A Change Can Do You Good? The Adaptability of Three Forest Birds to the Moose-browsed Grassland of Cape Breton Highlands National Park

by

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DEDICATION PAGE

I would like to dedicate this thesis to the birds, plants, and moose that call North Mountain home.

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Abstract

Bird Studies Canada (BSC) found that Blue-headed Vireo (BHVI) (*Vireo solitarius*), Yellow-bellied (YBFL) (*Empidonax flaviventris*), and Black-and-white Warbler (BAWW) *(Mniotilta varia*) showed no preference for forest amongst the moose-browsed grassland of North Mountain, Cape Breton Highlands National Park (CBHNP). We used point-counts and forest vegetation metrics from remote sensing data to test whether expanding the scale of vegetation characterization around point locations would increase the association of these songbirds to forest. We used song modes to determine BAWW pairing success in the grassland as well as vegetation sampling to identify differences between paired and unpaired territories. Results showed more unpaired males, weak evidence of differences between the song modes between paired and unpaired BAWW males, as well as no differences in habitat quality. BHVI and BAWW showed seven significant relationships to forest in some years, but overall there was high between-year variation for all the three species.

LIST OF ABBREVIATIONS USED

AMRE	American Redstart
ANOVA	Analysis of Variance
BAWW	Black-and-white Warbler
BBS	Breeding Bird Survey
BHVI	Blue-headed Vireo
BSC	Bird Studies Canada
BTBW	Black-throated Blue Warbler
CBHNP	Cape Breton Highlands National Park
MOWA	Mourning Warbler
P	Paired
P/A	Presence and absence
UP	Unpaired
YBFL	Yellow-bellied Flycatcher

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CHAPTER 1   INTRODUCTION

Amidst the cliffs, beaches, and small communities of Cape Breton, something mysterious was happening in the trees. In the 1970s, a massive outbreak of small insects, the spruce budworm (*Choristoneura fumiferana*) hit with unusual ferocity, killing large portions of the boreal forest species (MacLean, 1988; Franklin, 2013). Just as leaders shift in politics, so too do the dominant species of ecosystems. Starting in the 1970s, the spruce budworm killed off balsam fir (*Abies balsamea*), and in its place grass, alder, fern ecosystems thrived (Franklin, 2013). Moose (*Alces alces* ssp. *andersoni*) like to eat balsam fir in addition to white birch (*Betula papyrifera*). The introduced moose population on Cape Breton has no effective predators, as wolves (*Canis lupus*) had been extirpated by early human settlers (Pulsifer and Nette, 1995). This lack of predation coupled with an overabundance of food and little concern over getting eaten, the moose population flourished (Bridgland et al., 2007). Over the next decades (1980s-present), moose browsing impacted 11% of Cape Breton Highlands National Park (CBHNP), to the extent that regrowth of the boreal forest was curtailed and *Calamagrostis*-dominated grasslands were a new steady-state (Basquil and Thompson, 1996). In the place of spruce (*Picea* spp.) and fir grew extensive savannah-like grasslands, dense alder thickets, and fields of ferns - a stark contrast from a typical boreal forest (Franklin et al., 2015). This patchwork of open areas with remnant forest is most obvious on North Mountain, in CBHNP.

Parks Canada managers, with the goal of protecting the boreal forest within the park, saw this transformation to grassland and shrub thicket as a problem. They began planting boreal trees in nearby French Mountain and culling moose to protect the habitat of species requiring mature boreal forest to breed, feed, and shelter, such as American marten (*Martes americana*), lynx (*Lynx canadensis*), and Bicknell's thrush (*Catharus bicknelli*) (Smith et al., 2015). Field surveys were conducted by Bird Studies Canada (BSC) to try to understand how diversity and abundance of songbirds were responding to these landscape changes (Campbell, 2015).

BSC remained uncertain about whether some forest birds would use this new environment of grass, dotted with sparse trees. It was clear some forest birds had declined such as Swainson's Thrush (*Catharus ustulatus*), which are selective about nesting at specific heights but grassland species such as Lincoln's Sparrows (*Melospiza lincolnii*) were now abundant in these grassy semi-treed areas. Species with preference for grassland and were able to build their nests on the ground or in shrubs and take advantage of the new insects in these habitats (Smith et al., 2015). For a moment it seemed intuitive - breeding grassland birds had moved into the grasslands of North Mountain, while forest songbirds had declined due to forest loss. Historical Breeding Bird Survey data from the 1970s onward suggest generally that Blue-headed Vireo (BHVI) (*Vireo solitaries*) have declined on North Mountain while Yellow-bellied (YBFL) (*Empidonax flaviventris*), and Black-and-white Warbler (BAWW) *(Mniotilta varia*) have increased (Pardieck et al., 2017). However, BSC point-counts showed uncertainty about the current habitat preferences of BHVI, BAWW, and YBFL (Campbell, 2015). The question arose: are these birds adopting different approaches to better use the mix of grassland and thicket habitats in addition to their treed environment? Or was the lack of habitat associations for these species simply due to the inadequate scale of the BSC study.

