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Nesting Ecology of White-throated Sparrows

(Zonotrichia albicollis) :

The effects of variation in clutch-initiation date
and the application of prescribed fire on nesting success

by

Melissa Olmstead

B.Sc.H., Queen's University, 2011

A thesis

submitted to the

Department of Biology, Faculty of Science

in partial fulfillment of the requirements for the degree of

Master of Science in Integrative Biology

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Abstract

The study of nesting success is one of the most widely-used methods for examining the factors governing recruitment in birds. Many ecological influences act together to increase or decrease nesting success, and knowledge of these mechanisms is crucial for determining the habitat or conservation requirements of a given species. One ecological influence is the timing of breeding, which in many species is related to a decline in nest success later in the breeding season. Much of the research on this subject has focused on cavity-nesting species, and the hypothesis that this seasonal decline is caused by a mismatch between clutch-initiation date and peak food availability for young. I tested this hypothesis in a population of white-throated sparrows (*Zonotrichia albicollis*) in Algonquin Provincial Park, Ontario, and I offer the alternate hypothesis that this decline may be caused by increased predation later in the season. Another influence on nest survival is disturbance caused by habitat management, such as the use of prescribed fire to conserve open- and early-successional habitats. While the goal of these restoration initiatives is to maintain landscape heterogeneity, the level of disturbance required to improve a habitat cannot exceed the tolerance of target species. Much of the research on this subject has focused on community-level studies quantifying the change in species abundances after a fire event. These studies capture only the most coarse-grained effects of fire, and may not be used to elucidate the mechanisms driving these changes in population size. I investigate the effect of spring burning on the nesting success of a single species, white-throated sparrows, and reveal that, while overall nesting success is not affected, fire has a substantial impact on nest site selection. This has implications for future controlled burn initiatives, since a matrix of suitable nesting habitat must be left untouched in order to allow breeding in the first year after the burn. Observing the same population in both a natural and managed system represents a valuable contribution to our knowledge of the effects of management strategies on avian nesting success.

Co-authorship and Formatting

This thesis document has been written in the manuscript style. Chapter 2 was co-authored by Melissa Olmstead and Scott Ramsay, and submitted for publication to the Journal of Avian Biology. Data collection and analysis was carried out by Scott Ramsay. For inclusion in this document, some aspects of formatting have been modified to match the other chapters. Chapter 3 was written by Melissa Olmstead, and will be submitted for publication to a journal such as the Auk or the Journal of Wildlife Management. The findings in Chapter 3 are based on historical data collected in 2006-2010 (Chapter 2), as well as new data collected by Melissa Olmstead in 2012-2013. As such, some information may be duplicated between chapters, and there may be some differences in writing and/or formatting style.

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Chapter 1

General Introduction

The main objective of this research is to explore the factors influencing avian breeding success in a ground-nesting species. Here, I consider the relationship between nesting success and biotic and abiotic determinants of life history traits, such as fecundity, the timing of breeding, and nest failure through predation. This includes an observational study of variation in clutch-initiation date and its influence on nest success via ecological constraints (Chapter 2), and an experimental investigation of the acute effects of prescribed fire on nesting success (Chapter 3).

In the field of ecology, one of the most widely-used metrics of habitat quality is a combined measure of the number of species that can be supported, and the number of individuals that can survive in the area (Stirling and Wilsey 2001). However, the relative importance of community-level surveys versus species-by-species investigations of habitat quality must be considered when planning management or conservation projects. While many conservation initiatives involve large-scale implementation of management strategies and community-wide monitoring, the responses of individual guilds or species are often mixed (Kleijn and Sutherland 2003; Whittingham et al. 2007). Furthermore, species abundances alone may not be reliable indicators of habitat quality in disturbed areas (Horne 1983; Bock and Jones 2004). Although community-level sampling can provide an overview of the observed changes in species richness and

abundance, after management programs are put in place these metrics should be considered preliminary results. The effect of management at the species level should be investigated further in order to characterize the potential responses to habitat management. Such insight is crucial for evaluating the effectiveness of management strategies, and for troubleshooting cases in which the desired outcome has not been achieved. Therefore species-level examinations of the factors influencing species abundances in natural systems are required in order to better understand population dynamics and how they might be affected by management strategies.

1.1 Determinants of Population Size

The population size of a given species can be controlled by a number of factors, which are connected in a complex web of influence: climate and temperature, predation risk, juvenile recruitment, adult survival, dispersal, and immigration represent only a few of these factors. Each differs in importance depending on habitat, species, population size, and population density, and therefore care must be taken to focus on the largest influence on a given population. In birds, nesting success is generally accepted as the most important determinant of recruitment into the population (Johnson 2007). Nest success can be measured in a variety of ways (reviewed in Johnson 2007), including nest survival over time, and the proportion of nests that fledge young. A number of factors may influence nest success, such as female condition or age, abiotic stressors, nest predation, nest parasitism, food availability, and parental care (Forslund and Pärt 1995; Martin 1995). Many of these factors are in turn influenced by habitat quality, which in birds may be indicated by predation risk or the availability of resources such as food, shelter, and nest sites (Enoksson and Nilsson 1983; Martin 1993; Newton 1994). These may be directly affected by habitat management or restoration initiatives, and will ultimately impact the size of a given population. Therefore in order to predict and evaluate the large-scale effect of these initiatives on avian communities, it is important to first study the determinants of nesting success in individual

populations and species. In Chapter 2, I examine the effect of variation in clutch-initiation date on nest success, and relate this to increased nest predation risk later in the breeding season. In Chapter 3, I then use the insights gained from the research outlined in Chapter 2 to predict and examine the acute effects of prescribed fire on nesting success in the first two years after a burn.

1.2 Clutch-initiation Date and Nest Success

Constraints on a life history trait that involve different trophic levels are thought of as ecological limitations. In the field of nesting ecology, when food availability presents the largest constraint, it is said that bottom-up limitation is acting on nest survival; conversely, when predation of adults or young is the largest constraint, this is called top-down limitation. In this context, competition with other species for resources may also play a role in limiting food availability, or increasing nest predation through limiting high-quality nest sites. Depending on the constraint, certain strategies may be used to lessen its influence on nesting success and to improve population size. For example, in bottom-up systems it has been demonstrated that even short-term food supplementation will increase population density or growth in birds (reviewed in Boutin 1990), and in these cases habitat management is recommended to improve food availability. In top-down systems, predation can impact fecundity and nest success both directly and indirectly (Chalfoun and Martin 2010; Zanette et al. 2011), and predator-exclusion experiments have resulted in increased nest survival (reviewed in Smith et al. 2011). There can also be a synergistic interaction between food and predator constraints, with the implementation of both management strategies producing a stronger effect than either alone (Clinchy et al. 2004; Zanette et al. 2006). Therefore it is important to determine which type of limitation represents the most powerful influence on the population size of a given species, and the mechanism by which that limitation affects nesting success.

In 1966, David Lack observed a seasonal decline in nesting success, which he related to decreased food availability later in the season (Lack 1966). It has been postulated that the timing of spring leaf bud burst is directly correlated to the availability of insect prey, and so nest success later in the season is constrained by the dietary needs of the young (Rowe et al. 1994; Nager and Van Noordwijk 1995). Thus directional selection would favour earlier nests, but food availability is often low in the early spring (Perrins 1965). Therefore, in food-limited systems, the optimal clutch-initiation date (CID) would be determined by the date that most closely matches peak food availability for both the mother and the young. However, this constraint may not operate equally in all avian guilds, and it is important to also consider the role of predator-limitation as an influence on the timing of breeding. Much of the research on clutch-initiation date that puts forth bottom-up limitation as the most important constraint was performed on cavity-nesting species (reviewed in Ramsay and Otter 2007). A wide variety of terms is used to describe this research, and so I performed literature searches using different combinations of terms such as clutch-initiation date, laying date, breeding phenology, timing, nest success, nest survival, and breeding success. Many of the articles containing these terms described research on food availability and how it constrains the nesting success of cavity-nesting species, in the family Paridae in Europe (Table 1.1). Research on cavity-nesting species is often carried out in artificial nest box systems, which experience reduced nest predation rates compared to natural cavities, and therefore in these systems the effect of top-down limitation is confounded (Møller 1989). Furthermore, nest predation has been found to be higher in North America than in Europe, possibly due to differences in the history and extent of anthropogenic habitat disturbance between continents (Martin and Clobert 1996); in shrubland habitats, ground-nesting species have been shown to be more vulnerable to nest predation than other guilds (Martin 1993). Therefore in Chapter 2, I test the hypothesis that bottom-up limitation represents the most powerful influence on optimal laying date in birds, and investigate the impact of top-down limitation on clutch-initiation date and nesting success in a ground-nesting shrubland species.

1.3 Prescribed Fire and Nest Success

The impact of habitat degradation, fragmentation, and loss has been highlighted as a leading cause of population decline in many taxa, including birds (Butchart et al. 2010). In many cases habitat management methods can be successful in halting population decline, or even promoting population growth and recovery. One method for restoring habitats, such as open- and early-successional forest areas, is the controlled application of fire, which can be used to reverse succession and keep a habitat at a desired stage (Angelstam 1998). However, this method involves an initial reduction in habitat quality for some species, as even low-intensity prescribed burns will immolate a large portion of ground cover and some trees. Habitat management as a management strategy would be counter-productive if it resulted in an irreversible negative impact on the targeted breeding bird populations, and therefore the response of local species must be carefully considered before beginning a restoration project. While much is known about the community-level effects of fire on species abundances, and the effects of fire over long time periods after an event, information on species-specific responses immediately after a fire is scarce (reviewed in Saab and Powell 2005). Such information is crucial for predicting the effect of fire on local breeding birds, since community-level studies have shown mixed responses between guilds and fire intensities (Bagne and Purcell 2011, Haney et al. 2008, Knick et al. 2005). For example, out of 209 articles found through a search of the effects of fire on avian nesting success, only 37 articles are grouped in the research areas of ecology and conservation, or ecology and forestry; the majority of fire research is also conducted in the United States, with only a few studies in Canada (Table 1.2). The pool of available literature is further limited by excluding research on the effect of stand-replacing fire, since for safety and logistical reasons, applied habitat management fires are mainly low-intensity, low-severity burns. Important characteristics to consider when predicting species-level responses to fire are territory usage and nesting guild. Territories may be either all-purpose spaces in which both nesting and foraging occur (Hinde 1956), or they may have a central location for nesting alone, while individuals range far and wide to

forage (Nice 1941). The effects of management practices may be larger in species with all-purpose territories, as the likelihood of impacting the entire territory is greater when individuals only use one contiguous area. Factors indicating a “good” territory include food availability, which can be inversely related to territory size (Enoksson and Nilsson 1983; Smith and Shugart 1987), as well as the availability of nest sites and nesting material. Prescribed burns may result in no effect or a positive effect on breeding in cavity- or tree-nesters, since they may cause only low rates of tree loss, or they may increase the availability of standing deadwood for cavities (Koivula and Schmiegelow 2007). Conversely, even low-intensity fires will result in a substantial reduction of ground cover vegetation and litter depth, thus significantly reducing the availability of nesting habitat for ground- and shrub-nesters (Artman et al. 2003). This effect has been demonstrated in community-level studies, which indicate that fire results in decreasing abundances of ground- and shrub-nesting species (Klaus et al. 2010; Bagne and Purcell 2011). However, large-scale monitoring of abundances may not reveal the full impact of management practices on the health of a population, and more research is required to investigate effects on the nesting ecology of individual species (Hannah et al. 2008). Therefore in Chapter 3, I investigate the acute effects of prescribed fire on a ground-nesting species in the first two years after a controlled burn.

1.4 White-throated Sparrows

White-throated sparrows (*Zonotrichia albicollis*) are small ground-nesting birds that breed in open and edge habitats of Canada and the north-eastern United States. They occupy a wide range across the continent, and are considered habitat generalists (Drapeau et al. 2000, Falls and Kopachena 1994). They are short-distance migrants, with some likely breeding in Northern Ontario and overwintering in Southern Ontario (Falls and Kopachena 1994). Spring arrival occurs in mid-April, and the breeding season begins in early May (Tozer 2012). In early spring, white-throated sparrows feed on the ground, foraging for seeds and plant matter; during the nesting

season they glean insects from trees, and feed their young an almost exclusively insectivorous diet (Falls and Kopachena 1994). Further details on white-throated sparrow life history traits can be found in Chapters 2 and 3, as pertaining to respective investigations of the relationship between variation in clutch-initiation date, prescribed fire, and nesting success. As ground nesters, they are vulnerable to predation on eggs and young, and as they have a mainly insectivorous diet, nest timing and parental investment may also be constrained by food availability. Thus, they represent a good study species with which to investigate the effect of variation in clutch-initiation date on nest success (Chapter 2). Furthermore, the low shrubby vegetation that white-throated sparrows use as nesting habitat is the first to be impacted by a low-intensity prescribed burn. However, as habitat generalists, they may be more flexible in territory or nest site selection, and may be better able to escape any negative long-term or population-level effects of this disturbance. Therefore they represent a good study species with which to investigate the acute effect of prescribed fire on nesting success (Chapter 3).

1.5 The Old Airfield

The main study site is located in Algonquin Provincial Park, Ontario, Canada (Lat. 45° 34' 30", Long 78° 30' 30"), in a patch of cleared forest that was once used as an airfield. This area was cleared in the 1930s as a Depression relief project, and cottagers used it as a private airstrip until the 1970s (Clemson 2006). After 40 years of undisturbed forest succession, this area has developed into a heathland habitat characterized by woody shrubs and low-nutrient soil (Whittaker 1979). Ground cover is lowbush blueberry (*Vaccinium angustifolium*) and bracken fern (*Pteridium aquilinum*), with scattered conifers (*Pinus*, *Abies*, and *Picea* spp.), and isolated stands of trembling aspen (*Populus tremuloides*). As an old airstrip, this area also represents a heritage site preserving a piece of Algonquin Park history. This site was selected for preservation by Ontario Parks, through the use of controlled burning to reverse succession. This application of

prescribed fire is also part of a developing fire management plan, one of the goals of which is to enable policy implementation that allows some forest fires in the Park to burn naturally, rather than being completely suppressed. This has a two-fold benefit of facilitating a more natural fire regime in Algonquin Provincial Park, and creating the opportunity for a scientific investigation of the effects of fire on breeding birds.

The Airfield provides ample nesting habitat for white-throated sparrows, since it contains low ground cover to camouflage nests, as well as mature scattered conifers to serve as song posts and foraging habitat for adults (Falls and Lowther 1968; Peck and James 1987). This area has been used as a study site for white-throated sparrow research for many years, including an investigation by Falls and Lowther (1968) into general life history traits, a comparison of nesting ecology between colour morphs by Knapton and Falls (1982) and Knapton et al. (1984), and a summary of the known characteristics of white-throated sparrows by (Falls and Kopachena 1994). Furthermore, although white-throated sparrows have been declining in other areas of the Park, the Airfield has continued to sustain a healthy breeding population (Barker 2006; Tozer 2012). Therefore, with a source of historical data to serve as a baseline, and a stable population of individuals, this study site provides an excellent opportunity to study the nesting ecology of white-throated sparrows.

In summary, my research focuses on the study of nesting ecology in an individual species, and represents a valuable contribution to our knowledge of the effects of management strategies on the nesting success of breeding birds. Observing the same population in both a natural and post-management system widens the breadth of aspects of nesting ecology that can be studied, and improves our interpretation of community-level findings on prescribed fire and nesting success.

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1.7 Tables

Table 1.1: Summary of gathered literature concerning clutch-initiation date and nest success in birds. Literature searches were conducted over the course of 18 months in 2012 and 2013. Results are grouped by ecological constraint, nest guild, family, and geographic location.

Category	Number of Articles	Proportion of Articles (%)
Clutch-initiation date and nest success	33	100.00
Food availability	25	75.76
Nest Predation	6	18.18
Food and Predator Effects	2	6.06
Cavity or Box Nests	25	75.76
Ground Nests	1	3.03
Shrub or Tree Nests	9	27.27
Parid species	23	69.70
Non-Parid species	10	30.30
Europe	22	66.67
North America	14	42.42

Table 1.2: Summary of a literature search conducted in November 2013 on the study of fire ecology of breeding birds. The search structure using Boolean operators and wildcards was as follows: bird* and (nest or breed* or reproduc*) and (success or survival or mort*). Results are grouped by Web of Science categories, and by geographic location.

Category	Number of Articles	Proportion of Articles (%)
Nest Success + Fire + Birds	209	100.00
Ecology	100	47.80
Ornithology	59	28.20
Zoology	49	23.45
Conservation	33	15.79
Forestry	29	13.88
Ecology + Conservation	32	15.3
Ecology + Forestry	5	2.39
USA	152	72.70
Canada	17	8.13
Australia	16	7.66

Chapter 2

Clutch-initiation date and nesting success in white-throated sparrows (*Zonotrichia albicollis*) : early nesting avoids predation

Abstract – In 1966, David Lack made three main observations about avian nesting seasons that have been used as predictions for the relationship between clutch size, a measure of fecundity, and clutch-initiation date. 1) Clutch size varies negatively with clutch-initiation date. 2) In years when average clutch-initiation dates are earlier, the average clutch size for a population will be larger. 3) Clutch size varies positively with breeding latitude. The objective of this study was to test Lack's first two predictions in a population of white-throated sparrows (*Zonotrichia albicollis*) breeding in Algonquin Park, Ontario, Canada. In many species, it has been demonstrated that the strongest constraint on nesting success is food availability for the young. In these species, selection pushes clutch-initiation dates to coincide with peak food availability. However, the role of predation in limiting nest success must also be considered. In predation-limited systems, selection pushes clutch-initiation dates to coincide with the time of least risk of predation on eggs or nestlings. Here we test Lack's first and second predictions, and show that nest predation provides a selective pressure on clutch-initiation date. Over four breeding seasons in Algonquin Provincial Park, white-throated sparrow nests were monitored to determine clutch-initiation date, reproductive effort, and nest fate. Lack's first and second predictions were not met in this population, which may indicate that female white-throated sparrows are not limited by food availability in their offspring investment. However, an effect of variation in clutch-initiation

date was found in overall nest success. Nests with an earlier clutch initiation date were more likely to achieve the fledgling stage and nest success, which may indicate that in white-throated sparrows nest success is limited by predation rather than food availability.

2.1 Introduction

In many avian species, understanding the factors influencing nesting ecology can give vital insight into the determinants of recruitment into the population. Other life cycle elements may also come into play, one of which is adult survival; however, nesting success has the greatest effect on recruitment, and is also the most easily studied and managed (Johnson 2007). Song birds, or passerines, employ a variety of tactics when nesting: these include nesting on the ground, in shrubs, on tree branches, or within cavities in trees. Some elements, such as climate change, may influence species of all nesting strategies, while other elements, such as nest predation, may impact certain strategies more than others. Understanding the influences on nesting success is important for conservation purposes, and for predicting how a population may be affected by a disturbance. In many species it has been observed that nest success declines over the course of the breeding season (Lack 1966, Perrins 1965). This may have a number of causes, including a decrease in food availability for nestlings, an increase in predation pressure, or a decline in habitat quality. It would seem that breeding as early as possible would be ideal, but the breeding female is constrained by low food availability in the early spring (Perrins 1965). Therefore, the breeding female must strive for an optimum date to begin laying. This laying date varies among individual females, populations, and species. Investigating the variation in clutch-initiation date (CID), and the effect that this has on nesting success, can give vital clues into the mechanisms influencing population growth or decline.

Lack (1966) made three main observations that have been used as predictions for the relationship between clutch size and clutch-initiation date: 1) Clutch size varies negatively with

clutch-initiation date; i.e., females that begin laying later produce smaller clutches; 2) In years when average clutch-initiation dates are earlier, the average clutch size for a population will be larger; and 3) Clutch size varies positively with breeding latitude; i.e., populations at higher latitudes will have larger average clutch sizes than populations at lower latitudes.

The effect of variation in laying date on nesting success has been studied in several cavity-nesting species of birds in both Europe and North America (Lack 1966, reviewed in Ramsay and Otter 2007). This effect can be investigated in a number of ways, including documenting the variation in laying date among individual females and its effects on nesting success, and determining the mechanisms driving these differences. Research performed in the 1990's focused primarily on differences in CID among individual females. Considering that later laying dates in the spring should coincide with increased resources for a female, investigators sought other explanations for the seasonal decline in clutch size, and found consistent evidence for a relationship with the timing of leaf bud burst and insect prey availability (Nager et al. 1997, Rowe et al. 1994, van Noordwijk et al. 1995). The general conclusion of these studies has been that nest success is constrained by the dietary needs of the young, a phenomenon also known as a bottom-up limitation. In these studies, it was found that laying date was synchronised to match the peak of offspring food demands with the peak abundance of caterpillars, thus maximizing the potential growth and survivorship of offspring. These investigators concluded that females that mistimed breeding with respect to this peak had both poorer body condition and produced nestlings of lower fitness, and these effects could carry on into subsequent breeding seasons.

These studies were performed only on cavity-nesting species, however, and further inquiry is required to determine the effects of variation in laying date on the nesting success of ground-nesting species, such as the white-throated sparrow (*Zonotrichia albicollis*). Cavity-nesters are often observed in artificial box nests, which present a controlled environment where nest predation is reduced or eliminated. Conversely, ground-nesters are highly vulnerable to predation on eggs and nestlings. While most nest failures in box nests can be attributed to

starvation, species with open-cup nests are more likely to be subject to top-down limitation, where predation is the leading cause of nest failure (Knapton et al. 1984, Whillans and Falls 1990, Zanette et al. 2006). Although some studies of nesting success in great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) have considered predation, they have focused on the effects of sparrowhawks (*Accipiter nisus*), which prey on fledglings and adults rather than on eggs or nestlings (Götmark 2002, Both et al. 2009). To date, evidence of a link between clutch-initiation date and nest predation is inconsistent across species, with reduced predation on earlier nests (e.g., red-winged blackbirds, Weatherhead and Sommerer 2001; northern flickers, Fisher and Wiebe 2006; cackling geese, Kellett and Alisauskas 2011; Pacific common eider, Wilson et al. 2012), increased predation on earlier nests (e.g. wrentits, Preston and Rotenberry 2006; northern cardinals, Shustack and Rodewald 2011), or no relationship (e.g. dusky flycatchers, Kroll and Haufler 2008).

A further limitation of the earlier studies, in the context of examining the combined role of nest predation and nest timing in constraining nest success, is the focus on species such as titmice (Paridae) that have relatively large clutch sizes for passerines, suffer relatively low levels of nest predation, and have a large scope of variation in clutch size (reviewed in Ramsay and Otter 2007). In sparrows (Emberizidae), clutch sizes are smaller and show a much narrower range of variation; e.g. mean clutch size in white-throated sparrows is approximately 4 eggs, and clutches vary from 3 to 5 (Falls and Kopachena 1994). Therefore constraints on clutch size in some species may limit a female's ability to vary the number of eggs laid across the season. An alternative strategy that may be available to females with limited abilities to vary egg number is to vary egg mass. A female in good condition may not have sufficient resources available to add an extra egg to a clutch, but she may be able to add extra investment in each offspring through an increase in egg mass, which may improve offspring survival (Williams 1994).

2.1.1 Study Species

White-throated sparrows are small ground-nesting birds that breed in open and edge habitats of Canada and the north-eastern United States. They are short-distance migrants, with some breeding in Northern Ontario and overwintering in Southern Ontario (Falls and Kopachena 1994). Spring arrival occurs in mid-April, and the breeding season begins in early May (Tozer 2012). In early spring, white-throated sparrows feed on the ground, foraging for seeds and plant matter; during the nesting season they glean insects from trees, and feed their young an almost exclusively insectivorous diet (Falls and Kopachena 1994).

Both males and females exhibit a plumage colour polymorphism, with associated behavioural and ecological characteristics (Formica et al. 2004, Knapton and Falls 1984). Plumage differs by the colouration of the crown stripes on the head, and includes both white-striped (WS) and tan-striped (TS) colour morphs. This polymorphism is linked to a chromosomal inversion, and disassortative mating maintains the colour morphs at roughly equal proportions in the population (Tuttle 2003). White-striped males are more aggressive and often intrude on other territories to attempt copulation with extra-pair females, while tan-striped males exhibit higher levels of mate-guarding behaviour and provide more parental care (Formica et al. 2004, Tuttle 2003). In spite of the differences in male provisioning rates, females whose partners were removed were able to compensate for this by increasing their own provisioning rates, and fledged young at the same rate as intact pairs (Whillans and Falls 1990). Thus, the difference in male provisioning rates appears to have little effect on nesting success (Knapton et al. 1984, Whillans and Falls 1990).

