative impacts of edges through nest predation or parasitism, and may alter within-patch vegetation structure, composition, and

microclimates; and 4) anthropogenic land use (disturbance hypothesis): different matrix types have different levels of human activity (e.g., mining, logging, noise, and traffic) that can impact birds in their primary habitat (Kennedy et al. 2010). A multi-species meta-analysis showed that patch area and isolation alone are poor predictors of habitat occupancy (Prugh et al. 2008), so quantifying species' responses to different types of matrix land cover may provide a better understanding of occupancy and population dynamics.

I investigated the source-sink dynamics of a federally threatened habitat specialist to better understand the relationships among fluctuating demographics, population viability, habitat characteristics at multiple scales, and matrix composition. Golden-winged Warblers (*Vermivora chrysoptera*) are a rapidly declining, threatened species (Sauer et al. 2014) that require disturbance-created early- successional forest patches embedded within mature forest to nest and raise young (Buehler et al. 2007, Confer et al. 2011). They have declined as much as 8.5% annually since 1966 throughout their range (Larkin and Bakermans 2012, Sauer et al. 2014). Golden-winged Warbler declines have been attributed to numerous, likely interacting factors including habitat loss, Brown-headed Cowbird parasitism, and hybridization with and subsequent replacement by Blue-winged Warblers (*Vermivora cyanoptera*; Buehler et al. 2007, Vallender et al. 2009, Confer et al. 2011). However, the multi-scale impacts of human disturbance on source-sink population dynamics are not well understood (but see Thogmartin 2010 for indirect impacts to occupancy). In Manitoba, early-successional forests used by Golden-winged Warblers are mostly created anthropogenically through logging or resource extraction. The result is a landscape mosaic of young forests in various stages of regeneration embedded within a matrix of varying amounts of mature forest and human land uses such as agriculture and livestock grazing. This allows us to compare sub-populations within habitat patches embedded in a landscape

matrix reflecting varying amounts of anthropogenic disturbance. Golden-winged Warblers are at the northern periphery of their range in Manitoba and provide us with an opportunity to examine source-sink dynamics of a declining species at a range extreme, where species can be at greater risk of extinction (Mehlman 1997). Moreover, the Manitoba population of Golden-winged Warblers is the only one that remains allopatric to the closely related Blue-winged Warbler, thus providing a unique opportunity to evaluate the impacts of human disturbance on source-sink dynamics of this species without the potentially confounding effects of competition or hybridization with Blue-winged Warblers.

To gain a better understanding of warbler population dynamics its relationship with habitat characteristics at multiple scales, I measured warbler seasonal productivity and survival throughout the region. I also assessed whether breeding sites were source or sink populations over a five-year period. To identify the most important drivers of warbler population dynamics, I determined the relative importance of seasonal productivity and adult and juvenile survival. I predicted that warbler survival would be similar to that in other parts of the range (Bulluck et al. 2013), and that the major driver of population dynamics would be low or variable seasonal productivity. I predicted that sites with lower forest cover and greater amounts of edge at a landscape scale would have lower seasonal productivity as a result of increased brood parasitism and predation of nests and fledglings (Peterson 2013). I also predicted that Golden-winged Warbler subpopulations would consist of temporally and spatially variable sources and sinks, as has been observed in other warbler populations (Foppen et al. 2000, Zannette 2000, Perkins et al. 2003, Boves et al. 2013). Demographic monitoring can provide managers with information about whether management should be focused on increasing survival rates or increasing productivity;



distinguishing between the two is critical for a migratory species because the factors that impact survival and productivity may be seasonally and geographically distinct.

## Methods

### *Study Area*

I established seven 1000-m<sup>2</sup> study plots sites across the aspen parkland transition zone (APTZ) in southeast Manitoba (49° 46' N, 96° 29' W). Sites were chosen to represent a gradient of fragmentation amounts, had at least four Golden-winged Warbler territories, and were a minimum of 2-km apart to ensure independence. The APTZ is the transition zone between the former tallgrass prairie (now agriculture dominated) ecosystem to the west and the southern boreal forest to the east. The sites with higher amounts of fragmentation were embedded within landscapes of low-density human housing, agriculture, grazing, and/or active resource extraction, especially of aggregate used for building and maintaining roads. The remaining sites were located within the Sandilands provincial forest, which is used for forestry, conservation, and recreation, and dispersed across 125 km<sup>2</sup> (Figure 3.1). Sites varied in amounts of forest cover, edge densities, and matrix types (Table 3.1) and were widely dispersed across the limited range of the Golden-winged Warbler in SE Manitoba to avoid any geographical bias based on location of sites. The patches of early seral forest preferred by Golden-winged Warbler in Sandilands either occur naturally as a result of hydrology or are regenerating after being logged in 1996. Golden-winged Warbler prefer to nest in areas with a three-tier vertically stratified habitat structure, including a tree, shrub, and herbaceous layer (Artuso 2009, Confer et al. 2012). All study sites were dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), paper birch (*Betula papyrifera*), and/or bur oak (*Quercus macrocarpus*). The most

common shrubs included beaked hazel (*Corylus cornuta*), saskatoon (*Amelanchier alnifolia*), high bush cranberry (*Viburnum opulus*), and choke-cherry (*Prunus virginiana*).

### *Field Methods*

Field assistants and I monitored Golden-winged Warblers at each plot from May 15 – July 15 in the 2011 - 2015 breeding seasons. To distinguish among individuals and determine survival, we color-banded >90% of the adult males and >50% of the adult females in each sub-population. We target mist-netted territorial males using conspecific playback. The playback recording included both song types I and II (Highsmith 1989), and was broadcast from a speaker placed underneath the mist net for a maximum of 30 minutes. We captured females incidentally while targeting a male or by locating the nest and setting the net nearby during incubation or the nestling stage and captured them as they returned to the nest. We banded all adult birds with a USGS aluminum band and three unique color-bands to distinguish individuals. We aged birds as second year (SY) or after second year (ASY) based on plumage characteristics and feather wear (Pyle 1997).

We observed color-banded warblers for a minimum of 30 minutes every other day from May 15 – July 15 to determine annual return rates of birds, territory boundaries, pairing status, and reproductive activities. We tracked territorial males using behavioral clues such as singing and calling. To define territory boundaries, we followed singing males and took a minimum of 30 GPS points per male. We located nests using the behavioral clues of adults, which helped to minimize damage to vegetation that can be caused by systematic searching of an area. When we were sure of a nest location from behavioral clues, we approached a nest site. Once located, we monitored nests until they fledged or failed. Because Golden-winged Warbler nests are on the ground, the contents are easy to observe but also easy to disturb. We took precautions not to

trample nest vegetation by using a stick to check nest contents rather than closely approaching the nest and staying on already established trails to avoid impacting nest fates. When possible, we recorded the date the first egg was laid, the date that incubation began, the hatch date, and the fledge date. We monitored nests every other day so that we had an accurate date for hatching, fledgling, or failure. We banded nestlings with a single USGS aluminum band and one color-band on day five of the nestling stage or as close to it as possible. We considered a nest to be successful if banded adults were observed feeding banded fledglings. A nest was unsuccessful if adults abandoned the nest prior to the fledge date or if no fledglings were located post fledging.

While nesting success is one critical component of productivity, other important factors that influence the total number of fledglings produced per territory in a season should be considered (Thompson et al. 2001). Other studies of Golden-winged Warbler have revealed high mortality during the days immediately post-fledging (e.g., Petersen et al. 2013), so the number of fledglings that leave the nest will overestimate productivity. Conversely, nest survival alone can underestimate productivity because it does not account for re-nesting or double brooding (Thompson et al. 2001). Post-fledging, we attempted to locate each family group three times within the first week and count the number of fledglings to get as accurate an estimate of fledgling survival as possible. Each visit lasted until fledglings were successfully counted, or for up to one hour. Fledglings often beg loudly and are easy to locate and count. However, some fledglings are silent and adults cryptic when delivering food to a fledgling in the presence of a potential predator (i.e., a biologist). Therefore, my results should be interpreted with caution, as relying on fledgling counts alone may underestimate the true number of fledglings that survive to independence. If a nest failed prior to fledging, we immediately looked for a re-nest attempt. While we never observed double-brooding in Golden-winged Warblers, in the northern portion

of their range they will make up to two re-nesting attempts if nests fail early enough in the nesting cycle (L. Moulton, unpublished data).

### *Habitat metrics*

To quantify the impact of habitat characteristics on nest success and productivity, I calculated habitat metrics within a 200- and 1000-m buffer around each nest. The 200-m buffer represents a territory scale and corresponds to the average territory size for Golden-winged Warblers, as well as the home range size of common nest predators in our study area (e.g., chipmunks and other small mammals; Livoreil and Baudoin 1996, Marmet et al. 2009). The 1000-m buffer represents the landscape extent to which Golden-winged Warblers most strongly responded (Chapter 2). It is also the home range size often considered relevant for evaluating egg-laying behaviour for the brood parasitic Brown-headed Cowbird (Rothstein et al. 1984, Rothstein et al. 1986). At the landscape scale (1000-m), I calculated the percent forest cover and the edge density (ED). In this study area, anything that is not forest cover has been anthropogenically altered. I defined an edge as the boundary between contiguous forest and a recently or continually human-disturbed land-use type, which was most often an active aggregate mining operation, an agricultural field, or a road. I also measured the percent cover and edge densities of each matrix type individually. At the territory (200-m) scale, I calculated the percent forest cover and measured the distance (m) to the nearest human-disturbed edge (DTE). I used land cover classification data from GIS layers supplied by the Manitoba Land Initiative (MLI 2015, Tables 3.1 and 3.2), which distinguish among 18 distinct land cover classes. I overlaid the nest locations onto the land use layer and used analysis tools (proximity → buffer) in ArcMap 10.2 (ESRI 2014) to create 200-m and 1000-m buffers around each nest.

### *Survival analysis*

I used a Cormack-Jolly-Seber model structure to estimate annual adult or after-hatch-year (AHY) survival  $\phi$  (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992). My analysis included capture-resight information from 225 AHY male and female Golden-winged Warblers captured from 2011 to 2015 at the eight study sites. In addition, I calculated the AHY resight probability ( $p$ ). Though I banded 266 hatch year (HY) birds from 2011-2014, I could not estimate  $\phi$  due to the return of only one individual, presumably due to high dispersal rates and high mortality. I observed little movement within or among sites, and no banded birds outside of site boundaries, indicating high adult site fidelity. AHY survival might be underestimated, as survival estimates cannot account for dispersal among seasons (Marshall et al. 2004).

To estimate territorial adult  $\phi$ , I considered the unique effects of individual study site ( $p$ ), study year ( $t$ ), and sex ( $s$ ) as well as the combined effects of site, year, and sex, or  $\phi(t+s+p)$ . For adult recapture models, I considered a single-variable model of sex ( $s$ ). Including null survival and recapture models, I considered fifteen candidate models to examine the impacts of year, sex, and fragmentation on AHY apparent survival and resight probability. I then used an information theoretic approach using Akaike's information criterion corrected for small sample size ( $AIC_c$ ) to evaluate support for these *a priori* candidate models (Burnham and Anderson 2002). I conducted all analyses using program Mark (White and Burnham 1999) and assessed the goodness of fit for the top models using bootstrapping and median  $\hat{c}$  implemented in program Mark (White and Burnham 1999; Cooch and White 2014).

#### *Nest survival and fecundity*

Although I attempted to document all nesting attempts, there were some nests that failed early in the nesting cycle or that fledged before they were located. In addition, it is possible that biases in nest detection varied among sites due to differences in habitat conditions and

difficulties of locating nests. To account for potential biases in nest detection, I calculated nesting survival using the logistic exposure method (Shaffer 2004, Shaffer and Thompson 2007) and fecundity following Donovan et al. (1995). I estimated daily nest survival with a binomial response for each exposure period (success = 1, failure = 0; Shaffer 2004, Shaffer and Thompson 2007). I excluded the intervals during which a nest was not active (e.g., building and pre-laying). Per Dinsmore et al. (2002), I did not standardize individual covariates. I fitted all models using SAS proc GENMOD (SAS 2014).

I used an information-theoretic approach to compare the fit among alternative models derived from *a priori* hypotheses concerning the relationships between avian nest survival and habitat characteristics (Burnham and Anderson 2002). My set of ten candidate models consisted of: 1) a landscape-scale habitat model including percent forest cover and anthropogenic edge density within 1000 m; 2) a territory-scale habitat model including percent forest cover and distance to forested edge within 200 m; 3) a landscape-scale matrix model including percent cover of each matrix type (agriculture, mining, or roads), and edge density of each matrix type within 1000 m; 4) a local-scale nest habitat model including percent canopy cover, percent concealment of the nest at nest height, canopy height, and nest substrate height, measured at the nest; 5) an overall habitat model including variables from 1, 2, 3, and 4 above; 6) a temporal effects model with year (2011, 2012, 2013, 2014, 2015), Julian date, quadratic Julian date, and nest stage (laying, incubation, or nestling); 7) a brood parasitism model including whether the nest had been parasitized by one or more Brown-headed Cowbirds or not parasitized; 8) a parasitism and landscape model designed to examine additive effects of Brown-headed Cowbird parasitism and landscape scale habitat factors (% forest cover and edge density); 9) a global model including all effects; and 10) a null model with only an intercept.

My landscape and territory-scale models were intended to measure how nest survival related to habitat amount and fragmentation independently of matrix type and composition. My matrix model measured how nest survival was impacted by the amount and edge densities of specific matrix elements within the landscape. My overall habitat model measured how habitat characteristics at both territory and landscapes scales were related to nest survival in comparison to temporal and brood parasitism effects. My nest habitat model was intended to examine the effects of habitat structure immediately surrounding the nest. I included an explicit temporal effects model because day of year, quadratic day of year, year, and nest stage (laying, incubation, nestling) are known to have an impact on nest survival in other species (Dinsmore et al. 2002, Grant et al. 2005, Hoover 2006) and I wanted to compare the influence of these factors to those of habitat characteristics. Finally, I included a brood parasitism effects model to determine whether Brown-headed Cowbird parasitism impacted nest survival in this population.

To assess collinearity, I used PROC REG (SAS 2014) to estimate the tolerance for variables in the global model. Percent forest cover at 200 m and percent forest cover at 1000 m had tolerance values lower than 0.20 in the global model, suggesting that multicollinearity may be an issue. I explored reducing the collinearity by centering the variables on their means; however, this did not reduce the collinearity, so I presented the models as they were originally formulated. All other variables had tolerances greater than 0.20, indicating no issue with multicollinearity. I plotted the standardized deviance residuals from each global model against the explanatory values and found no patterns, suggesting that transformations of the data were not necessary. No outliers (standardized residual deviance  $> 3$ ) occurred within the data set. I evaluated the goodness-of-fit of the global model with a Hosmer-Lemeshow test (Hosmer and Lemeshow 2000).

I ranked candidate models using Akaike's information criteria adjusted for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002). The  $\Delta AIC_c$  allowed direct comparison of models in relation to the optimum; models with  $\Delta AIC_c < 2$  were considered to have strong support. Only the temporal model was given strong support, so I based final conclusions on this model alone (Burnham and Anderson 2002, Arnold 2010). To estimate the cumulative nest survival over the complete nesting period, I used the estimate of (daily survival)<sup>24</sup> because 24 is the average number of days to complete a nest cycle (Thompson and Shaffer 2007).