There is evidence that the selected species all use small openings, and forested habitat at the edge of a wetland or alder boundary (Gross and Lowther, 2001; Kricher, 2014; Morton and James, 2014). Yet using these edge habitats comes with a risk, as nesting in edge habitat makes their young more vulnerable to predators (Gates and Gysel, 1978). If the grasslands, thickets, and abundant edge habitats of North Mountain are not ideal it may be that the populations in these habitats consist of fewer and less-fit individuals (Van Horne, 1983).

There are substantial gaps in the scientific literature on how BAWW breeding behaviour differs in a fragmented landscape (Kricher, 2014). Compared to other forest species, BAWWs have inconsistent habitat preferences, although it is unclear whether there are regionally-specific patterns in their habitat-choice; and exhibit diverse nesting and foraging strategies (Rudnicky and Hunter, 1993). It is unclear how much forest is “good enough” for BAWW. Small islands of trees may be useful but likely only when they are beside larger tracts of forest.

Some of the uncertainties about bird distribution in this fragmented habitat can be explored by using spatial data, while we may be able to determine if there are differences in the distribution between paired versus unpaired males. One way to test if BAWW are paired is interpreting their songs. Pushing the boundaries of bird-song knowledge may help avian ecologists to see how the birds' ability to find a mate is affected by this newly patchy landscape (Staicer, 1989). Are there characteristics unique to territories of males with mates relative to those without? Can we hear whether a male bird has a mate purely from the types of song he sings (Spector, 1992)?

This study aims to address these knowledge gaps by using field-based bird and vegetation surveys, song interpretation, and spatial analysis, focusing on North Mountain. The first objective is to test whether we can consistently distinguish a male BAWWs pairing status using his song. The second objective is to describe the vegetation characteristics unique to the territories of paired or unpaired BAWW males in fragmented habitats. This research project provides a baseline study of BAWW territory establishment and pairing status from song types in the North Mountain plateau.

Our second objective was to examine the relationship between YBFL, BHVI and BAWW presence and absence and the amount of forest nearby. To do this we used multi-year point-counts and obtained forest vegetation metrics from remote sensing data, (SPOT5 (2013) imagery). We hypothesized that expanding the scale of vegetation characterization around point locations from 100 to 140 m would increase the likelihood of BAWW, YBFL, and BHVI occurrence at points with a higher proportion of forest at a 140 m radius.

CHAPTER 2 FOUNDATIONAL CONCEPTS

2.1 Thesis Layout & Ideological Approach

The thesis is organized into five main chapters, beginning with an introduction to the thesis (Chapter 1). Chapter two explores the foundational concepts most relevant to the thesis topic including: boreal forest community ecology, implications of spatial scale for bird-habitat relationships, adaptability of passerines to changes in breeding habitat, and Cape Breton Highlands National park fragmentation due to moose. A global methods section (Chapter 3) follows the foundation concepts and covers broad sampling techniques for assessing breeding birds and their habitat, description of our study area, field methods of data collection, and data analysis sections. Key findings are discussed in the format of two academic journal manuscripts: the first (Chapter 4) on song mode use in determining pairing status in avian ecology, and the second (Chapter 5) on species-habitat associations. The thesis conclusion (Chapter 6) summarizes key messages (Chapter 1-5). The final section contains a list of literature cited and appendices.

When field-studies are communicated in creative ways, the knowledge becomes more transferable to communities (Schmidly, 2005), a research quality that is imperative in polarized topics such as hyper-abundant moose in CBHNP. A common thread in the thesis components is a natural history approach. In studies such as ours that work at a macro-level, the findings are more easily relayed to the public compared to micro-level research. In Cape Breton towns and cities, boreal forest ecosystem dynamics and management (moose cull, tree planting) within the park are relatively well known and polarizing topics; living in the community for a month we observed active community-groups against the moose cull based on ethical concern, fear of economic loss as hunting guides and economic concern and resistance by some residents who instead supported a hands-off approach to wildlife management in the park. Although communities on the island are updated from CBHNP about moose browse monitoring and the importance of planting trees, this information is likely less well received by the public because the source has ordered the politically-charged moose cull.

This project aims to challenge perspectives that view the grassland as a problem. CBHNP is right to be concerned about the loss of boreal forest threatening forest species in the park. In some cases, the changing boreal forest has also created novel extensive alder and fern ecosystems that, unlike the savannah, do provide vegetation structure for YBFL, BHVI, and BAWW as this study demonstrates empirically. Northern Cape Breton communities would find this research familiar and relevant as it is based in their backyards. People may also more likely openly receive the findings since the work comes from an independent graduate thesis

2.1.1 A Natural History Approach

When the term natural history was conceived, ‘history’ referred to ‘description’ (Schmidly, 2005). It was a way of “revealing and explaining regularities of nature” (Grant, 2004 in Schmidly, 2005, p.4), conditions which First Nations people have long observed. Understanding the patterns of organisms in their environments was the earliest form of studying wildlife (Bartholomew, 1986; Schmidly, 2005). Currently, wildlife studies currently use sophisticated modelling, remote sensing, and spatial statistics, often relegating natural-history-based studies to an inferior status. Although technological applications are crucial to large-scale theories and predictive science, the value of empirical field-based evidence is often undervalued even though it is the living proof of observations (Noss, 1996).