Nests are constructed out of grasses, pine needles, and dead bracken ferns. They are commonly found on the ground under blueberry shrubs or dead bracken ferns, and are placed in close proximity to a conifer at least 1m tall. Nest construction materials and placement can be flexible, and the amount of nest camouflage varies from completely covered to completely

visible. Nest construction begins within a few days of female arrival, and there may be a lag of a few days between nest completion and clutch initiation. One egg is laid per day, and 4-5 eggs may be laid; incubation lasts approximately 12 days, and during this time the female will only leave the nest for short bouts of foraging (Falls and Kopachena 1994). During the nestling stage, both parents are involved in food provisioning, and trips may be made to and from the nest once every 5-7 minutes (Whillans and Falls 1990). Fledging, which is considered the standard measure of nest success, occurs when the young leave the nest (Johnson 2007).

Since white-throated sparrows nest on the ground, the eggs and nestlings are highly vulnerable to predation by small mammals, snakes, and other birds. Females will normally nest only once per season, unless the first nest is predated (Falls and Kopachena 1994). Predation can affect 30-60% of the total nests in an area, resulting in egg and nestling mortality. Nest predators may include deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Clethrionomys gapperi*), red squirrels (*Tamiasciurus hudsonicus*), blue jays (*Cyanocitta cristata*), eastern garter snakes (*Thamnophis sirtalis sirtalis*), and eastern chipmunks (*Tamias striatus*) (Falls and Kopachena 1994). This nest predation changes the optimal laying date, which must occur at the right time during the breeding season to coincide with peak food availability without incurring the costs of increased nest predation (Richmond et al. 2011).

2.1.2 Objectives

Our objective in this study was to test Lack's predictions for the relationship between clutch size and clutch-initiation date in a population of white-throated sparrows breeding in Algonquin Park, Ontario, Canada (Figure 1). Specifically, we predicted that females would show a negative relationship between clutch size and clutch-initiation date, through variation in either egg number or egg mass. We also predicted that the average clutch size of the population would vary negatively with the mean clutch-initiation date, again via changes in either egg number or egg

mass. Because this study was based on a single population we were unable to test Lack's third prediction. Aside from these predictions we also tested the effects of variation in clutch-initiation date and clutch mass on nest survival, as well as the effects of morph and habitat. We tested these predictions using nesting data collected over four years.

2.2 Methods

2.2.1 Field Methods

Data were collected in April and June of the years 2006-2008 and 2010. Two study sites were established in Algonquin Provincial Park, Ontario, Canada (45° 34' 30" N, 78° 30' 30" W). The first site (Airfield) covers a former airfield near Mew Lake Campground, an open area of low vegetation, forest edge and small tree stands. Ground cover is predominately wild blueberry (*Vaccinium* spp.) and bracken fern (*Pteridium aquilinum*), with scattered conifers (*Pinus*, *Abies*, and *Picea* spp.), and isolated stands of trembling aspen (*Populus tremuloides*). The second site (Station Road) lies along a stretch of secondary roadway, located approximately 1 km NE of the Airfield, and is the access to Algonquin Wildlife Research Station. The area around this road is comprised mainly of forest edge, with some open areas of low vegetation in hydro line cuts, and additional edge habitat along the North Madawaska River. Most nesting data were collected in areas of moderate tree density in the Airfield, and along the forest edge of the Station Road.

All adult white-throated sparrows were closely observed for nesting activity throughout the breeding season. Behavioural cues from the parent birds helped with nest location. Once the nest was found, a monitoring protocol was initiated that allowed sufficiently frequent nest checks to collect data, without attracting predators or causing undue disturbance to the parents. Nests found during building were checked every second day for the presence of eggs. Once the first egg

was laid, the next visit was scheduled for the date when the fifth egg would be laid, and at that point the number of eggs was noted and the complete clutch was weighed to the nearest 0.1 g using a spring balance (Avinet 30 g \pm 0.1 g). Nests that were found with fewer than five eggs were checked on the day when they should reach five; i.e. two days later for a clutch of three, one day later for a clutch of four. On the subsequent visit the number of eggs was noted and the clutch was weighed. Any additional eggs in the nest were considered evidence that the nest was found during egg-laying. A nest with no additional eggs was considered to have been in the incubation phase when found. For these nests, we used hatch date and clutch size to estimate the clutch-initiation date, allowing 12 days for incubation plus one day less than clutch size for laying, to account for the onset of incubation with the laying of the penultimate egg. We were able to compare nests with equal clutch sizes that hatched on the same day to verify the accuracy of this back-dating procedure.

Nests were checked during incubation for continuing female presence, nest contents and hatching at 5, 10 and 12 days following clutch completion. Nests that were found during the incubation stage were checked every second day for evidence of hatching. Hatch day was determined based on the contents of the nest at the day 10 and 12 checks. If all eggs were hatched, then hatch day was determined to be the previous day; if the clutch had partially hatched, then the day of the check was determined to be hatch day.

Once a nest hatched, it was checked again 5 days later for signs of continued activity, and depending on the growth of the nestlings, they were banded between days 5 and 7 post-hatch. During banding, chicks were weighed to the nearest 0.1 g using a spring balance (Pesola 60 g \pm 0.1 g); tarsus was measured to the nearest 0.01 mm using dial calipers; and the feather with the longest broken tuft on the left wing was noted and the length of the tuft was measured to the nearest 0.01 mm with dial calipers. Nests that were found during the nestling stage were banded and measured when the nestlings were estimated to be 5 to 7 days post-hatch, based on a comparison of size and appearance with nestlings of known age. Nests that were found when the

nestlings were greater than 7 days post-hatch were banded immediately.

Between 10 and 12 days after hatching, nests were checked for signs of activity, and any nestlings in the nest were deemed to have fledged. For nests that were empty, the parents were monitored for evidence of food carrying. If no evidence of fledging success could be found on the first visit, a second visit to the territory was conducted two days later to look for further evidence. Again, if no evidence was apparent the nest was deemed to have failed.

2.2.2 Statistical Analysis

Figure 2.1 provides a schematic of the analyses we performed. Our analyses can be thought of as a path of causation from clutch-initiation date to clutch size/mass, brood mass, and nesting success. We treat year, site and male morph as external variables that may affect a female's nesting parameters, and therefore include all three as factors in addition to those of our main predictions. To test for external influences on clutch-initiation date (our most basic predictor) we used a three-factor ANOVA with all three external variables as main effects. All other predictions were tested using GLMs, with additional subordinate factors added as we progressed from effects on clutch size to nesting success. The GLMs for clutch size and clutch mass included year, site, male morph and clutch initiation dates as independent variables, with a normal distribution and an identity link function. The GLM for brood mass included the additional factor of mean egg mass, also with normal distribution and identity link. The test of nesting success included the three external variables, clutch-initiation date (standardized to the annual mean), and mean egg weight, with a binomial distribution and a logit link function. All statistical analyses were carried out using JMP 9.0 (SAS Institute 2010).

2.3 Results

Our analysis includes 55 nests across the four years of study for which we had complete information on clutch-initiation dates. The nests were distributed as follows: 2006 – 14, 2007 – 16, 2008 – 16, 2010 – 9; Airfield – 35, Station Road – 20; White-Striped Male – 32, Tan-Striped Male – 23). In all cases individuals within pairs were opposite morphs (WS-TS or TS-WS in male-female pairs). A three-factor ANOVA of clutch-initiation dates revealed a significant effect of year, with 2008 being later than all other years (2006: 26.57 ± 1.79 , mean \pm S.E., 2007: 27.05 ± 1.63 , 2008: 33.88 ± 1.68 , 2010: 25.89 ± 2.24 , $p = 0.00069$; $F_{5,49} = 3.477$, $p = 0.0091$; Table 2.1, Figure 2.2). There were no effects of male morph or site on clutch-initiation dates ($p > 0.5$).

Analysis of clutch size variation yielded a non-significant GLM (Whole model, $n = 55$, $\chi^2 = 5.3658$, $df = 6$, $p = 0.4978$; Table 2.2), however male morph was a significant main effect, with females mated with TS males laying larger clutches than females mated with WS males (TS: 4.04 ± 0.13 vs. WS: 3.67 ± 0.10 , $\chi^2 = 3.9781$, $df = 1$, $p = 0.0461$; Figure 2.3a). Clutch-initiation date, year, and site did not predict clutch size ($p > 0.5$). Analysis of clutch mass rather than size did yield a significant GLM (Whole model, $n = 40$, $\chi^2 = 15.0615$, $df = 6$, $p = 0.0198$). As with clutch size, male morph was a significant effect, with females mated with TS males producing heavier clutches than females mated with WS males (TS: 11.29 ± 0.40 g, vs. WS: 9.60 ± 0.32 g, $\chi^2 = 10.0270$, $df = 1$, $p = 0.0015$; Figure 2.3b). There was a marginally non-significant relationship between clutch-initiation date and clutch mass, with later clutches trending toward higher masses (slope = 0.0771 ± 0.0415 , $\chi^2 = 3.3142$, $df = 1$, $p = 0.0687$). Neither year nor site was related to clutch mass ($p > 0.45$).

Total brood mass is affected by the number of nestlings in the brood and their age at weighing (Least-squares Regression, $r^2 = 0.7350$, $F_{2,25} = 34.67$, $p < 0.0001$). Therefore we used

the residual brood mass in grams to test for additional factors affecting offspring growth. Including egg mass in the model reduced the sample size for analysis to only 18 nests, therefore, we generated two models for brood mass: the first included year, sample location, male morph, standardized clutch-initiation date, and mean egg mass (Whole model, $n = 18$, $\chi^2 = 15.5931$, $df = 7$, $p = 0.0291$), the second included all effects except egg mass (Whole model, $n = 28$, $\chi^2 = 3.6622$, $df = 6$, $p = 0.7223$; Table 2.3). In the model that included egg mass, the independent variables of year, sample location, standardized clutch-initiation date, and mean egg mass were all significantly related to brood mass. In the model that excluded egg mass, there were no significant effects on brood mass. Because of the relatively small sample size in comparison with the number of factors entered in the model, we feel we must be conservative in interpreting our results, favouring the reduced model with the larger sample size.

Out of a total of 72 nests that were found, 28 were lost prior to hatching, 19 were lost during the nestling stage, and 20 survived fledging. Five others survived at least to the nestling stage, but whether they survived to fledging was not determined; therefore, we excluded them from further analysis. Which factors significantly affected nesting success depended on whether clutch size (Whole model, $n = 51$, $\chi^2 = 23.8448$, $df = 7$, $p = 0.0012$) or clutch mass was entered into the model (Whole model, $n = 39$, $\chi^2 = 23.3379$, $df = 7$, $p = 0.0015$; Table 2.4). In both models, earlier-laid clutches were significantly more likely to survive to fledging than later clutches (**model including clutch size**: logistic slope = -0.1714 ± 0.0821 , $\chi^2 = 5.9602$, $p = 0.0146$; **model including clutch mass**: logistic slope = -0.4047 ± 0.1897 , $\chi^2 = 9.6748$, $p = 0.0019$, Figure 2.4). Year was a significant effect in both models, with nesting success significantly poorer in 2008 compared to all other years (2006: 44.44%; 2007: 45.45%; 2008: 4.17%; 2010: 41.67%; **model including clutch size**: $\chi^2 = 13.9136$, $p = 0.0030$); **model including clutch mass**: $\chi^2 = 12.0882$, $df = 3$, $p = 0.0071$, Figure 2.5). Sample location was a significant effect only in the model including clutch mass, with nests at the Airfield significantly more likely

to survive to fledging than nests on the Station Road (Airfield: 40.54% vs. Station Road: 16.67%, $\chi^2 = 4.3189$, $df = 1$, $p = 0.0377$). Male morph was not a significant effect in either model. Only 4 out of 25 nests that survived to nestling banding age failed to survive to fledging; thus, we excluded brood mass from the analysis of nesting success.

2.4 Discussion

Lack's (1996) first prediction, that clutch size varies negatively with clutch-initiation date in individual females, was not met in this population. This matches our prediction for white-throated sparrows, as their clutch size cannot vary as much as Parid clutches. White-throated sparrow females might, however, be able to vary investment in offspring by altering clutch mass. Therefore we also considered clutch mass in testing Lack's first prediction. The relationship between clutch-initiation date and clutch mass, however, was non-significant and, if anything, weakly counter to the predicted direction. Therefore we must reject the first of Lack's predictions. Male morph had a consistent effect on both clutch size and clutch mass, with females mated to tan-striped males laying larger and heavier clutches. To our knowledge, this is the first demonstration of a difference in clutch output by pair-type (reviewed in Falls and Kopachena 1994). This pattern will require further investigation to confirm, first, that it is not simply a short-term effect that might disappear over longer time-frames; second, that it is not an effect that is unique to this population; and, third, to test hypotheses that might explain the pattern. Enhanced clutch size and mass in white-striped females may be indicative of higher foraging efficiency of the more aggressive morph. Dominance rank within winter flocks of white-throated sparrows is known to affect an individual's access to food (reviewed in Falls and Kopachena 1994). Other possible explanations include more effective foraging for females due to the lower stresses that

are associated with mate guarding by tan-striped males (Tuttle 2003), and differential allocation among females based on the attractiveness of their partners (Sheldon 2000). We know from lab studies that females of both morphs prefer tan-striped males (Houtman and Falls 1994), and that tan-striped males invest more in parental care than white-striped males (reviewed in Falls and Kopachena 1994), giving us good reasons to predict that females should practice differential allocation.

Lack's second prediction, that mean clutch sizes will be larger in years with earlier mean clutch-initiation date, was not met in this population. Although 2008 had a later mean CID than other years, no differences were found in clutch size or mass. This may indicate that female white-throated sparrows are not limited by food availability in their offspring investment. Brood mass was examined in addition to clutch size and clutch mass. Our two models of brood mass gave us different results; however, the one with the larger sample size, and therefore more conservative of the two, showed no effects explaining variation in brood mass, adding further support to the idea that offspring growth is not food-limited in this population.

Although clutch size, clutch mass and brood mass did not follow Lack's predictions in this population, CID was significantly related to overall nesting success. Earlier-laid clutches had a greater chance of survival to fledging both between individual females within years, and among populations of females between years. Most nest failures in this population can be attributed to nest predation rather than starvation or hypothermia, which indicates that predation on white-throated sparrow nests increases later in the breeding season. This may be due to an adaptation in the timing of predator breeding phenology to coincide with peak availability of prey: white-throated sparrow eggs and nestlings (Götmark 2002). For example, small mammals such as deer mice experience an increased need for food when the young are dependant on the mothers for milk. The increased demand of deer mouse litters birthed in early May coincides with the avian breeding season, and therefore may result in higher rates of nest predation (Sharpe and Millar

1991). Further investigation in collaboration with small mammal researchers studying populations overlapping ours is warranted to test this hypothesis.

The results of this study are consistent with other work investigating variation in laying date, and how that may be related to predator effects on nesting success (Götmark 2002, Hušek et al. 2012, Morton 1971). Through our study we have shown that nest predation can provide a directional selective pressure favouring earlier laying dates, and that this predation is a limiting factor in achieving the fledgling stage. Many ecological studies focus on single factors; however, food availability and predation risk may act synergistically to further reduce nesting success (Dunn et al. 2010, Zanette et al. 2003). When this is the case, treatments that include both food supplementation and predator reduction may have a greater effect on population size than either treatment alone (Zanette et al. 2003). Experimental feeding studies are warranted in this population to determine whether white-throated sparrows also experience the kind of interaction effects between food availability and predation that have been observed in song sparrows.

David Lack's influential work focused the study of animal numbers on bottom-up ecological processes, a focus that continues to this day. This study serves as a valuable reminder that species vary, and that top-down regulation operates in some populations.

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2.6 Tables

Table 2.1: Three-way ANOVA table for variation in clutch-initiation date, as a function of year, sample location, and morph. Clutch initiation was significantly later in 2008 ($p = 0.0069$), but there was no effect of site or morph

Independent Variable	d.f. (Effect)	d.f. (Error)	<i>F</i>	<i>p</i> -value
Year	3	49	4.5199	0.0071
Sample Location	1	49	0.3918	0.5342
Morph	1	49	0.2476	0.6210

Table 2.2: GLM table for variation in clutch size. The whole model was not significant ($n = 55$, $p = 0.4978$), but colour morph was a significant main effect, with females mated with tan-striped males laying larger clutches than females mated with white-striped males.

Effect	d.f.	χ^2 Likelihood Ratio	<i>p</i>-value
Year	3	0.8660	0.8336
Sample Location	1	0.0045	0.9464
Morph	1	3.9781	0.0461
Standardized Clutch-initiation Date	1	0.3972	0.5285

Table 2.3: GLM table for variation in residual brood mass including clutch mass as an effect ($n = 18$, whole model $p = 0.0291$), and excluding clutch mass ($n = 28$, whole model $p = 0.7223$). The reduction in sample size when including clutch mass suggests the model should be treated with caution.

Effect	d.f.	χ^2 Likelihood Ratio	p -value
Year	3	10.0156	0.0184
Sample Location	1	11.3686	0.0007
Morph	1	3.1806	0.0745
Standardized Clutch-initiation Date	1	6.7084	0.0096
Mean Egg Mass	1	5.4806	0.0192
Year	3	0.3751	0.9453
Sample Location	1	0.7477	0.3872
Morph	1	0.7133	0.3984
Standardized Clutch-initiation Date	1	1.2537	0.2628

Table 2.4: GLM table for variation in nesting success ($n = 51$, whole model $p = 0.0012$). Nesting success varied by year and clutch-initiation date, but not male morph or clutch size. Substituting clutch mass for clutch size in the model ($n = 39$, whole model $p = 0.0015$), resulted in sample location also being a significant effect.

Effect	d.f.	χ^2 Likelihood Ratio	p -value
Year	3	13.9136	0.0030
Sample Location	1	1.4423	0.2298
Morph	1	0.6522	0.4193
Standardized Clutch-initiation Date	1	5.9602	0.0146
Clutch Size	1	0.2663	0.6058
Year	3	12.0882	0.0071
Sample Location	1	4.3190	0.0377
Morph	1	1.6813	0.1948
Standardized Clutch-initiation Date	1	9.6748	0.0019
Clutch Mass	1	0.2565	0.6125

2.7 Figures

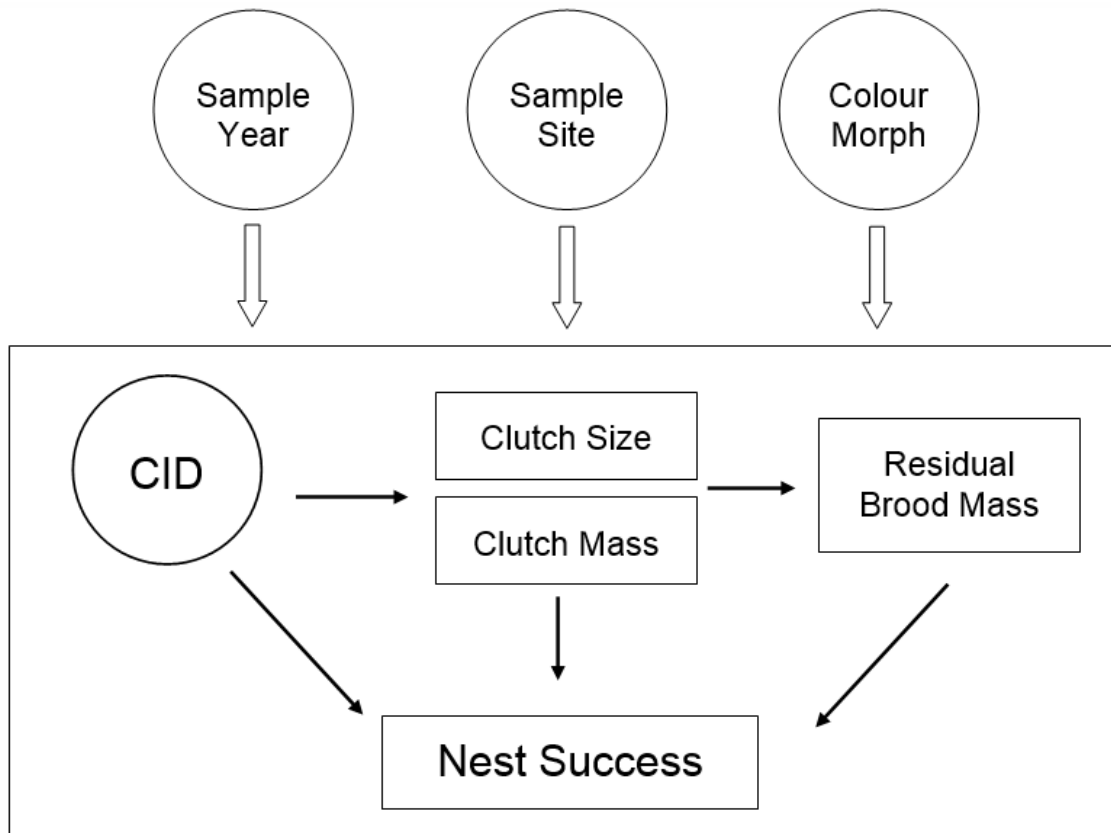


Figure 2.1: Schematic of statistical analyses. Our analyses can be thought of as a path of causation from clutch-initiation date (CID) to clutch size/mass, brood mass, and nesting success. Circles represent explanatory variables, and rectangles represent response variables. Open arrows represent factors in a three-way ANOVA. Solid arrows represent a predicted path of causation from clutch-initiation date to clutch size/mass, brood mass, and nesting success. Predictions were tested using GLMs, with additional subordinate factors added as we progressed from effects on clutch size to nesting success.

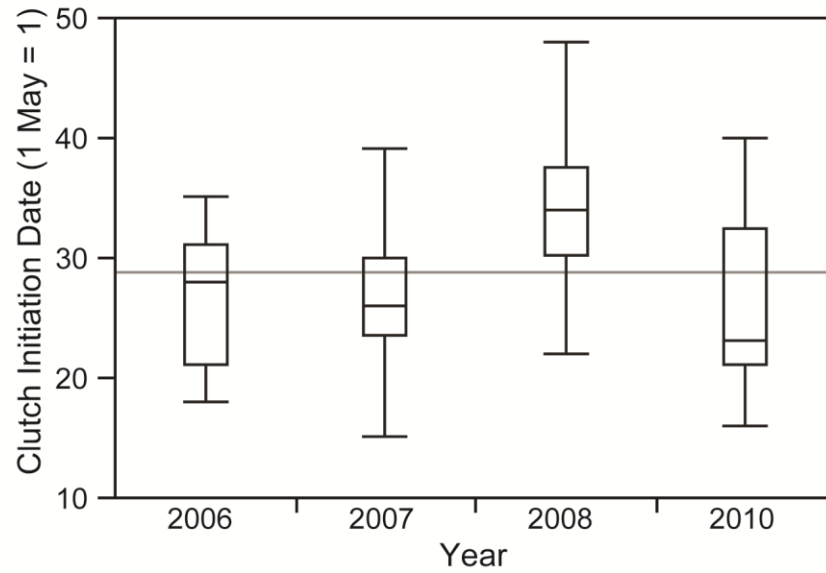


Figure 2.2: Box plots for between-year variation in mean clutch-initiation date, which was significantly later in 2008 compared to other years ($p = 0.0069$). The upper and lower boundaries of the boxes represent the 75th and 25th percentiles, and the middle lines in the boxes represent the median. The grey line represents the sample mean.