Estimates of nest survival are not able to account for partial nest failures and simply count all nests that fledge >1 young as successful. Yet, partial nest losses impact productivity by reducing the number of nestlings fledged from each successful nest. Partial nest failures can result from predation, brood parasitism, illness, or starvation (pers. obs.). Golden-winged Warblers are a particularly difficult species to estimate accurate productivity for because nests are hard to locate and family groups can brood split and move outside of the established territory within a few days (Petersen et al. 2013). I used a combination of nest-monitoring and fledgling surveys to obtain fledged brood sizes and verify territory success. I defined productivity as the total number of fledglings produced per female per season and defined fecundity ( $F$ ) as the total number of juvenile females produced per adult female, assuming a 50% sex ratio (Vallender et al. 2007). To determine the effects of temporal, patch, landscape, and matrix elements on seasonal productivity, I fitted generalized linear models with a Poisson distribution (proc GENMOD, SAS Institute) and used the same model set that I used for nest survival, except that I omitted the nest characteristics model and the 'stage' and 'day of year' covariates of the temporal model as they did not apply. I evaluated the goodness-of-fit of the global nest survival model with a Hosmer and Lemeshow (2000) goodness-of-fit test and the global seasonal



productivity model using a  $k$ -fold cross validation (Boyce et al. 2002). I assessed multicollinearity in the global models by examining tolerance values for the covariates (Allison 1999) and checked for overdispersion in the data by examining the Pearson  $\chi^2$  test statistic for the global models divided by degrees of freedom (Burnham and Anderson 2002).

To further explore whether Brown-headed Cowbird parasitism rates were impacted by fragmentation at a territory- or landscape-scale, I fitted a logistic regression model in Proc GENMOD (SAS 2014) and used a similar model selection approach as before (Burnham and Anderson 2002) to evaluate support for six candidate models: 1) a landscape model including the covariates percent forest cover and edge density at a 1000-m scale; 2) a territory model including the covariates percent forest cover at a 200-m scale, and distance to edge; 3) a temporal model including nest initiation date; 4) a total fragmentation model including both landscape and territory fragmentation covariates [edge density at a 1000-m scale and distance to edge]; 5) a global model including all covariates; and 6) a null model. I evaluated the goodness-of-fit of the global model with a Hosmer-Lemeshow test (Hosmer and Lemeshow 2000). Because Brown-headed Cowbirds often remove host eggs in nests they parasitize and Brown-headed Cowbird young can outcompete host nestlings for resources (Lowther 1993), the number of host nestlings that fledge may differ between successful nests that are parasitized or not parasitized. For nests that successfully fledged host young, I compared the mean number of fledglings per parasitized nest to the mean number of fledglings in non-parasitized nests using a  $t$ -test.

### *Population dynamics*

To determine the population growth rate of Golden-winged Warbler populations in south-east Manitoba at each of my study sites, I followed methods outlined by Caswell (2001) and Pulliam (1988) and commonly used in other migratory bird species (Donovan et al. 1995,

Buehler et al. 2008, Bulluck et al. 2013). I built simple two stage population matrices (Caswell 2001) across all sites to calculate the growth rate,  $\lambda$ , of the population. Matrix elements were largely based on population-specific data I collected. I calculated fecundity from nesting data collected from 2011 through 2015 and estimated adult and juvenile survival by analyzing my banding and resighting data (2011-2015).

I defined annual fecundity ( $F$ ) as the number of juvenile females produced annually per breeding female (Ricklefs 1973). To calculate fecundity, I used the equation:

$$F = \text{seasonal productivity} \times \text{sex ratio}$$

where the sex ratio was assumed to be 0.5 (Vallender et al. 2007). To calculate  $\lambda$ , I used the equation defined by Pulliam (1988):

$$\lambda = P_A + P_J * F$$

where  $P_A$  is AHY female apparent survival, and  $P_J$  is HY female survival, and  $F$  is fecundity. I assumed female juvenile survival to be half that of female adult survival (Temple and Cary 1988, Donovan et al. 1995). In a finite population,  $\lambda = 1$  for a population at equilibrium,  $\lambda > 1$  for a source population, and  $\lambda < 1$  for a sink population (Pulliam 1988).

To better define the relationship between survival, fecundity and population growth rates, I calculated the sensitivity. Sensitivity is the rate of change in the population growth rate with respect to a numerical change in fecundity or survival (Caswell 2001). Survival and fecundity are measured with different units, however, so to compare them I also calculated the elasticity, or proportional sensitivity, for fecundity and survival values. To determine the survival and fecundity values required for a stable population growth rate, I modeled the relationship between deterministic population growth and a range of fecundity values (0–3.0 young fledged/year) and

adult and juvenile survival rates (0–100%). I used PopTools (Hood 2010) to estimate lambda ( $\lambda$ ) and elasticity values.

## Results

### *Apparent Survival*

I banded 225 AHY and 259 HY Golden-winged Warblers beginning in 2011. From 2012 to 2015, 78 AHY warblers returned in a subsequent year and 147 were not seen again. However, of those that returned, I found no evidence that AHY males dispersed any more than 100 m between seasons. Territory shifts did occur, but in every case the new territory still included a portion of the previous year's territory. AHY females moved up to 450 m between seasons, but I found no evidence of among-plot movements. Only a single female HY warbler was resighted early in the 2014 season and dispersed outside the plot before I was able to recapture and determine her identity. The lack of HY returns suggests low natal philopatry in this species.

The goodness of fit test provided no evidence of a lack of fit for the global model after being corrected for overdispersion ( $\hat{c} = 1.06$ ), thus, I used the estimates of territorial adult survival from the top model in the population assessments. The most supported model was  $\phi(.)p(s)$ , indicating constant survival and resight probabilities that vary by sex (Table 3.3). I estimated apparent survival ( $\phi$ ) at 0.41 (SE = 0.02). Male resight probability was 0.84 (SE = 0.04), and female resight probability was 0.66 (SE = 0.11). Though fewer females were marked, the resight probability accounts for this (Lebreton et al. 1992, White and Burnham 1999), suggesting that female site fidelity is simply lower than male site fidelity. The most highly ranked survival/resight models all included a resight probability that varied by sex only. There was no evidence for an impact of sex, year, or study site on AHY  $\phi$ .

### *Nest survival and seasonal productivity*

I monitored 115 nests from 2011 – 2015. I found no evidence of double-brooding, although females made up to three nesting attempts in one season if a previous attempt was unsuccessful, with a mean of 6 days between the time a previous nest failed and the first egg was laid in the re-nest (range = 3 – 9,  $n = 21$ ). The mean date of first nest initiation (first egg laid) was 31 May (19 May – 10 June,  $n = 82$  nests), the mean date of second nest initiation was 15 June (5 June – 30 June,  $n = 28$ ), and the mean date of third nest initiation was 20 June (16 June – 23 June,  $n = 5$ ). The mean number of nestlings that fledged per nest was 2.22 ( $SE = 0.20$ ), but the mean number of fledglings that could be accounted for post-fledging was 1.94 ( $SE = 0.17$ ) because not all fledglings survived after leaving the nest.

There was no evidence of lack of fit of the global nest survival model based on the Hosmer and Lemeshow (2000) goodness-of-fit test ( $\chi^2 = 2.63$ ,  $p=0.95$ ) and the dispersion parameter ( $\hat{c} = 1.03$ ). The only nest survival model receiving any support was the temporal model, which included the covariates year, nest stage, day of year, and quadratic day of year (Table 3.4). The only factor with confidence intervals that did not include zero was day of year (Table 3.5). Daily nest survival decreased as the breeding season progressed in all years ( $\beta = -0.71$   $SE = 0.27$ ), from 0.986 to 0.856 over the observed length of the breeding season (Figure 3.2). The habitat fragmentation models at both scales were poor predictors of daily nest survival, as was the matrix model. Interestingly, I did find a significant correlation between nest attempt and distance to edge (0.20,  $p=0.033$ ), indicating that Golden-winged Warbler place nests closer to a forested edge for early nest attempts and further from a forested edge for later nest attempts. However, there was no evidence to suggest the distance to edge impacted nest survival. The mean daily nest survival was 0.964 ( $SE = 0.013$ ) and overall nest survival was 0.418 ( $SE = 0.104$ ).

The  $k$ -fold validation of the global seasonal productivity model indicated that the Poisson distribution provided a good fit to the data with a positive mean correlation between observed and predicted fledglings per territory ( $r = 0.40$ , 95% CI = 0.18 – 0.84). The most supported seasonal productivity models included BHCO parasitism and landscape characteristics (Table 3.6). For nests that survived to fledging, Brown-headed Cowbird brood parasitism reduced productivity ( $t(72) = 2.87$ ,  $p = 0.005$ ) from 3.51 (SE = 0.15) to 2.25 (SE = 0.37) fledglings per female. Although confidence intervals of forest cover and forest edge density included zero, their inclusion improved model fit, suggesting that in combination, these variables influence productivity. As forest cover increased, seasonal productivity increased while the opposite was true for forest edge density. An alternate explanation may be that this result is a consequence to the tendency for AIC to select overly complex models (Mundry 2011) and thus, it may be spurious. The mean annual seasonal productivity per female across all years was 2.34 (SE = 0.10), so fecundity ( $F$ ) was 1.17.

Brood parasitism rates were most strongly impacted by landscape-level habitat characteristics (forest cover and edge density; Table 3.7). The top-ranked model included only percent forest cover ( $\beta = -21.7$ , SE = 7.65) and edge density ( $\beta = 0.005$ , SE = 0.002) at a 1000-m scale. Though brood parasitism did not directly impact whether a nest fledged or did not fledge, it impacted productivity via reductions in the number of young fledged.

#### *Population dynamics*

I estimated  $\lambda$  for the southeast Manitoba population as 0.65, suggesting that this population would decline at a rate of 35 % per year unless mortality was offset by immigration from other source populations. For females whose nests were parasitized by Brown-headed Cowbirds,  $\lambda$  was reduced to 0.62 compared to a  $\lambda$  of 0.75 for those not parasitized. Elasticity

values show that population growth rates were most impacted by changes in adult survival when juvenile survival is low (Table 3.8). To achieve stable growth rates, Manitoba populations on average would need a fecundity of 2.88 female young fledged per year. Juvenile survival would need to increase to 0.51 to achieve a stable population growth rate, a rate that is greater than the apparent adult survival, and thus unlikely. To reach stable growth, adult survival would need to increase to 0.80 if juvenile survival and fecundity were held constant.

## **Discussion**

Apparent survival and seasonal productivity estimates were below levels needed for population stability and indicate a declining Golden-winged Warbler metapopulation in this region of southeast Manitoba. In contrast to my predictions, population growth rates were consistently negative temporally and across all sites. My  $\lambda$  estimate suggests this population is declining at a mean rate of 35% per year, a greater rate than was calculated for both Tennessee and Ontario populations (Bulluck et al. 2013). In contrast, breeding bird survey data for Manitoba indicates a 21.85% (95% CI: 5.59, 55.96) increase in abundance from 2005 – 2015; however, the level of confidence is low and the results are imprecise due to the small sample size of only six survey routes (Sauer et al. 2017). If this portion of the southeast Manitoba population cannot sustain itself, the value of this population as a refugia for phenotypically pure Golden-winged Warblers free from contact with Blue-winged Warblers is in jeopardy.

Increased nest predation along habitat edges of temperate forests has been frequently reported (Gates and Gysel 1978, Andrén et al. 1985, Wilcove et al. 1986, Andrén and Angelstam 1988, Möller 1989, Peak 2007) The prevailing explanation for increased predation near forest edges has been the high concentration of predators based in the surrounding matrix entering the forest to forage (Angelstam 1986, Andrén and Anglestam 1988, Small and Hunter 1988).

However, I found no direct impact of forest cover, edge, or matrix composition on overall nest success of Golden-winged Warblers. Chalfoun et al. (2002) found that the response of nest predators to fragmentation is complex, and dependent upon predator/parasite species and context. Multiple studies in both predominately forested and agricultural landscapes have found that small mammals were equally abundant at edges and in the interior of forests (Heske 1995, DeGraaf et al. 1999, Menzel et al. 1999, Chalfoun et al. 2002). Similarly, I suggest that nest predators in this landscape are ubiquitous and nest predation is more strongly influenced by predator activity and search patterns in close proximity to the nest. Thompson et al. (2002) hypothesized that local habitat conditions may be more important than landscape structure if nest predators are not constrained by habitat at larger scales.

Brown-headed Cowbirds are known to concentrate at habitat edges (Brittingham and Temple 1983) and my results confirmed that Brown-headed Cowbird parasitism was more frequent as the edge density between forest and human lands uses increased. Although not the primary cause of nest failure, my results suggest that cowbird parasitism is a limiting factor for Golden-winged Warbler population growth across all study sites because it leads to decreases in productivity. Cowbirds can contribute to lower productivity directly by destroying eggs or nestlings (Arcese et al. 1996, Hoover and Robinson 2007, Conkling et al. 2012). Cowbirds can also decrease the number of fledglings produced indirectly as a consequence of increased competition for parental care, which can decrease host brood size and condition (McGeen 1972, Donovan et al. 1995, Rasmussen and Sealy 2006, Peterson et al. 2012, Jenkins and Faaborg 2016). Cowbird nestlings grow faster, beg more, and often receive higher rates of provisioning than nestlings of host species (Dearborn et al. 1998, Lichtenstein and Sealy 1998). The population growth rate for Golden-winged Warblers dropped to 0.62 with brood parasitism and

increased to 0.75 in the absence of brood parasitism. Though this was not the difference between a source and a sink habitat, it was the only mechanism I was able to define as having a direct impact on Golden-winged Warbler productivity and population growth rate.

Although it is of conservation concern, Brown-headed Cowbird brood parasitism cannot be easily managed. Like nest predators, Brown-headed Cowbirds are ubiquitous across the landscape, and were detected at every study site. Brown-headed Cowbird control programs have been successful elsewhere, particularly for increasing nest success of the Black-capped Vireo (*Vireo atricapillus*), another early-successional specialist, but the costs for a wide-ranging bird would be prohibitive (Wilsey et al. 2014). Instead, the best approach would be to limit the amount of anthropogenic edge in the landscapes where Golden-winged habitat is created or maintained. While this may not be possible for existing habitat, this should be considered if early successional habitat is created for use by Golden-winged Warblers.

Adult survival was independent of year, sex, and habitat. The mean apparent survival of adult Golden-winged Warblers ( $0.41 \pm 0.02$ ) was at the lowest end of the range of estimates observed in other Neotropical migrants ( $0.41 - 0.83$ ; Faaborg et al. 2010). Apparent  $\phi$  estimates for other warblers of conservation concern include the Golden-cheeked Warbler (*Setophaga chrysoparia*) at  $0.47 \pm 0.02$  (Duarte et al. 2014); Black-throated Blue Warbler (*S. caerulescens*) at  $0.43 \pm 0.04$  (Sillett and Holmes 2002); and Cerulean Warbler (*S. cerulea*) at  $0.54 \pm 0.06$  (Buehler et al. 2008). Adult apparent survival was 33% lower than other declining Golden-winged Warbler populations (Bulluck et al. 2013) yet Tennessee ( $0.62 \pm 0.11$ ) and Ontario ( $0.62 \pm 0.08$ ) (Bulluck et al. 2013) populations have been declining by ~8% per year (Sauer et al. 2008), indicating that a higher survival rate still did not offset low seasonal productivity. Elasticity values indicated adult survival was the biggest driver of population trends, a result



frequently observed in species with high adult survival (Festa-Bianchet et al. 1998, Cooch et al. 2001).

I was unable to quantify the amount of immigration and emigration among subpopulations or between years so my apparent  $\phi$  estimates cannot account for dispersal events and therefore underestimate true  $\phi$  (Brawn and Robinson 1996, Cilimbur et al. 2002). Dispersal events between high- and low-quality habitat patches could help alleviate demographic pressures placed on less productive populations, and although I did not directly observe any adult dispersal between breeding sites, I know from my estimates of population growth that immigration must occur for these populations to have persisted through the course of this study. A study of Prothonotary Warblers found that true  $\phi$  was underestimated by 17% for males and 19% for females when dispersal was unaccounted for (Marshall et al. 2004), so future studies would benefit from incorporating a way to calculate dispersal rates.