Natural history has melded with technological applications which take observations of organisms outdoors and create enormous databases for current ‘big science’(Noss, 1996). Whether in backyards or national parks, the focus of documenting sightings is an enjoyable pastime and a method of integrating smart-phone technology with the outdoors. Apart from recreational species identification, research in ecology could do better to engage in less data-mining and use natural history to inform biologically relevant and unique hypotheses (Greene, 2005). “Natural history tells us unequivocally that we are foolish to look for general answers to specific questions about how organisms perform” (Bartholomew, 1986, p. 325).

Seeking generalized and reductionist answers to bird-habitat relationships results in misleading conclusions that thwart our understanding of a population’s ability to adapt but asking where three forest songbird species breed in a fragmented moose-browsed grassland is complex and has a basis in natural selection. The value and practice of rigorous outdoors behavioural observation of a species are lacking in conservation biology where species abundance and diversity are more often used as the overarching indication of a species wellbeing (Sutherland, 1998). In short-term field studies, obvious variation may be unclear, but we should be unsurprised as the small changes in an organism`s territory components, or any small habitat-induced behavioural changes, are the essence of natural selection (Bartholomew, 1986).

Despite the steep decline of natural history in academia (Noss, 1996), this research takes a more descriptive approach to analyzing case-specific empirical data rather than focusing on making generalized predictions about selected species habitat choice. Knowledge of a species' natural history is critical to determining if statistically significant differences are biologically relevant. Furthermore, the spatial data and the biological statistics in this study remain interpreted in the context of what was observed in the field and the literature about confounding aspects of bird behaviour.

In this study we used a scientific approach grounded in natural history; in other words, results statistically significant were not automatically relevant without reference to a species' natural history. The inconsistent habitat requirements of our focal species meant it would be unreliable to make claims based on predictive models. For example, a bird's preference for non-coniferous forest may only be relevant when coniferous forest is absent. We recognize that generalist songbirds are represented in contrary ways in the bird-habitat literature, where one study indicates a preference for edge habitat and another indicates an avoidance. We accept that the term *forest* includes a continuum of treed and semi-treed openings and wetlands, while the term *treed* naturally excludes the non-treed components of a forest. The characterization of boreal forest in this study comes from remote sensing data which has defined 2.5 m x 2.5 m cells based on their dominant cover type as treed or alder. In the context of moose browse, which has specifically reduced fir and spruce trees, not semi-treed wetlands, we have used the terms forest and treed area interchangeablyOur approach asserts that identifying key habitat variables as solely explaining species preference is unreasonable in two respects: first, the focus species have generalist foraging and nesting preferences; second, their presence is linked to inter-and intra-species communications and predator dynamics, which are unaccounted for in the scope of this study. Field studies such as ours help build judgement and empathy gained from trudging through field and forest, experience which allows for more holistic and realistic interpretation of data and informs management (Noss, 1996a). Although "some would call this experience-based conservatism emotional and biased; I would call it prudent and precautionary" (Noss, 1996a, p.6).

2.2 Boreal Forest Community Ecology

2.2.1 Disturbance agents: climate change, insect outbreaks, and herbivory

Climate change alters the patterns of natural succession, creating intense forest fires, insect outbreaks in the boreal forest (Kurz et al., 1995). These disturbances are the foundation of forest succession, which may alter and transform boreal ecosystems in sometimes unpredictable ways. The result of these forces is the creation of more novel conditions to which boreal species must further adapt (Chapin et al., 2000). The result of more extreme natural disturbances such as wind, fire, insects, and herbivore browsing have led ecologists to conclude that boreal species must have more plasticity than temperate species (Cardinal et al., 2012). Forest composition is likely to change as tree species range limits move northward; these range shifts can transform boreal ecosystems to mixedwoods, heathland, or shrub landscapes (Pureswaran et al., 2015). As anthropogenic-caused climate changes increase, these biome changes will continue.

A key aspect of community ecology is the relationship between insect outbreaks, large mammal herbivory, and the affected tree communities. After the insect-affected trees die and new young trees and shrubs take over, the plentiful browse benefits herbivores (Persson et al., 2000). Moose are a selective force in the natural succession of boreal and taiga landscapes (McInnes et al., 1992; Kielland and Byrant, 1998). Moose browsing creates clearings in canopy and alters hydrological regimes, and these new conditions support shade-intolerant shrubs like speckled alder (*Alnus incana)* (Newton et al., 1989). Speckled alder adapts to moderate and temporary flooding, a competitive advantage over other early successional plants. The reproductive strategy of alders involves saplings growing from root masses, also contributing to its successful dense thickets (Tilton and Bernard, 1975). In the Copper River Watershed of Alaska, moose browsing on willow species resulted in the shrub Sitka alder (*Alnus viridis* ssp. *sinuate*) expanding throughout the area by competitive advantage (Hammersmark, 2002).