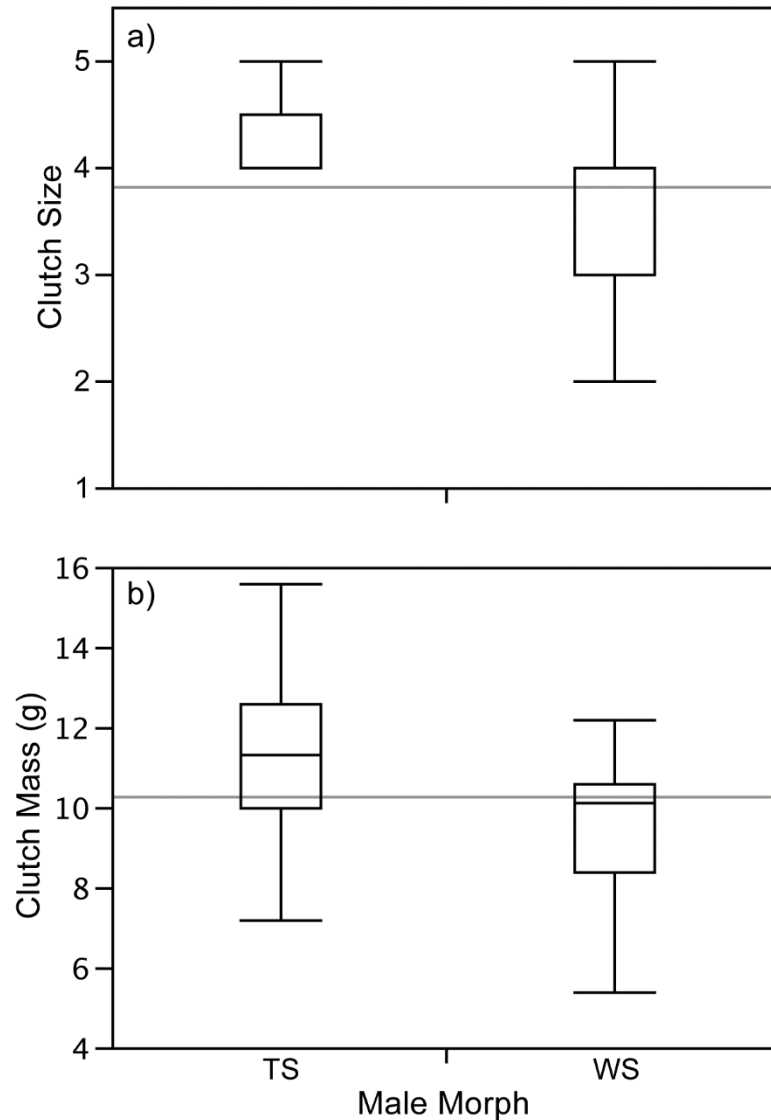


Figure 2.3: Box plots for the effect of morph on (a) clutch size and (b) clutch mass. Colour morph (TS, WS) was a significant main effect, with females mated with tan-striped males laying larger clutches ($p = 0.0461$), and producing heavier clutches ($p = 0.0015$), than females mated with white-striped males. The upper and lower boundaries of the boxes represent the 75th and 25th percentiles, and the middle lines in the boxes represent the median. The grey line represents the sample mean.

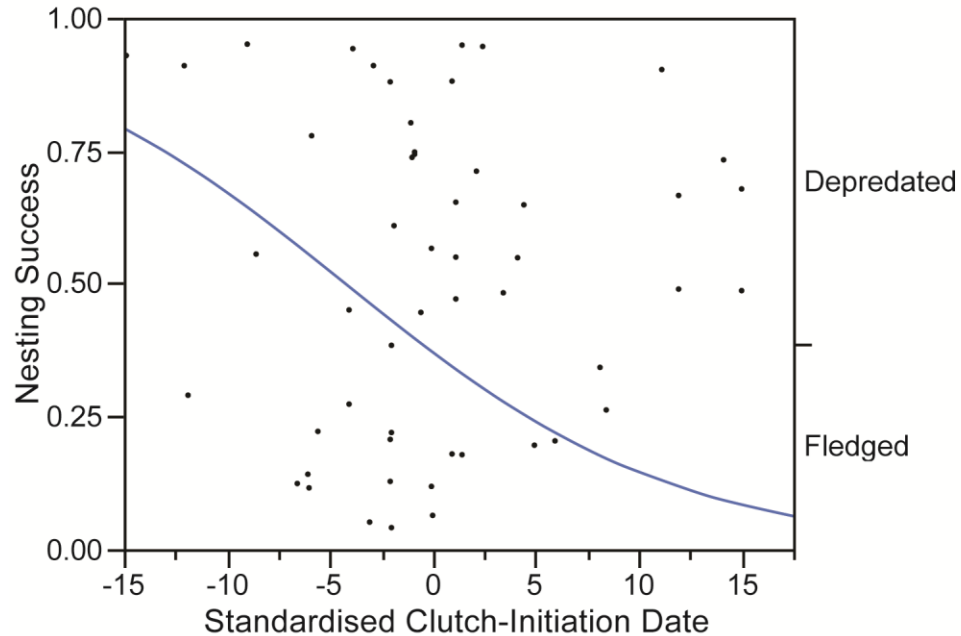


Figure 2.4: Scatterplot for the effect of variation in clutch-initiation date on nest success. Earlier-laid clutches were significantly more likely to survive to fledging than later clutches ($p = 0.0019$). The curved line shows the proportion of nest successes and failures over time: points below the line represent successful nests, and points above the line represent failed nests. Points were jittered in the y-axis by default in JMP, and do not reflect percentages of nesting success between 0 and 100.

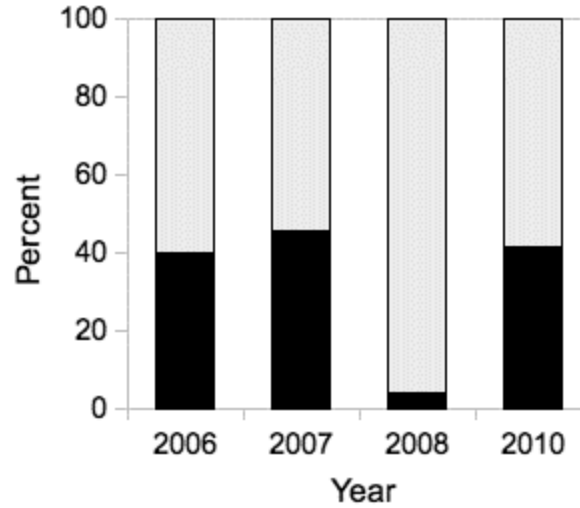


Figure 2.5: Stacked bar graph for between-year variation in nest success. Nesting success was significantly poorer in 2008 compared to all other years ($p = 0.0071$). Black bars represent the percentage of successful nests, and grey bars represent the percentage of failed nests.

Chapter 3

Acute effects of prescribed burning on the nesting ecology of white-throated sparrows (*Zonotrichia albicollis*) : low-intensity fire alters nest site selection

Abstract—The use of prescribed burning as a habitat management tool is becoming more widespread, but little is known about the effects of this conservation strategy on individual species. A before-after-impact-control experiment was used to investigate the acute effects of low-intensity prescribed fire on white-throated sparrow nesting success in Algonquin Provincial Park, Ontario. Two controlled burns were conducted in April 2012, and nesting was monitored in the subsequent breeding seasons in May-July 2012 and 2013. Impact-control analysis revealed that nest site selection was significantly affected, with pairs exhibiting an almost complete avoidance of nesting in burned areas in the first nesting season after the fire. This can be attributed to a short-term loss of nesting habitat in burned areas, where near 100% of all ground cover was immolated. However, some nesting occurred in burned areas in 2013, indicating that the recovery of ground vegetation is sufficiently rapid to minimize long-term negative impacts. This is supported by randomised quadrat surveys, which indicate that the structure of ground vegetation was similar between treatment and control plots in 2013. However, the density of ground cover and nest site camouflage was lower in treatment plots, suggesting an increased vulnerability of these nests to predation. Before-after analysis revealed that site-wide nest success was not affected by the fire, nor did it change one year after the fire. The results of this investigation serve as a valuable starting point to inform predictions about future prescribed burns. Due to the acute effects of fire on nest site selection, it is important that a matrix of suitable nesting habitat is left undisturbed to allow breeding in the first growing season after a burn.

3.1 Introduction

For many decades, wildfire has been viewed as damaging and costly, and as a result complete fire suppression has become a widespread management practice in North America. However, current research indicates that fire suppression negatively affects biodiversity, and that certain habitats are declining without the regular occurrence of forest fires (MacDougall et al. 2013). Many open-habitat and early-successional birds are also in decline, mainly due to a decrease in the abundance of these habitats following the succession of undisturbed areas (Brawn et al. 2001). One example of an important habitat of this type is the heathland. Heathlands are characterized by the presence of one or more heath families (Vaccinaceae, Ericaceae, Epacridaceae, Diapensiaceae, Empetraceae, Grubbiaceae, or Prionotaceae) and low-nutrient soils; as such, even areas that are anthropogenic in origin may be considered heathland habitat, if the area is maintained by disturbance (Whittaker 1979). In North America, examples of these habitats are often limited to small, scattered patches (Whittaker 1979). One such patch can be found in Algonquin Provincial Park, Ontario, Canada. Although it was originally a man-made clearing for an airstrip, forest succession has since transformed this area into an open habitat that supports a mix of shrubland, grassland, and early-successional birds (Tozer 2012). These species have been declining in abundance in recent decades due to habitat loss: in many areas, fire suppression and forest succession have created homogenous, closed-canopy, even-aged forests that cannot support a large diversity of species (Tozer 2012; MacDougall et al. 2013). Left undisturbed, this area will undergo further succession and will eventually be filled in by the surrounding forest, becoming unsuitable for open- or early-successional species. The use of controlled burns to simulate a natural disturbance regime can stabilize the habitat at this early-successional stage, and maintain populations of local breeding birds (Angelstam 1998). However, before any habitat management

initiatives can be put in place, the potential impacts of such practices on the nesting success of these species must be investigated.

Much of the research in the field of avian fire ecology has focused on community-level changes in species abundances after fire, and a variety of habitats and species assemblages have been examined in North America (Saab and Powell 2005). These studies include opportunistic investigations after wildfire events (Brooker and Rowley 1991; Hobson and Scheick 1999; Morissette et al. 2002; Lowe et al. 2012), and field experiments using targeted burns or established prescribed burn regimes (Artman 2001; Greenberg et al. 2007; Pons and Clavero 2010). However, wildfire studies are usually limited by a focus on the delayed effects of fire years or decades after it has occurred (Watson et al. 2012). Furthermore, the authors of many community-level studies prioritize quantifying changes in local abundances, and these methods have been shown to underestimate the impact of disturbance on avian populations (Brooker and Rowley 1991; Bock and Jones 2004; Hannah et al. 2008). Additionally, species assemblage data reveal mixed responses among avian nesting guilds, among habitat types, and across fire intensities (Knick et al. 2005; Blake 2005; Haney et al. 2008; Bagne and Purcell 2011; Rush et al. 2012). The body of literature concerning individual populations and species is limited, and also reveals mixed responses among species: Birds may exhibit an increase in nest survival (Churchwell et al. 2008; Hovick et al. 2012; Long et al. 2012), no effect on nest survival but altered nest placement (Artman et al. 2003; Almario et al. 2009), and decreased nest survival or no nesting at all (Brooker and Rowley 1991). Therefore there is a marked need for additional empirical, species-specific studies which track the nesting success of individuals in a population immediately after a fire event. Furthermore, there is a paucity of fire research conducted in North American heathlands. While heathland habitats do exist in greater sizes and abundances in a similar temperate climate in Europe, the focus of most prescribed fire studies performed in those systems is the effect of fire on the plant community (Angelstam 1998; Davies 2010; Ascoli et al.

2013). Australia is a source of avian fire research in heathlands (Woinarski 1990; Pons and Clavero 2010; Long et al. 2012), but a lack of temperate habitats restricts the ability to make inferences about the impact of fire on North American heathland and shrubland birds.

The heathland bird of interest here is the white-throated sparrow (*Zonotrichia albicollis*). White-throated sparrows are small, ground-nesting birds that breed in open and edge habitats of Canada and the north-eastern United States. They have been called “habitat generalists,” (Drapeau et al. 2000, Falls and Kopachena 1994), though in Algonquin Park they are found most often in clearings with semi open stands of conifers (*Picea*, *Pinus*, and *Abies* spp.) with some birches (*Betula papyrifera*) and aspens (*Populus tremuloides*) (Falls and Lowther 1968). They are short-distance migrants, with some wintering in areas as close as Southern Ontario (Falls and Kopachena 1994). Their average spring arrival date is April 16th in Algonquin Provincial Park, and nest construction begins in early May (Tozer 2012). Nests are constructed out of grasses, pine needles, and dead bracken ferns. They are commonly found under blueberry shrubs or dead bracken ferns, and are placed in close proximity to a conifer at least 1 m tall (Peck and James 1987). Nest construction materials and placement can be flexible, and the amount of nest camouflage varies from completely covered to completely visible. Females will normally nest once per season, unless the first nest is depredated (Falls and Kopachena 1994). In Algonquin Provincial Park, an average of 40% of clutches laid in May are depredated (Chapter 2; J.G. Kopachena pers. obs. in Falls and Kopachena (1994). Nest predators may include deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Clethrionomys gapperi*), red squirrels (*Tamiasciurus hudsonicus*), blue jays (*Cyanocitta cristata*), eastern garter snakes (*Thamnophis sirtalis sirtalis*), and least chipmunks (*Tamias minimus*) (Falls and Kopachena 1994). In the last 40 years, white-throated sparrow populations have been in decline in other areas of Algonquin Provincial Park (Tozer 2012), but there has been a steady increase in territory density in a patch of developing heathland (Barker 2006). Furthermore, this area has been used as a study site for

white-throated sparrow research for many years, including an investigation by Falls and Lowther (1968) into general life history traits, a comparison of nesting ecology between colour morphs by Knapton and Falls (1982) and Knapton et al. (1984), and a summary of the known characteristics of white-throated sparrows by (Falls and Kopachena 1994). This indicates an ideal study system in which to conduct a fire experiment, as there is a healthy population in an area that has been previously-studied.

3.1.1 Objectives and Approach

The original goal of this experiment was to test the impact of prescribed fire on nesting success, when that fire occurred during an early stage in the nesting season, rather than before or after the breeding period. Since white-throated sparrows are short-distance migrants, it was predicted that they would arrive before or during the ideal weather window for spring prescribed fires, which occurs in early May in Algonquin Park. Conversely, neotropical migrants, upon which many of the previously-mentioned fire investigations were based, normally arrive after this weather window has closed (Tozer 2012). Therefore the original design of this study would have provided a unique opportunity to investigate the acute effects of prescribed fire on birds that had already completed spring migration, territory establishment, and possibly also the early stages of nesting. However, unusual weather in 2012 led to an early spring (see 3.3.1 Weather Conditions), and the ideal window for spring burning occurred a full month earlier than planned. This placed the burn at a time before the spring arrival of white-throated sparrows, and thus the April 2012 fire could not be used to investigate the original study question. The temperatures in spring 2013 were more normal for the region, and in order to recreate the original experimental time frame, plans were made to conduct a new burn in the southern portion of the Airfield. However, in April 2013 a high amount of rainfall in a short time period and rapid snowmelt resulted in widespread flooding and structural damage throughout Algonquin Park (Environment Canada 2013a). All available

resources were diverted to making repairs, and additional rainfall throughout May 2013 precluded any possibility of conducting another prescribed burn (Environment Canada 2013b). Therefore the experimental design was modified to investigate the effect of a fire that occurred immediately before spring migration and the onset of breeding, using a partial before-after-impact-control experimental design.

Territory and nesting data collected in previous years (2006-2010) were used to determine baseline conditions, and two treatment and two control plots were used to determine the impact of the prescribed burn in 2012 and 2013. I predicted that there would be a short-term decline in nesting success immediately after the burn and in the following year, but that this impact would be minimal and would not affect the Airfield population in the long term (five or more years after the burn). To test this prediction I monitored all known nests for two breeding seasons immediately following the burn, and I evaluated the structure of ground cover vegetation in control and treatment plots in the second year after the burn was conducted. Here I departed slightly from the normal before-after-impact control design, as I did not have baseline data on the structure of ground cover vegetation in treatment plots before the burn. However, since control and treatment plots were relatively small and located close together, I predicted that the vegetation in the control areas would serve as an acceptable proxy for baseline data.

Vegetation surveys were designed to determine the effect of the burn on nest site selection. Without behavioural nesting experiments, it cannot be determined whether the measured vegetative characteristics were considered by female white-throated sparrows when choosing nest sites. However, previous studies have quantified the vegetative structure at white-throated sparrow nests, and the characteristics measured in 2013 were chosen with these in mind (Knapp and Falls 1982; Peck and James 1987). Thus some insight may be gained into the influence of the burn on nest placement in and around treatment areas. Additionally, since the

diversity of herbaceous and shrubby ground cover species was low and not likely to differ between sites, I focused on quantifying the physical structure of ground vegetation in each plot.

The effect of the burn on nest survival was determined using a three-step approach: (1) I compared apparent nest success across the entire study site before and after the burn, (2) I used Kaplan-Meier survival analysis to generate survival curves for the treatment control plots, and asymptotic log-rank tests to make comparisons between them, and (3) I used logistic-exposure survival analysis for an information-theoretic exploration of nest survival conditions throughout each breeding season. A wide variety of methods may be employed for estimating nest success, and the effectiveness of each method has been evaluated in different situations (Dinsmore et al. 2002; Johnson 2007). Although apparent nest success is said to overestimate true nest success (Dinsmore et al. 2002) and can only be used to evaluate success at a basic pass/fail level, it is still valuable for certain applications, such as the preliminary exploration of a data set. Additionally, the date of initiation and completion for each nest in a sample is required for Kaplan-Meier analysis and logistic-exposure methods. While adults whose identities are known may be found with fledglings after successful nest completion, without known start and end dates these nests cannot be included in these analyses. Thus in certain systems, such as those with small sample sizes, analysis using a method that allows all known nests to be included can help ensure the most well-rounded results. In addition to the analysis of apparent nest success, Kaplan-Meier and logistic-exposure survival analysis were used in conjunction, as each method reveals part of the story behind daily nest survival in this population. Kaplan-Meier analysis, first developed for use in medical research, has an advantage over traditional Mayfield estimates in that it minimizes the bias created by the fact that not all nests are found at the same stage (Nur et al. 2004). It also allows for hypothesis testing, using the asymptotic log-rank test to compare two survival curves. Logistic-exposure analysis is a modified form of logistic regression developed by Shaffer (2004). This method allows inclusion of variable nest check intervals, and has been found to be more

robust than the Mayfield method or survival estimates calculated using the program MARK (Shaffer and Burger 2004; Lloyd and Tewksbury 2007). In this particular analysis, the logistic-exposure method is used to explore the structure of daily nest survival estimates across the breeding season.

A secondary objective in this experiment was to contribute to the ongoing examination of the nesting ecology of white-throated sparrows in Algonquin Provincial Park, and to further investigate the effect of variation in clutch-initiation date on nest success. Based on the findings from analysis of nesting data in previous years (Chapter 2), I predicted that nests initiated earlier in the season would be more likely to succeed than those initiated later in the season. I also predicted that increased vulnerability to predation in treatment plots would enhance this effect. To test these predictions, I estimated daily nest survival rates using standardized clutch-initiation date as an effect in both Kaplan-Meier and logistic-exposure analysis.

3.2 Methods

3.2.1 Field Methods

Study sites

Data were collected from early April to mid-July in 2012 and 2013. The main study site covers a former airfield in Algonquin Provincial Park, Ontario, Canada (45° 34' 30" N, 78° 30' 30" W). This is an open area of low vegetation, forest edge, and small mixed stands of trees. Ground cover is lowbush blueberry (*Vaccinium angustifolium*) and bracken fern (*Pteridium aquilinum*), with scattered conifers (*Pinus*, *Abies*, and *Picea* spp.), and isolated stands of trembling aspen (*Populus tremuloides*). Two control and two treatment plots were defined within the breeding habitat of white-throated sparrows, based on the potential for a safe controlled burn (Figure 3.1). This study

site was also used to collect data on white-throated sparrow nesting ecology in 2006-2010, which are used as historical data in this experiment (Chapter 2).

Three alternate sites were used in 2012 and 2013 to measure white-throated sparrow territory density in other areas of the Park, and to serve as a control for the Airfield population. All three sites are located within 5 km of the Airfield, and at each site territory mapping was carried out over one or two days, using conspecific song playback (Falls 1981). This involved “pulling” males to the ends of their territories by playing a conspecific song recording at regular intervals while walking along the road. When the males stopped following the speaker, they were considered at or near the edge of their territory. In the context of this study the size and shape of territories at the alternate sites was not as important as the absolute number of males occupying territories along the roadways before and after the burn. The Station Road site follows a secondary road that leads from Highway 60 to the Wildlife Research Station (Highway 60 at km 30.8, 45°34'44.76" N, 78°30'56.73" W). This road is approximately 2 km long, characterized by forest edge with open areas in power line cuts and along the North Madawaska River. The Centennial Ridges Road site follows a secondary road that leads from Highway 60 to Whitefish Lake (Highway 60 at km 37.6, 45°34'17.07" N, 78°25'46.09" W). This road is approximately 2.8 km long, characterized by forest edge and an open area near Whitefish Lake. The Old Railway site follows a portion of railway embankment that runs along the southern edge of the Airfield, extending east along the southern shore of Lake of Two Rivers (45°34'17.87" N, 78°30'0.55" W—45°34'16.74" N, 78°28'55.23" W). This portion of railway embankment is approximately 1.4 km long and is characterized mainly by forest edge. Territory mapping also took place at these sites in 2006-2010 (S.M. Ramsay, unpub. data).

Prescribed Burn

The burn was conducted on April 5th 2012 by Ontario Ministry of Natural Resources staff (Figures 3.2-3.3). Fire breaks were established along treatment plot perimeters, and fires were set with drip torches along the edge. The fire in Treatment Plot 1 took approximately one hour to burn the entire area, and flames were roughly 0.5 m in height. The fire in Treatment Plot 2 exhibited a burn time of 40 minutes and flames 1-2 m in height. In both plots, the heat of the fire (average 575 °C) did not penetrate more than 3-5 cm into the soil, and the ground was cool enough to walk on within 20 minutes after burn completion (Figure 3.4-3.5).

Structure of Ground Vegetation after the Prescribed Burn

Since near 100% of ground vegetation was immolated in 2012, only qualitative observations of vegetative recovery were made throughout the first spring and summer after the fire (April 10th to August 1st 2012). Quantitative vegetation surveys were conducted in spring 2013, between May 14th and June 5th 2013. This time frame was chosen to characterize nesting habitat during the nest site selection phase one year after the fire. Vegetation was characterized by 1 m² quadrat surveys at waypoints determined through stratified random sampling (Figure 3.6). Treatment and control areas were divided into roughly equal 4ths at the largest stratum, 16ths at the mid-sized scale, and 5 m² sections at the finest scale. Waypoints were generated in the middle of the selected 5 m², and 1 m² quadrats were measured at the generated waypoint when possible. If the waypoint fell on an area with no vegetation, outside the plot, or was occupied by a tree or footpath, the quadrat was laid on the nearest suitable area. Quadrats were surveyed at nest sites found in control areas in 2012, but not on nest sites found in 2013. This was due to the limited time frame in which vegetation surveys could be conducted, which could not accommodate the delay required for each 2013 nest to reach failure or completion days or weeks after the peak nest building period. The number of quadrats to be sampled in treatment and control areas was determined through an

adaptive method, by which the data was examined in each plot after every 5-10 quadrat surveys to determine whether the total variation present had been captured. Measurements of each characteristic were sorted from smallest to largest, and then plotted in ascending order on the y axis of a line graph. If the line appeared to be rising at the last point, then further sampling was required. If the line appeared to reach a plateau on or before the last point, then a sufficient number of quadrats had been sampled.

Quadrats were framed by two wooden metre sticks tied together with string approximately 1 m apart, and were laid on top of ground vegetation (Figure 3.7). Within each quadrat I measured the height of the shrub layer, the depth of the vegetative debris layer, and the number of dead bracken fern stems. These measurements were chosen to characterize the structure of the vegetation used as camouflage for white-throated sparrow nests (Peck and James 1987; Falls and Kopachena 1994). I also measured the distance from the edge of the quadrat to the nearest conifer taller than 1 m, since trees may be used as lookout posts by both adults when moving to and from the nest (Falls and Lowther 1968). Finally, a photograph was taken of each quadrat approximately 1 m above the ground. These photographs were used to determine the percent of ground covered by vegetation in the quadrat, quantified through polygon measurements in ImageJ (version 1.47v). Whichever metre stick was completely visible was used as a scale, and the area of ground covered by vegetation was recorded as a proportion of the total area within each quadrat. If both metre sticks were not completely visible, the distance between two numbers on the metre stick was used as the scale. All heights and depths were measured to the nearest 0.5 cm, with a metal ruler if under 30 cm (maximum precision 0.5 mm), or with a flexible measuring tape if over 30 cm (maximum precision 0.5 mm). All distances were measured with a flexible measuring tape to the nearest 10 cm (maximum precision 0.5 mm).

The effect of the fire on coniferous trees was also quantified using photographs taken before and after the burn (Appendix A). This was included in the initial sampling design because white-throated sparrows may use low-hanging conifer branches as nest cover (Peck and James 1987). However, tree survey data were not included in the statistical comparison of nesting vegetation between treatment and control plots. Almost all low-hanging branches were completely scorched, and since it was predicted they would not quickly grow back, these data would lend no value to the examination of vegetative recovery in treatment plots one year after the fire.