The overall daily nest survival (0.964) was within the range of estimates found in other Golden-winged Warbler populations (Bulluck et al. 2008, Bulluck et al. 2013, Aldinger and Wood 2014, Aldinger et al. 2015, see Appendix 3). Nest survival decreased over the breeding season and productivity decreased as a result of Brown-headed Cowbird brood parasitism, again consistent with Golden-winged Warbler nest survival elsewhere in the breeding range (Bulluck et al. 2013, Aldinger et al. 2015) and other passerines in a range of habitat types (Grant et al. 2005, Davis et al. 2006, Peak 2007). Arrival and territory establishment date can strongly influence breeding success as birds that initiate nests earliest have the highest chance of success. The primary cause of avian nest mortality is predation (Ricklefs 1969, Martin 1993) and Golden-winged Warblers are no exception (Bulluck et al. 2008, Kubel and Yahner 2008, Bulluck et al. 2013, Aldinger and Wood 2014). In our study area, the most commonly observed nest predators

include mammals such as the eastern chipmunk (*Tamias striatus*), thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*), and the eastern garter snake (*Thamnophis sirtalis*). Small mammals and snakes become noticeably more active as the temperature increases and they are feeding their own young, so birds that can fledge nests more quickly have an advantage. Arrival time generally depends on climatic conditions and we observed later first arrival dates during cold years (pers. obs.), so changes in climate are an important factor to consider in future studies.

Donovan and Thompson (2001) suggest that a nest survival rate of 0.25 to 0.30 is needed to balance juvenile and adult mortality. My nest survival estimates average well above that (0.42) over the past five breeding seasons, yet the population is still a sink (Pulliam 1988). More important than nest survival is the number of young that survive from each nest, a number that appears to be lower in Manitoba than elsewhere (Bulluck et al. 2013). Management of this species in Manitoba could focus on increasing fecundity by decreasing Brown-headed Cowbird brood parasitism. While it is not realistic to call for direct reductions of Brown-headed Cowbird populations due to the expense of cowbird control programs, an increase in fecundity could be accomplished indirectly by increasing forest cover and minimizing anthropogenic edges at a landscape scale. Golden-winged Warbler habitat should be created and maintained with this goal in mind.

Efforts to conserve threatened and endangered species frequently focus on the creation and maintenance of high-quality source habitats but it is important not to discount the contributions of sink habitats to the overall stability and long term survival of a metapopulation (Howe et al. 1991, Foppen et al. 2000, Murphy 2001). Perhaps some sinks function as sources in years with higher reproduction or survival than observed in the limited time period of this study (Dias 1996, Johnson 2004). Because I was not able to calculate emigration, it is also possible that

adults or juveniles may eventually disperse to higher-quality source habitats (Foppen et al. 2000). While sink populations are individually more vulnerable to a year of poor productivity or to a stochastic event, a high abundance of small sink subpopulations helps buffer population variation across the overall metapopulation and provide time for managers to determine needed actions (Heinrichs et al. 2015).

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Table 3.1. List of habitat variables used in nest success models for Golden-winged Warblers in southeast Manitoba, 2011-2015.

Variable type	Units	Calculated with	Variable name
<b>Nest (5m)</b>			
Canopy cover	%	densiometer	CC
Canopy height	Meters	visual estimate	CH
Nest cover	%	visual estimate	NC
Nest substrate height	Meters	meter stick	SH
<b>Territory (200m)</b>			
Forest cover	%	ArcGIS	FC
Distance to forested edge	Meters	ArcGIS	DTFE
<b>Landscape (1000m)</b>			
Forest cover	%	ArcGIS	FCplot
Forested edge density	meters/hectare	ArcGIS	FED
<b>Matrix (1000m)</b>			
<i>Composition</i>			
Agriculture amount	%	ArcGIS	AG
Mining amount	%	ArcGIS	MIN
Roads/development amount	%	ArcGIS	RDS
<i>Configuration</i>			
Agriculture edge density	meters/hectare	ArcGIS	AED
Mining edge density	meters/hectare	ArcGIS	MED
Roads/development edge density	meters/hectare	ArcGIS	RED

Table 3.2. Range of values for forest cover, matrix type, and edge density at each study site.

Study Site	% forest cover	% agriculture	% bare ground	% anthropogenic infrastructure	% forest cutover	edge density (m/ha)
Monominto	69	0	17	14	0	983
Gravel Pit	75	0	21	4	0	312
Uppingham	56	17	1	26	0	1876
Ostenfeld	86	2	8	6	0	65
Sandilands	92	0	0	1	7	57
FR 13	93	0	1	6	0	34
13 South	98	0	1	1	0	181

Table 3.3. Cormack-Jolly-Seber models representing the apparent survival and resight probability for adult Golden-winged Warblers in southeast Manitoba, 2011-2015. Model selection was corrected for overdispersion (QAIC<sub>c</sub>). Global model is indicated in bold. Time (year) is represented by 't', sex by 's', and plot by 'p'.

Model	K	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	ω <sub>i</sub>	QDeviance
φ(.)p(s)	3	912.56	0	0.52	78.08
φ(s)p(s)	4	913.59	1.03	0.31	77.16
φ(p)p(s)	5	916.20	3.64	0.08	77.69
φ(t)p(s)	9	917.20	4.64	0.02	71.04
φ(s+t)p(s)	12	918.75	6.19	0.01	70.71
φ(s)p(.)	3	920.14	7.58	0.00	85.10
φ(p)p(.)	3	923.16	10.6	0.00	86.02
φ(.)p(.)	2	923.20	10.64	0.00	86.06
φ(t+p)p(s)	9	928.51	15.95	0.00	85.96
φ(s+p)p(s)	6	936.83	24.27	0.00	94.91
<b>φ(s+t+p)p(s)</b>	<b>18</b>	<b>938.23</b>	<b>25.67</b>	<b>0.00</b>	<b>66.71</b>
φ(t+p)p(.)	9	939.79	27.23	0.00	91.95
φ(s+p)p(.)	5	946.08	33.52	0.00	105.36
φ(t)p(s)	5	960.42	47.86	0.00	107.24
φ(s+t+p)p(.)	17	962.62	50.06	0.00	97.63

Table 3.4. Model selection for nest survival of Golden-winged Warblers in southeast Manitoba, 2011-2015.

Model	K	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>
<b>Temporal</b>	<b>4</b>	<b>371.5</b>	<b>0</b>	<b>1.00</b>
Global	19	410.9	39.4	0.00
Matrix	6	420.3	48.8	0.00
Nest	4	420.6	49.1	0.00
Landscape	2	424.7	53.2	0.00
Landscape + Parasitism	3	425.4	53.9	0.00
Habitat (Landscape + Territory + Nest)	8	425.7	54.2	0.00
Territory	2	425.9	54.4	0.00
Parasitism	1	426.7	55.2	0.00
Null	0	575.8	204.3	0.00



Table 3.5. Beta coefficients ( $\beta$ ), standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence intervals for temporal factors identified as affecting nesting success of Golden-winged Warblers in southeast Manitoba, 2011-2015. The only factor with a confidence interval that excludes zero is in bold.

Parameter	$\beta$	SE	LCL	UCL
2011 vs 2015	0.53	0.62	-0.60	1.74
2012 vs 2015	0.74	0.53	-0.29	1.78
2013 vs 2015	0.96	0.49	-0.02	1.92
2014 vs 2015	0.26	0.48	-0.69	1.21
Laying vs nestling	-0.08	-2.09	-2.10	0.04
Incubation vs nestling	0.15	0.35	-0.54	0.84
<b>DOY</b>	<b>-0.65</b>	<b>0.28</b>	<b>-1.20</b>	<b>-0.10</b>
(DOY) <sup>2</sup>	0.00	0.00	0.00	0.00

Table 3.6. Model selection for seasonal productivity of Golden-winged Warblers in southeast Manitoba, 2011-2015.

Model	K	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	ω <sub>i</sub>
<b>Parasitism</b>	<b>1</b>	<b>261.6</b>	<b>0</b>	<b>0.40</b>
<b>Landscape + Parasitism</b>	<b>3</b>	<b>262.9</b>	<b>1.3</b>	<b>0.21</b>
<b>Landscape</b>	<b>2</b>	<b>264.3</b>	<b>2.7</b>	<b>0.10</b>
Null	6	264.4	2.8	0.10
Matrix	2	264.6	3	0.09
Habitat (Landscape + Territory)	4	265.5	3.9	0.06
Territory	2	266.9	5.3	0.03
Temporal	1	271.8	10.2	0.00
Global	12	279.7	18.1	0.00

Table 3.7. Model selection for Brown-headed Cowbird brood parasitism rates of Golden-winged Warblers in southeast Manitoba, 2011-2015.

Model	K	AIC <sub>C</sub>	$\Delta$ AIC <sub>C</sub>	$\omega_i$
<b>Landscape fragmentation</b>	<b>2</b>	<b>76.7</b>	<b>0</b>	<b>0.44</b>
Global	5	77.6	0.9	0.28
Total fragmentation	4	77.7	1	0.27
Territory fragmentation	2	88.8	12.1	0.00
Null	0	89.9	13.2	0.00
Nest initiation date	1	90.2	13.5	0.00

Table 3.8. Sensitivity and elasticity of demographic parameters for Golden-winged Warbler populations across southeast Manitoba, 2011–2015. Sensitivity is the response of population growth rate,  $\lambda$ , to a numerical change in an individual parameter while elasticity reflects a proportional change. The estimate of juvenile survival was half that of adult survival (0.205).

	Sensitivity	Elasticity
Adult survival	0.95	0.62
Juvenile survival (low)	1.17	0.38
Fecundity	0.22	0.41

Table 3.9. Demographic parameters for Golden-winged Warblers in southeast Manitoba, 2011-2015. Number in parentheses represents the standard error.

Demographic parameter	Manitoba
Number of nests	115
Number of exposure days	1571
Mean clutch size	4.63 (0.07)
Mean first nest initiation date	31-May
Mean young fledged per successful nest	4.06 (0.16)
Daily nest survival	0.964 (0.013)
Period survival	0.418
Adult male survival ( $\Phi$ )	0.41 (0.02)
Male recapture/re-sighting rate (p)	0.84 (0.04)
Adult female survival ( $\Phi$ )	0.41 (0.02)
Female recapture/re-sighting rate (p)	0.66 (0.11)
Lambda ( $\lambda$ )	0.650

Figure 3.1. Map of Golden-winged Warbler study sites in southeast Manitoba.

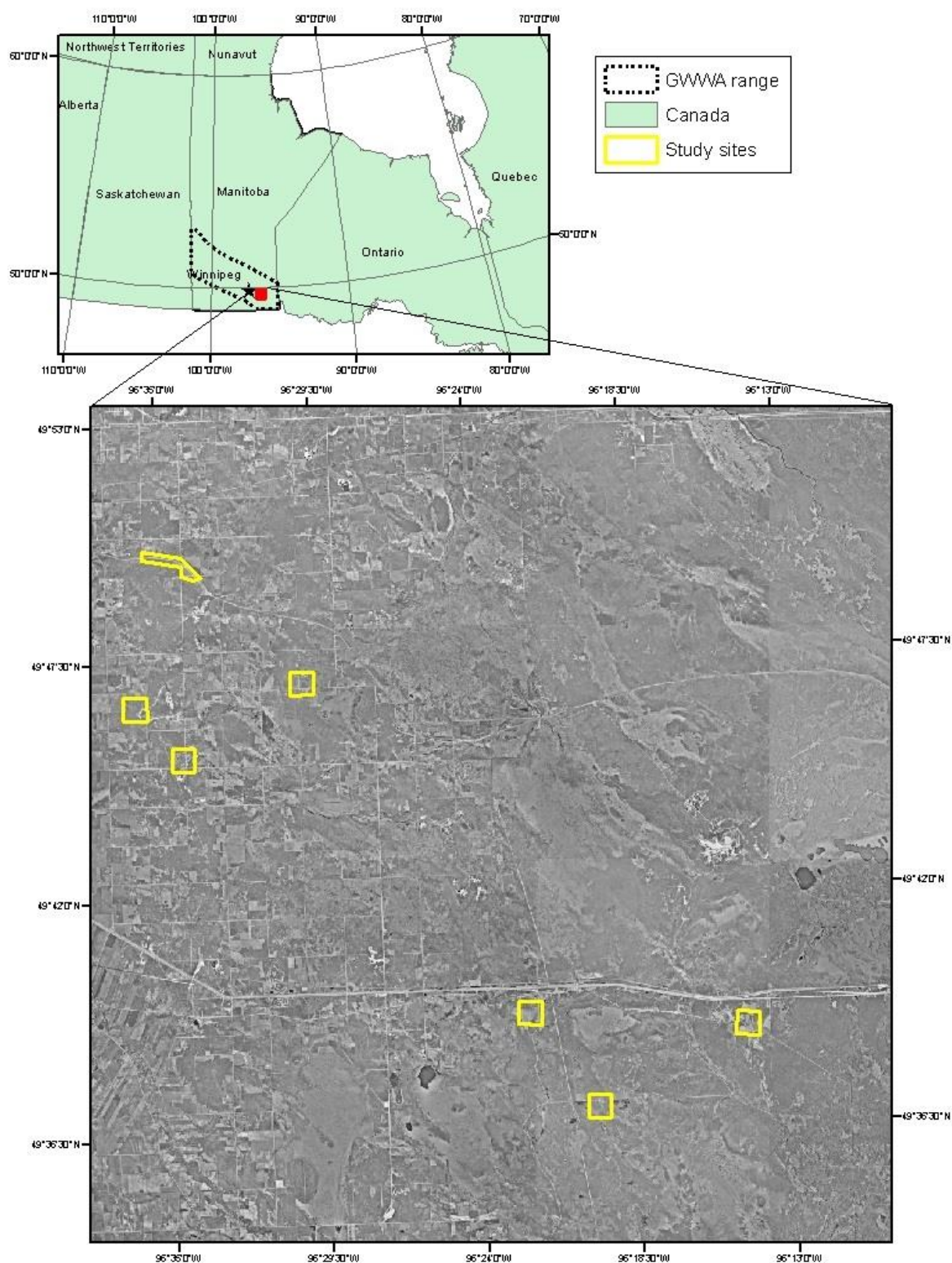
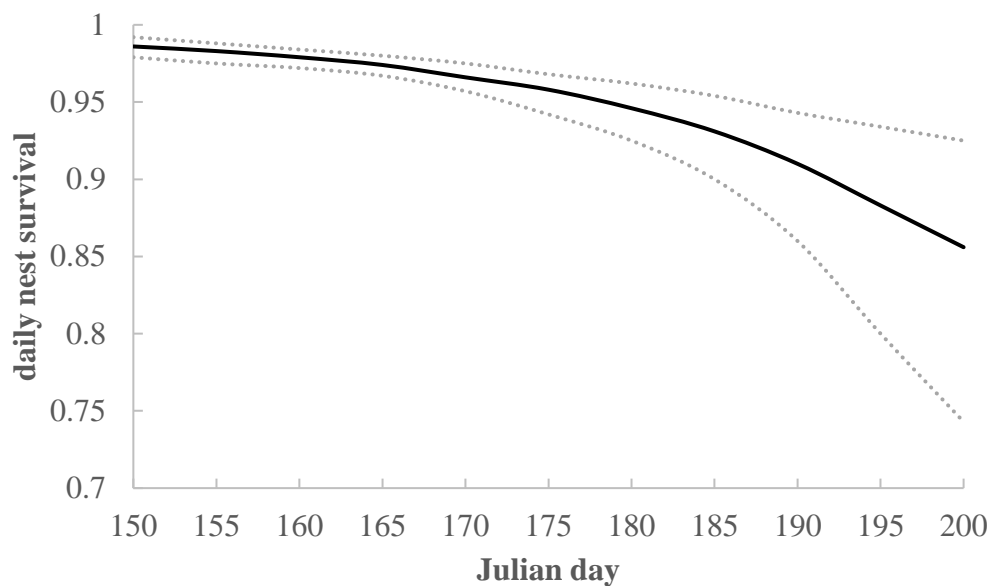


Figure 3.2. Daily nest survival varied by year and decreased non-linearly as the nesting season progressed for Golden-winged Warblers in SE Manitoba, 2011-2015. Dotted lines indicate the upper and lower standard errors.