By feeding on the plants moose can be deemed a keystone species in many ecosystems as they determine the succession of vegetation (Newton et al., 1989; Persson et al. 2000); but the effects of browsing also reduces the amount Mycorrhizal fungi (Rossow et al., 1997). Mycorrhizal fungi require nutrients in the form of carbohydrates from the leaves of plants, when moose also feed on the plant leaves there is less available for the fungi. As a result, the Mycorrhizal fungi are less abundant on trees browsed by moose. Thus, a positive feedback loop is created where the trees are not only stressed by the loss of foliage by moose browsing, but also the decline of beneficial Mycorrhizal fungi that would normally contribute to the trees` uptake of carbon (Rossow et al., 1997). In a moose exclusion experiment in Tanana River, there was less mycorrhizal activity on the roots of willow, balsam fir, and poplar outside of the fenced area and more mycorrhizal activity inside the fenced-off area (Rossow et al., 1997). As such moose dictate pathways of biogeochemical cycling, although excluding litter decomposition rates or soil quality (Ellis et al., 2017).

2.2.2 Effects on passerine abundance, diversity, distribution

The effects of forestry, agriculture, and fire disturbance on boreal forest songbirds are well documented (Tewksbury et al., 1998; Dalley., 2003), but studies evaluating the impacts of intensive moose browsing upon the avian communities are limited (Matsuoka et al., 1997; Rae et al., 2014; Ellis et al., 2017). For example, moose-browsed areas may revert to vastly different landscape types, such as shifting from forest to grassland, and this heterogeneity creates more edge habitat. Browsing-created edges experience more depredation for ground-nesting birds, and thus nests in edge habitat have higher mortality in some species (Gates and Gysel, 1978; Poulin and Villard, 2011; Etterson et al., 2015). Other influences of moose on birds include trampling nests, moose mostly influence songbirds through their browsing activity which influences tree growth, litterfall biomass, and the associated invertebrate abundance.

Specialist species are more vulnerable to the altered landscape than generalist species. Forest songbirds such as Bicknell's thrush (*Catharus bicknelli*) require interior coniferous-dominated areas which may be compromised by the habitat changes caused by moose browsing (McKinnon et al., 2014). With fewer forest specialist species able to adapt to moose-browsed areas, overall species richness in an area may decline. Sometimes browsing can reduce the understory canopy of a forest. On Anticosti Island (Quebec, Canada), elevated levels of deer browsing and foraging have created openings in the canopy and have reduced the understory vegetation significantly (Cardinal et al., 2002). A loss of understory vegetation may reduce avian diversity by limiting the nesting and foraging options for shrub-forest species (Cardinal et al., 2012). However, generalist forest songbirds able to nest and forage in a variety of habitats may be resilient to the horizontal and vertical vegetation changes of browsed areas.

2.3 Implications of Spatial Scale for Bird-Habitat Relationships

2.3.1 Landscape Level

Moose browsing affects the boreal forest at a landscape level, though the impact to forest songbirds is contingent on the level used for evaluation (Toerrenta and Villard, 2017). Landscape-level studies often assess bird-habitat relationships based on species diversity (Drapeau et al., 2016). The diversity of breeding songbirds is more often determined by habitat at landscape levels (>1 km^2) rather than determined by the habitat composition of each individual defended territory (0.5-5.0 ha approximately) (Collins, 2014). This is also the level at which ecosystem shifts, such as from forest to grassland, may be examined, and how the numbers, configurations, and edges of these cover types affect birds (Villard and Metzger, 2014). Birds are mainly affected by landscape patch configuration if more than 30% of their habitat is considered fragmented (Andrén, 1994; Villard and Metzger, 2014). In cases where landscape patchiness is high, the layout of patches can alleviate some detrimental impacts associated with habitat loss (Villard and Metzger, 2014).

At a landscape level, researchers often use point-counts as a reliable method to estimate species abundance and diversity, especially for noticeable birds with modest territories (Toms et al., 2006), and for studies collecting vegetation data (Bibby et al*.,* 2000). To cover large areas, Breeding Bird Surveys (BBS) or Breeding Bird Atlas Surveys are used, though species observations are confounded by road disturbance (Bart et al., 1995). Breeding Bird Atlas Surveys use multiple indices of bird behaviour to confirm breeding success, sometimes without finding a nest. One index of breeding status used by researchers is observing adults carrying food; this behaviour is widely used, and often produces similar estimates of nesting success when compared with known nest sites (Vickery et al., 1992; Morgan et al., 2010).