Nesting Data

In both 2012 and 2013, daily site visits occurred from dawn to mid-morning. Observations of white-throated sparrow activity were made across the entire study site, although focus remained on the control and treatment plots for the two-year study period. Territories were mapped by tracking the daily movements of males, and by using conspecific song playback (Falls 1981). Territory boundaries were determined by locating song posts used by males, boundary disputes that took place between two or more males, and foraging areas used by male-female pairs without interruption by disputes involving other individuals. All known adults were closely observed for nesting activity throughout the breeding season. Behavioural cues from adults helped with nest location, and once a nest was found, a monitoring protocol was initiated (Chapter 2.2.1). Nesting data collected included location, date of clutch initiation, size of clutch, mass of total clutch, nest stage achieved, the fate of the nest, and the last date it was known to be active. Nest stages included building, laying, incubation, nestling, and fledgling. A successful nest was defined as one that produced at least one fledgling, a common measure of nest success in avian systems (Etterson et al. 2011). The most prevalent cause of whole-nest loss during this study was nest predation. Therefore a failed nest was defined as one where the nest was found empty, and no live nestlings or fledglings could be detected near the parents.

3.2.2 Statistical Analysis

Analyses of interest include comparisons of the whole site between past study years (2006-2010) and present study years (2012-2013), between 2012 and 2013 control plots, and between control and treatment plots in 2013. A comparison of nesting data between control and treatment plots in 2012 was not conducted, since there was only one nest found in a treatment plot in 2012. For the same reason, a statistical comparison of nesting data between treatment plots in 2012 and 2013 was not conducted. Comparisons of vegetation data were only made between control and treatment plots in 2013, and between 2012 nest sites (sampled in 2013) and other plots in 2013. All statistical analyses were carried out in R Statistical Package (versions 3.0.1 and 3.0.2).

Nesting Habitat and Nest Site Selection

The effect of the prescribed burn on nesting habitat was determined using a Principal Components Analysis (PCA) of five vegetative variables: percent nest vegetation, shrub height, depth of vegetative debris, number of bracken ferns, and distance to the nearest tree. The PCA was based on a correlation matrix, since each vegetative variable was measured on a different scale. Principal Components 1, 2 and 3 (PC 1, PC 2 and PC 3) were selected for use in further analyses, since together they explained 81.2% of the total variation in the vegetative data (PC 1: 43.94%, PC 2: 19.89%, PC 3: 17.40%). Although these three principal components were analysed further, PC 1 explains the most variation in the data, and therefore emphasis should be placed on PC 1 scores. Principal component scores were compared between plot type, and between 2012 nests that failed or succeeded. A Shapiro-Wilk test was used to determine whether principal component scores were normally-distributed. For normally-distributed scores, a Bartlett's test was used to determine whether variances were equal between plot types, and for non-normal scores, a Fligner-Killen test was conducted. Based on whether assumptions of normality and equal variances were met, either a parametric or non-parametric analysis of variance (ANOVA)

was performed to determine whether PC scores differed by plot type (Table 3.1). For parametric analyses, a one-way ANOVA and Tukey HSD test were performed; for non-parametric analyses, a Kruskal-Wallis one-way ANOVA by ranks and a Multiple Comparison test were conducted.

The effect of the prescribed burn on nest site selection was determined using a Fisher's Exact Test comparing the number of nests found in treatment plots before and after the burn.

Territory Density and Territory Placement

Territory density was defined as the number of territories recorded at a given location. The overall density of territories was compared between plots, sites, and years. Historical data from 2006-2010 was used to investigate the effect of the burn on the overall number of territories on the Airfield, and the alternate sites were used as a control. A two-sample t-test was used to compare territory density on the Airfield between past and present study years. G-tests were used to compare territory density at alternate sites between past and present study years, as well as between 2012 and 2013. A Fisher's Exact Test was used to compare territory placement between treatment and control plots among past and present study years. Finally, a Fisher's Exact Test was used to compare the nest site selection between treatment and control plots among past and present years, and among 2012 and 2013.

Nest Survival

I used a three-step approach to investigate the effect of the prescribed burns on nest success: a preliminary test to determine whether whole-site estimates differed before and after the burn, followed by a Kaplan-Meier survival analysis with hypothesis testing, and then logistic-exposure analysis with model selection. In the preliminary step I used an R x C test of independence to compare apparent nest success before and after the burn. I then investigated nest success in 2012

and 2013 using Kaplan-Meier analysis with survival curves (Pollock et al. 1989; Nur et al. 2004), and a logistic-exposure model with predicted daily nest survival (Shaffer and Burger 2004). Kaplan-Meier analysis and logistic-exposure analysis were also conducted to investigate the effect of variation in clutch-initiation date on nest survival.

The effect of sample year on apparent nest success was tested using a G-test of independence, with an R x C contingency table of sample years in rows, and with nest successes and failures in columns (Table 3.3). Sample years included 2006-2010 and 2012-2013, with each year in a separate row. Observed and expected frequencies were obtained using a chi-square test of independence, and then the G-test was calculated in R as per Sokal & Rohlf (1995).

Kaplan-Meier survival curves were generated using the “survival” package (Terry Therneau version 2.37-4). The Kaplan-Meier Survival formula was used to generate survival curves by comparing, within each time interval, the number of nests at risk to the number of nests that had failed or had been censored. In this sample a nest could be “right-censored”: the outcome was unknown after a certain date, including after young successfully fledged; or a nest could be “interval censored”: nest failure occurred in the interval of time between two nest checks (Nur et al. 2004). Median interval length was three days in both 2012 and 2013. Kaplan-Meier estimates of survival were obtained from each curve, and asymptotic log-rank tests for interval-censored data were conducted to compare survival curves using the “interval” package (Sun 1996).

Logistic-exposure models were fitted using a survival response variable, two continuous predictors (nest age and standardized CID), and the logistic-exposure link function developed by Shaffer (2004b). Exposure days were calculated as the time from nest discovery to nest completion. Two subsets of the data were used, and two models fitted to the data in order to investigate survival as predicted by date and standardized clutch-initiation date. These models were selected using Akaike’s Information Criterion for small sample sizes (AIC_c, Table 3.2; Burnham and Anderson, 2002).

3.3 Results

3.3.1 Weather Conditions

Weather varied between 2012 and 2013: spring 2012 started unusually early, and lower temperatures and higher precipitation were observed in May 2013 than in May 2012. The local “ice out” date, the day when all ice has thawed from largest lake in Algonquin Park (Lake Opeongo, 45°41'27.94" N, 78°22'32.42" W), was March 29th—25 days earlier than the current average, and 32 days earlier than the 2013 ice out date of April 30th (Friends of Algonquin Park 2013). Mean daily temperatures were lower in 2013 during May 10th-29th, and daily precipitation was higher during May 9th-11th and May 21st-23rd (Figure 3.8; Environment Canada 2013a, b).

3.3.2 Trees and Ground Cover after the Fire

See Figure 3.9 for photos of conditions before, during, and after the burn. Direct fire damage to trees was apparent in scorch marks on the outer surfaces of branches and trunks, as well as the complete immolation of needles on lower branches (Appendix A). Indirect fire damage was apparent less than one week after the prescribed burn in yellowing pine needles, which later turned orange and dropped off the branches. Crowns of some partially-burned trees also showed signs of yellowing late in the summer. Bracken ferns were observed sprouting in treatment plots on May 21st, and new growth of *Cladina* spp. was recorded on May 22nd. Blueberry shrubs were 5-10 cm tall by June 10th, and 10-15 cm tall by early July. A period of drought occurred in late July and early August, and dead bracken ferns and grasses were observed in Treatment Plot 2 (Environment Canada 2013c, d).

Vegetative recovery after the burn continued throughout the 2013 growing season, with the growth of bracken ferns, trailing arbutus (*Epigaea repens*), fire weed (*Chamerion*

angustifolium), and fruiting blueberries. Grasses and blueberry shrubs were noticeably sparser and shorter in Treatment Plot 1, and more bare ground was visible compared to Treatment Plot 2. Many trees that had been partially damaged by the fire were still alive, with green needles on the top third or more of the crown. Some trees with fire damage to more than two thirds of the crown developed additional yellowing during the 2013 field season.

Various avian species were observed moving through the burned areas, and foraging on the ash (Appendix B). In 2013 an active black-capped chickadee (*Poecile atricapillus*) nest was found in a stump approximately 1.5 m tall, which had been present as standing deadwood before the burn.

3.3.2 Nesting Habitat and Nest Site Selection

See Figures 3.10-3.12 for photos of quadrats in treatment plots, control plots, and 2012 nest sites, and see Tables 3.3-3.4 for a summary of vegetative data. Principal Components Analysis of vegetative characteristics produced five principal components (PC). Three principal components were retained, as together they explained 81.22% of the total variation (PC 1: 43.94%, PC 2: 19.89%, PC3: 17.40%, Table 3.5). See Figure 3.13 for a graph of Principal Components 1 and 2 scores separated by plot. High Principal Component 1 scores represent shorter shrubs and a shallower layer of vegetative debris; high Principal Component 2 scores represent fewer dead bracken ferns; high Principal Component 3 scores represent a very low percentage of available nest vegetation, and a longer distance to the nearest tree (Table 3.6). Principal Component 1 scores differed significantly among plots (Kruskal-Wallis Test, $p < 0.001$). Treatment Plot 1 was similar to Treatment Plot 2, but significantly different from all other plots; Treatment Plot 2 was also similar to Treatment Plot 1 and significantly different from all other plots (Multiple Comparison Test, Table 3.7). Principal Component 2 scores did not differ among plots (one-way ANOVA, $p = 0.231$). Principal Component 3 scores were significantly different among plots

(Kruskal-Wallis test, $p < 0.001$). Treatment Plot 1 differed from Treatment Plot 2 but not from Control Plot 1; Treatment Plot 2 differed from Treatment Plot 1 but not from 2012 nest sites or Control Plot 2 (Multiple Comparison Test, Table 3.8). Principal component scores did not differ between 2012 nests that succeeded or failed (PC 1: one-way ANOVA, $p = 0.672$; PC 2: one-way ANOVA, $p = 0.832$; PC 3: Kruskal-Wallis test, $p = 0.4957$).

Nest site selection was significantly different between pre-burn and post-burn years, with a higher proportion of nests located outside treatment plots after the burn (Fisher's Exact Test, $p = 0.0392$; Figure 3.14).

3.3.3 Territory Density and Territory Placement

Territory density on the Airfield ranged between 25-37 territories in pre-burn years, and 30-31 territories in post-burn years (Table 3.9). The total number of territories on the Airfield was not significantly different between pre-burn and post-burn years (Welch two-sample t-test, $t = 0.85$, $df = 4.044$, $p > 0.44$). Likewise, the number of territories at each alternate site was not significantly different between pre-burn and post-burn years (G-test, $G = 1.085$, $df = 2$, $p = 0.581$), nor was it different between 2012 and 2013 (G-test, $G = 0.3705$, $df = 2$, $p = 0.831$).

Many territories overlapped the perimeter of the treatment plots, and both males and females were observed foraging in burned areas. In both years, the portion of each territory that overlapped a treatment plot ranged from 0 to 100 percent. Qualitative observations indicate that conifer song posts were used in both treatment and control plots; in treatment plots males were observed singing in both fire damaged and dead trees. Both males and females were observed foraging in trees with varying amounts of fire damage.

The number of territories overlapping with treatment plots was not significantly different between pre-burn and post-burn years (Fishers' Exact Test, $p = 0.572$), nor was it different between 2012 and 2013 (Fishers' Exact Test, $p = 1$).

3.3.4 Nest Survival

In 2012, 19 nests were found on the Airfield, with 14 of those nests occurring in treatment or control plots. In 2013, 14 nests were found on the Airfield, all of which occurred in treatment or control plots. The number of nests found in previous years ranged from 12-22 (2006—14, 2007—21, 2008—22, 2010—12).

Apparent Nest Success

Apparent nest success ranged from 27.27 – 71.43% between 2006 and 2013 (Table 3.10).

Apparent nest success was not dependant on sample year (R x C test of independence, $df = 5$, $p > 0.17$). Likewise, there was no difference in apparent nest success when comparing control plots between 2012 and 2013 (Fisher's Exact test, $p > 0.44$), nor when comparing control and treatment plots in 2013 (Fisher's Exact test, $p > 0.53$).

Kaplan-Meier Survival Analysis

Kaplan-Meier survival estimates for 2012 and 2013 (control plots only) were 0.53 ± 0.30 and 0.48 ± 0.39 , respectively (Figure 3.15). Survival was not significantly different between control plots in 2012 and 2013 (asymptotic log-rank test, $p > 0.96$). Kaplan-Meier survival estimates for 2013 treatment and control plots were 0.52 ± 0.39 and 0.25 ± 0.30 , respectively (Figure 3.16). Survival was not significantly different between treatment and control plots in 2013 (asymptotic log-rank test, $p > 0.36$).

The mean clutch-initiation date in 2012 was May 23rd, with the earliest clutch initiated on May 15th, and the latest clutch initiated on June 10th. One outlier was omitted from analysis, with a clutch-initiation date of July 6th, 2012. This outlier was the only nest found in a treatment plot in 2012 (Figure 3.14). Mean clutch-initiation date in 2013 was June 3rd, with the earliest clutch

initiated on May 26th, and the latest clutch initiated on June 19th. In 2012, 8 of 11 nests were initiated before the mean clutch-initiation date. In 2013, 6 of 12 nests were initiated before the mean clutch-initiation date. Kaplan-Meier survival estimates for early and late nests in 2012 and 2013 were 0.72 ± 0.28 and 0.31 ± 0.26 , respectively (Figure 3.17). Survival was not significantly different between early and late nests in pooled years (asymptotic log-rank test, $p > 0.50$).

Kaplan-Meier survival estimates for early and late nests 2012 and 2013 are as follows: 2012 early— 0.63 ± 0.46 ; 2012 late— 0.58 ± 0.39 ; 2013 early— 0.32 ± 0.36 ; 2013 late— 0.58 ± 0.39 . Survival was not different between early and late nests in 2012 (asymptotic log-rank test, $p > 0.95$), nor in 2013 (asymptotic log-rank test, $p > 0.55$).

Logistic-exposure analysis

The model used to predict survival by date in control plots (pooled and separate years) was not the most highly ranked ($\Delta AIC_c = 2.51$), but it was within the 90% confidence set by cumulative weight (Cumulative $\omega_i = 0.9$). In pooled years, daily nest survival estimates in control plots started and ended at similar points, with an increase to approximately 20% greater chance of survival at the midpoint of the breeding season (Figure 3.18). Daily nest survival estimates predicted by date were noticeably different between 2012 and 2013 (Figure 3.19). Daily survival estimates in 2012 exhibited a peak around 5 days after the earliest nest, followed by a trough around 10 days into the season, and a large peak around the midpoint of the season. Daily survival estimates in 2013 exhibited a trough around 5 days after the earliest nest, followed by a peak around the midpoint of the season. The model used to predict survival by date in treatment and control plots in 2013 was not the most highly ranked ($\Delta AIC_c = 1.5$), but it was within the 90% confidence set by cumulative weight (Cumulative $\omega_i = 0.73$). Daily nest survival estimates predicted by date were slightly different in treatment and control plots in 2013, with treatment plots exhibiting decreased nest survival at the midpoint of the season compared to nests in control plots (Figure 3.20).

The model used to predict survival by standardized clutch-initiation date in control plots (pooled and separate years) was not the most highly ranked ($\Delta AIC_c = 2.5$), but it was within the 90% confidence set by cumulative weight (Cumulative $\omega_i = 0.74$). In pooled years, daily nest survival estimates in control plots varied with standardized clutch-initiation date: survival was estimated at approximately 70% with the earliest nest, declined at 5 days before the mean date, and then peaked at approximately 85% approximately 5 days after the mean date (Figure 3.21). Daily nest survival estimates predicted by standardized clutch-initiation dates differed in 2012 and 2013. Nest survival in 2012 peaked at near 100% survival probability shortly after the mean date, which was sustained for a further 6-7 days; nest survival in 2013 exhibited a W-shaped curve, with a peak at approximately 80% survival probability 3 days after the mean date, and troughs of 65% survival probability at 5 days before and 10 days after the mean date (Figure 3.22). The model used to predict survival by standardized clutch-initiation date in treatment and control plots in 2013 was not the most highly ranked ($\Delta AIC_c = 2.03$), and it was just outside the 90% confidence set by cumulative weight (Cumulative $\omega_i = 0.91$). Daily nest survival estimates predicted by standardized clutch-initiation date in treatment and control plots in 2013 were similar to those predicted by survival by date in the same comparison. (Figure 3.23).

3.4 Discussion

3.4.1 Nesting Habitat and Nest Site Selection

The similarity in principal component scores between control plots and 2012 nest sites indicates that the measurements taken at randomised waypoints captured the same vegetative characteristics present at actual nest sites. In addition, species occurrences measured at 2012 nest sites and in treatment and control plots were similar to those found at nest sites in Algonquin by

Knapton and Falls (1982). The near-complete immolation of ground cover occurred as predicted, since blueberry shrubs and grasses are highly flammable (Duchesne and Wetzel 2004). The speed and extent of vegetation growth after the burn was unexpected, with Treatment Plot 2 resembling control plots and 2012 nest sites by May and June 2013, and with blueberries fruiting simultaneously in treatment and control plots in 2013. This growth rate is likely normal, however, as blueberries can regenerate quickly after a prescribed burn by sprouting from unburned stems and roots (Duchesne and Wetzel 2004). The difference in shrub height and ground cover density between Treatment Plots 1 and 2 was also unexpected, with blueberry shrubs and grasses growing more quickly in Treatment Plot 2. This difference in recovery speed after the controlled burn may be attributed to differences in microclimate conditions, or to differences in fire intensity between treatment plots. Overall, post-fire recovery was rapid, with vegetation coverage in treatment plots becoming more similar to unburned areas by 2013. However, in 2012, white-throated sparrows exhibited a distinct avoidance of nesting in areas with the most distinctly different vegetation from unburned areas. This avoidance decreased in 2013, but fewer nests were found in treatment plots than in control areas, indicating that nesting vegetation had not yet fully recovered by the second year after the burn.

The pronounced change in nest site selection in post-burn years indicates that the prescribed burn had an immediate and acute effect on female nest site selection, and that the quality of nesting habitat was much lower in burned areas. A noticeable shift away from treatment areas occurred in both 2012 and 2013, with nests arranged outside the perimeters (Figure 3.14). Some change in nest site selection was predicted, since white-throated sparrows require low-hanging conifer boughs, shrubs between 15-30 cm in height, grasses, and dead bracken ferns to conceal nests (Peck and James 1987; Falls and Kopachena 1994), all of which were almost completely immolated in the controlled burn. The distinct avoidance of nesting in burned areas observed in the first year after the burn was not expected, as other avian species

have been reported nesting in recently burned areas (Brooker and Rowley 1991; Artman et al. 2003). Some nesting occurred in treatment plots in 2013, suggesting that ground vegetation recovered sufficiently quickly after the burn to provide some cover for nests during the next spring. However, not all females in territories overlapping treatment plots selected burned areas for nests in 2013, which may indicate that quality of nesting one year after the burn was still poorer than in control areas. Altered nest placement after a fire was also observed in seaside sparrows (*Ammodramus maritimus*), which chose unburned patches over burned areas (Almario et al. 2009), wood thrushes (*Hylocichla mustelina*), which placed nests higher off the ground in recently burned areas (Artman et al. 2003), and splendid fairy-wrens (*Malurus splendens*), which nested only in plants that regenerated from sprouts as opposed to seeds (Brooker and Rowley 1991).

3.4.2 Territory Density and Territory Placement

The lack of differences observed in past and present territory density suggest that the prescribed burn did not have any effect on the overall number of white-throated sparrows using the Airfield study site. Any negative impacts of the burn may have been outweighed by site fidelity, which in Algonquin white-throated sparrows is $26 \pm 7\%$ — roughly 55% of surviving adults return to the site where they were banded (Schlossberg 2009). This rate is comparable to that observed after the burn, where 46% (8 of 17) of banded males sighted in 2012 returned to the Airfield in 2013. The similarity observed between pre-burn and post-burn territory density on the Airfield is supported by a lack of change in the recorded territory density at alternate sites. Likewise, low variation in territory density across years indicates that the Airfield and alternate study sites were used consistently by white-throated sparrows from 2006-2013. These results differ from some community-level surveys, which reported a decrease in abundance of ground-nesting species after a prescribed burn (Greenberg et al. 2007; Gaines et al. 2010). This may be due to differences in

fire intensity or in the proportion of nesting habitat burned: Artman (2001) observed that ovenbirds (*Seiurus aurocapillus*) will continue to breed in burned areas, as long as they have access to suitable nesting habitat in unburned areas nearby.

The similarity in territory placement between past and present study years suggests that the prescribed burn did not have an effect on the spatial arrangement of male territories. This is supported by qualitative observations of male and female foraging activity, which took place in both treatment and control areas where territories overlapped both plot types. Additionally, white-throated sparrows, as “habitat generalists” (Falls and Kopachena 1994, Drapeau et al. 2000, may not be constrained by strict requirements for territory selection. However, since territory placement is not a large component of this study, the historical territory placement data that I utilized consisted of single waypoints recorded in the perceived center of a territory, and I did not include detailed data on the size or shape of male territories. It is likely that these midpoints do not represent the areas which were used most by the males and females occupying these territories. For future investigations, I recommend analyzing estimations of territory size and shape. These data could be useful in quantifying the effects of the burn on territory selection, since ecological factors such as food availability are known to affect territory size in birds (Enoksson and Nilsson 1983; Smith and Shugart 1987).

3.4.3 Nest Survival

The lack of an observed decrease in whole-site nest success after the burn went against predictions, since nesting habitat on parts of the Airfield were dramatically altered. However, since females were able to select nest sites outside of burned areas, and since overall nest success was not affected by the burn, I conclude that there was a sufficient matrix of suitable nesting habitat left untouched to allow normal nesting immediately after the burn. This is similar to the site-level nesting success observed in seaside sparrows, in an area subjected to yearly prescribed

burns (Almario et al. 2009). On the other hand, although there were no significant differences in Kaplan-Meier survival estimates between control and treatment plots in 2013, the sample size of nests found in burned areas is greatly limited. In order to lend more statistical power to the investigation of nest survival in treatment plots, either more sampling in future years is required, or this experiment should be repeated on the Airfield in new treatment plots. Although information on the post-fire nest survival of an individual species is rare, results of similar fire studies suggest that prescribed burns conducted before spring migration negatively affect ground-nesting birds in burned areas (Zimmerman 1992; Artman 2001; Gaines et al. 2010; Greenberg et al. 2013). Furthermore, due to the reduction of ground cover, nests in burned areas may be more vulnerable to avian and mammalian nest predators (Jones et al. 2002). As ground cover grows back, the species composition of nest predators may shift towards small mammals and snake predation (Jones et al. 2002; Ellis-Felege et al. 2012). However, fire has been shown to have a null effect on *Peromyscus* mouse survival, but a negative effect on reproduction in the years after the fire (Morris et al. 2011). Therefore I cannot predict how fire may alter nest predation rates in burned areas. Experimental nest predation studies are required to determine which species contribute the most predation risk to white-throated sparrow nests in Algonquin Provincial Park.

The early start date of the 2012 nesting season, as revealed by the logistic-exposure analysis, may be attributed to an abnormally early spring. Furthermore, the start of nesting in 2013 may have been delayed due to a drop in temperature and a large amount of precipitation that occurred in the week before May 28th, the earliest recorded clutch-initiation date (Figure 3.9). This cold-temperature delay in nesting has also been observed by Visser et al. (2009). The differences between survival curves in treatment and control plots in 2013 were as predicted, with lower survival occurring in treatment plots at the midpoint of the season. However due to limited sample size, additional sampling in future years is required to test this prediction further.

3.4.4 Clutch-initiation Date and Nest Survival

Although Kaplan-Meier analysis found no statistical differences in survival between nests with an early standardized clutch-initiation date and those laid later than the mean, logistic-exposure analysis affords a more detailed examination of the relationship between CID and nest survival. In each year, peak daily nest survival occurred within 5 days after the mean CID. Interestingly, daily nest survival estimates for nests with the latest standardized clutch-initiation date were similar to those laid on or before the mean date. This contrasts with the seasonal decline in nesting success observed by Lack (1968) and seen in Chapter 2. However, the small sample sizes in 2012 and 2013 may be exaggerating the observed changes in daily nest survival estimates. On the other hand, the point at which the lowest daily nest survival estimate occurs varies by year. In 2012, the lowest daily nest survival occurs with nests laid just before the mean date, but in 2013, the lowest daily nest survival occurs twice at 5 or more days before the mean date, and 10 or more days after the mean date. In 2013 early clutch-initiation coincided with a five-day period of heavy rainfall and below-average temperatures, weather conditions similar to the spring of 2008 (Environment Canada 2013e). Thus periods of time with lower temperatures and higher precipitation may result in lower nest survival. This may be due to nest loss from flooding, or from higher vulnerability to predation when the mother spends more time away from the nest to forage and keep dry. The results of clutch-initiation date analysis in this study provide partial support for the findings from Chapter 2. However, a larger data set is needed for a more powerful analysis; this may be achieved by re-analyzing nesting data from 2006-2010 using logistic-exposure analysis, and pooling data from past and present sample years together.