**Chapter Four.** Pairing success and extra-pair paternity rates are impacted by male age and percent forest cover in an early successional songbird.

### **Abstract**

Pairing success and extra-pair paternity are two important aspects of avian mating systems that contribute to variation in male reproductive success. Because the first response to anthropogenic change by wildlife is often behavioral, these two factors can help us understand the behavioral mechanisms underlying potential changes in productivity and population viability due to anthropogenic landscape change. I developed spatially explicit, multifactor models to test competing hypotheses that ecological (habitat amount and fragmentation) and social (breeding density and male age) factors influence an individual's opportunity for pairing success and extra-pair paternity in a socially monogamous bird, the Golden-winged Warbler (*Vermivora chrysoptera*). I monitored Golden-winged Warbler territories across the breeding range in south-east Manitoba, Canada. The average pairing success rate across all plots was 88%. A male's probability of pairing successfully increased with greater landscape forest cover and with male age, but was not impacted by distance to edge or edge density. Extra-pair young were present in 25.4% of all nests, while 16.9% of all young were extra-pair. A male's probability of siring extra-pair young increased with age but was not impacted by forest cover, distance to edge, or edge density. My study demonstrates that both ecological and social conditions can constrain pairing success and opportunities for extra-pair paternity and ultimately impact variation in mating success. Further, loss of forest cover can potentially impact target populations via mating system disruption.



## Introduction

Anthropogenic activity is changing the environment in novel ways, and at unprecedented rates. While most species have been exposed to environmental change and variation during their evolutionary history, the current rate of change is problematic. Many species have been unable to adapt quickly enough to avoid population declines and extinctions, leading to a worldwide decline in biodiversity (Stockwell *et al.* 2003, Kinniston and Hairston 2007). Habitat loss and fragmentation are examples of anthropogenic change that animals must adapt to on very short timescales. The initial response of animals to sudden disturbance is often behavioral, such as altered habitat selection or changes in mate selection (Price *et al.* 2003, Kinniston and Hairston 2007). In turn, this influences the survival, reproductive success, and distribution of the individual and ultimately the dynamics of a population.

Breeding habitat for birds in North American forests has become increasingly fragmented due to anthropogenic activity, resulting in many population declines and extinctions (Saunders *et al.* 1991, Tilman *et al.* 1994, Henle *et al.* 2004). Habitat loss and fragmentation can change the size, structure, and connectivity of habitat patches. These changes can influence the availability of resources, possibility of dispersal, and the risk of predation (Bender *et al.* 1998, Fletcher 2009), and consequently can affect survival and productivity of individuals and induce behavioural changes in response to those effects. While a large body of research has examined the impacts of fragmentation on avian nesting success and brood parasitism (Brittingham and Temple 1984, Wilcove 1985, Porneluzi *et al.* 1993, Paton 1994, Robinson *et al.* 1995), impacts on other aspects of animal mating systems have been largely ignored (Reed 1999, Banks *et al.* 2007, Stutchbury 2007).

Though social monogamy is the most prevalent avian mating system (Lack 1968, Emlen and Oring 1977), we now know that genetic monogamy is rare and the acquisition of extra-pair mates and resulting extra-pair paternity is part of the reproductive strategy of most bird species (Griffith et al. 2002, Westneat and Sherman 2003). Extra-pair paternity provides direct benefits for the lifetime fitness of males, and some research shows direct benefits to females in the form of increased resources provided by an extra-pair male or indirect benefits in the form of increased genetic quality of offspring (Griffith et al. 2002, Foerster et al. 2003). Most research on extra-pair paternity rates focuses on population- or individual-level variation such as male physical characteristics or age and breeding density (Westneat and Sherman 1997, Griffith et al. 2002, Westneat and Stewart 2003), but does not address how anthropogenic landscape changes such as fragmentation may alter this important aspect of mating systems. Ultimately, the ability of an individual to reproduce is critical to the long-term persistence of a population; therefore, documenting changes in mating systems in response to anthropogenic disturbance can aid researchers in understanding population trends (Peacock and Smith 1997).

Despite extensive research on the topic, the underlying factors explaining variation in pairing success and extra-pair paternity (EPP) among species, as well as among populations of the same species, are still not fully understood. The debate mostly focuses on how population-specific demographics influence EPP. For example, variation in population density is often proposed as way to explain inter- and intraspecific variation in pairing success and EPP in avian mating systems. In higher density habitats, individuals have increased encounter rates and more opportunities for pairing/extra-pair mating and the cost of searching for mates is reduced (Hoogland and Sherman 1976, Birkhead 1978, Møller 1985). If density increases, pairing success and the rate of EPP should also increase (Westneat et al. 1990). Another consistently

observed correlate of successful pairing and EPP is male age (Griffith et al. 2002). The age-dominance hypothesis suggests that older males have survived longer as a result of better genetic quality (Trivers 1972, Manning 1985) and have an advantage in male-male competition for mates because they are genetically superior and more experienced (Weatherhead and Boag 1995, Brooks and Kemp 2001, Johnsen et al. 2003). Indeed, older males are often more successful at gaining mates and EPP (Yasukawa 1981, Searcy 1982, Sæther 1990, Weatherhead and Boag 1995, Griffith et al. 2002). However, the evidence supporting these hypotheses has been mixed, even within the same species (Kempnaers et al. 1997, Griffith et al. 2002, Charmantier et al. 2004). Variation in environmental factors such as habitat configuration and quality should also be considered when examining intraspecific variation in pairing success and EPP because it may increase or decrease the impact of demographic factors (Komdeur 2001, Westneat and Mays 2005).

As habitat is fragmented, food, mates, or nest sites may become spatially disjunct, and may require an organism to change dispersal patterns to gain access to sufficient resources (Dale 2001, Norris and Stutchbury 2001, 2002). The ability to disperse could also be impacted by fragmentation because it increases habitat isolation and decreases connectivity among fragmented patches (Doak et al. 1992, Desrochers and Hannon 1997, Ricketts 2001, Rodriguez et al. 2001). As a result, the cost of dispersing from a territory in a fragmented patch to seek mates could increase (Debinski and Holt 2000, Fraser and Stutchbury 2004, Stutchbury et al. 2005, Banks et al. 2007). Norris and Stutchbury (2002) found that female Hooded Warblers (*Setophaga citrina*) in small fragments spent less time off-territory and sought fewer extra-pair copulations in contrast to females in continuous habitat. They concluded that isolation restricted females to a single fragment during the breeding season, and that this lack of extra-pair

copulation opportunity likely contributed to the observed female avoidance of small, isolated fragments (Norris and Stutchbury 2002). Evidence of decreased extra-pair copulation opportunity was also observed in Least Flycatchers breeding in fragmented habitats (Kasumovic et al. 2009). In contrast, male Hooded Warblers and Wood Thrushes in fragmented habitat made extra-territorial forays that were longer and of greater distance, indicating increased energetic requirements to pursue extra-pair copulations (Stutchbury 1998, MacIntosh et al. 2011). Thus, fragmentation can alter mating behavior and decrease male and female fitness via mechanisms that relate to extra-territorial movement ability.

Fragmentation can also impact pairing success via changes to habitat structure that alters the availability of resources, such as nesting sites and shelter from predators (Bender et al. 1998, Debinski and Holt 2000). Numerous studies have observed lower pairing rates in isolated forest patches (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1885, Burke and Nol 1998, Rodewald and Yahner 2000). Gibbs and Faaborg (1990) hypothesize that this could be a result of female preference for larger tracts with more resources and higher nesting success, or to higher predation on females in fragments. Burke and Nol (1998) concluded that the reduction in pairing success was a result of lower arthropod biomass in fragments compared to contiguous forest. Bayne and Hobson (2001) found that fragmented landscapes had an age ratio skewed toward younger males with lower pairing success, suggesting that older males are able to out-compete younger males for territories in more desirable patches and force younger males into sub-optimal patches (Bayne and Hobson 2001). Thus, a reduction in pairing success could act as an early behavioural warning that a population has been impacted by fragmentation even if other aspects of reproduction do not seem to be impacted.

Predicting and mitigating population declines and extinctions requires an understanding of the way that both demographic and environmental factors can alter the behavioural responses of animals and of the consequences that these responses may have for populations and species (Sutherland 1998, Berger-Tal et al. 2011). I examined mating behavior in the Golden-winged Warbler (*Vermivora chrysoptera*), focusing on pairing success and EPP. Golden-winged Warblers breed in southeast Manitoba, where the landscape varies in the amount of anthropogenic activity and resulting fragmentation. Golden-winged Warblers are federally listed as Threatened in Canada (SARA 2007) because of increasing habitat loss and fragmentation of the breeding grounds (Buehler et al. 2007). Successful conservation and management of this species will require an understanding of the behavioral responses to habitat change and how they could impact fitness.

In Manitoba, human alteration to the landscape has resulted in early-successional fragments that are no longer embedded solely within a forested landscape, but are often located within anthropogenic landscapes dominated by croplands, livestock grazing, resource extraction and ex-urban development. I established seven study sites throughout southeast Manitoba in landscapes with varying amounts of fragmentation resulting from resource extraction, agriculture, and/or ex-urban development to investigate whether pairing success and extra-pair mating varied in relation to male age, male density, fragmentation and habitat amount, or a combination of these factors. I predicted that pairing success and EPP rates would be lower for younger males but that these aspects of the mating system would not vary with male density. As an early-successional specialist, Golden-winged Warblers evolved to be distributed patchily across the landscape and so may not be impacted as much by isolation or lower densities. I also predicted that increased fragmentation would decrease habitat quality and attract younger males,

resulting in lower pairing success and higher rates of extra-pair paternity in patches embedded within anthropogenic landscapes than in patches embedded within intact forest.

## **Methods**

### *Field sampling*

Field assistants and I monitored Golden-winged Warbler breeding activity at seven 100-hectare study sites within southeast Manitoba (49°N -96°W) from May 15 to July 25 in 2012, 2013, and 2014. The sites were located at least 2 km apart to ensure independence of individuals among sites, as Golden-winged Warbler territories are less than 6 hectares (Confer et al. 2011). The sites were embedded within landscapes that varied from 56% to 99% forest cover (Table 4.1). The landscape in this area of Manitoba has four primary anthropogenic land uses: agriculture, livestock grazing, aggregate resource extraction, and ex-urban development. Crops grown in this region include row crops such as wheat, barley, soy, and canola. The parcels of land with livestock were often partially deforested or lacking understory vegetation. Resource extraction is dominated by aggregate removal of the sandy, gravelly soils.

I measured habitat characteristics of my study sites using a combination of metrics. I used ArcGIS 10 (ESRI 2013) to calculate the percentage of forest cover within a 1000-m buffer around each territory, the anthropogenic edge density within a 200-m and 1000-m buffer around each territory, and the distance from the center of each territory to the nearest anthropogenic edge. I used a 200-m radius to represent the patch scale because this corresponds to an average territory size for the Golden-winged Warbler (Confer et al. 2011), as well as the home range size of common nest predators in our study area, e.g., chipmunks and other small mammals (Livoreil and Baudoin 1996, Marmet et al. 2009). I used a 1000-m radius to represent a landscape scale because Golden-winged Warblers respond most strongly to this scale when selecting breeding

habitat (see Chapter 2). I defined anthropogenic edge as the boundary where suitable early-successional habitat abutted an agricultural or grazed field, a major paved roadway, or a mining operation. I defined male density at each site as the quotient of the number of breeding males by the total area (ha) of suitable habitat within each site. In our study area, suitable habitat included open deciduous or mixed-wood forest with an herbaceous, shrub, and canopy layer. The standardization of breeding density allowed for it to be compared among sites.

Within each study site, we banded as many territorial male and female Golden-winged Warblers as possible. 90% of the territorial males at each site were banded and over 90% of the females (with known nests) were banded. We collected standard morphometrics and feather samples (P1 or R1) from all captured adults. We aged adult birds as either second year (SY) or after second year (ASY) by molt limit and rectrix shape (Pyle 1997). We delineated territory boundaries by observing singing males and territorial disputes and calculated breeding density at each site with the use of ArcMap 10.2 (ESRI 2014). I included all known territorial males in my calculation of male density, even if they were unbanded. We determined that a male was paired if: 1) he was observed interacting (following, copulation) with a female on his own territory at least two separate times during the season, or 2) a nest was found within his territory, or 3) no nest was found but he was observed carrying food or feeding fledglings. We were confident in our ability to determine pairing status for this species as we spent at least two hours every other day within each territory, and additional time when females first arrived. The arrival of females on the breeding ground occurs over about seven days, during which time the females are conspicuous and courtship behaviors are easy to observe.

We monitored 168 Golden-winged Warbler territories and located 99 nests from 2012-2014 using behavioral clues such as female nest building, direct flights to the nest area after

foraging, alarm calling near nest, and/or food delivery to a nest. We checked nests every two days, and every day around the time of hatching and fledging. We identified the social father of each nest by observing which male fed the nestlings. To determine paternity, on day 5 after hatching, I collected a blood sample from each nestling (~15 µl blood from brachial vein) and stored it in a lysis buffer at room temperature until DNA extraction. If we found a nest during the nestling stage and determined it was safe to handle with no risk of force fledging (i.e., female still brooding and feathers still in pin), then I sampled blood until day 6 after hatching. If we found a nest after day 6 of the nestling stage, I took samples after fledging had occurred to avoid force-fledging. After fledging, I collected two body feathers from each individual in lieu of blood.

I completed parentage analysis on 67 of the 99 nests (N=266 nestlings); the other 32 nests failed before day 5 of the nestling stage due to predation, cowbird parasitism, or abandonment. I excluded one nest with two nestlings from the analysis because I was unable to capture the social father. In addition, I captured 5 fledglings from 4 known territories where the nest was not located but the social male was sampled.

#### *Laboratory methods*

I extracted DNA from blood and feathers using a homemade DNA extraction kit (Ivanova *et al.* 2006). I amplified fragments from 4 microsatellite regions [three microsatellite loci were isolated from the Golden-winged warbler genome (Stenzler *et al.* 2004) and one was isolated from Swainson's Warbler (*Limnothlypis swainsonii*) genome (Winker *et al.* 1999); Table 4.2] with PCR using the following conditions: 1.0 µl 10x reaction buffer (JumpStart; Sigma-Aldrich, St. Louis, MO, USA), 1.5-3.0 mM MgCl<sub>2</sub> (Sigma; varied by locus, Table 4.2), 0.2 µM forward primer labeled with 5'-fluorescent tags (6-FAM or HEX; Alpha DNA, Montreal,



Quebec), 0.2  $\mu\text{M}$  reverse primer, 0.02  $\mu\text{M}$  deoxyribonucleotide triphosphate (dNTP; each), 0.08  $\mu\text{L}$  2.5 units  $\mu\text{L}^{-1}$  JumpStart Taq DNA polymerase (Sigma), 100-250 ng DNA template, and DNA grade ddH<sub>2</sub>O (Fisher Scientific, Hampton, New Hampshire) to a final volume of 10.0  $\mu\text{L}$  per sample. I amplified microsatellites using the following temperature-cycling conditions in an Eppendorf Mastercycler ep gradient S (Eppendorf Canada, Mississauga, Ontario) thermal cycler: 94°C for 3 min, followed by 35 cycles at 94°C for 30 s,  $X^\circ\text{C}$  for 1 min ( $X$  = locus-specific annealing temp; Table 4.2), and 72°C for 5 min. I confirmed the presence of a PCR product and then prepared samples for analysis on an ABI 3130 XL automated sequencer (Applied Biosystems Canada, Burlington, Ontario). I scored microsatellite genotypes using GENEMARKER, version 2.6.3 (SoftGenetics, State College, Pennsylvania).