2.3.2 Territory/ Community Level

When studying bird-habitat relationships, working at a territory level, often 0.5-8.0 ha for songbirds or at a home-range level of 4-12 ha (Collins, 2004), allows researchers to collect local vegetation data, in addition to conducting standard point-counts. This contributes to a better understanding of food availability and reproductive success. When assessing how well a species is thriving in a disturbed area, researchers may use the density of male songbird territories as an indicator of species habitat preferences (Whitaker et al., 2008). Higher densities of males in an area may indicate favourable vegetation characteristics and lower densities as less favourable habitat, intuitively (Whitaker et al., 2008). But the reality may be the exact opposite: Van Horne (1983) states that there will not be a higher density of birds in superior habitat "unless territory size is treated as a sampling unit, not individual species" (p.4). If a density estimate is based on counting the number of singing males at each point-count, as is widespread practice (Bibby et al., 2000), the researcher is bound to arrive at misleading conclusions, first, because unpaired males often have smaller, more tightly-packed territories than paired males, and second because unpaired 'floater' males sing more than paired males (Byers et al., 2015).

The quality of breeding habitat may be determined by the number of paired males with established territories (Dale, 2001). Those with successfully fledged young are believed to have had territories on high quality habitat, though this is dependent upon dominant tree type and bird species density (Morse, 1976). Paired males may also have lower fledgling success in poorer quality fragmented areas. However, fledgling success is best studied at the nest-site level, as it is more difficult to locate fledglings within a territory than it is around an immediate nest site. Still, we can assume that nesting is occurring when a pair is observed foraging closely, carrying nesting material, or, in the case of warblers, singing particular songs (Staicer, 1989).

The degree of fragmentation and scarcity of preferred cover types can affect the territory size. Territory size is a factor in whether a bird successfully finds a mate. Often the fittest males are the most experienced breeders in the area and arrive on the breeding territory earlier than younger less-experienced males (Byers et al., 2015). Arriving first, these males determine which areas have high habitat quality and defend large portions of the quality areas as their territory to attract mates, and defend against other males by competitive exclusion (Van Horne, 1983). These large territories are often spread out inherently because of their size, leaving the leftover areas for males arriving late, immigrants, and young inexperienced breeders (Van Horne, 1983; Byers et al., 2015).

Forest songbirds with smaller territories and a high degree of fragmentation may experience decreased pairing success (Villard et al. 1993) and fledgling success (Darveau et al., 1995; Dale, 2001). The density of territories and the number of nearby neighbouring males affect the frequency of interactions between male birds. There is the potential for more disputes in areas with food shortages as males compete for prime foraging at the edges of their territories (Spector, 1992). Studies which accurately map territories and measure territory spacing are advantageous in deciphering how territory size may be linked to reproductive success – although this remains a challenge for species with naturally variable territory sizes (Kricher, 2014).

2.3.3 Nest-site Level

For specialist species, such as woodpeckers, it may be important to measure vegetation immediately around the nest (Cunningham and Johnson, 2016). This nest-level assessment of habitat allows the researcher to get detailed information about crucial habitat features, for example the height and thickness of snags (standing deadwood) for woodpeckers. Such detailed information may be more difficult to obtain from remote sensing data, and therefore nest-site vegetation is often measured in the field.

In poorer quality habitat, birds may still pair and hatch eggs, but their chicks may not survive (Corbani et al., 2014). However, when the nest site is known we can also study the evolutionary processes of parent-chick behaviour and nest-calls. For conservation purposes, the nest level also allows researchers to better understand specific causes of changing bird populations e.g. whether mortality is occurring at the nest-building stage, hatchling stage, or fledgling stage. As one cause of mortality is nest predation, when a nest site is known, it may be possible for the researcher to determine, sometimes based on the condition of depredated eggs, the type of nest predator (Thompson, 2007).

The nest-site level is a difficult one at which to obtain data for songbirds, as finding enough nests for a reasonable sample size is enormously time-consuming (Collins, 2004). Finding nests may not always be necessary: one study that sampled the site characteristics of 0.04 ha nest sites and non-nest sites within a single BAWW territory found that slope was the only habitat difference (Collins, 2004). BAWW are generalists when choosing nest sites, and as such, researchers may make inferences from habitat data collected at a territory level compared to forest specialists where researchers may be required to sample the nest site. For generalist bird species, vegetation sampling might be favourable at a territory level as it does not require finding a nest and yields similar vegetation characteristics. Overall, questions concerning the breeding success of birds best operate with a nest-site component; however, field-season logistics often prevent researchers from finding nests so indirect indices of breeding success such as pairing status are used instead (Thompson, 2007).

2.4 Adaptability of Passerines to Changes in Breeding Habitat

The obstacles to successful reproduction are plentiful and often compounding (Collins, 2004). A forest songbird's adaptability to habitat change can be conceptualized in two main ways: adult survival and breeding success. An area may provide enough for adults to survive but not enough for them to feed and protect their young. Even if quality forage is somewhat limited in a male's territory, one could still expect his young to be nourished assuming that good foraging resources are reasonably within his undefended home range. However, his home range may overlap with another songbird’s territory, limiting his access to foraging, especially if their foraging niches overlap. Furthermore, if a male must travel too far for regular foraging, his fitness may decline which would affect his ability to raise the young.