3.4.5 Conclusion

The results of this investigation serve as a valuable starting point to inform predictions about future prescribed burn initiatives. Due to the acute effects of the prescribed burn on nest placement, it is imperative that enough suitable nesting habitat is left undisturbed to allow breeding in the first growing season after a burn. This may be more difficult to achieve in smaller patches, or in a linear space such as a power line cut. The average territory size of the focal species must also be taken into consideration, since higher territory density and smaller territory sizes may limit the ability of females to select nest sites outside of the burned area. Future studies on prescribed fire and white-throated sparrows should investigate the effect of variation in the timing of prescribed burns, such as those occurring after the birds have arrived in the spring, or in the fall after the birds have left for the wintering grounds. Since white-throated sparrows are short-distance migrants, they arrive early in the spring and territories may already be established at the time of the burn. A burn conducted in this situation may disrupt territory boundaries, causing a potential delay in territory establishment, mate acquisition, and resulting in a decline in reproductive success for males (Brooker and Rowley 1991; McKellar et al. 2013). Finally, if females have already begun laying before the burn, this disturbance may lead to nests being disrupted or abandoned, resulting in a decline in reproductive success for both parents.

3.5 References

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3.6 Tables

Table 3.1: Summary of the results of assumptions tests to determine whether to use parametric or non-parametric analysis of variance tests to compare principle component (PC) scores among plots, and between nests that succeeded or failed.

	Distribution	Variances	Test type
PC 1 (all plots)	Non-normal	Equal	Non-parametric
PC 2 (all plots)	Normal	Equal	Parametric
PC 3 (all plots)	Normal	Unequal	Non-parametric
PC 1 (2012 nest success)	Normal	Equal	Parametric
PC 2 (2012 nest success)	Normal	Equal	Parametric
PC 3 (2012 nest success)	Non-normal	Equal	Non-parametric

Table 3.2: Comparison of logistic-exposure models for daily nest survival estimates, predicted by date or standardized clutch-initiation date (St.CID). Models were ranked within each data set by Akaike's Information Criterion for small sample sizes (AIC_c). K is the number of parameters, ΔAIC_c is the difference between each model's AIC_c and that of the highest-ranked model (row 1), and ω_i is the Akaike weight. Only models within the 90% confidence set by Cumulative ω_i were considered for further analysis. The constant is the model containing no predictor variables.

Data	Model	K	AIC_c	ΔAIC_c	ω_i	Cumulative ω_i
2012 and 2013 (control plot subset) (pooled and separate years)	Constant	1	27.52	0	0.58	0.58
	St.CID	2	30.02	2.5	0.16	0.74
	Date	2	30.03	2.51	0.16	0.9
	St.CID * Date	4	32.22	4.7	0.05	0.96
	St.CID + Date	3	32.81	5.29	0.04	1
Between plots (2013 subset)	Constant	1	17.09	0	0.5	0.5
	Date	2	18.59	1.5	0.24	0.73
	St.CID	2	19.12	2.03	0.18	0.91
	St.CID + Date	3	21.79	4.7	0.05	0.96
	St.CID * Date	4	22.2	5.11	0.04	1

Table 3.3: Summary of vegetative characteristics measured in 103 quadrat surveys, including the number of quadrats sampled per plot, and the mean (\pm SE) of each aspect measured. Characteristics measured include the percent of ground covered by vegetation suitable for nesting habitat (Nest Veg.), the height of the shrub layer (Height), the depth of the vegetative debris layer (Depth), the number of dead bracken ferns (Ferns), and the distance from the outer edge of the quadrat to the nearest conifer taller than 1 m (Dist. to T.).

	Control 1	Control 2	Treatment 1	Treatment 2	2012 Nest Sites
Sample Size	25	25	20	20	13
Nest Veg. (%)	53.8 (5.4)	69.2 (3.9)	16.8 (4.1)	70.8 (3.5)	79.5 (5.0)
Height (cm)	33.3 (1.3)	32.5 (1.2)	17.9 (0.7)	21.3 (0.6)	34.0 (1.9)
Depth (cm)	8.2 (0.5)	7.5 (0.3)	0.7 (0.1)	0.9 (0.1)	6.5 (0.5)
Ferns (No.)	5.3 (0.6)	4.3 (0.9)	3.3 (0.7)	3.2 (0.7)	4.2 (0.6)
Dist. to T. (m)	4.6 (0.6)	4.2 (0.8)	8.5 (1.3)	10.5 (2.1)	3.0 (0.5)

Table 3.4: Summary of the proportional occurrence of the most common ground cover species in sampled quadrats. Incidentals include *Rubus* spp., *Epigaea repens*, *Lycopodium* spp, and *Teraxacum* spp.

	Control 1	Control 2	Treatment 1	Treatment 2	2012 Nest Sites
Sample Size	25	25	20	20	13
<i>Vaccinium angustifolium</i>	100.0	100.0	100.0	100.0	100.0
<i>Pteridium aquilinum</i>	96.0	64.0	80.0	75.0	84.6
<i>Gaultheria procumbens</i>	64.0	16.0	30.0	5.0	53.8
Grass	60.0	57.5	56.0	44.0	84.6
<i>Cladina</i> spp.	56.0	20.0	80.0	10.0	23.1
<i>Comptonia peregrina</i>	0.0	16.0	0.0	75.0	23.1

Table 3.5: Summary of Principal Components (PC) Analysis of vegetative data across all plots.

	PC 1	PC 2	PC 3	PC 4	PC 5
Standard Deviation	1.48	0.997	0.933	0.819	0.518
Proportion of Variance	0.4394	0.1989	0.1740	0.1342	0.0536
Cumulative Proportion of Variance	0.4394	0.6383	0.8123	0.9464	1.00
Eigenvalues	2.197	0.9946	0.8699	0.6708	0.2679

Table 3.6: Mean loadings of Principal Components 1, 2 and 3 for each vegetative characteristic, across all plot types.

	PC 1	PC 2	PC 3
Shrub Height	-0.5697	0.2967	-0.2104
Vegetation Depth	-0.5413	0.2151	0.2258
Percent Nest Vegetation	-0.3841	-0.3147	-0.7475
Distance to Tree	0.4257	-0.0874	-0.5033
Number of Bracken Ferns	-0.2317	-0.8712	0.3046

Table 3.7: Results of Multiple Comparison test of Principal Component 1 scores between plot types. Significant observed differences occurred at $p < 0.05$.

	Observed Difference	Critical Difference
Treatment 1 – Treatment 2	12.00	26.52
Treatment 1 – 2012 Nests	60.84	29.88
Treatment 1 – Control 1	55.39	25.16
Treatment 1 – Control 2	56.43	25.16
Treatment 2 – 2012 Nests	48.84	29.88
Treatment 2 – Control 1	43.39	25.16
Treatment 2 – Control 2	44.43	25.16
2012 Nests – Control 1	5.45	28.68
2012 Nests – Control 2	4.41	28.68
Control 1 – Control 2	1.04	23.72

Table 3.8: Results of Multiple Comparison test of Principal Component 3 scores between plot types. Significant observed differences occurred at $p < 0.05$.

	Observed Difference	Critical Difference
Treatment 1 – Treatment 2	52.30	26.52
Treatment 1 – 2012 Nests	42.39	29.88
Treatment 1 – Control 1	15.22	25.16
Treatment 1 – Control 2	30.90	25.16
Treatment 2 – 2012 Nests	9.91	29.88
Treatment 2 – Control 1	37.00	25.16
Treatment 2 – Control 2	21.40	25.16
2012 Nests – Control 1	27.17	28.68
2012 Nests – Control 2	11.49	28.68
Control 1 – Control 2	15.68	23.72

Table 3.9: Territory densities at the Airfield and three alternate sites in pre-burn (2006-2010) and post-burn (2012-2013) sample years. Territory placement in control and treatment plots in pre-burn years was approximated from GPS waypoints recorded at the center of each territory.

Sample Year	Airfield	Station Road	Centennial Ridges Road	Old Railway	Airfield Control Plots	Airfield Treatment Plots
2006	37	16	--	--	23	3
2007	22	11	--	10	10	6
2008	25	--	12	--	9	10
2009	30	14	14	11	10	12
2010	37	20	13	10	21	9
2012	31	13	13	12	15	5
2013	30	12	12	8	17	6
2006-2010	181	61	39	31	73	40
2012-2013	61	25	25	20	32	11

Table 3.10: Apparent nest success on the Airfield for pre-burn (2006-2010) and post-burn (2012-2013) sample years. This data set includes nests found in areas outside of treatment and control plots, and fledglings found after they left the nest.

Sample Year	Successful Nests	Failed Nests	Apparent Success (%)
2006	10	4	71.43
2007	12	9	57.14
2008	6	16	27.27
2010	5	7	41.67
2012	10	9	52.63
2013	5	9	35.71
Pre-burn (2006-2010)	33	36	47.82
Post-burn (2012-2013)	15	18	45.45

3.7 Figures

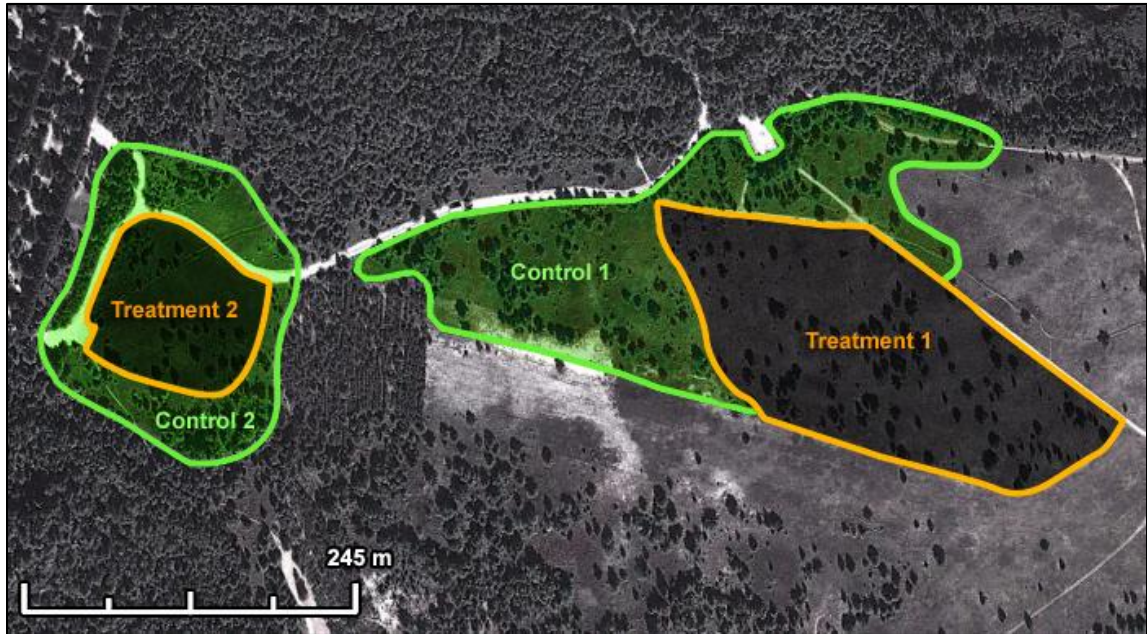


Figure 3.1: Aerial view of the Airfield study site, with treatment and control plots outlined.

Approximate areas are as follows: Treatment Plot 1 – 4.71 ha, Control Plot 1 – 4.37 ha, Treatment Plot 2 – 1.58 ha, Control Plot 2 – 1.97 ha.



Figure 3.2: Controlled burn in progress in Treatment Plot 1 (April 5th 2012).



Figure 3.3: Controlled burn in progress in Treatment Plot 2 (April 5th 2012).



Figure 3.4: Photo taken immediately after burn completion in Treatment Plot 1. Patches of brown highlight a footpath that was not burned as completely as the surrounding vegetation. Nearly 100% of ground vegetation was completely immolated.



Figure 3.5: Photo taken immediately after burn completion in Treatment Plot 2. Nearly 100% of ground vegetation was completely immolated.

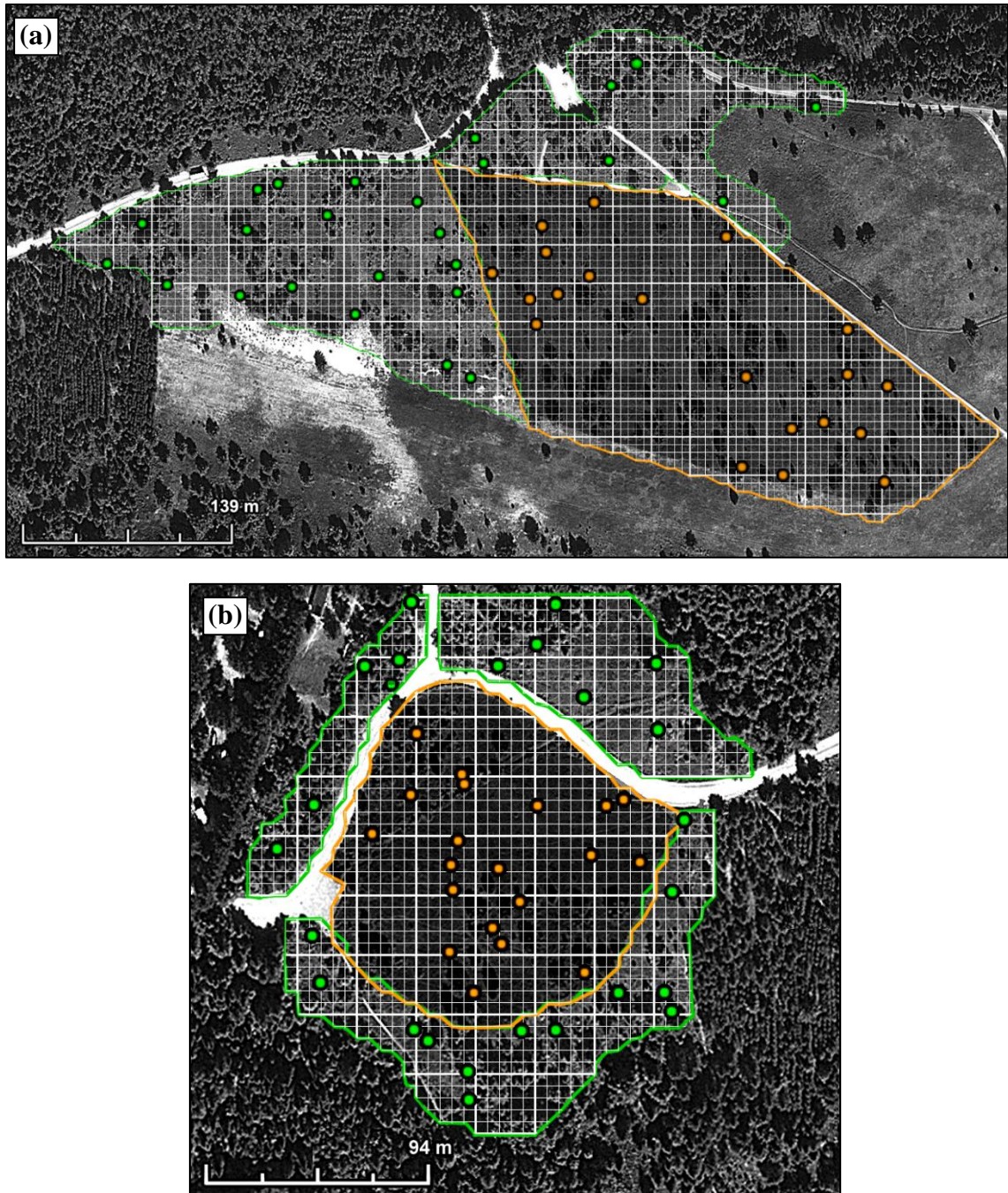


Figure 3.6: Locations of quadrat surveys in (a) Treatment and Control Plot 1 and (b) Treatment and Control Plot 2. Orange dots represent treatment quadrats, and green dots represent control quadrats. Plot areas are overlaid with a 5 x 5 m grid, the smallest unit used in the stratified random sampling procedure. See Figure 3.14 for 2012 nest site locations within the control plots.

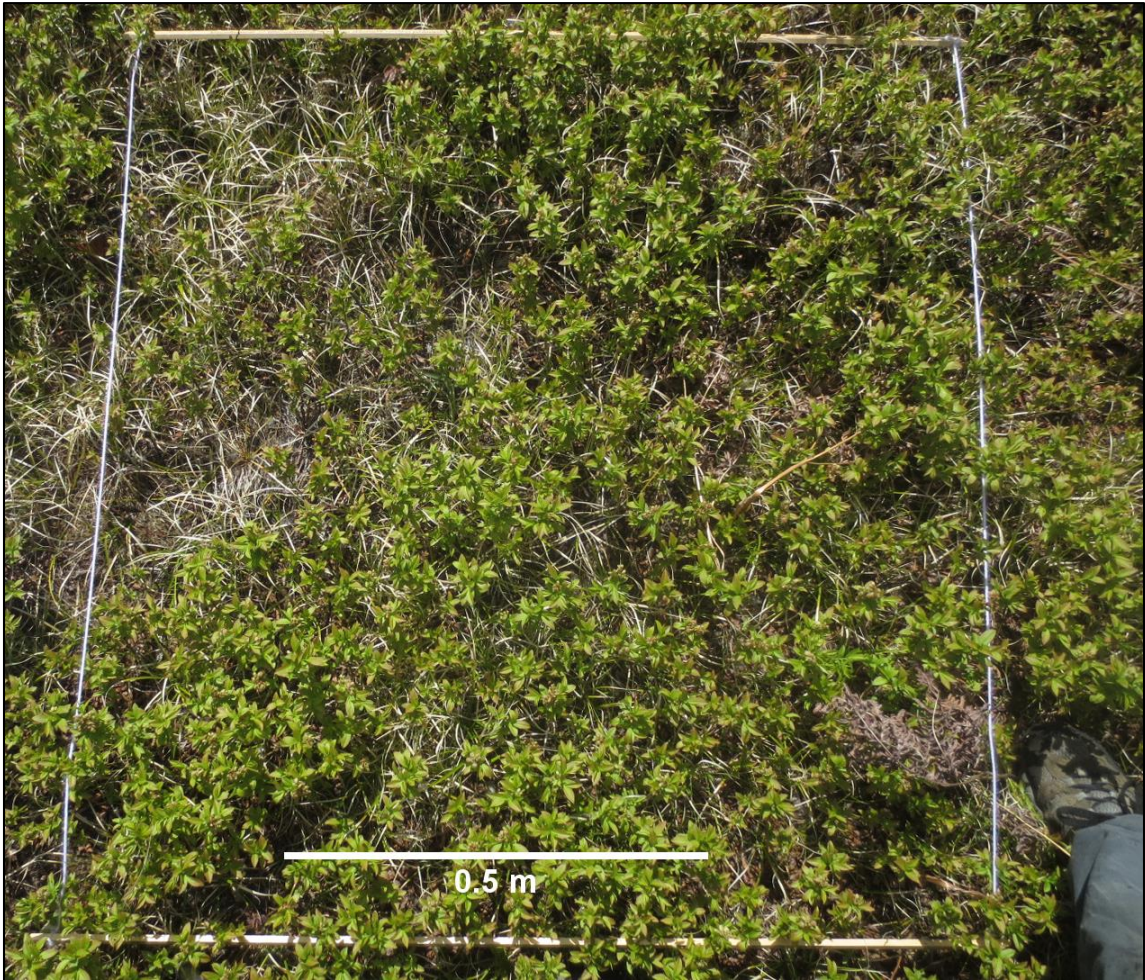


Figure 3.7: Overhead view of a vegetative quadrat survey. The quadrat frame consisted of two wooden metre sticks tied together with string approximately 1 m apart, and each photo was taken from approximately 1 m above the quadrat. Photos were taken at a slight angle, as the tripod used was not tall enough for a centered overhead shot. In this particular quadrat, the metre stick at the top was used as a scale in ImageJ, as both ends were clearly visible.

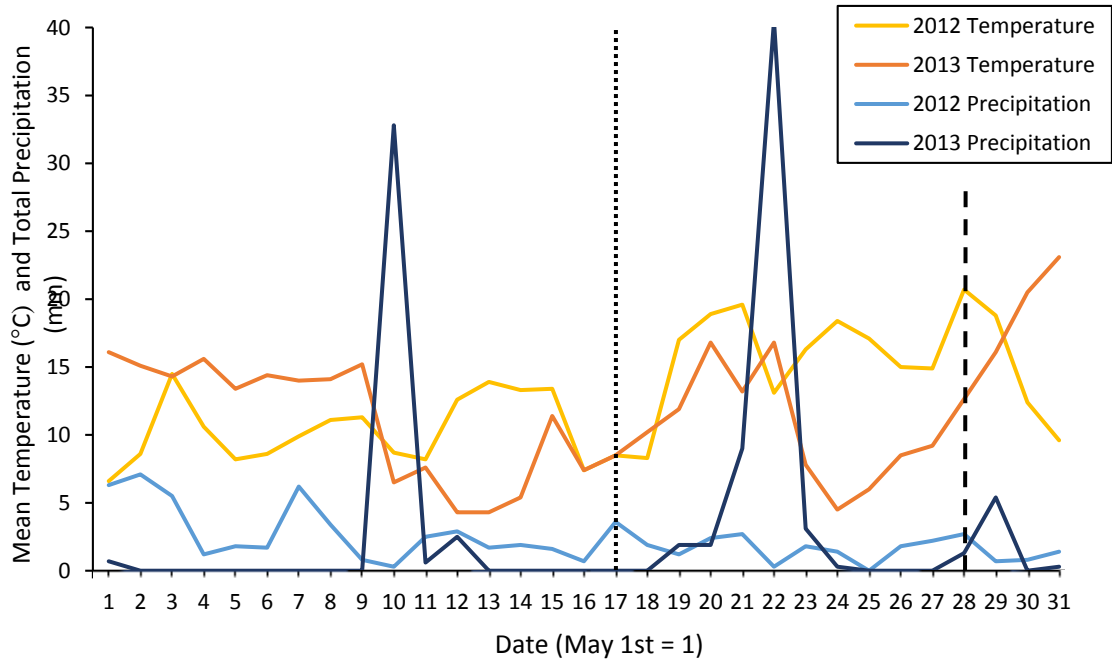


Figure 3.8: Daily mean temperatures and total precipitation recorded at the East Gate weather station (Lat: 45°32'00.000", Long: 78°16'00.000") in May 2012 and 2013 (Environment Canada 2013c, d). The dotted line is the earliest recorded clutch-initiation date in 2012 (May 17th), and the dashed line is the earliest recorded clutch-initiation date in 2013 (May 28th).

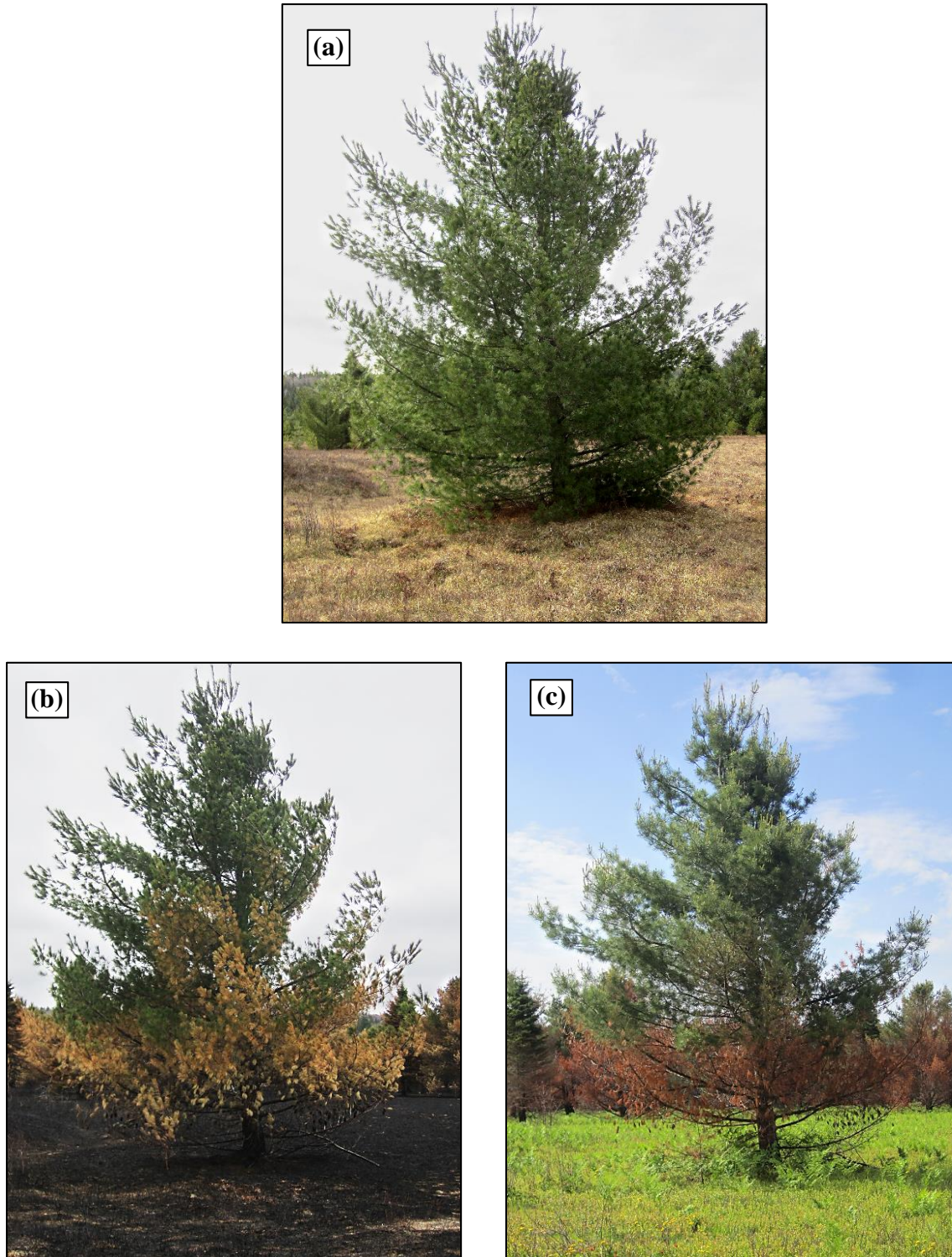


Figure 3.9: Photos of a white pine (*Pinus strobus*) located within Treatment Plot 1 taken (a) one week before the burn, (b) one week after the burn, and (c) two months after the burn.