#### *Parentage analyses*

I used Cervus, v 3.0.7 (Marshall et al. 1998; available at [http://www.fieldgenetics.com/pages/aboutCervus\\_Overview.jsp](http://www.fieldgenetics.com/pages/aboutCervus_Overview.jsp)), to calculate allele frequencies of all adult birds, including the expected frequency of heterozygotes ( $H_e$ ), the observed frequency of heterozygotes ( $H_o$ ), and the null allele frequencies at all loci (Table 4.2). The combined probability of falsely assigning paternity given a known mother was  $3.0 \times 10^{-3}$ . Allele frequencies did not deviate from Hardy-Weinberg equilibrium indicating no evidence of genetic drift.

I used Cervus to conduct paternity exclusions and assignments (given a known mother) with the following simulation parameters: 10,000 cycles, 140 candidate fathers, and 90% of all possible candidate fathers sampled, with the latter variable based on knowledge of territorial males at our study sites. I confirmed that each nestling shared at least one allele with the social mother. The remaining allele was compared to the social father as well as to all other males in the population for which I had DNA. Cervus uses likelihood ratios when comparing candidate

males to nestlings, such that all males in the population are ranked from most to least likely sire (Marshall *et al.* 1998).

I hand-checked all assignments made by Cervus and excluded a male as sire if: (1) the male was not yet born ( $n=1$ ); or (2) the sire was on a different study site than the nest ( $n=1$ ). I only accepted a Cervus-assigned sire if he matched the nestling at a minimum of three loci and considered a single loci mismatch to be the result of mutation or genotyping error (Dakin and Avise 2004). In situations where this did not apply, I considered the male parent to be an unbanded male for whom I had no DNA ( $n=16$ ).

### *Statistical Analyses*

I evaluated the effects of proportion of forest cover (200- and 1000-m scale), distance to edge, and edge density (1000-m scale), male age, and male density on pairing success and extra-pair paternity in the Golden-winged Warbler. I combined the data over three years, which allowed an increase in sample size, so I could evaluate longer-term rather than annual patterns (Martin 1998). Although the proportion of forest cover at a 200- and 1000-m scale is collinear ( $r=0.75$ ), Smith et al. (2009) found that including all variables of interest in a model is the least biased way to obtain estimates of the relative effects of each, even if they are highly correlated, thus I included all variables of interest in my models. To investigate whether pairing success and extra-pair paternity rates vary with habitat characteristics, male age, or male density, I used generalized linear mixed models (GLMMs, proc GLIMMIX in SAS 9.4) with site as a random effect to account for the temporal interdependence of sampling the same sites over multiple years, and spatial interdependence of territories within sites. To assess the impacts of both demographic and habitat characteristics on pairing success, I included percent forest cover (200- and 1000-m scale), distance to anthropogenic edge, edge density (1000-m scale), male age, and

breeding density as fixed effects. Males were either paired or not paired, so I used a binomial distribution. To examine the effects on extra-pair paternity, I modeled the proportion of extra-pair nestlings within broods using male age, male density, percent forest cover (200- and 1000-m scale), distance to anthropogenic edge, and edge density (1000-m scale) as fixed effects. I used a negative binomial distribution because it had the lowest model deviance. For both models, I assessed the significance of fixed terms using Null Hypothesis Significance Testing (NHST, Mundry 2011). Finally, I examined the difference in age ratio among sites with different amounts of forest cover by using a simple linear regression with a normal distribution (proc REG in SAS 9.4). I conducted all statistical analyses in SAS, version 9.4 (SAS Institute 2012) with an  $\alpha$  value of 0.10 to determine statistical significance, because the risk of Type II error is a concern in conservation biology (Taylor and Gerrodette 1994).

## Results

The number of Golden-winged Warbler territories ranged from two to 16 per plot and the average male density per site ranged from 0.030 to 0.126 per ha. Average male density increased as landscape-level forest cover decreased (0.107 vs 0.059 per ha,  $F = 103.9$ ,  $p < 0.001$ ). As predicted, a higher proportion of SY males were present in sites with less forest cover at a landscape scale ( $t = -2.93$ ,  $p = 0.03$ ,  $R^2 = 0.63$ , Figure 4.1).

I confirmed the presence of a female on 147 of 168 male territories (88%). Pairing success ranged from 79 - 100% among sites (Table 4.3). There were two significant fixed effects (Table 4.4). Landscape-level forest cover was positively related to pairing success. Pairing success was higher for ASY males (94% paired) compared to SY males (75% paired); the odds of being paired was 1.25 times higher for ASY males than SY males. I found no evidence that

pairing success was impacted by the amount of territory-level forest cover, anthropogenic edge density, or male density (Table 4.4).

From these 147 pairs, I located 99 active nests. Sixty-seven survived to day five of the nestling period and were sampled. Seventeen of these nests had at least one extra-pair young (25.4%) and 45 out of 266 total nestlings were extra-pair young (16.9%) (Table 4.5). I determined the genetic father for 250 of 266 nestlings (94%); the remaining 16 nestlings were fathered by unknown males that were either present within the study site but unable to be captured and sampled, were males who defended a territory outside the study plot but traveled to the plot for extra-pair copulation, or were floaters that did not defend a territory. There were two bigamous males (both ASY) for whom I sampled both nests, one with both nests in a contiguous site, and the other with nests on opposite sides of a road in a fragmented site.

Nests with extra-pair young contained nestlings from up to three different fathers. At all sites, the sires that could be identified were most often immediate neighbors (27/32, 84%). However, some extra-pair young were sired by males from several territories away or unknown males that likely came from a greater distance. The farthest a banded male was known to travel to father young in another nest was 320 m.

I examined the relationship between the number of extra-pair young and factors that represent male demographics and habitat characteristics. The only significant fixed effect was male age, with greater extra-pair paternity in nests of SY males compared to ASY males (Table 4.6). Male density, forest cover at both scales, distance to edge, and edge density did not impact the number of extra-pair young.

## Discussion

My study is the first to examine changes in the Golden-winged Warbler mating system as a result of habitat characteristics and population demographics. Although Golden-winged Warblers are found in naturally patchy early-successional habitats, they suffered reduced pairing success in sites with lower landscape forest cover. Nonetheless, males were found in higher densities in more disturbed sites with less forest cover, indicating that male density may not be an accurate indicator of habitat quality or of population viability.

Pairing success was not impacted by edge density or distance to edge, providing support for a greater impact of habitat loss over fragmentation (Debinski and Holt 2000, Fahrig 2003). Golden-winged Warblers are a highly vagile species that have evolved to exploit ephemeral early-successional habitat patches, so their ability to encounter mates may not be impacted by isolation or lack of connectivity in the same way as a more sedentary species. The negative impacts of fragmentation on pairing success in other bird species has been attributed to lower nest success (Van Horn et al. 1995), increased brood parasitism (Bayne and Hobson 2001), or decreased body mass of nestlings (Huhta et al. 1999), all of which can reduce productivity. I found increased brood parasitism and decreased productivity in territories that were closer to an edge (Chapter 3), suggesting a potential mismatch between female mate choice (and breeding territory) and productivity.

Extra-pair paternity rates did not vary by forest cover, distance to edge, or edge density. My results contrast with similar studies where extra-pair paternity increased with greater forest cover (Kasumovic et al. 2009, Evans et al. 2009). However, unlike these studies, I did not find lower male densities in more fragmented sites so access to extra-pair mates did not appear to be a limiting factor. The majority of extra-pair mates that I was able to verify were neighbors within

one to two territories away, and all territories had at least one available neighbor. The relatively high levels of forest cover remaining in this region may not have reached the threshold at which habitat loss or fragmentation impact mating systems (Andr  n 1994). Alternatively, because the mating system of this species evolved to exploit ephemeral, early-successional habitats that are naturally patchy across the landscape, the extra-pair mating system may not be impacted by habitat or landscape characteristics.

The age dominance hypothesis was strongly supported, with young male Golden-winged Warblers pairing at lower rates than older males and losing paternity at higher rates than older males. Numerous studies have shown older birds to have greater pairing success than younger birds (S  ther 1990, Holmes et al. 1996, Bayne and Hobson 2001), finding that ASY males arrive earlier to the breeding grounds and outcompete younger males for territories in preferred habitats. Consequently, SY males are forced into suboptimal habitat where they are less likely to attract mates (Van Horne 1983, Lanyon and Thompson 1986, Sherry and Holmes 1989, Lozano et al. 1996, Smith and Moore 2005). I found that males at sites with less forest cover tended to be younger, suggesting that indeed these sites may be less preferred by older (more experienced) males. Nevertheless, the majority (75%) of SY males were able to successfully pair. Moreover, SY and ASY reproductive success did not differ (see also King et al. 2001), suggesting that females do not suffer a fitness cost in choosing to mate with an SY male (see Ch. 4). SY males lost paternity at higher rates than ASY males, indicating that younger birds may not be able to guard mates as effectively as older males (Charmantier and Blodel 2003, Bouwmen and Komdeur 2005).

I found no support for the hypothesis that higher male density increased pairing success or extra-pair paternity in contrast to a study of a Wisconsin population of Golden-winged

Warblers where male densities above 0.2 males/ha indicated consistently high pairing success (Roth et al. 2014). While lower breeding density in fragmented habitats may lead to fewer encounters with primary or extra-pair mates and thus may be a mechanism that decreases both pairing success and extra-pair paternity rates (Banks et al. 2007), I did not find lower male densities in more fragmented habitat patches. While I had a range of densities across sites, the sites with the fewest territorial males also had the oldest, most experienced males. These sites also had higher rates of returning females, often pairing with the same male from previous years and potentially confounding the impacts of lower density. Other studies have found that the relationship between male density and extra-pair paternity is variable and likely determined by an interaction between density and species-specific behavior (Griffith et al. 2002, Westneat and Stewart 2003).

Overall, pairing success in this population of Golden-winged Warblers was higher than reported in populations in Michigan and Wisconsin (Will 1986, Roth et al. 2014). Extra-pair paternity rates were close to the average observed in other passerines (Griffith et al. 2002), but lower than those observed in an Ontario Golden-winged Warbler population, where 55% of nests and >30% of nestlings were extra-pair (Vallender et al. 2007). To understand these differences, the age ratios and forest cover should be examined to determine whether pairing success is higher in landscapes with more forest in other parts of the breeding range. Because fragmentation is higher in other parts of the Golden-winged Warbler range, further study is needed to determine whether fragmentation impacts extra-pair paternity rates elsewhere. Although the aspen parkland region of southeast Manitoba has so far been spared the high levels of habitat loss and fragmentation that exist in other portions of the Golden-winged Warbler range, local increases in mining operations (Brian Kiss, pers. comm.), ex-urban development,

and the construction of a hydro-line through primary Golden-winged Warbler habitat (Manitoba Hydro 2015) may result in future threats to keeping this unique ecosystem intact.

While it is known that variance in mating success can vary across environments (Emlen and Oring 1977, Cornwallis and Uller 2010), there has been minimal research into the social changes that occur as a result of anthropogenic landscape change. Both pairing success and extra-pair paternity can increase variance in male mating success (Webster et al. 1995, 2007), so it is imperative to understand how these behaviors are impacted as the landscape is altered. My study demonstrates that both ecological (forest cover) and social factors (age) affect male opportunities for pairing success and extra-pair paternity. Reduced levels of pairing success will exacerbate effects of habitat loss and ultimately reduce population viability. Because disturbance-dependent habitats are ephemeral, species that depend on them require continuous habitat management (DeGraaf and Yamasaki 2003). This makes it particularly important to account for links between forest cover and mating system variation when developing plans for habitat management or creation for the conservation of this species at risk.



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Table 4.1. Range of values for forest cover, matrix type, and edge density at each study site.

Study Site	% forest cover	% agriculture	% bare ground	% anthropogenic infrastructure	% forest cutover	edge density (m/ha)
Monominto	69	0	17	14	0	983
Gravel Pit	75	0	21	4	0	312
Uppingham	56	17	1	26	0	1876
Ostenfeld	86	2	8	6	0	65
Sandilands	92	0	0	1	7	57
FR 13	93	0	1	6	0	34
13 South	98	0	1	1	0	181

Table 4.2. Microsatellite loci and PCR conditions used in paternity assignments of Golden-winged Warblers (*Vermivora chrysoptera*). Temp = annealing temperature,  $K$  = # of alleles,  $H_o$  = observed heterozygosity,  $H_e$  = expected heterozygosity.

Locus	Temp (°C)	[MgCl <sub>2</sub> ] mM	$K$	$H_o$	$H_e$	Null freq.
VeCr02	51.5	3	19	0.721	0.696	0.022
VeCr07	59.5	1.5	12	0.662	0.729	0.045
VeCr08	55	1.5	44	0.814	0.943	0.074
Lswμ12	50	3.5	34	0.863	0.929	0.043

Table 4.3. Pairing success of after-second-year (ASY) and second-year (SY) Golden-winged Warbler (*Vermivora chrysoptera*) territorial males in southeast Manitoba, 2012-2014.

Site	% forest cover	2012		2013		2014		Total
		ASY paired	SY paired	ASY paired	SY paired	ASY paired	SY paired	
Monominto	0.69	5/5	4/5	4/4	2/2	5/5	3/4	23/25 (92%)
Gravel Pit	0.75	4/4	5/7	6/6	3/4	7/9	4/6	29/36 (81%)
Uppingham	0.56	5/6	1/4	7/8	3/5	6/6	4/4	26/33 (79%)
Ostenfeld	0.84	4/4	5/7	8/9	1/1	8/8	3/3	29/32 (91%)
Forestry 13	0.93	4/4	1/1	3/3	1/2	3/4	0/0	12/14 (86%)
Sandilands	0.92	7/7	1/1	4/4	2/2	5/5	0/0	19/19 (100%)
Wetland 13	0.98	3/3	1/1	2/2	1/1	2/2	0/0	9/9 (100%)
Total		32/33 (97%)	18/26 (69%)	33/36 (92%)	13/17 (76%)	36/39 (92%)	14/17 (82%)	147/168 (88%)

Table 4.4. Global model measuring the effect of male age, male density, and habitat characteristics on pairing success of male Golden-winged Warblers (*Vermivora chrysoptera*) in southeast Manitoba, 2012-2014.

Parameter	Estimate	SE	t-Value	<i>p</i>
Intercept	-10.263	7.7607	-1.32	0.2433
<b>Age: 0</b>	<b>-1.6214</b>	<b>0.546</b>	<b>-2.97</b>	<b>0.0035</b>
<b>Age: 1</b>	<b>0</b>	<b>.</b>	<b>.</b>	<b>.</b>
Edge density	0.0021	0.001526	1.39	0.1679
<b>Forest cover 1000m</b>	<b>16.3426</b>	<b>9.7357</b>	<b>1.68</b>	<b>0.0955</b>
Forest cover 200m	-1.8598	26.7338	-0.07	0.9447
Distance to edge	0.00063	0.00245	0.26	0.7993
Male density	-0.2072	0.3718	-0.56	0.5784

Table 4.5. Extra-pair paternity observed in Golden-winged Warblers (*Vermivora chrysoptera*) at seven sites in southeast Manitoba, 2012-2014.