2.4.1 Breeding Behaviour

To understand whether a songbird population is at risk from the habitat fragmentation of its breeding site, researchers may study pairing success, nesting attempts, hatching success, and fledgling success. For songbirds such as warblers, pairing success is a reasonable index since nests are difficult to locate (Collins, 2004). Measuring pairing success for songbirds involves noting the presence of a female and male foraging closely, making soft call notes to each other - visual confirmation of copulation is rare. However, for species with more-conspicuous nests, marking the success of egg-laying, egg-hatching, and finally fledgling success delivers sequentially stronger indicators of population health. If songbirds can successfully raise their young, we can assume the habitat was of good enough quality. In one field study, Black-throated Blue Warblers (*Setophaga caerulescens*) (BTBW) had unexpectedly high pairing rates in edge habitat which was later found to have high invertebrate density (Harris and Reed, 2002).

Low-quality habitat is associated with unpaired males, which are not contributing to the population viability since they cannot reproduce successfully (Van Horne, 1983). Yet defining the role of unpaired males in the breeding success of a population is complex. One role of unpaired 'floater' males is their potential contribution to reproduction by engaging in extrapair copulations with females (Whitaker et al., 2008); their other contribution is occasionally assisting in feeding young, in the case of BAWW (Collins, 2004). It is suggested that females mate with multiple males to maximize paternal help (Cant and Reeve, 2002) although instances of cooperative breeding remain rare (Collins, 2004).

2.4.2 Foraging Behaviour

Changes in the vegetation composition of breeding habitat may create novel opportunities for some forest songbirds with diverse foraging abilities, but simultaneously may limit food availability for specialists. Forest species such as BAWW may be able to feed on diverse insects provided by non-forested areas such as grasslands, using alternative techniques such as 'hawking,' capturing insects in the air, and, as their preferred method, gleaning insects from bark (Kricher, 2014; Dunn and Garrett, 1997).

The types of food songbirds prioritize depend on the time of year and how the prey is caught. Most songbirds feed nutrient-rich insects to their young, leaving seeds and berries for fall and winter diets (Tufts, 1986). One type of habitat disturbance, moose herbivory, caused a decline in invertebrates in the boreal forests of Norway, resulting in insectivorous passerines foraging less and fledging fewer young (Mathisen et al., 2011). In contrast, aerial insectivores captured more insects and exhibited higher breeding success in moose-rich habitat (Mathisen et al, 2011).

2.4.3 Song and Breeding Indication

If adaptation to disturbance is framed as surviving and establishing a territory and successfully finding a mate despite the presence of a perturbation, much can be uncovered by paying attention to the types of songs sung by male warblers. For centuries, researchers exhaustively described bird behaviour, diet, and interspecies interactions for common species (Chisholm and Leonard, 2008), but relatively few paid attention to the meaning of bird song. Unfolding the meaning from a bird's song is an untapped resource to understand life-history traits such as pairing status.

Analyzing birds with complex songs such as paruline species offers an effective method of determining interspecies relationships (Demko et al., 2016).

Singing rates may also indicate pairing status since unpaired birds sing more than paired birds (Byers et al., 2015). However, singing rates are influenced by any combination of time of day, proximity to the nest (Weary et al., 1994), the quality of territory habitat (Manica et al., 2014), and proximity to a neighbour (Morse, 1967). For example, a male may sing less not because he has a mate, but because his territory is isolated from neighbours (Morse, 1967). Although singing rates may be associated with the ability of a male to successfully rear young, there is no confirmation of female preference for high-singing males; extra-pair copulations add a further layer of complexity as these extracurricular interactions often go undocumented before sunrise (Staicer et al., 2006).

Natural and experimental behavioural studies show that, in many cases, song types indicate whether a male is mated (Kroodsma et al. 1989; Staicer 1989, 1996; Spector 1991). Male birds sing increasingly complex songs or multiple song types to attract females (Byers et al., 2015); thus, male repertoire size is a trait influenced by pairing status (Reid et al., 2004). These complex songs in a male bird's repertoire may also be sung to defend their territories from other males. A-songs are repeated continually while B-songs are more likely sung in combination with A-songs or within-song variation called ‘serial mode’ (Spector, 1992). A-songs resonate for longer distances in repeat mode, so they are better at attracting a mate, while B-songs, less frequently repeated, may be for close neighbour interactions and communications once the male is paired, later into the breeding season (Wiley et al., 1994 in Woodward 1997). In addition to song complexity, the frequency of singing is postulated to indicate that a male has acquired a mate.