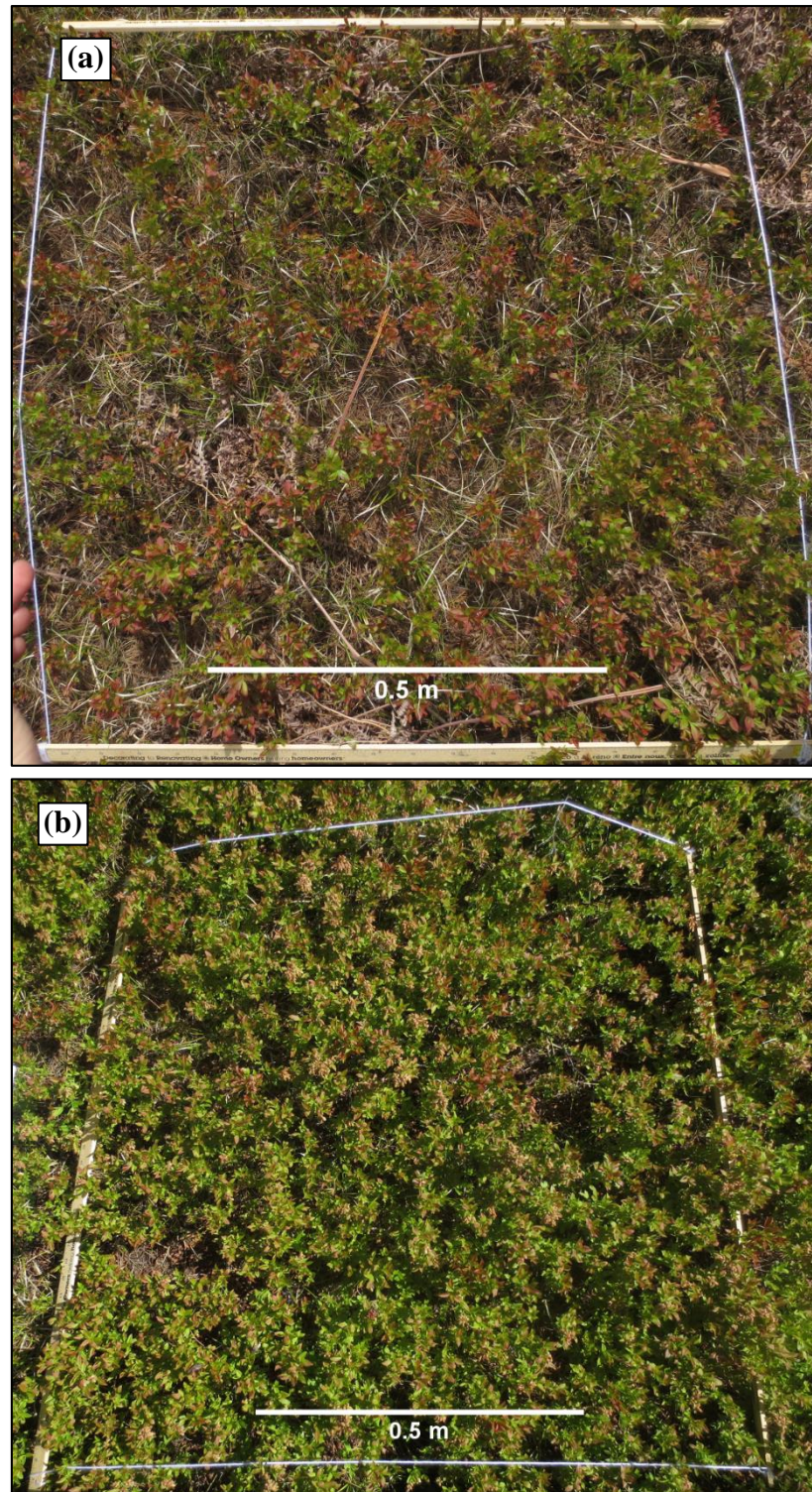


Figure 3.10: Overhead view of quadrats in (a) Treatment Plot 1 and (b) Treatment Plot 2.

Quadrat frames are two wooden metre sticks tied together with string approximately 1 m apart.



Figure 3.11: Overhead view of vegetative quadrats in (a) Control Plot 1 and (b) Control Plot 2.

Quadrat frames are two wooden metre sticks tied together with string approximately 1 m apart.

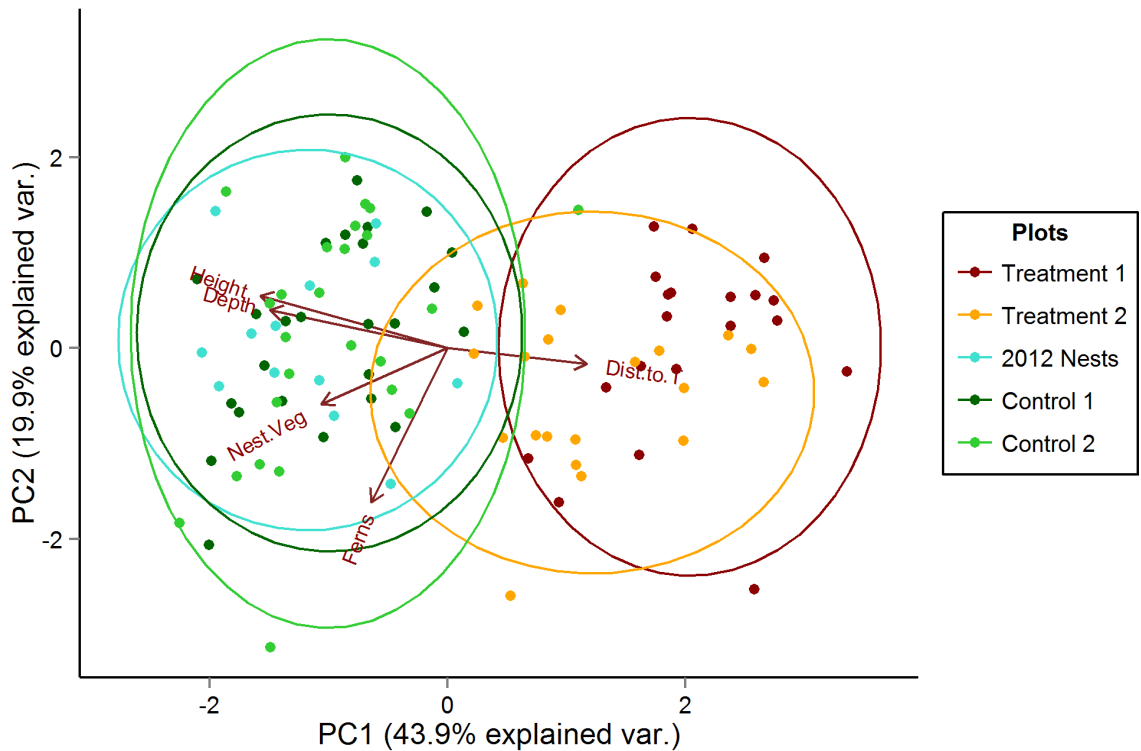


Figure 3.13: Scatterplot representing Principal Components Analysis of vegetative characteristics. Principal Component 1 and 2 (PC1 and PC2) scores are separated out by plot type. Ellipses represent 95% density. Red arrows represent vegetative characteristics: height of the shrub layer (Height), the depth of the vegetative debris layer (Depth), the percent of ground covered by nest habitat vegetation (Nest Veg.), the number of dead bracken ferns (Ferns), and the distance from the outer edge of the quadrat to the nearest conifer taller than 1 m (Dist. to T.).

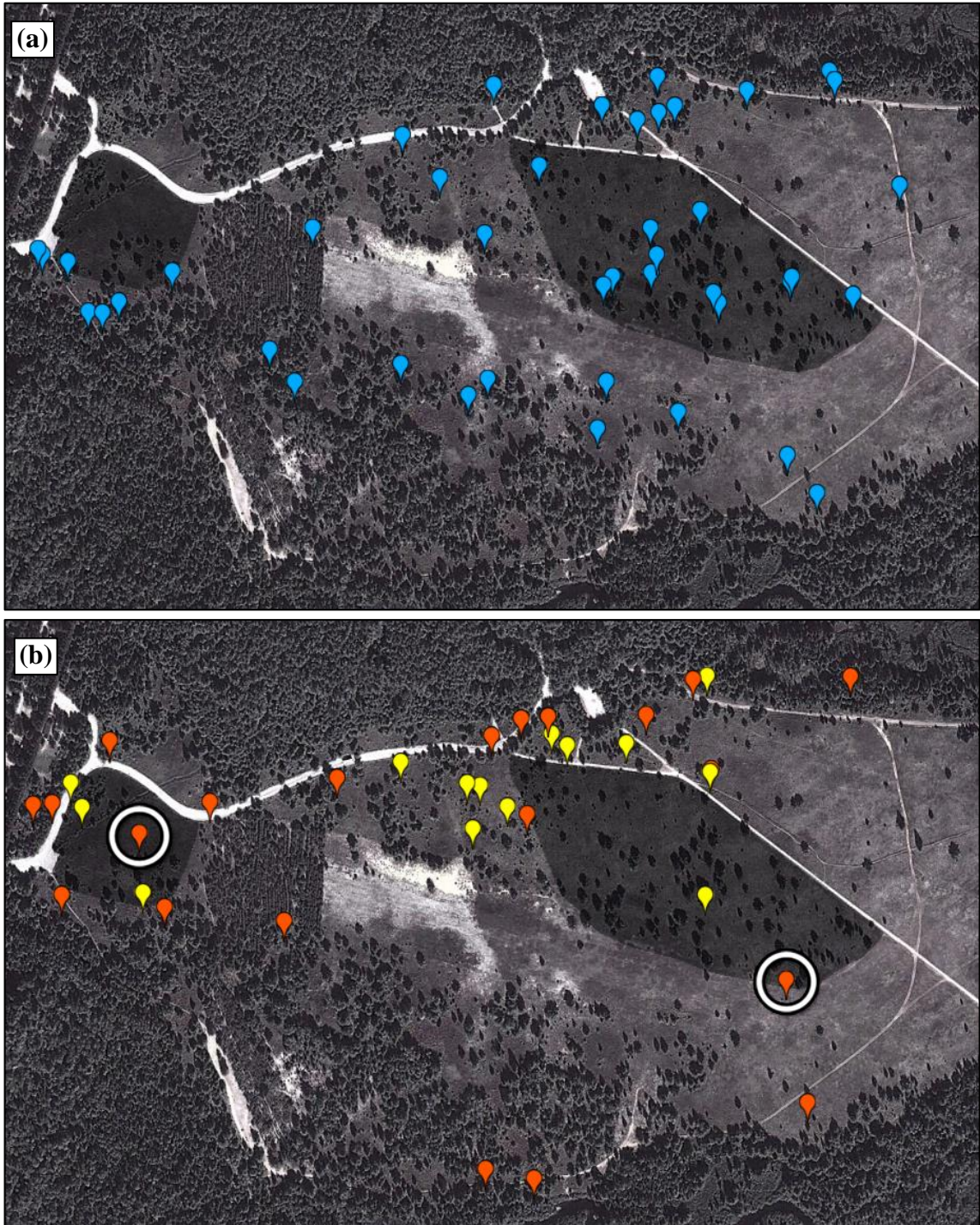


Figure 3.14: Aerial view of nest placement in (a) 2006-2010 and (b) 2012 and 2013. Pre-burn nests are labeled in blue, 2012 nests in orange, and 2013 nests in yellow. White circles highlight nests of interest in 2012, including the only nest to be found in a treatment plot that year (left) and a nest found in sub-par habitat just outside the perimeter of a treatment plot (right).

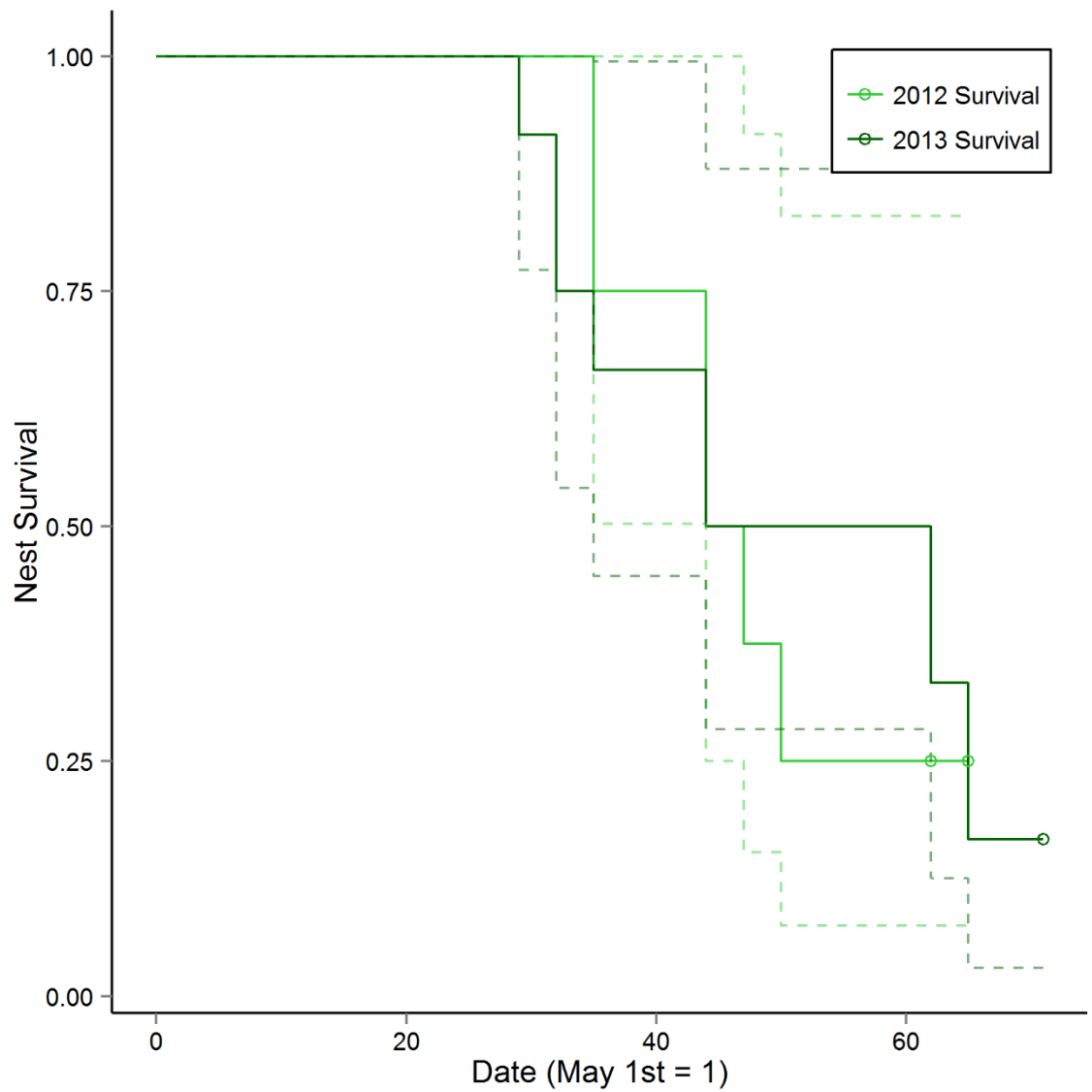


Figure 3.15: Kaplan-Meier survival curves representing nest survival in control plots in 2012 (N = 22) and 2013 (N = 9). Open circles represent censored nests, and dashed lines represent upper and lower confidence bands.

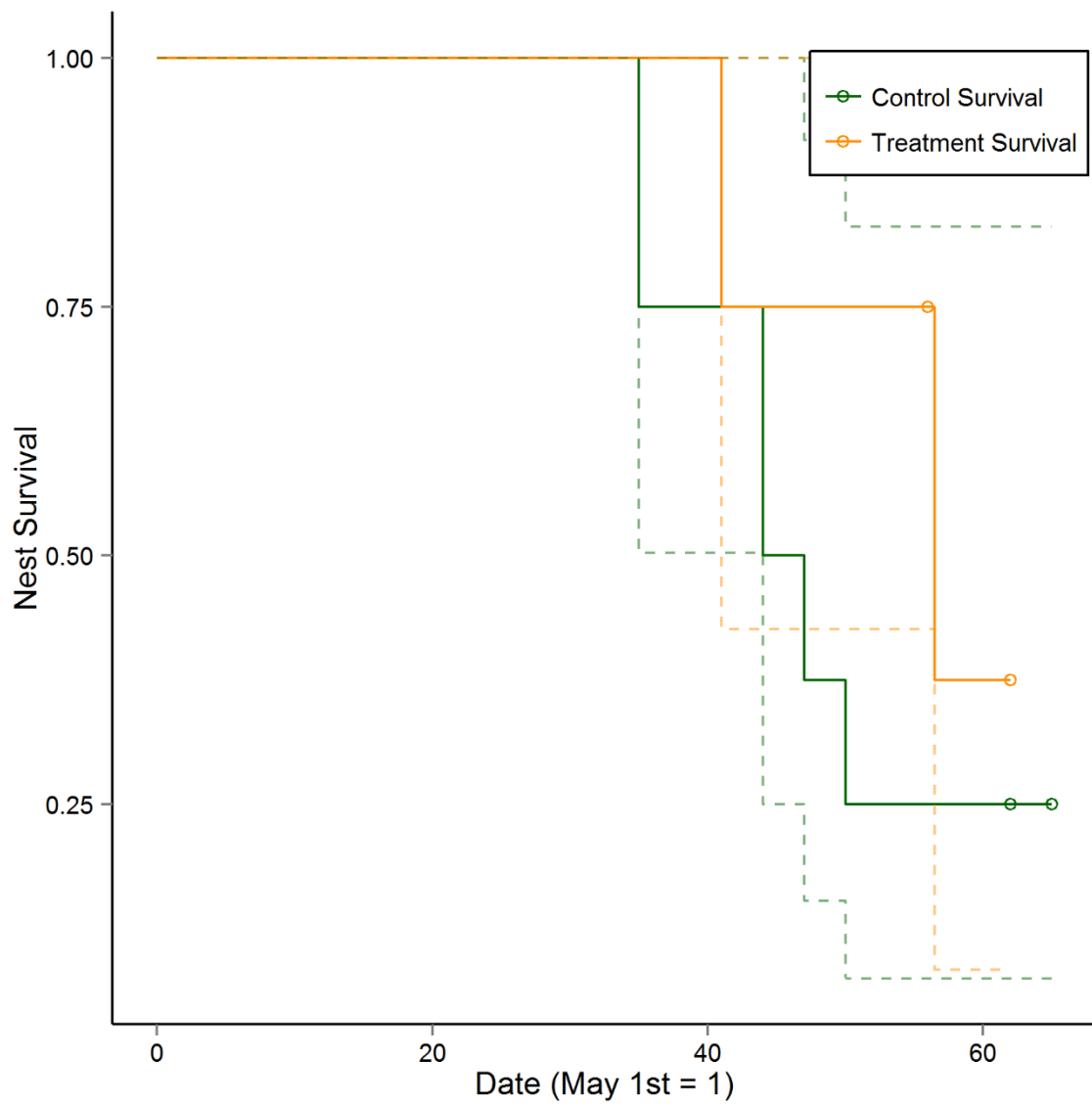


Figure 3.16: Kaplan-Meier survival curves representing nest survival in control plots ($N = 10$) and treatment plots ($N = 4$) in 2013. Open circles represent censored nests, and dashed lines represent upper and lower confidence bands.

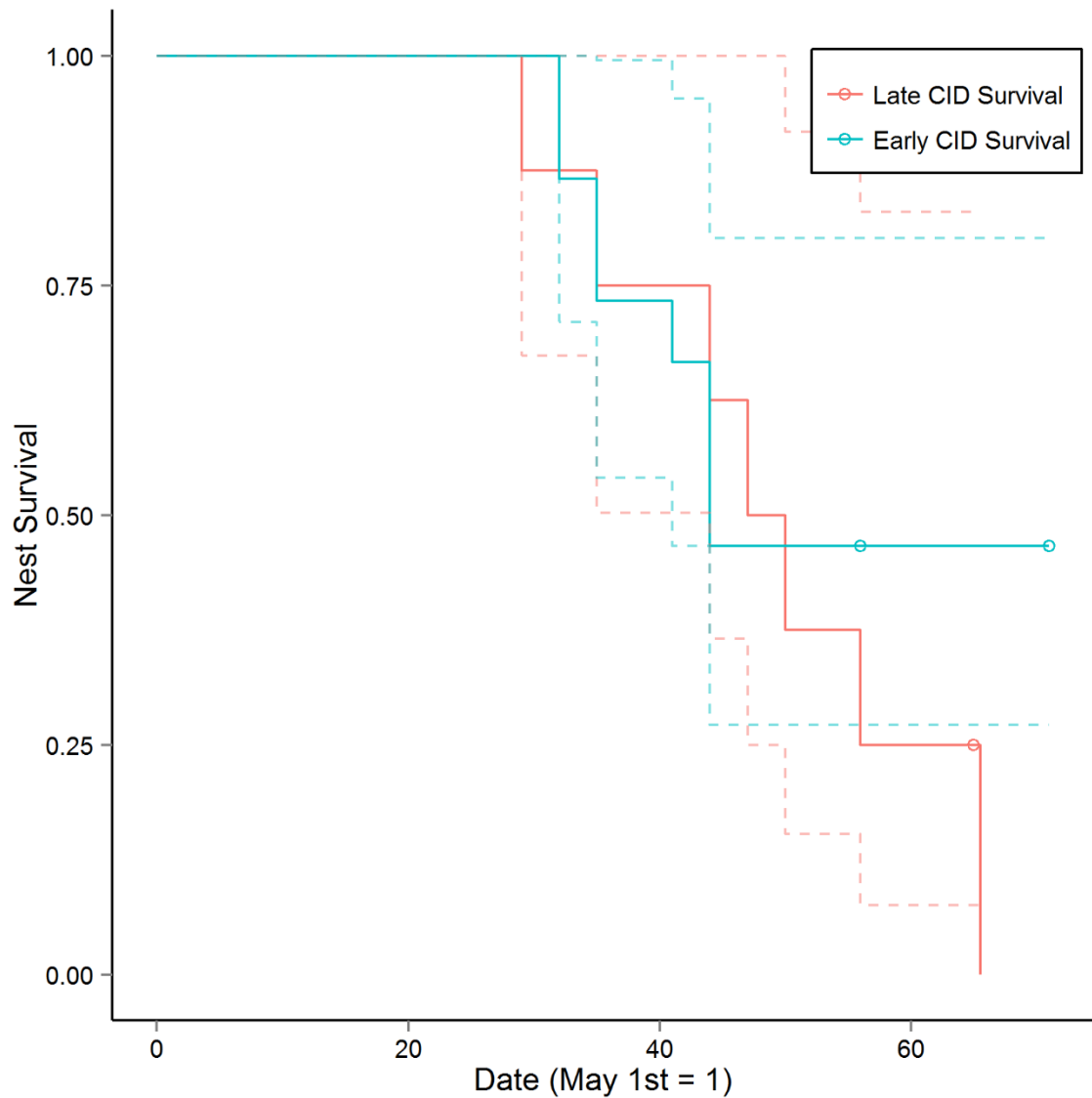


Figure 3.17: Kaplan-Meier survival curves representing survival of nests with an earlier than average clutch-initiation date (CID, $N = 9$) and nests with a later than average clutch-initiation date ($N = 13$) in 2012-2013. Open circles represent censored nests, and dashed lines represent upper and lower confidence bands.