Site	Location	Forest cover (%)	Avg. Male density (males/ha)	Extra-pair paternity	
				Nests	Nestlings
Monominto	49.75° N, -96.57° W	0.69	0.083	5/10	18/47
Gravel Pit	49.77° N, -96.59° W	0.75	0.126	3/11	9/34
Uppingham	49.83° N, -96.58° W	0.56	0.09	4/12	8/48
Ostenfeld	49.78° N, -96.49° W	0.84	0.126	2/12	3/41
Forestry 13	49.65° N, -96.36° W	0.93	0.05	1/6	2/26
Wetland 13	49.61° N, -96.33° W	0.98	0.03	1/7	2/33
Sandilands	49.65° N, -96.24° W	0.92	0.073	1/9	3/37
Total				17/67 (25.4%)	45/266 (16.9%)

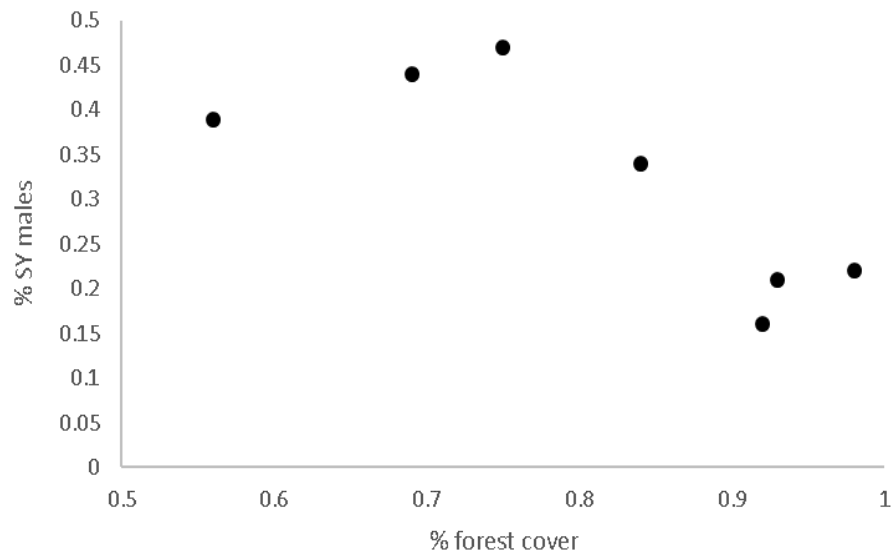
Table 4.6. Global model measuring the effect of male age, male density, and habitat characteristics on the number of extra-pair young in nests of Golden-winged Warblers

(*Vermivora chrysoptera*) in southeast Manitoba, 2012-2014.

Parameter	Estimate	SE	t-value	<i>p</i>
Intercept	4.9525	6.2124	0.64	0.4253
<b>Age: SY</b>	<b>1.7039</b>	<b>1.0156</b>	<b>2.81</b>	<b>0.0934</b>
<b>Age: ASY</b>	<b>0</b>	<b>0</b>	<b>.</b>	<b>.</b>
Forest cover (200m)	-2.7448	4.2891	0.41	0.5222
Forest cover (1000m)	-3.9175	6.1464	0.41	0.5239
Distance to edge	-0.0018	0.0026	0.49	0.4862
Edge density	-0.0004	0.0012	0.09	0.7684
Male density	-0.0321	0.4799	0	0.9466



Figure 4.1. Percentage of second-year (SY) males by amount of forest cover per study plot in southeast Manitoba, 2012-2014. Each point represents a single study plot.



**Chapter 5:** The final frontier: Early-stage genetic introgression and hybrid habitat use in the northwestern extent of the Golden-winged Warbler breeding range

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### **Abstract**

Anthropogenic changes to the landscape and climate have resulted in secondary contact between previously allopatric species. This can result in genetic introgression and reverse speciation when closely related species are able to hybridize. The Golden-winged Warbler has declined or been extirpated across much of its range where it has come into secondary contact with the Blue-winged Warbler. Genetic screening previously showed that introgression had occurred range-wide with the exception of Manitoba, Canada. My goal was to reassess the genetic status of the Golden-winged Warbler population in Manitoba and to examine the demographics and habitat use of phenotypic and genetic hybrids. From 2011-2014, I sampled and screened mtDNA from 205 Golden-winged Warblers and hybrids in southeast Manitoba. In 2012, I monitored all Golden-winged Warbler territories within those sites and measured territory- and landscape-level habitat variables. Of the birds screened, 195 had a phenotype that matched their mtDNA type, 2 were phenotypic hybrids, and 8 showed a phenotypic-mtDNA mismatch (cryptic hybrids). I found no difference in the habitat used by Golden-winged Warblers compared with hybrids at either scale. The low proportion of hybrids found in Manitoba and the lack of a distinguishable difference in habitat use by Golden-winged Warblers and hybrids indicates that the exclusion of hybrid birds from Golden-winged Warbler habitat is unlikely to be a successful conservation strategy. The best way to manage for Golden-winged Warblers is to slow the habitat loss and fragmentation that continues within Manitoba and to actively manage early-successional deciduous forest using tools such as fire and logging.

## Introduction

The role of hybridization in both evolutionary diversification (Seehausen 2004) and extinction (Rhymer and Simberloff 1996) has become an important area of study as humans increasingly alter ecosystems and bring species into secondary contact. Hybridization and the resulting introduction of one species genetic material into another, known as genetic introgression (Anderson 1949), aids in the maintenance of genetic diversity and can introduce novelty into the gene pool (Lewontin and Birch 1966, Dowling and Secor 1997, Arnold *et al.* 1999, Seehausen 2004). However, the increased temporal rate and geographic scale of anthropogenic hybridization brought about by habitat fragmentation, climate change, and species introductions can reverse evolutionary processes that resulted in divergence over hundreds of thousands or millions of years within just a few generations (Rhymer and Simberloff 1996, Rieseberg *et al.* 2007, Taylor *et al.* 2014). Genetically distinct populations that developed unique adaptations over significant amounts of time can become so introgressed that genetic boundaries dissolve, or a population may be replaced and leave no genetic trace behind (Rhymer and Simberloff 1996, Allendorf *et al.* 2001, Seehausen 2006, Brumfield 2010). The loss of species through this mechanism is often unpredictable and irreversible and may become one of the most difficult conservation problems to manage in modern times (Rhymer and Simberloff 1996). A decrease in biodiversity can have devastating consequences for ecosystem stability and evolutionary potential (Chapin *et al.* 2000), many of which are not well understood or even foreseeable.

Habitat fragmentation can remove barriers between previously allopatric species, bring them into secondary contact and provide an opportunity for interbreeding (Rieseberg *et al.* 2007). The Golden-winged Warbler (*Vermivora chrysoptera*) and Blue-winged Warbler (*V.*

*cyanoptera*) hybridization complex is one of the best-known examples. Geographic isolation resulted in separate evolutionary trajectories and speciation of Golden-winged Warbler and Blue-winged Warbler about three million years ago according to mitochondrial DNA (Gill 1980, Shapiro et al. 2004, Dabrowski et al. 2005) although a recent study shows the nuclear genome differs by only a few genomic regions (Toews et al. 2016). While both species prefer early-successional habitat in the breeding range, Golden-winged Warbler were historically distributed across more northerly latitudes and higher altitudes than Blue-winged Warbler and large patches of contiguous forest prevented contact. However, over the last 150 years in eastern North America, humans have cleared large expanses of forest for agriculture, which has resulted in allopatric populations of Golden-winged Warbler and Blue-winged Warbler becoming sympatric. In most cases, sympatry has resulted in hybridization and genetic introgression and follows a predictable pattern of localized Golden-winged Warbler extirpation within 50 years or less (Gill 1997, but see Confer *et al.* 2010). Also of concern, the rate of hybridization is increasing as the range of the Blue-winged Warbler continues to expand northward into areas previously dominated by Golden-winged Warbler (Gill 1980). The range expansions seen in both species have been attributed to habitat fragmentation/alteration but climate change may also be a factor (COSEWIC 2006). Because of both habitat loss and genetic introgression, Golden-winged Warbler are one of the most rapidly declining songbirds in North America with declines greater than 3% per year over the last decade (Sauer *et al.* 2014). In Canada, the species declined by 79% from 1993 to 2002 (COSEWIC 2006), and in 2006 was listed as ‘threatened’ under the federal *Species at Risk Act* (SARA 2007).

An exception to the typical hybridization and replacement pattern has been observed in a New York population located in Sterling Forest State Park, where Golden-winged Warbler and

Blue-winged Warbler have coexisted for over 100 years (Eaton 1914, in Confer *et al.* 2010; Confer and Larkin 1998; Confer and Tupper 2000) with very little documented hybridization, and stable population sizes (Confer and Knapp 1981, Confer *et al.* 2010). This successful coexistence appears to be related to differences in habitat selection, with Blue-winged Warbler exclusion from swamp forests used by Golden-winged Warbler (Confer *et al.* 2010). These results suggest that a stable hybrid zone is being maintained by exogenous selection (Kruuk *et al.* 1999) and that potential refugia for Golden-winged Warbler occur where Blue-winged Warbler do not breed. Patton *et al.* (2010) also found local-scale differences in habitat use by the two species and Thogmartin (2010) found that Golden-winged Warbler avoid areas occupied by Blue-winged Warbler at a landscape scale. Further, Wood *et al.* (2016) found Golden-winged Warbler prefer undisturbed contiguous forest far from urban areas at a landscape scale, Blue-winged Warbler preferred the opposite, and hybrids showed intermediate associations. Wood *et al.* (2016) suggest that this intermediate habitat preference by hybrids may actually be facilitating genetic introgression by allowing reproductive access of Golden-winged Warbler and Blue-winged Warbler to hybrids. If habitat preferences can segregate hybrids or parentals by physically separating them or impacting mate selection, then this mechanism could potentially be used to predict the likely location for a hybrid zone to occur, expand, or remain stable.

The manipulation and/or preservation of habitat to benefit pure Golden-winged Warbler and exclude Blue-winged Warbler has been suggested as a conservation strategy for Golden-winged Warbler (Vallender *et al.* 2009, Roth *et al.* 2012). Confer and Knapp (1981) suggested that Blue-winged Warbler may be more habitat generalists and use habitat later into succession than Golden-winged Warbler, whereas Confer *et al.* (2003) found evidence that Golden-winged Warbler prefer more herb cover and less tree cover. Wood *et al.* (2016) found that Golden-

winged Warbler prefer more highly structured patches embedded within large landscapes of contiguous forest with little fragmentation while Blue-winged Warbler prefer the opposite. This suggests that habitat could be manipulated to favor Golden-winged Warbler while providing an opportunity to avoid secondary contact with Blue-winged Warbler who may not prefer to settle there. However, the presence of hybrids (both phenotypic and cryptic) could alter habitat preferences and impact the effect of habitat management that favors one species over the other if hybrids do indeed prefer an intermediate habitat type.

Presently, the only Golden-winged Warbler populations that remain allopatric to Blue-winged Warbler and without active Blue-winged Warbler x Golden-winged Warbler hybridization are in Manitoba, northern Ontario, and the highest altitudes of the Appalachian Mountains (Vallender *et al.* 2009). Extensive research and monitoring has been conducted in the Appalachian region for the last 20 years (Buehler *et al.* 2007), but little is known about the status of introgression within Manitoba. Because it is at the northwestern extent of the range and Blue-winged Warbler have yet to expand their range here, Manitoba provides a unique opportunity to study the population before and during the initiation of genetic introgression. My study aimed to document the present level of genetic introgression in the southeast Manitoba population of Golden-winged Warbler and the rate at which introgression is occurring, if at all. In addition, I examined habitat use by hybrids (both phenotypic and cryptic) compared to parentals. In the absence of Blue-winged Warbler, I expected the maintenance of low levels of introgression each year. The presence of Blue-winged Warbler is reportedly what initiated the genetic swamping in other populations (Gill 1980, Gill 1997), so I did not expect to see such rapid introgression in the Manitoba population. I also did not expect to see significant differences in habitat use by hybrids compared to parentals simply due to the low expected number of hybrids and need to stay in

habitats where they could successfully breed with Golden-winged Warbler. While Manitoba is currently outside the range of the Blue-winged Warbler, further range expansions are likely inevitable (Buehler *et al.* 2007). Conserving and managing habitat refugia or stable hybrid zones for Golden-winged Warbler may provide the best opportunity for the continued survival of the species.

## Methods

### *Field*

I established eight study sites in southeast Manitoba (49° 46' N, 96° 29' W) to represent a variety of habitat types used by Golden-winged Warbler within both fragmented and contiguous forests (Figure 5.1). The four fragmented sites occur in an area with active and ever-expanding resource extraction, especially of aggregate used for building and maintaining roads.

Additionally, these sites are interspersed with low-density human housing. The contiguous forest sites occur within Sandilands provincial forest. Early seral forests in Sandilands either occur naturally as a result of hydrology or are regenerating after being logged. All study sites were dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), paper birch (*Betula papyrifera*), and/or bur oak (*Quercus macrocarpus*).

Field assistants and I captured >90% of the population of all breeding male and female Golden-winged Warbler at each of these sites from May 15 - July 15, 2011-2014. We target mist-netted territorial males using conspecific playback. The playback recording included both song types I and II (Highsmith 1989) and was broadcast from a speaker placed underneath the mist net for a maximum of 30 minutes. We captured females by locating the nest and setting up the net nearby during incubation or nestling stage, and captured them as they returned to the nest. We banded all birds with a Canadian Wildlife Service aluminum band and three unique color-

bands to distinguish individuals. We aged birds as second-year (SY) or after-second-year (ASY) based on plumage characteristic and feather wear (Pyle 1997). We collected a single rectrix (R1) feather from each bird and stored at room temperature until DNA was extracted.

We monitored banded birds a minimum of every other day from May 15 – July 15 each year. We located and tracked territorial males using behavioral clues such as singing and chipping. To define territory boundaries, we took a minimum of 30 GPS points per male to determine territorial boundaries. We sampled territory-level vegetation characteristics previously found to be indicators of habitat suitability for both Golden-winged Warbler and Blue-winged Warbler (Confer et al. 2010, Patton et al. 2010) at 10 random points within each territory. Within a 5-m radius circle of each random point, we measured the percent of woody, shrub and herbaceous vegetation, the average canopy height (m), and the percent canopy cover. Additionally, we measured the distance to the nearest forested edge (m) and to the nearest anthropogenic edge (m). To examine landscape-level variables, I used land cover classification data from GIS layers supplied by the Manitoba Land Initiative (MLI 2015). These data include 18 distinct land cover classes that were simplified into anthropogenic and forested land-use types. I overlaid the territory polygons onto the land-use layer and used analysis tools in ArcMap 10.2 (ESRI 2014) to create a 1000 m buffer around each territory. Within the buffers, I measured the percent anthropogenic (representing the percent non-forested), forest edge density (m/ha), and anthropogenic edge density (m/ha). A previous multi-scale study by Thogmartin (2010) found these to be important predictors of Golden-winged Warbler habitat use in the northwestern prairie-hardwood transition zone of the United States.

*Lab*



I screened 205 feather samples (28 in 2011, 66 in 2012, 66 in 2013, and 45 in 2014) from our eight study sites. I extracted DNA from feathers using a homemade DNA extraction kit (Ivanova *et al.* 2006). Golden-winged Warbler and Blue-winged Warbler mitochondrial DNA (mtDNA) have a 4.2 – 4.9% nucleotide divergence at the NDII gene (Dabrowski *et al.* 2005; Shapiro *et al.* 2004) that can be used to determine the ancestral maternal lineage of an individual. Vallender *et al.* (2009) discovered a single nucleotide polymorphism (SNP) at position 277 and 279 relative to the Zebra Finch NDII gene (Stapley *et al.* 2008; GenBank reference #DQ422742) at which the Golden-winged Warbler variant (GCAT) differs from the Blue-winged Warbler variant (ACGT). The Blue-winged Warbler variant is cut by the restriction enzyme MaeII (HpyCHIV; New England Biolaboratories) while the Golden-winged Warbler variant remains intact. Vallender *et al.* (2009) designed primers F2 (5' – AGC CAT TGA AGC CGC TAC CAA GTA - 3') and R1 (5' – GGA GTT TTA TGA TGG TTG ATA GGA GGA G – 3') to flank the cut site and generate a 282-bp fragment via PCR. I amplified this locus with PCR using the following conditions: 1.0 µL 1X reaction buffer (Sigma-Aldrich, St. Louis, Missouri, USA), 0.2 µM each F2 and R1 primers, 0.02 mM deoxyribonucleotide triphosphate (dNTP), 2.5 mM MgCl<sub>2</sub> (Sigma), 0.2 U JumpStart *Taq* polymerase (Sigma), 100–250 ng genomic DNA, and DNA-grade water (Fisher Scientific, Hampton, New Hampshire, USA) to a final volume of 10 µL per sample. I used the following temperature-cycling conditions in an Eppendorf Mastercycler ep gradient S (Eppendorf Canada, Mississauga, Ontario) thermal cycler: one cycle at 95°C for 3 min, followed by 34 cycles at 95°C for 1 min, 1 min at 53°C, and 1 min at 72°C. The program ended with one cycle at 72°C for 5 min, followed by a continuous hold at 10°C.