Using a combination of singing frequency data and song types accurately advertises pairing status in a variety of warblers including Grace’s Warbler *(Setophaga graciae*) (Staicer, 1989), Adelaide’s Warbler *(Setophaga adelaidae)* (Staicer, 1996), American Redstarts (*Setophaga ruticilla*) (Staicer et al., 2006), and BAWW (Tyler, 1953; Woodward, 1997; C. Staicer, *pers. comm.* November 20, 2016). Recognizing distinct song types is a more reliable method of determining pairing status than singing rates (Bourque and Villard, 2001; Harris and Reed, 2002). This is because an unpaired male holding a territory may defend its perimeter singing type-B songs (Byers et al., 2015) which are also sung for mates, and could be interpreted by the researcher as a paired male. Other factors affecting when a male sings type-B songs include the proximity to female (in CSWA, singing declines if the female is close) and its position in the territory, edge or middle (Lein, 1978). Efforts to understand the meaning of songs are also confounded to an extent by the individual variation in singing for some genera of warblers. Evidence shows that the type-A songs of one male were similar to a neighbouring male's type-B song (Spector, 1992).

2.4.3.1 BAWW song types and modes

Male BAWW's broad preferences for habitat and mysterious nest-site location conceal their mate and make observing their `personal` life a challenge. But by analyzing his songs, it may be possible to interpret whether he has a mate. In dense vegetation, utilizing song modes may allow researchers to potentially determine the pairing status of BAWW. Like other warblers including Chestnut-sided Warbler and Yellow Warbler (Kroodsma, 1981; Byers et al., 2015), BAWW sing two main songs for distinct purposes. The first is a high pitched squeaky wheel sound known as the A-song which is sung rapidly (repeat mode) to attract a mate and a slightly longer, quicker and more variable B-song is sung back and forth with the A-song (serial mode) in breeding territory when the female is present (Kroodsma, 1981). It is suggested males sing in repeat mode until he has found a mate, after which he may continue to sing in repeat mode, but far less than before and with a combination of serial mode singing (C. Staicer, pers. *comm*., 2017).

2.5 On the Edge: Cape Breton Highlands National Park and Fragmentation due to Moose

2.5.1 Herbivore and Predator Populations

When the abundance of one species is drastically altered, cascading effects can occur to other organisms inhabiting that ecosystem (Chapin et al., 2000). Cascading effects are top-down interactions, sometimes between predator and prey (Schmitz et al., 2000). Since the outbreak of spruce budworm diminished balsam fir in the 1970s, moose have become hyper-abundant in CBHNP (MacLean, 1988; Franklin, 2013). This one perturbation has had lasting cascade effects on flora and fauna (Smith et al., 2010).

2.5.2 Moose Browsing Following Budworm

The story of moose and their impacts on Cape Breton starts, for our purposes here, in the late 1940s when 18 individuals of the western sub-species (*A. a. andersoni)* were introduced (Pulsifer and Nette, 1995). In the 1970s a particularly intense outbreak of spruce budworm caused extreme spruce (*Picea* spp.) and fir mortality; approximately 87% mortality of balsam fir and 27% of white spruce (Franklin, 2013). Following the budworm outbreak, the boreal forest became dominated by young white birch (*Betula papyrifera*) and balsam fir, which are ideal moose winter browse (Basquil and Thompson, 1996; Franklin, 2013). With a burgeoning food resource and no natural predators, moose abundance increased from 66 animals in the 1970s to over 2000 individuals in the 2000s (Bridgland et al., 2007). Current park-wide densities are greater than an average of two moose per km^{22} based on aerial surveys in March, 2015 (M. Smith, *personal comm*., November, 2015). Moose herbivory, fecal waste, urination, and trampling cumulatively change the landscape of the park, altering nutrient cycling regimes, soil chemistry, and vegetation structure in the process (Suominen, 2008; Ellis et al., 2017). Foraging 'hot spots' exist throughout the park (Basquil and Thompson, 1996) such as North Mountain where forests have not regenerated. These areas, formerly dominated by spruce and fir, have transitioned to a savannah-like grassland, disrupting the ecological functioning and altering bird species composition in 11% of CBHNP (Suominen et al., 2008).

National Parks management policies in Canada support reducing hyper-abundant wildlife species where they threaten the ecological integrity of the park (Waithaka, 2008). CBHNP initiated the '*Bring Back the Boreal*' project in 2014 to restore the forest and conserve boreal species at risk due to the increasing grasslands. The project involves an annual moose cull in a 20 km^{22} area of savannah-like moose-impacted habitat on North Mountain during the period 2015-2017 (Smith et al., 2015). Following the cull, some trees are regenerating on North Mountain, but the landscape remains a patchy mosaic of ecosystems dominated by dense alder regrowth, grasses, and ferns.