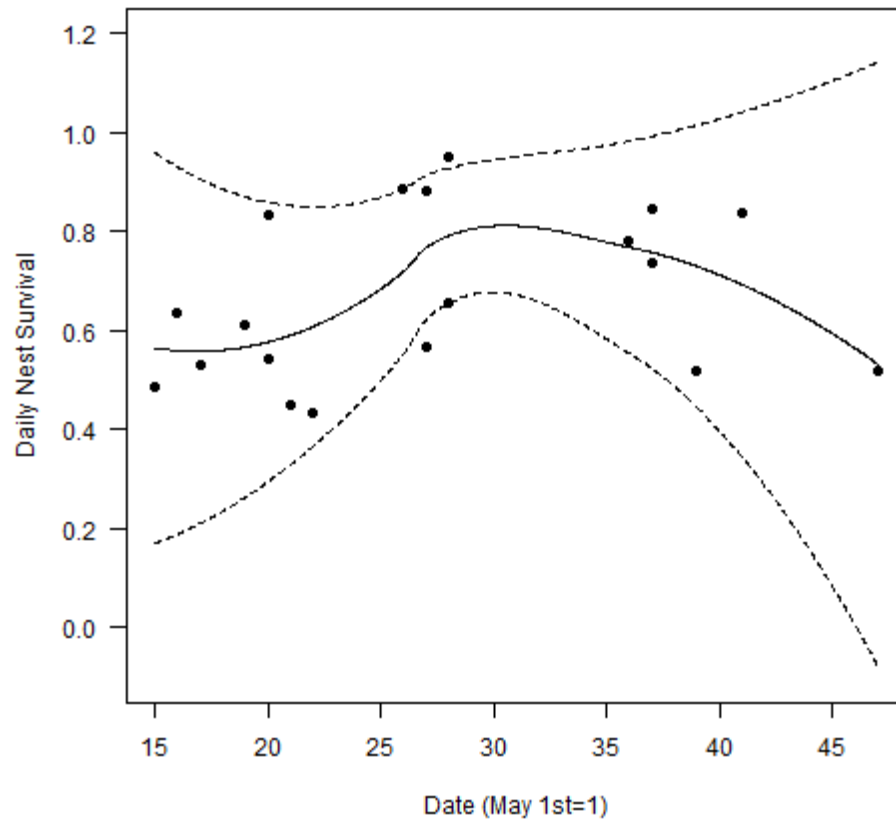


Figure 3.18: Logistic-exposure plot: daily nest survival probabilities for control plots in pooled sample years (2012-2013, $N = 23$). The dots represent individual nests, the solid line is the predicted model curve, and the dashed lines represent the 95% confidence interval. The points were generated using the logistic exposure model, with date as a predictor. The curve was fit to the points using Loess smoothing.

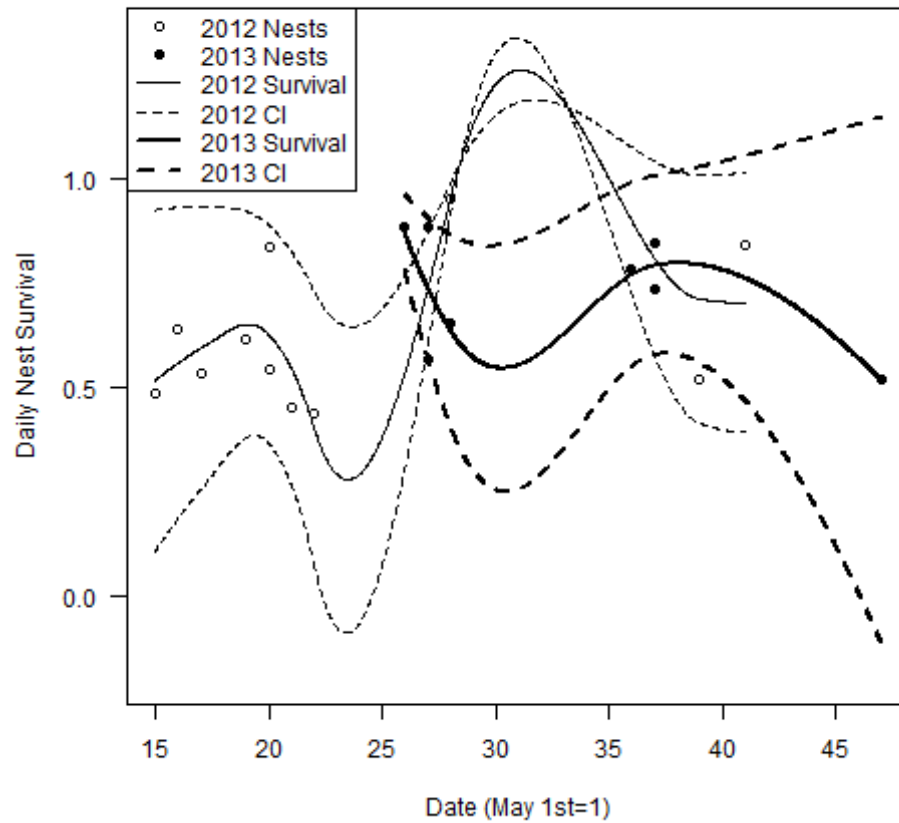


Figure 3.19: Logistic-exposure plot: daily nest survival probabilities for control plots in 2012 (N = 11) and 2013 (N = 12). The points were generated using the logistic exposure model, with date as a predictor. The curve was fit to the points using Loess smoothing.

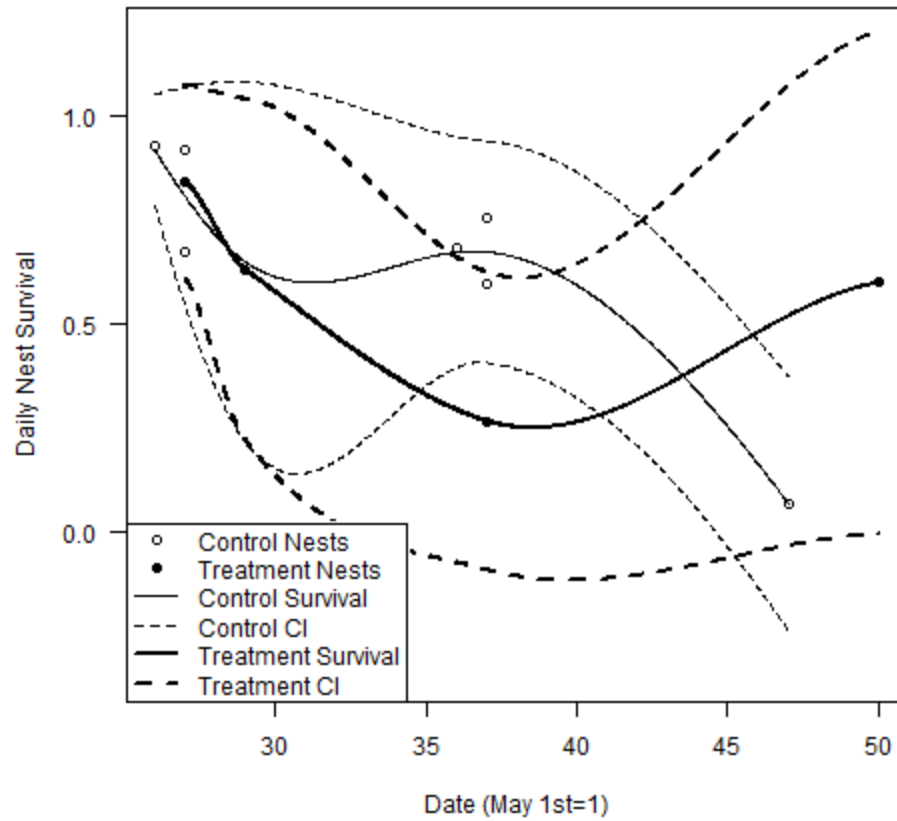


Figure 3.20: Logistic-exposure plot: daily nest survival probabilities for control ($N = 8$) and treatment plots ($N = 4$) in 2013. The points were generated using the logistic exposure model, with date as a predictor. The curve was fit to the points using Loess smoothing.

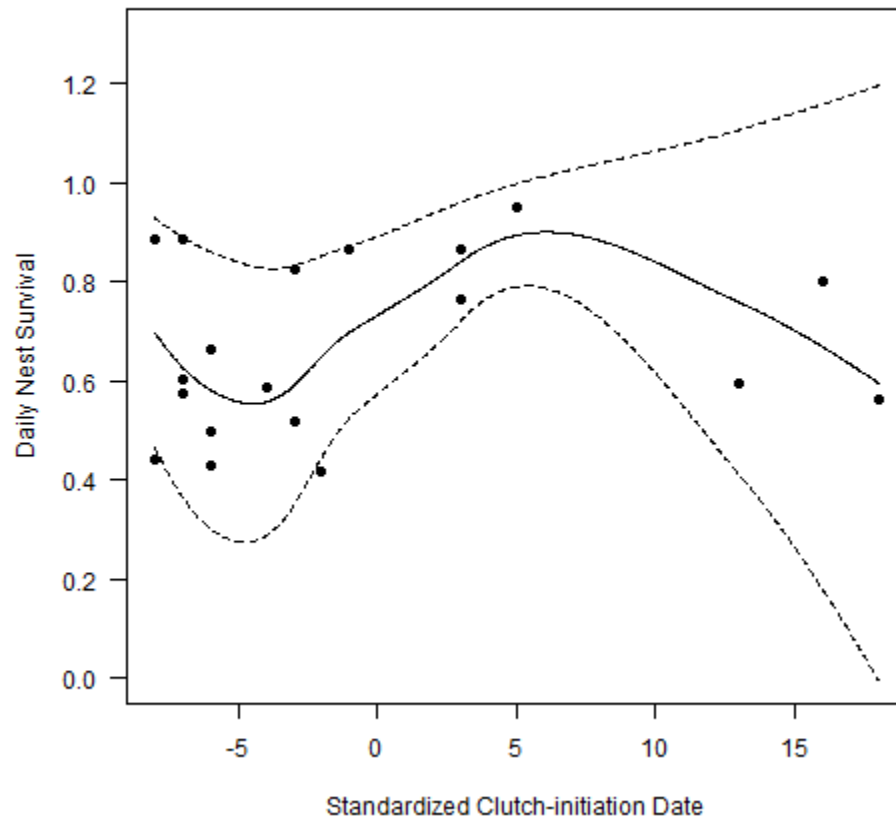


Figure 3.21: Logistic-exposure plot: daily nest survival probabilities for control plots in pooled sample years (2012-2013, $N = 23$). The dots represent individual nests, the solid line is the predicted model curve, and the dashed lines represent the 95% confidence interval. The points were generated using the logistic exposure model, with standardized clutch-initiation date as a predictor. The curve was fit to the points using Loess smoothing.

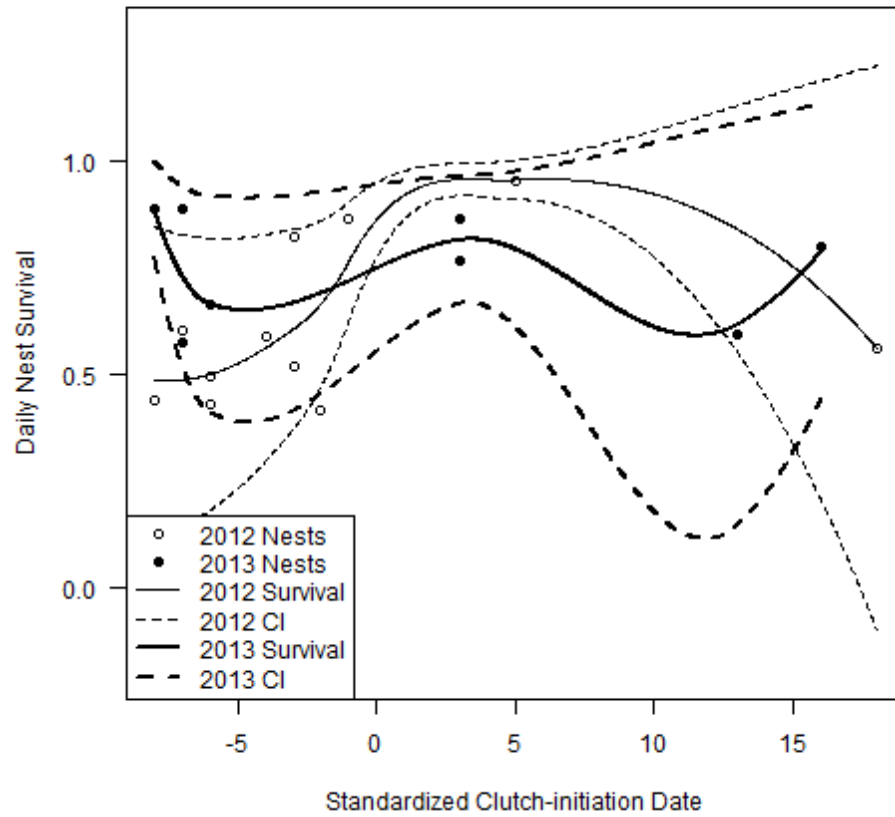


Figure 3.22: Logistic-exposure plot: daily nest survival probabilities for control plots in 2012 (N = 11) and 2013 (N = 12). The points were generated using the logistic exposure model, with standardized clutch-initiation date as a predictor. The curve was fit to the points using Loess smoothing.

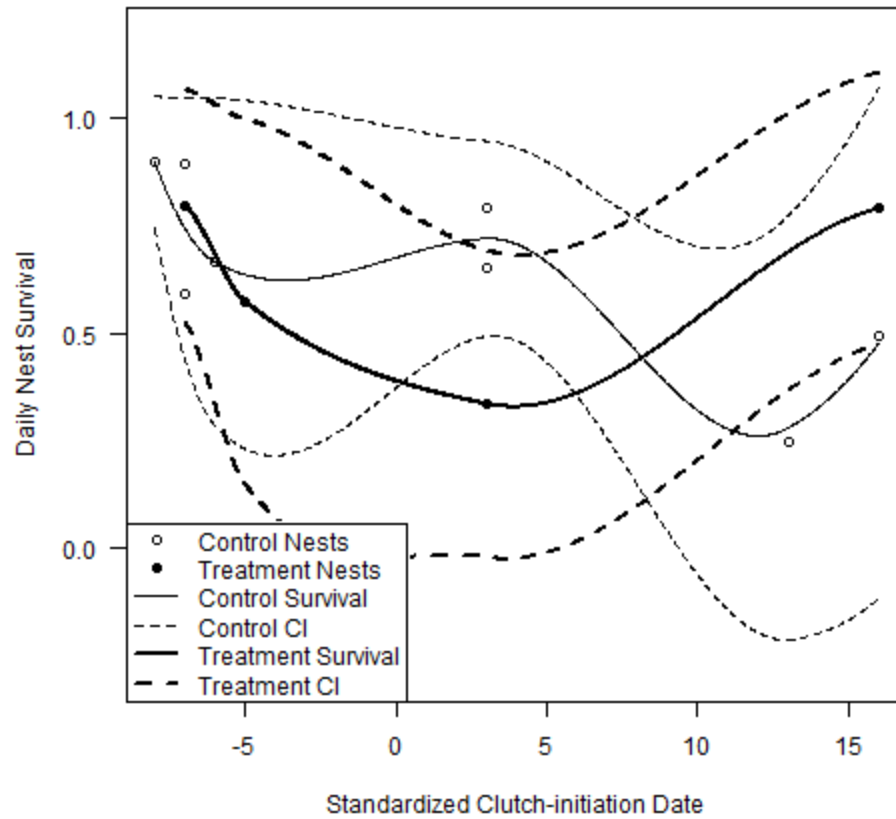


Figure 3.23: Logistic-exposure plot: daily nest survival probabilities for control ($N = 8$) and treatment plots ($N = 4$) in 2013. The points were generated using the logistic exposure model, with standardized clutch-initiation date as a predictor. The curve was fit to the points using Loess smoothing.

Chapter 4

General Discussion

The study of nesting success and population size in birds continues to be a valuable source of information about the management and conservation requirements of a given species. My research provides a more complete picture of the mechanisms driving changes in species abundances, through the examination of nesting success in the same system before and after habitat management. In this white-throated sparrow population the largest influence on nesting success in a natural system is the timing of breeding, and the limiting factor in the post-management system is the availability of ground cover vegetation during nest site selection. In the natural system I conclude that there is an interaction between timing of breeding and nest predation rates, since predation was the leading cause of nest loss, and nests later in the season showed a higher probability of failure. However the relative contribution of food-limitation and synergistic effects between predation and food availability were only indirectly explored, presenting an avenue of further inquiry in this system. In the post-management system there may be an interaction between changes in the structure of nesting vegetation and predation rates, with increased vulnerability to nest predation in burned areas. Further monitoring of nesting in burned areas is required to observe how white-throated sparrow nesting ecology will change as ground vegetation recovers. Long-term effects on the size of this population will likely be positive, since repeated application of fire can be used to conserve the openness of the breeding site.

My findings highlight the need for more research on the species-specific determinants of avian nesting success, in both natural systems and managed populations. While community-level studies may be the most efficient way to carry out long-term monitoring of the effects of large-scale management initiatives, the interpretation of these effects can be improved by information on species-specific determinants of population size.

4.1 Recommendations

The wide variety of habitats and conditions in which a species may live suggests that conclusions made in one area may not be applicable to another area of the same species range. Furthermore, literature concerning the influences of nest predation on the timing of breeding remains scarce. Therefore I recommend that this question be investigated further, both in other white-throated sparrow populations and in other ground-nesting species in North America. Based on the varied results given by different survival analysis methods used in Chapter 3, I also recommend that all such replications employ a standard method for survival analysis to improve the interpretation of results and comparison between studies. Furthermore, a thorough study of the suite of predators affecting white-throated sparrow nesting success is required to better understand why nest predation rates increase later in the breeding season. An investigation into the power of predator-limitation in cavity-nesting species should also be conducted in North America, and populations breeding in natural cavities should be used in order to minimize the confounding factors present in artificial nest box systems. Although the theory of food-limitation effects on the timing of breeding have been explored in many cavity-nesting species, the contribution of predator-limitation as well as synergistic effects between the two must also be considered.

Further examination of the effects of prescribed fire on the reproductive success of ground-nesting birds is required to help predict the response of individual species to habitat management. More research on acute effects occurring in the first months and years immediately

following a burn is suggested, as well as research on the effect of burning at other times: after nesting has begun, or in the fall outside of the growing season. In addition, the effect of variation in burn patch size should be investigated, as well as the effect of variation in territory density and spatial arrangement. Long-term monitoring following these investigations is also recommended, to aid in determining the appropriate fire-return interval that would maintain a habitat without negatively affecting breeding bird populations. Finally, this experimental application of prescribed fire should be replicated across many species, in many different habitats and nesting guilds in order to further our understanding of the effect of fire on avian populations.

4.2 Integration

My exploration of the nesting ecology of white-throated sparrows incorporates multiple aspects of ecological research, and also connects different fields. Various techniques were incorporated into this project, including the observational study of life history traits such as fecundity and breeding phenology, the application of the before-after-impact-control experimental design, and the use of vegetative measurements to help in quantifying the impact of prescribed fire on nesting ecology. The interpretation of Chapter 2 findings required an understanding of life history traits of other taxa, such as the breeding phenology of small mammals. The analysis of Chapter 3 data included both hypothesis-testing and information-theoretic approaches, where one alone would not be sufficient to explore the factors influencing daily nest survival across the season.

Furthermore, my findings in Chapter 3 have can be applied in the fields of conservation biology, public education, and policy. My research provides valuable empirical data to supplement the growing body of literature in the field of avian fire ecology, and this may be used to help design future habitat management initiatives. One example is the use of fire to restore and maintain pyrogenic jack pine (*Pinus banksiana*) stands in Ontario, which could serve as new breeding habitat for recovering populations of Kirtland's warbler (*Setophaga kirtlandii*). Moreover, the

perception of fire as a destructive force is still present in the public consciousness, a by-product of decades-long fire suppression campaigns. By conducting a fire study in a high-traffic tourist area, the positive effects of fire as a management tool can be—and already has been—demonstrated to the public (Figure 4.1). Finally, my data can be used to inform habitat management policy, such as forest fire protocols that contain guidelines on the appropriate fire severity, size, and fire return intervals to be used in the application of prescribed fire.

4.3 Figures



Figure 4.1: Photograph of interpretive sign placed on the eastern edge of Treatment Plot 1.

Text on the sign describes the prescribed burns and the benefits they provide to the Airfield as both a natural habitat and a heritage site. Two signs were placed around the perimeter of each treatment plot, with before and after photographs taken at each location.

Summary

The main objective of this research was to explore the factors influencing avian breeding success in a ground-nesting species. Here I considered the relationship between nesting success and biotic and abiotic determinants of life history traits, such as the timing of breeding, fecundity, and nest failure through predation. This includes an observational study of variation in clutch-initiation date and its influence on nest success via ecological constraints (Chapter 2), and an experimental investigation of the acute effects of prescribed fire on nesting success (Chapter 3).

In Chapter 2 I examined the effects of variation in clutch-initiation date on clutch-size, clutch mass, and nest success. Much of the research on this subject was conducted on cavity-nesting species in Europe, and in those systems it was concluded that increased food-limitation later in the season leads to decreased parental investment and nest success. I tested this hypothesis in a ground-nesting species in North America, and offered an alternative explanation for a seasonal decline in parental investment and nesting success. Clutch size was not smaller in later white-throated sparrow nests, which matched predictions since they cannot vary their clutch size by more than two eggs. Variation in clutch mass was considered as an alternative method of varying parental investment, but whole-clutch mass also did not decline with later clutch-initiation dates. Nest success, however, did exhibit the late-season decline predicted for other life-history traits. This was caused by an increase in nest predation with later initiation dates, which may be attributed to seasonal variation in nest predator abundance or activity. Therefore nest predation was found to be the most powerful limiting factor in nest success, in this population of white-throated sparrows. This provides an alternative to the food-limitation theory of seasonal

variation in nest success, and highlights the need for more research in clutch-initiation date and nest survival outside of cavity-nesting species.

In Chapter 3 I examined the effect of early-spring prescribed burning on nesting success. Much of the research on this subject was conducted using community-level surveys that measured changes in species abundances. While investigations of this nature can be carried out efficiently on the large-scale, more small-scale surveys are required to improve interpretation of the observed changes in population size. I tested the hypothesis that prescribed burning would have an immediate negative effect on nesting success, using a population of white-throated sparrows and previous research on their nesting ecology in a natural system (Chapter 2). While overall nesting success was not affected in the first two years after the burn, nest site selection was significantly altered: Nesting females exhibited an almost complete avoidance of burned areas in the first breeding season after the burn, and only some females nested in treatment plots in the second year. This indicates that a matrix of suitable nesting habitat must be left untouched, in order to allow normal breeding in the first nesting season after a burn. The lack of change in site-wide nesting success, coupled with the substantial impact on nest site selection, highlights the need to go beyond community-level surveys, since species abundances may not reveal the immediate, short-term effects of fire on breeding birds.

My findings represent a valuable contribution to two areas of research in avian ecology: the study of nesting success and determinants of population size, and the study of the immediate effects of habitat management on nesting success. The integration of these research subjects, on both the small and large scale, is recommended to best achieve management goals.

Appendix A

The Effects of Fire on Coniferous Trees

Fire damage to coniferous trees in treatment plots was quantified using photographic surveys. Surveys were conducted from late March to early May 2012 by taking photographs of each tree taller than 2.5 m, before and after the burn. The proportion of conifer branches severely damaged by the fire was determined using ImageJ and polygon measurements of the total area of each crown that still contained needles. The proportional difference between pre-fire crown area and post-fire crown area was recorded as the percent fire damage for each tree. The height of each tree was also measured in ImageJ, and the conifer species composition of the burn plots was characterized. These measurements were not repeated in control plots because conifer species and height were not considered sufficiently important nest cover characteristics to warrant quantitative comparison between control and treatment plots in this experiment.

See Table A.1 for a summary of tree survey data. Mean fire damage to coniferous branches was 34.88 % in Treatment Plot 1, and 56.00 % in Treatment Plot 2 (Figure A.1). In both treatment plots, fire damage was concentrated at the base of the crown, with complete immolation of needles on lower branches (Figure A.2). The most abundant coniferous species in both plots was white pine (*Pinus strobus*), and species composition was similar between treatment plots (Figure A.3). Average tree heights were also similar between treatment plots (Figure A.4), with the exception of two red pines (*Pinus resinosa*) in Treatment Plot 1.