After confirming successful PCR product, I diluted 5 µL of the PCR product in 9 µL DNA-grade water (Fisher Scientific). I added 2 µL of the restriction enzyme MaeII (New

England BioLabs) and 4  $\mu$ L of NEB buffer 1 (New England BioLabs) to the PCR dilution for a total volume of 20  $\mu$ L. These samples were placed back into the Eppendorf Mastercycler ep gradient S (Eppendorf Canada, Mississauga, Ontario) thermal cycler and held at 37°C for 3 hours and then at 65°C for 20 min to deactivate the restriction enzyme.

I scored fragments by running on a standard 2% agarose gel (Fisher Scientific Molecular Biology Grade Agarose, 1X TAE buffer, 0.25mg/mL EtBr). The samples that were cleaved by the restriction enzyme and showed two similar sized bands (~140bp) were assigned to the Blue-winged Warbler haplotype group, while the samples that were not cleaved and showed only one band (~280bp) were assigned to the Golden-winged Warbler group. I used several samples of known Blue-winged and Golden-winged Warbler haplotypes as controls (obtained from R. Vallender). Any mismatch between the assigned haplotype group and phenotype indicated that the individual was a cryptic hybrid (Vallender *et al.* 2007; 2009).

### *Analyses*

All of the hybrids discovered were present in 2012 (though some returned in subsequent years); therefore, I compared habitat use of hybrids and pure Golden-winged Warbler within this year only. Territory boundaries remained similar from year to year within our study sites so no loss of information occurred by using data solely from 2012. I used an information theoretic approach (Burnham and Anderson 2002) to determine support for four *a priori* candidate models to evaluate whether habitat selection at different spatial scales was influenced by hybrid status. My set of *a priori* candidate models included a landscape model that included only landscape-level variables; a territory model that included only territory-level variables; a global model, including both landscape- and territory-level variables; and a null model with only an intercept.

All models were fit using generalized linear models (GLMs) in PROC GENMOD (SAS 2014). The response variable, hybrid status, was fit using a binomial distribution with a logit link function. I evaluated the goodness of fit and model assumptions of each global model using the deviance/df as well as by visually examining the residuals (McCullagh and Nelder 1989). I used Akaike's Second-Order Information Criterion ( $AIC_c$ ) to rank models from the most to the least supported (Burnham and Anderson 2002).

## Results

I sampled 205 Golden-winged Warbler and hybrids from 2011-2014 in SE Manitoba. Of these 205 birds, 10 (4.9%) were hybrids (Table 5.1). Two birds showed phenotypic signs of genetic introgression and fit the stereotypical phenotype of the Brewster's Warbler (Parkes 1951). Genetic screening revealed both Brewster's Warblers to have Golden-winged Warbler mtDNA. Of the remaining 203 phenotypic Golden-winged Warbler, eight had Blue-winged Warbler mtDNA and were cryptic hybrids (Table 5.1). While ninety percent of hybrids were male and only 65% of the total sample was male, I did not find a significantly greater proportion of males in the hybrid sample compared to the rest of the population ( $\chi^2 = 2.818, p = 0.09$ ). SY birds made up 80% of the hybrid sample but only 55% of the total sample ( $\chi^2 = 4.13, p = 0.04$ ). Half (5/10) of the genetic and phenotypic hybrids returned to the same territories in subsequent years (Table 5.2); by comparison, 19 out of 41 (46%) pure Golden-winged Warbler returned in 2012, 39 out of 71 (55%) in 2013, and 33 out of 83 (40%) in 2014.

Hybrids co-occurred at sites with Golden-winged Warbler and did not overlap territories. Hybrids were found in five out of eight study sites. The standard errors overlapped for all of the habitat metrics at both spatial scales (Table 5.3). The null model received most of the support (Table 5.4) and I found no evidence that landscape- or territory-level variables were useful

predictors of hybrid status. I found no differences in habitat selection between hybrid and pure Golden-winged Warbler at either scale, at least for the variables that were measured.

At the patch scale, both hybrids and pure Golden-winged Warbler preferred predominantly deciduous forests and established territories within 100 m of a forested edge. The average distance from the center of a territory to an anthropogenic edge was 805 m but ranged from less than 10 m to over 3 km. Both hybrids and Golden-winged Warbler had territories made up of nearly equal ratios of canopy, shrub, and herbaceous components. At a landscape scale, hybrid and pure Golden-winged Warbler territories contained an average of 23% habitat that was anthropogenically disturbed in some way, generally through agriculture or aggregate mining, up to a maximum of 44% disturbed habitat.

## **Discussion**

My study provides the first published genetic evidence that introgression has occurred in the Manitoba population of Golden-winged Warbler. Vallender et al. (2009) previously found no phenotypic or genotypic hybrids in a sample of 95 birds. At this time, the rate of introgression does not appear to be increasing. While I did not find significant evidence that hybrids were more likely to be male, hybrids were more likely to be SY when first captured than expected by chance. It is likely that the Brewster's Warbler and cryptic hybrids were reared elsewhere and dispersed northwest to Manitoba for their first breeding season. Van Wilgenburg (unpub. data) completed stable isotope analyses of Golden-winged Warbler across the breeding range and the results suggest that hatch-year birds disperse north of their natal grounds.

Although not significant, the fact that 90% of hybrids were male might be noteworthy, because female passerines are generally the dispersing sex (Greenwood 1980). Gill (1997) asserted that females are leading the Blue-winged Warbler range expansion and that

introgression is initiated when they pair with pure Golden-winged Warbler males. My results suggest the opposite, in all but one case, introgressed males paired with pure Golden-winged Warbler females. Because mtDNA is inherited maternally, the offspring of these pairings will again be classified as pure Golden-winged Warbler if there are no phenotypic signs of introgression.

While the sample size is small, the return rate of hybrids was similar between the pure Golden-winged Warbler and hybrids in this population. Similar to others, I found no evidence that hybrids are at a survival disadvantage (Vallender et al. 2007b, Neville et al. 2008). The comparable survivorship of hybrids provides additional evidence that hybrids do not face post-zygotic selection (Reed et al. 2007, Harper et al. 2010, Vallender et al. 2012). Taken together with the lack of pre-zygotic selection against hybrids (Vallender et al. 2007b), the implication is that there are no barriers to the complete admixture of Golden-winged Warbler and Blue-winged Warbler populations once they come into secondary contact.

While differences may exist between Golden-winged Warbler and Blue-winged Warbler habitat preferences, I found no evidence of difference in the habitat used by pure Golden-winged Warbler and hybrids in Manitoba. The breeding habitat characteristics are similar to those used by Golden-winged Warbler elsewhere in the range, generally including some anthropogenic disturbance, a nearby forested edge, and a habitat structure composed of an herbaceous, shrub, and canopy component (Confer 1992; Aldinger and Wood 2014, Aldinger et al. 2015; Bakermans et al. 2015). In Manitoba, early successional habitat within a deciduous forest-dominated landscape has become scarce enough that the management technique of Blue-winged Warbler exclusion from areas with Golden-winged Warbler could have negative effects if it results in the permanent loss of any additional habitat. The current rate of introgression in

Manitoba is so low that the best strategy may be to conserve the maximum amount of intact deciduous forest as possible and avoid further losses or fragmentation. It seems unlikely that there are any habitat characteristics that could be manipulated or managed at a large enough scale to exclude hybrids while benefitting pure Golden-winged Warbler.

The coexistence of Blue-winged Warbler and Golden-winged Warbler in Sterling State Forest (Confer et al. 2010) appears to be an anomaly that has not been replicated elsewhere. The expansion of Blue-winged Warbler into Ontario (even in very low levels, Rondel, pers. comm.) has resulted in introgression rates up to 30% (Vallender et al. 2007*a, b*). Manitoba has avoided this fate so far, but Blue-winged Warblers have been observed more frequently in central Minnesota over the past ten years and there is no evidence to suggest that the northward expansion of Blue-winged Warbler will slow (Sauer et al. 2014). The Manitoba population of Golden-winged Warbler has the lowest levels of genetic introgression range-wide and is likely to serve as an important refugium for Golden-winged Warbler in the coming years. While afforded some habitat protection under the Species at Risk Act as a Schedule 1 – threatened species (SARA 2007), viable breeding habitat continues to be destroyed with no mitigation and little oversight. If development and fragmentation continue at their current rate in Manitoba, the Golden-winged Warbler will decline regardless of the impact of Blue-winged Warbler. Conservation efforts should be made to preserve and manage all possible habitat types for Golden-winged Warbler or further declines will be unavoidable.

Though hybridization is a common and natural process with an important evolutionary role, habitat fragmentation and climate change has broken down geographic and ecological barriers and caused a net loss of biodiversity (Chapin et al. 2000, Seehausen 2006). The resulting homogenization of the environment can lead to a reversal of the evolutionary processes that

initially led to speciation (Rhymer and Simberloff 1996, Seehausen 2006, Seehausen et al. 2008). Some of the consequences of hybridization and genetic introgression could include the erosion of genetic diversity, a loss of adaptation, and ultimately extinction (Rhymer and Simberloff 1996, Woodruff 2001, Rosenzweig 2001, Myers and Knoll 2001). Further, as hybridization rates increase and genetically distinct populations merge, not only is current genetic diversity lost but there may also be a loss of evolutionary potential (Myers and Knoll 2001, Rosenzweig 2001). The combination of modern extinction rates and increased hybridization could have evolutionary consequences far into the future, beyond when these processes themselves have stopped. Stated simply, there will be less diversity, fewer genetically distinct populations, and fewer separate starting points from which evolution can proceed.

The loss of a species through hybridization and introgression is likely to become an increasingly common threat to biodiversity as human impacts to ecosystems increase. In the case of the Golden-winged Warbler, secondary contact, genetic introgression, and species replacement has already been initiated throughout most of its range, with Manitoba acting as the ‘final frontier’. The documentation of this process from start to finish in a species such as the Golden-winged Warbler can serve as a blueprint for what could occur in other closely related species brought into secondary contact. If the process can be better understood, perhaps it can be better predicted and avoided.

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Table 5.1. Results of Golden-winged Warbler (*Vermivora chrysoptera*) mtDNA screening in southeast Manitoba, 2011-2014. Brewster's Warbler = F1 Golden-winged x Blue-winged hybrid; AGW = ancestral Golden-winged Warbler; ABW = ancestral Blue-winged Warbler.

Year	<u>Golden-winged Warbler</u>		<u>Brewster's Warbler</u>	
	AGW	ABW	AGW	ABW
2011	27	0	1	0
2012	57	8	1	0
2013	66	0	0	0
2014	45	0	0	0
Total	195	<b>8</b>	<b>2</b>	0

Table 5.2. Demographics of Golden-winged Warbler (*Vermivora chrysoptera*) x Blue-winged Warbler (*Vermivora cyanoptera*) hybrids found in southeast Manitoba, 2011-2014.

ID	Sex	Age	Year(s) present
2690-29039	M	SY	2011, 2012, 2013, 2014
2690-29055	M	SY	2012
2690-29079	M	SY	2012, 2013, 2014
2690-29101	M	SY	2012
2690-29119	F	SY	2012
2690-29138	M	ASY	2012, 2013
2690-29163	M	SY	2012
2690-29173	M	SY	2012
2690-29188	M	SY	2012, 2013
2690-29339	M	ASY	2012, 2013



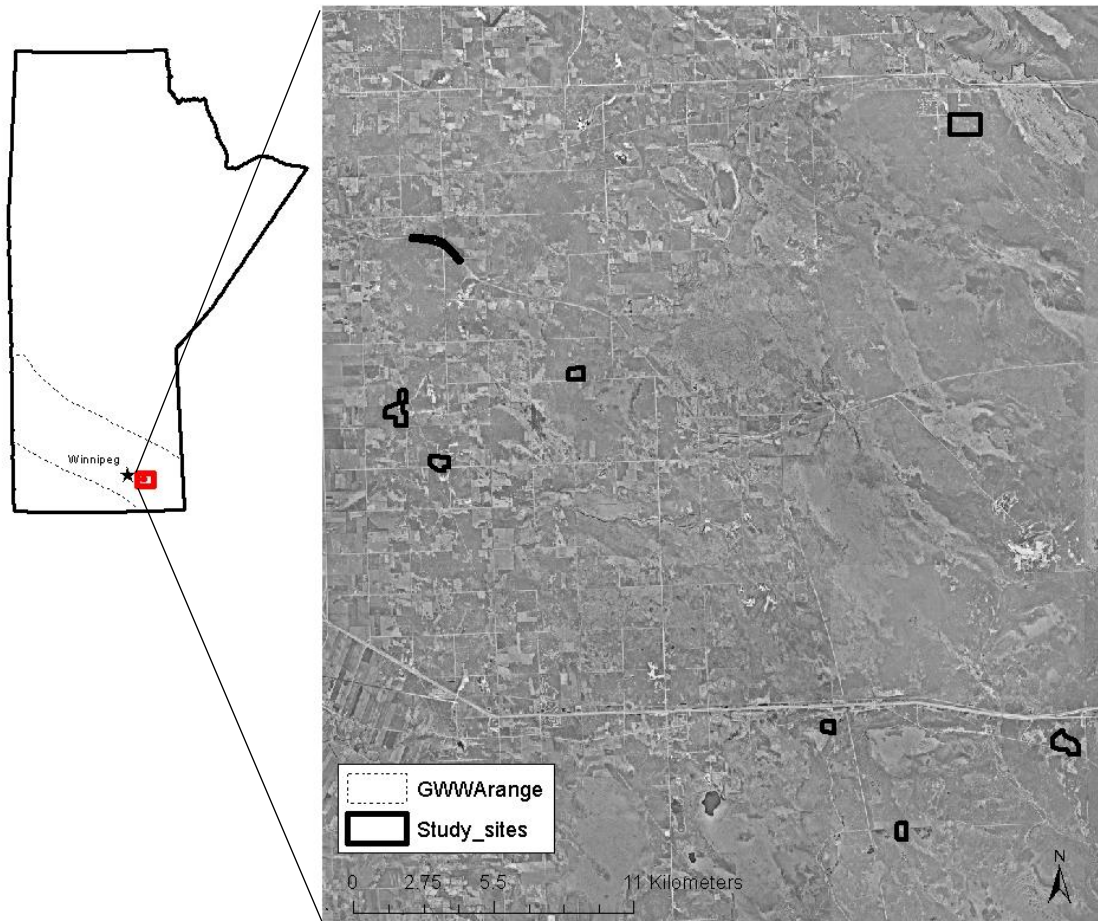
Table 5.3. Territory- and landscape-level habitat use of pure and hybrid Golden-winged Warblers (*Vermivora chrysoptera*) in southeast Manitoba, 2012.

Variable	<u>Golden-winged Warbler</u> (n=40)		<u>Golden-winged Warbler x</u> <u>BLUE-WINGED WARBLER</u> hybrid (n=8)	
	Mean (SE)	Range	Mean (SE)	Range
<b>Territory-level</b>				
% canopy cover	24.39 (2.31)	6 – 57	31.25 (4.61)	14 - 43
% shrub	34.70 (1.82)	10 – 65	37.87 (6.88)	15 - 80
% herbaceous	29.85 (1.79)	10 – 63	29.50 (5.22)	5 - 45
% woody	30.50 (2.42)	10 – 67	39.12 (6.62)	20 - 80
Distance to forest edge (m)	25.08 (4.04)	0 – 108	28.00 (7.98)	0 -55
Distance to anthropogenic edge (m)	861.01 (142.8)	9 – 3500	751.69 (404.0)	18 - 3500
% coniferous forest	1.9 (0.82)	0 – 25	0 (0)	0
<b>Landscape-level</b>				
Forest edge density (m/ha)	312.9 (37.04)	126 – 645	267.7 (95.21)	0 - 645
Anthropogenic edge density (m/ha)	556.1 (116.5)	0 – 1876	696.13 (278.3)	65 - 1876
% anthropogenic	21.25 (2.28)	2 – 44	25.37 (5.08)	2 - 44

Table 5.4. Results of model selection regarding the differences in habitat selection between pure and hybrid Golden-winged Warbler (*Vermivora chrysoptera*) in southeast Manitoba, 2012.

Model	K	$\Delta AIC_c$	$\omega_i$
Null	1	45.34	0.91
Landscape (% anthropogenic + forest edge density + anthropogenic edge density)	4	51.17	0.05
Territory (% shrub + % herb + % woody + DTE + canopy cover + % coniferous)	7	51.59	0.04
Global (Territory + Landscape)	10	57.84	0

Figure 5.1. Golden-winged Warbler (*Vermivora chrysoptera*) study sites in southeast Manitoba, 2011-2014.



## **Chapter 6. Conclusions and Management Implications**

### ***Conclusions***

The management of habitat for a species at risk requires an understanding of the species' resource needs. For an early-successional specialist like the Golden-winged Warbler, a primary requirement is locating suitable early successional habitat on the landscape. The availability of early-successional forest habitat for breeding Golden-winged Warblers has decreased due to suppression of natural disturbances and changes in forest management practices across North America (Askins 2001, Lorimer and White 2003). In southeast Manitoba, early-successional forests are fragmented by and converted to agriculture, human development, or resource extraction (pers. obs.). The result is a landscape no longer dominated by contiguous forest and tallgrass prairie that are subject to regular wildfires, but rather a patchwork of anthropogenically altered land-use types that have suppressed natural disturbances.

Much of the recent research on Golden-winged Warblers focused on habitat needs at a territory and nest-site scale (Aldinger et al. 2014, Roth et al. 2014, Aldinger et al. 2015, Leuenberger et al. 2017). My research shows that in addition, the surrounding landscape matrix may also be used as a proximate cue that influenced habitat selection. Golden-winged Warblers preferred landscapes with some anthropogenic disturbance, likely because it created the early-successional habitat that they prefer. In Manitoba, this early-successional habitat is most commonly created by small resource extraction operations that remove small areas of trees within a forested landscape. However, forested habitat that was fragmented by an agricultural matrix negatively influenced occupancy, with Golden-winged Warblers avoiding patches with higher agricultural cover and edge density at a 1000m scale. Agriculture and grazing tends to permanently remove forest cover and suppress forest regrowth. Habitat patches with otherwise suitable early successional forest remained unoccupied, suggesting that fragmentation and

conversion to agricultural habitat types may have impacts greater than the total amount of forest lost. This is not the first time that Golden-winged Warblers have been shown to be sensitive to landscape context as other studies have shown that mature forest is used by hatch-year birds post-fledging, and thus must be adjacent to early-successional breeding habitat to make the focal habitat patch suitable (Peterson 2014, Streby et al. 2015). Without both early-successional habitat required for nesting adults and late-successional habitat required by post-fledging young, Golden-winged Warblers will be absent. I was unable to locate Golden-winged Warblers in habitat patches with less than ~56% forest cover within a 1000m landscape buffer. These results add to the evidence that landscape factors often impact patterns observed within a patch and caution should be exercised when basing analyses on patch-scale characteristics alone (Fahrig 2001, Donald and Evans 2006, Brady et al. 2009, Prevedello et al. 2010).

Habitat selection is a hierarchical decision-making process in which individuals react to cues that are associated with habitat quality (Hildén 1965, Jones 2001). One potential flaw in the evaluation of habitat quality is the assumption of a positive relationship between habitat selection and fitness. Under certain circumstances, the link between habitat selection and fitness may become disconnected. Thus, the best measures of habitat quality test the effects of habitat on demographic parameters related to population growth and decline, and directly quantify the relationships between habitat preference and reproductive performance. In this study, I found that the anthropogenically created habitats preferred by Golden-winged Warblers do not confer the highest fitness levels in terms of pairing success or reproductive output and that the Golden-winged Warbler population in southeast Manitoba is declining. Overall, the relationships between male density, pairing success, daily nest survival, and annual fecundity were weak.

These findings imply that habitat selection decisions may be decoupled from realized fitness in this system.

Nest success is an attractive metric for researchers because it can be measured without color-banding individuals or tracking birds post-fledging, which is time and labor intensive. However, my results suggest the degree to which nest success accurately reflects habitat quality is questionable. The annual fecundity of a female bird is a function of the number of successful and unsuccessful nest attempts she makes, the probability that a nest will fledge young for any given attempt, and the number of young that are fledged from a successful attempt (Grzybowski and Pease 2005). I found a disconnect between nest success and annual fecundity, indicating that the use of nest success alone as a measure of productivity and habitat quality did not provide an accurate picture of population growth. Further, I found that the primary ecological mechanism driving the disconnect between nest success and annual fecundity was Brown-headed Cowbird (*Molothrus ater*) parasitism, which reduced clutch size and fledging success. The occurrence of parasitism was higher on fragmented sites with greater edge density.

Although density was highest on more fragmented sites with less forest cover and greater edge densities, females occupying these sites fledged fewer offspring. My results suggest that individuals use the presence of early-successional habitat as a proximate cue for territory selection, but realized fitness levels appear to be decoupled from the information associated with selection cues (Schlaepfer et al. 2002). Bock and Jones (2004) found similar patterns among species occupying human dominated landscapes and suggest that birds may fail to recognize suitable breeding habitats in landscapes that differ from those in which they evolved. Individuals may make poor habitat choices because they need time to adjust to changing landscapes, either through adaptation or learning (Purcell and Verner 1998, Misenhelter and Rotenberry 2000,

Battin 2004). Increased rates of brood parasitism by Brown-headed Cowbirds can negatively influence reproductive success for forest-nesting passerines (Robinson et al. 1995). This is the first study to document the costs of parasitism incurred by Golden-winged Warblers and it appears that increased reproductive failure in fragmented landscapes is strongly influenced by brood parasitism.

The discovery of habitat sinks is not unexpected of a population at the periphery of its range (Mayr 1963, Kirkpatrick and Barton 1997). Adult survival rates are on the low side of those observed in other North American warblers (Faaborg et al. 2010), which indicates there may be limiting factors on the wintering grounds or during migration that cannot be directly addressed by management efforts on the breeding grounds. My efforts to understand how local and landscape factors impacted productivity revealed only one potentially effective management action: decrease the amount of anthropogenic edge at a landscape scale to reduce Brown-headed Cowbird brood parasitism and increase pairing success. While other techniques for controlling cowbirds (e.g. trapping) have successfully increased productivity of Black-capped Vireo (Wilsey et al. 2014) and Kirtland's Warbler (Solomon 1998), these programs are expensive, labor intensive, and create a dependency on long-term intervention. In Manitoba, nest survival rates were similar to those in the declining populations in Ontario and Tennessee, but the number of young produced per nest was lower (Bulluck et al. 2013), so this is potentially an area where effective management could increase productivity.

Hybridization with Blue-winged Warblers (*Vermivora cyanoptera*) is an interesting aspect of these warblers' ecology that is still not fully understood and recent research raises questions about whether these should continue to be managed as two separate species or as a single species with various phenotypic morphs (Toews et al. 2016). Very few genes differ in the

nuclear genomes of Golden- and Blue-winged Warblers and those that do are related to plumage (Toews et al. 2016). However, the mitochondrial genomes show a clear distinction between the two species that indicate the ancestral species diverged around two million years ago (Gill 1987, Gill 1997, Shapiro et al. 2004, Dabrowski et al. 2005, Vallender et al. 2009). The greater genetic divergence of the mitochondrial genome is not unexpected; mitochondrial DNA evolves more rapidly than nuclear DNA in animals (Brown et al. 1979). Model simulations suggest that hybridization has been an ongoing part of the Golden- and Blue-winged warbler evolutionary history and not a recent phenomenon as was previously widely accepted (Toews et al. 2016). Hybridization does not appear to immediately threaten conservation of the Golden-winged Warbler in Manitoba. With Manitoba's low levels of introgression, I suggest the issue of hybridization should not be a focus of management and conservation at this time. Issues such as the loss of habitat and management of public lands are more urgent and can be addressed directly.

The results of my study illustrate the need for long-term demographic data from marked individuals (Sherry and Holmes 1999). While I observed negative population growth, there may have been factors outside the scope of my research (i.e., climate) impacting survival and productivity that could change with longer term monitoring. Hybridization and genetic swamping in this species is also ongoing and increasing across most of the breeding range (Vallender et al. 2009) so future studies in Manitoba should continue monitoring this aspect of Golden-winged Warbler ecology.

### ***Management implications***

Early-successional habitat should be created and maintained on a regular basis as part of a dynamic forest ecosystem. If forests are completely converted to other land use types as is



currently occurring at an increasing rate in the aspen parkland transition zone of Manitoba, it removes the option for any present or future occupancy by Golden-winged Warblers. One approach to maintaining early successional habitats is to manage forests based on the natural range of variation that was historically estimated (Lorimer and White 2003). That would require the establishment of a reference time period, agreement about what is natural vs unnatural, and the ability to implement management actions to maintain the historical variation. An alternative option would be a more proactive approach that identifies the desired future conditions and then creates those conditions. I suggest that managers focus on creating and maintaining habitat in forested areas that are only moderately or minimally fragmented by agricultural land uses because Golden-winged Warblers are not likely to occupy habitat patches otherwise. This does not mean that forestry, resource extraction, or development could not occur, but it would need to be managed to avoid permanently removing habitat.

The forestry industry, as currently managed by Manitoba Sustainable Development, provides a good example for other industries to follow. Patches of forest are removed from the landscape at a given time and then allowed to regenerate back to pre-harvest condition (Manitoba Forestry, <https://www.gov.mb.ca/sd/forestry/renewal/index.html>). This mimics natural disturbance conditions such as a fire. This type of management scenario creates a shifting mosaic of age classes and can sustain a target proportion of the landscape in a young forest condition. Leaving legacy trees intact by making selective cuts can also benefit the Golden-winged Warbler (Roth et al. 2014). Another way that timber harvesting could create Golden-winged Warbler habitat is by seeding both the cut slash that remains on the ground and the logging roads with native grasses, forbs, and shrubs which can help to more quickly create suitable habitat conditions (Klaus and Buehler 2001). Periodic fire in harvested stands could also help maintain

an herbaceous component and extend habitat suitability for a longer period of time. Though this is less likely to be agreed to by Manitoba Sustainable Development due to limited time and resources, it could be a management tool to use in areas that have been specifically targeted for Golden-winged Warbler conservation.

The biggest concern for the immediate future of Golden-winged Warblers in southeast Manitoba relates to the permanent removal of habitat as a result of the increasing amount of resource extraction in the aspen parkland region. Additionally, the Manitoba-Minnesota Transmission Line is currently pending approval and would cut directly through high density Golden-winged Warbler habitat in the southeast. However, mine restoration/reclamation and the transmission line project both have the potential to create and maintain habitat for Golden-wing Warblers in this region.

The removal of gravel aggregate to build and maintain roads is the most common resource extraction practice in this area of Manitoba. Golden-winged Warblers are attracted to the early successional habitats created when these mining operations cut down trees to prospect for areas to excavate. The standard practice of mining for aggregate removes large portions of earth and leaves open pits so that recovery to former conditions is nearly impossible without intensive restoration (Langer and Arbogast 2002). Manitoba Sustainable Development leases government lands to aggregate mining operations for an indefinite period of time (until mine depletion) and does not require restoration to occur during that time, which often lasts a century or longer (D. Sobkowich, pers. comm.). Once a mining operation has been started but not yet depleted, the pit is left open and may be abandoned. In my experience, the only species of plants that colonize the areas around the open pits and surrounding areas are invasive or weedy species such as Canada Thistle (*Cirsium arvense*), Bull Thistle (*Cirsium vulgare*), Perennial Sow Thistle

(*Sonchus arvensis*), Tansy Ragwort (*Jacobaea vulgaris*), and Absinthe Wormwood (*Artemisia absinthium*). The recovery of these areas to pre-mining conditions without any restoration would take longer than 50 years due to short growing seasons and steep-sided open pits.

With the recent increase in aggregate mining throughout the region, reclamation and restoration procedures should be required and clearly defined by the Manitoba mineral resources division, mining industries, and conservation agencies to determine the best strategy from both site-specific and landscape-level perspectives. The reclamation and restoration actions should be outlined and approved in the permitting stage before mining actually begins. The mine closure plan guidelines for revegetation currently state: “All areas affected by mining activities (building sites, tailings ponds, sedimentation ponds, waste rock piles, etc.) must be revegetated to control erosion and restore the site’s natural condition. However, if all or part of the mining site, particularly former mine rock piles and mine rock piles in use, cannot be revegetated, the proponent must prove that it is nevertheless in “satisfactory condition” (Manitoba Department of Mines Regulation 67/99). As it stands, this wording is vague and the enforcement procedures are unclear. More stringent requirements and enforcement of habitat restoration may also encourage companies to destroy less habitat initially, while also encouraging recolonization of disturbed lands more quickly. In addition, I suggest that companies be required to level out the open pits so that large areas of uninhabitable bare ground are not left with little chance of revegetation.

Transmission lines can be managed as both prairie and early-successional ecosystems for endangered species (Baker 1999). Manitoba Hydro’s Manitoba-Minnesota transmission line has the potential to benefit Golden-winged Warblers and other early-successional species through the creation and continual maintenance of habitat in an early-successional stage. Manitoba Hydro acknowledges that Golden-winged Warblers could both benefit from and be harmed by the

construction and maintenance of the Manitoba-Minnesota transmission line (Manitoba Hydro EIS 2015). 475 ha of potential Golden-winged Warbler habitat will be removed during construction of the transmission line (Manitoba Hydro EIS 2015), and Golden-winged Warbler nests could be destroyed annually because vegetation in the rights-of-way will be managed (e.g. sprayed and mowed) during the nesting season. While Manitoba Hydro acknowledges that selective spraying and feathered edges may improve habitat quality for Golden-winged Warblers (Confer and Pasco 2003, Kubel and Yahner 2008), they did not commit to follow these practices in the EIS (Manitoba Hydro EIS 2015). Overall, although Manitoba Hydro EIS (2015) concluded that the construction and maintenance of Manitoba-Minnesota transmission line would have a non-significant impact on the Golden-winged Warbler, I cannot support this finding, as my research has demonstrated that the creation of edges negatively impacts Golden-winged Warbler productivity (Ch. 3). Further, research in another part of the range found rights-of-way can act as an ecological trap for Golden-winged Warblers (Kubel and Yahner 2008). Therefore, changes to the habitat may be long-lasting and negative for the Golden-winged Warbler.

Manitoba Hydro states they will continue to monitor all threatened and endangered species post-construction to assess longer-term impacts (Manitoba Hydro EIS 2015), but standard monitoring practices only last a few years post-construction and will not be sufficient to monitor long-term impacts or assess changes in productivity. The Manitoba-Minnesota transmission line presents an opportunity to follow best management practices for Golden-winged Warblers and potentially could aid in the recovery of this species but it could also remove habitat and permanently decrease habitat quality.

Golden-winged Warblers in Manitoba have the good fortune to occur mostly within provincial and federal land, allowing the majority of the population to be managed by Manitoba

Sustainable Development and Environment Canada. This is a benefit to the species because management can be consistent across the Manitoba range; however, a broader strategic approach to conservation in the boreal-parkland transition zone is necessary and should include private land owners and industry. The management of habitat to benefit the Golden-winged Warbler will not only help to conserve this charismatic species, but will also protect a unique and declining ecosystem required by other species.

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