A.1 Tables

Table A.1: Summary of fire damage to coniferous trees, and species composition of both treatment plots. Only trees taller than 2.5 m were sampled.

Treatment Plot 1				
	Average Branches Burned (%)	Number of Stems	Proportional Abundance	Average Height (m)
<i>Pinus strobus</i>	35.89	222	76.03	5.26
<i>Picea glauca</i>	22.81	41	14.04	3.62
<i>Pinus resinosa</i>	50.85	2	0.68	8.17
<i>Pinus sylvestris</i>	29.96	27	9.25	3.56
Treatment Plot 2				
	Average Branches Burned (%)	Number of Stems	Proportional Abundance	Average Height (m)
<i>Pinus strobus</i>	60.45	90	74.75	3.81
<i>Picea glauca</i>	49.52	25	17.99	5.21
<i>Pinus resinosa</i>	60.86	23	16.55	4.63
<i>Pinus sylvestris</i>	53.16	1	0.72	2.57

A.2 Figures

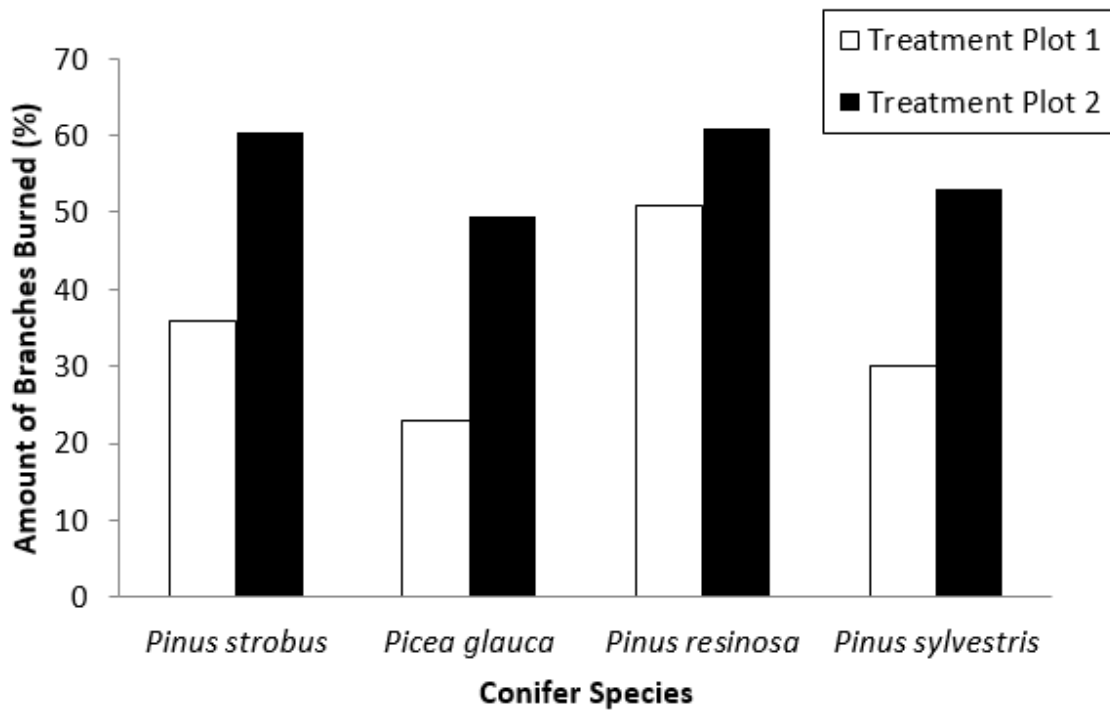


Figure A.1: Mean fire damage to coniferous trees in each treatment plot. Fire damage was most severe in lower branches at the base of the crown.



Figure A.2: Photo taken of a white pine (*Pinus strobus*) in Treatment Plot 1 on April 17th 2012, one week after the controlled burn. In this tree, fire damage is apparent in complete immolation of needles at the base of the crown, and needle death in approximately 60 % of the crown.

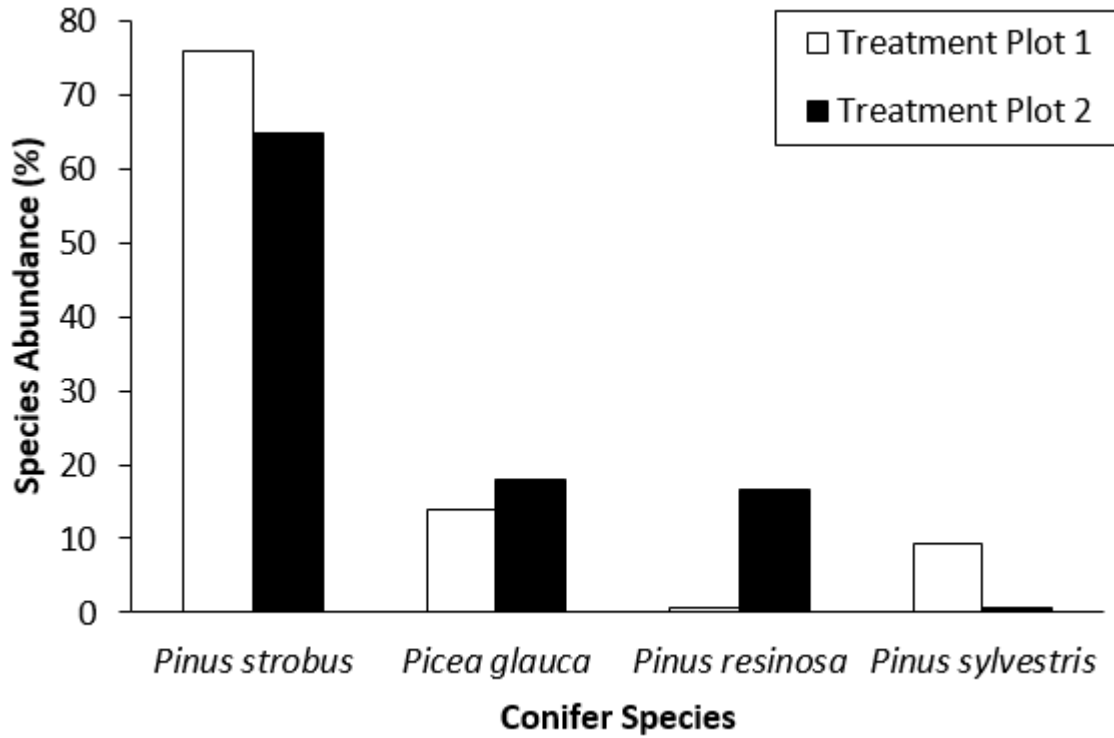


Figure A.3: Species composition of coniferous trees in each treatment plot. Only coniferous trees taller than 2.5 m were sampled.

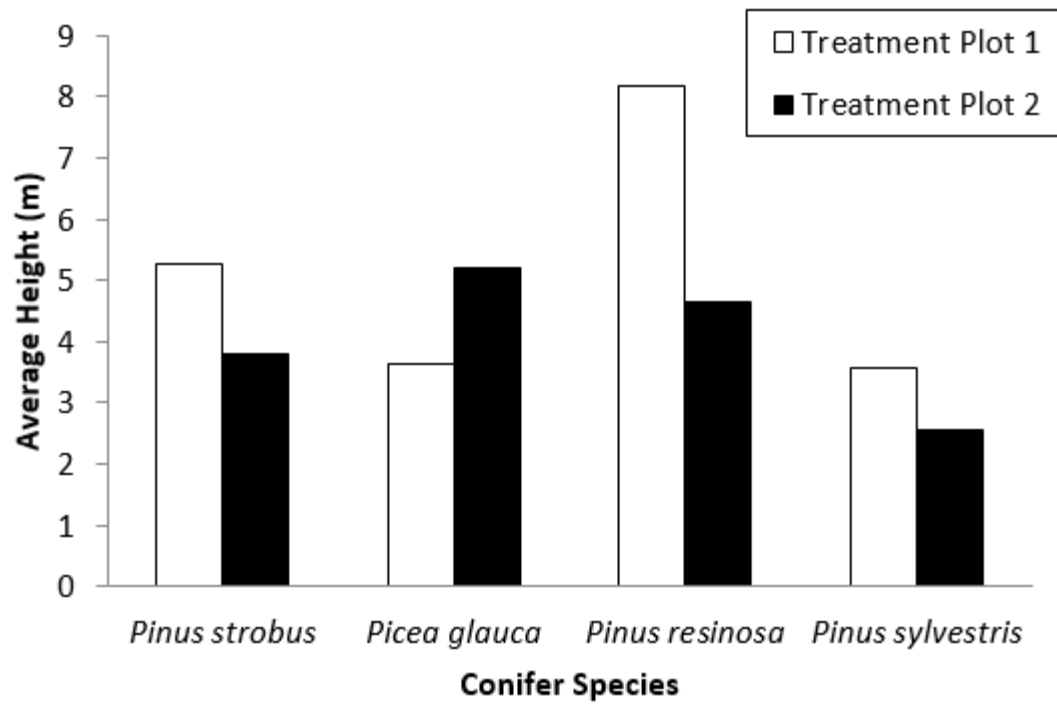


Figure A.4: Average height of coniferous trees in each treatment plot. Only trees taller than 2.5 m were sampled.

Appendix B

Other Avian Species Observed in Treatment Plots

Observations of other avian species on the Airfield and in treatment plots were collected in an opportunistic manner in both 2012 and 2013 (Table B.1). A new species was added to the list of observations whenever individuals appeared more than once, and were observed perching or foraging in treatment plots. These species were also observed on the Airfield in 2005 (Barker 2006). Notable observations include active nesting by other species in treatment plots, and the presence of an avian nest predator. An active black-capped chickadee (*Poecile atricapillus*) nest found in Treatment Plot 1 in 2013, located in a stump approximately 1.5 m tall that had been present as standing deadwood before the burn. Blue jays (*Cyanocitta cristata*) were observed in both control and treatment plots exhibiting a behaviour that appeared similar to predatory nest searching patterns. This behaviour was characterized by perching on low branches or landing on the ground, orienting the head towards low areas. Although no quantitative comparisons of nest predator activity can be made between control and treatment plots, Jones et al. (2002) attributed a higher proportion of predation events in burned areas to avian nest predators compared to small mammal nest predators.

B.1 Tables**Table B.1:** List of avian species observed perching or foraging in treatment plots.

Common Name	Latin Name
northern flicker	<i>Colaptes auratus</i>
american robin	<i>Turdus migratorius</i>
eastern meadowlark	<i>Sturnella magna</i>
american crow	<i>Corvus brachyrhynchos</i>
common raven	<i>Corvus corax</i>
canada goose	<i>Branta canadensis</i>
common grackle	<i>Quiscalus quiscula</i>
downy woodpecker	<i>Picoides pubescens</i>
chipping sparrow	<i>Spizella passerina</i>
white-crowned sparrow	<i>Zonotrichia leucophrys</i>
black-capped chickadee	<i>Poecile atricapillus</i>
yellow-rumped warbler	<i>Dendroica coronata</i>
dark-eyed junco	<i>Junco hyemalis</i>
cedar waxwing	<i>Bombycilla cedrorum</i>
hermit thrush	<i>Catharus guttatus</i>
ruby-throated hummingbird	<i>Archilochus colubris</i>
blue jay	<i>Cyanocitta cristata</i>
northern harrier	<i>Circus cyaneus</i>

B.2 References

Barker NK (2006) Relationships between abundances of forest bird species: Can the white-throated sparrow (*Zonotrichia albicollis*) be used as an indicator species? (Unpublished undergraduate thesis). Wilfrid Laurier University, Waterloo.

Jones DD, Conner LM, Warren RJ, Ware GO (2002) The effect of supplemental prey and prescribed fire on success of artificial nests. *The Journal of Wildlife Management* 66:1112–1117.

Appendix C

Sample R Codes for Statistical Analysis in Chapter 3

Nesting Habitat

```
vegPCA <- princomp(veg.data[,1:5], cor=T)
#PCA of shrub height, depth of vegetative
debris layer, percent nest vegetation, number
of bracken ferns, and distance to the nearest
tree taller than 1 m.
vegPCA$scores
vegPCA$loadings
vegPCA$sdev^2
#eigenvalues
```

Testing PC scores by plot (sample code)

Checking normality

```
shapiro.test(PC1)
# PC1 non-normal (p<0.05)
```

Checking for equal variances by plot

```
fligner.test(PC1, plot)
# PC1 equal variances
```

Kruskal-Wallis test for PC1

```
kruskal.test(PC1~plot.n)
# significant difference between plots
(p<0.05)
```

Multiple comparison test (non-parametric equivalent of Tukey HSD)

```
kruskalmc(PC1~plot.n)
# PC1 differs between BPs and everything
else but between BPs, between nests and
veg, or between veg plots
```


Plotting PC1 scores against PC2 scores

```

g <- ggbiplot(vegPCA, obs.scale = 1, var.scale = 1, groups = veg.data$plot, ellipse = TRUE,
ellipse.prob = 0.95, circle = FALSE)

g <- g + scale_color_manual(name="Plots", values=c("darkred", "orange", "turquoise",
"darkgreen", "limegreen"))

g <- g + theme(legend.direction = 'vertical', legend.position = 'right')

g <- g + theme(panel.background = element_blank())

g <- g + theme(panel.grid.major = element_blank())

g <- g + theme(panel.grid.minor = element_blank())

g <- g + theme(legend.key = element_blank())

g <- g + theme(legend.background = element_rect(fill="white", size=0.5, linetype="solid",
color="black"))

g <- g + theme(axis.line = element_line())

g <- g + guides(colour = guide_legend(title.hjust = 0.5))

g <- g + theme(axis.text.x = element_text(colour="black"))

g <- g + theme(axis.text.y = element_text(colour="black"))

```

Nest Placement

```
# Past = 2006-2010, current = 2012-2013
```

```
nests
```

```
Treatment Control
```

```
Past      12  14
```

```
Current   5  24
```

```
> fisher.test(nests)
```

```
# p<0.05 therefore significant difference in nest placement after the burn
```

Territory Density

AF = Airfield, RR = Old Railway Bike Trail, CRR = Centennial Ridges Road, SR = Station

Road

Terr

Burn	Control	AF	RR	CRR	SR	Year	Time
3	23	37	NA	NA	16	2006	Past
6	10	22	10	NA	11	2007	Past
10	9	25	NA	12	NA	2008	Past
12	10	60	11	14	14	2009	Past
9	21	37	10	13	20	2010	Past
5	15	31	12	13	13	2012	Present
6	17	30	8	12	12	2013	Present

Airfield

testing assumptions for past vs present t-test

```
apply(terr[,1:6], 2, shapiro.test)
```

all normal except perimeter

```
var.test(AF[1:5], AF[6:7])
```

variances equal so can use two-sample t-test

```
t.test(AF[1:5], AF[6:7])
```

p = 0.4428 therefore no difference in AF territory density between past and present

Alternate Sites (Past-Present)*alt*

	RR	CRR	SR
Past	27	20	25
Present	25	20	25

g.test(alt)

p = 0.581, therefore no difference in territory density at alternate sites before/after the burn

Alternate Sites (2012-2013)*alt2*

	RR	CRR	SR
Past	12	13	13
Present	8	12	12

g.test(alt2)

p-value = 0.8309, therefore no difference in territory density at alternate sites between 2012 and 2013

Nest Survival**Apparent Nest Success (by year)***nests*

	Successful	Failed
2006	10	4
2007	12	9
2008	6	16
2010	5	7
2012	10	9
2013	5	9

chisq.test(nests)

Pearson's Chi-squared test

data: nests

X-squared = 10.9395, df = 5, p-value = 0.05259

Warning message:

```
In chisq.test(nests) : Chi-squared approximation may be incorrect
#Calculate G Test Statistic, assigning O as observed and E as expected frequencies
O <- matrix(chisq.test(nests)$observed)
E <- matrix(chisq.test(nests)$expected)
# add one to both O and E so that 0 value in O doesn't screw up G-test statistic calculation
E <- E+1
O <- O+1
G <- 2*sum(O*log(O/E))
#Determine the Critical Value using the qchisq() function
#Set the Type 1 Error to alpha = 0.05
#Input the R = # Rows and C= # Columns to calculate the df
alpha <- 0.05
R <- 6
C <- 2
df <- (R-1)*(C-1)
CV <- qchisq(1-alpha,df)
#Calculate the Probability for the G and X Test Statistic
PG <- (1-pchisq(G,df))
Xsq <- sum(((O-E)^2)/E)
PX <- (1-pchisq(Xsq,df))
> PX
[1] 0.1799545
> df
[1] 5
# therefore apparent nest success is not dependant on year
```

Apparent Nest Success (control plots**2012-2013)***ctrl*

	successful	failed
2012	10	8
2013	4	9

fisher.test(ctrl)

p-value = 0.2749, therefore no difference

in success/fail in 2012/2013

Apparent Nest Success (treatment vs**control 2013)***plot*

	Successful	failed
control	2	7
treatment	2	2

fisher.test(plot)

p-value = 0.5301, therefore no difference

in success/fail in treatment vs control

Kaplan-Meier Survival Analysis**Control 2012-2013***main.ctrl (head)*

nest.i	start.i	stop.i	time.i	event.i	year.i	plot.i	CID.i
AN01	31	33	20	3	yr1	ctrl	early
AN02	34	36	20	3	yr1	ctrl	middle
AN03	50	NA	35	0	yr1	ctrl	early
AN04	50	NA	30	0	yr1	ctrl	early
AN05	31	33	9	3	yr1	ctrl	late
AN06	43	45	27	3	yr1	ctrl	late

Survival Curve (sample code)

surv1 <- survfit(Surv(main.ctrl\$start.i, main.ctrl\$stop.i, type="interval2")~main.ctrl\$year.i)

summary(surv1)

Call: survfit(formula = Surv(main.ctrl\$start.i, main.ctrl\$stop.i, type = "interval2") ~

main.ctrl\$year.i)

```
main.ctrl$year.i=yr1
```

time	n.risk	n.event	survival	std.err	Lower CI	Upper CI
29	11	1	0.909	0.0867	0.7541	1
32	10	2	0.727	0.1343	0.5064	1
35	8	1	0.636	0.145	0.4071	0.995
44	7	2	0.455	0.1501	0.2379	0.868
65	2	1	0.227	0.1774	0.0492	1

```
main.ctrl$year.i=yr2
```

time	n.risk	n.event	survival	std.err	Lower CI	Upper CI
35	7	2	0.714	0.171	0.4471	1
44	5	1	0.571	0.187	0.3008	1
47	4	1	0.429	0.187	0.1822	1
50	3	1	0.286	0.171	0.0886	0.922

Asymptotic Logrank Test (sample code)

```
ictest(Surv(main.ctrl$start.i, main.ctrl$stop.i, type="interval2")~main.ctrl$year.i,
scores="logrank1")
```

Exact Logrank two-sample test (permutation form), Sun's scores

```
data: Surv(main.ctrl$start.i, main.ctrl$stop.i, type = "interval2") by main.ctrl$year.i
```

```
p-value = 0.9625
```

```
alternative hypothesis: survival distributions not equal
```

```
n Score Statistic*
```

```
main.ctrl$year.i=yr1 11 -0.09313730
```

```
main.ctrl$year.i=yr2 7 0.09313719
```

* like Obs-Exp, positive implies earlier failures than expected

```
# p-value = 0.9625, therefore no difference in survival curves between 2012/2013
```

Plotting Survival Curves using Ggplot2 (sample code)**#ggplot with date, year (just ctrl)**

```
ctrl.survframe <- createSurvivalFrame(survfit(Surv(main.ctrl$start.i, main.ctrl$stop.i,  
type="interval2")~main.ctrl$year.i))  
  
ctplot <- qplot_survival(ctrl.survframe, TRUE, 1)  
  
ctplot <- ctplot + theme(legend.direction = 'vertical', legend.position = c(0.85,0.9))  
  
ctplot <- ctplot + theme(legend.background = element_rect(fill="white", size=0.5,  
linetype="solid", color="black"))  
  
ctplot <- ctplot + theme(panel.background = element_blank())  
  
ctplot <- ctplot + theme(panel.grid.major = element_blank())  
  
ctplot <- ctplot + theme(panel.grid.minor = element_blank())  
  
ctplot <- ctplot + theme(legend.key = element_blank())  
  
ctplot <- ctplot + theme(axis.line = element_line())  
  
ctplot <- ctplot + xlab("Date (May 1st = 1)") + ylab("Nest Survival")  
  
ctplot <- ctplot + theme(legend.title= element_blank())  
  
ctplot <- ctplot + theme(axis.text.x = element_text(colour="black"))  
  
ctplot <- ctplot + theme(axis.text.y = element_text(colour="black"))  
  
ctplot <- ctplot + scale_color_manual(labels = c("2012 Survival", "2013 Survival"),  
values=c("limegreen", "darkgreen"))  
  
print(ctplot)
```

Logistic Exposure Analysis*main.exp (head)*

nest.m	exp.m	age.m	event.m	year.m	treat.m	factor.m	CID.m	group.m
AN01	3	21	1	yr1	ctrl	ctrl_1	-3	early
AN02	3	22	1	yr1	ctrl	ctrl_1	0	middle
AN03	2	34	0	yr1	ctrl	ctrl_1	-4	early
AN04	2.5	29	0	yr1	ctrl	ctrl_1	-2	early
AN05	5	8	1	yr1	ctrl	ctrl_1	1	late
AN06	2	27	1	yr1	ctrl	ctrl_1	1	late

AIC and Model Selection (sample code): Ctrl plots in pooled years with CID and date

library(AICcmodavg)

Cand.models <- list()

```
Cand.models[[1]] <- glm(main.exp.c$event.m~main.exp.c$CID.m * main.exp.c$date.m,
family=binomial(logexp(days=main.exp.c$exp.m)))
```

```
Cand.models[[2]] <- glm(main.exp.c$event.m~main.exp.c$CID.m + main.exp.c$date.m,
family=binomial(logexp(days=main.exp.c$exp.m)))
```

```
Cand.models[[3]] <- glm(main.exp.c$event.m~main.exp.c$date.m,
family=binomial(logexp(days=main.exp.c$exp.m)))
```

```
Cand.models[[4]] <- glm(main.exp.c$event.m~main.exp.c$CID.m,
family=binomial(logexp(days=main.exp.c$exp.m)))
```

```
Cand.models[[5]] <- glm(main.exp.c$event.m~1,
family=binomial(logexp(days=main.exp.c$exp.m)))
```

modnames <- paste("mod", 1:length(Cand.models), sep = " ")

aictab(cand.set=Cand.models, modnames = modnames, sort= TRUE)

Model selection based on AICc :

Model #	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
5	1	27.52	0	0.58	0.58	-12.64
4	2	30.02	2.5	0.16	0.74	-12.64
3	2	30.03	2.51	0.16	0.9	-12.64
1	4	32.22	4.7	0.05	0.96	-10.68
2	3	32.81	5.29	0.04	1	-12.61

based on AIC values, weights, and variables of interest, Candidate model # 3 is the best model.

Creating Logistic Exposure Plot (sample code)

```
# predictor: date, pooled years (ctrl plots)#
main.logexp2 <- glm(main.exp.c$event.m~main.exp.c$date.m,
family=binomial(logexp(days=main.exp.c$age.m)))

# set up new table to hold CID at mean

newdata2 <- main.exp.c
newdata2$CID.m <- mean(main.exp.c$CID.m)

newdata2 <- cbind(newdata2, predict(main.logexp2, newdata2, type="response", se.fit=TRUE))

newdata2 <- within(newdata2, {
  DNS <- fit
  LL <- fit - 1.96 * se.fit
  UL <- fit + 1.96 * se.fit })

plot(newdata2$date.m, newdata2$DNS, xlab="Date (May 1st=1)", ylab="Daily Nest Survival",
ylim=c(-0.1,1.2), las=1, pch=16)
```

fit main curve to points

```
x <- newdata2$date.m
y <- newdata2$DNS
lo <- loess(y~x)
x1 <- seq(min(x),max(x), (max(x) - min(x))/1000)
lines(x1, predict(lo,x1), lty=1)
```

fit upper CI curve

```
x <- newdata2$date.m
y <- newdata2$UL
lo <- loess(y~x)
x1 <- seq(min(x),max(x), (max(x) - min(x))/1000)
lines(x1, predict(lo,x1), lty=2)
```

fit lower CI curve

```
x <- newdata2$date.m
y <- newdata2$LL
lo <- loess(y~x)
x1 <- seq(min(x),max(x), (max(x) - min(x))/1000)
lines(x1, predict(lo,x1), lty=2)
```