2.5.3 Savannah and Alder Establishment

The moose-browsed savannah is spatially diverse. In some areas, wide-open fields contain scattered snags and low shrubs, which have avoided browsing by snow cover and the minimum browsing height of moose (Franklin et al., 2015). In other areas, cover types dramatically change from grass to valleys dominated by bracken fern (*Pteridium aquilinum*). Severely browsed balsam fir and white birch are prominent and downed deadwood is common, although covered by graminoids such as *Calamagrostis* sp. (Franklin et al., 2015). There are many tall un-browsed dead saplings where the grassland transitions to forest. In these edges, speckled alder and herbaceous plant species richness is lower than in forest patches (Franklin et al., 2015). Although the grassland supports many ecotypes and associated species, CBHNP aims to plant trees and remove moose with hopes of bringing back the forest. Many areas that used to be dominated by spruce, balsam fir, and birch have been replaced by alder which has a competitive advantage in areas with low nutrients. The expansion of alders has implications on future tree regeneration of North Mountain. Moose browsing creates clearings in the canopy and alters hydrological regimes, and these new conditions support shade-intolerant shrubs like speckled alder (Newton et al., 1989).

On North Mountain, moose do not browse alders, only mountain ash (*Sorbus americana*) and willow (*Salix* spp*.)* growing at the edges of alder thickets (J. Bridgland, *pers. comm*., September 2017). Therefore, by way of being unpalatable to moose, possible conifers growing under alder thickets may be protected from browsing. Although alder thickets are seemingly homogeneous, there are cases in the French Alps where shade- and wet-tolerant saplings were observed growing under green alders (*Alnus viridis*), though only where alders made up less than 50% of the shrub canopy (Anthelme et al., 2001). At North Mountain, this pattern is as yet un-documented.

Overall the dynamics and trajectory of alder expansion on North Mountain are uncertain (C.D'Orsay, Parks Canada *pers. comm.,* October, 2017). A park ecologist formerly from CBHNP predicts that as moose continue browsing, the grass areas will continue to grow and the shrub species will decline (M. Smith, *pers. comm.,* 2016). CBHNP long-term vegetation monitoring of browsing effects on the boreal forest exclude alder swales as moose avoid browsing this shrub. Since alders are shade-intolerant, they will not expand into forest edges. Although spruce budworm densities have been slowly increasing in the Maritimes since 2006 (Pureswarna, et al., 2016), moose may have prevented the insects from causing another outbreak on North Mountain. The smaller stands of forest remaining are not ideal as spruce budworm thrives mostly in large continuous stands of mature Balsam Fir.

The wide bands of alders and ferns along the forest island edges on North Mountain still provide habitat for forest songbird species. Alder thickets provide different food options for songbird species adapted to foraging on conifer-dominated forest (Anthelme et al., 2001). In one study, arthropods (*i.e.,* Hemiptera, Coleoptera, Hymenoptera, and Orthoptera) decreased with the expansion of alder (Anthelme et al., 2001). Yet overall invertebrates are usually in high densities in alder thickets because of the high productivity of these areas due to the ability of alder to fix nitrogen. Fields of tall ferns and enormous alder thickets are more common in the temperate forests on the western coast of Canada, but this type of regrowth is rare in the eastern boreal forest (Cardinal et al., 2012). Where ungulate browsing in other areas homogenizes the understory (Cardinal et al., 2012), North Mountain has productive tall shrubs and ferns, both with complex structure where some low-story songbirds forage, shelter, and nest. However, the forest patches are not as complex with little undergrowth and most trees at canopy height (Campbell, 2015).

2.5.4 Putative Effects on Passerine Distribution

Open-woodland songbirds such as Mourning Warbler (MOWA), which feed on invertebrates in the grassland (Cox, 1960), were abundant on North Mountain (Campbell, 2014). Though the abundance of some forest specialist songbirds has declined in the savannah (Campbell, 2015), new opportunities exist for adaptable species with diverse foraging abilities and a preference for ground/shrub nest sites (Tufts, 1986; Dunn and Garrett, 1997). However, with only coarse-level habitat information (Campbell, 2015), it is unclear whether forest songbirds are using primarily alder thickets and tree islands within the savannah mosaic or foraging in areas dominated by sparse trees and grass.

Three forest songbirds - YBFL, BAWW, and BHVI - were not associated with either treed or grassland cover types in the BSC analysis of North Mountain (grassland-dominated) and French Mountain (forest-dominated) (Campbell, 2015). Explanations for BHVI and YBFL may be due to their wide-ranging habitat choice and the inability of local-level habitat analysis to detect differences. It is somewhat more reasonable for BAWW to adapt to open areas since they also showed no preferences for forest in a study of the moose-browsed habitat of Gros Morne National Park (Rae et al., 2014). Trends in declining forest songbirds but stable forest generalist and shrub-nesting songbird abundance are also found in the moose-browsed areas of Gros Morne National Park. There, hyper-abundant moose populations also have reduced forests to shrub-lands, impeding Black-throated Green Warbler (BTGW) and other canopy-nesters, but benefitting early-successional songbirds such as Mourning Warblers (MOWA) (Bergerud and Manuel, 1968; Rae et al., 2014). Whereas Gros Morne moose-browsed areas resulted in more shrub species than grasslands, the North Mountain grasslands produced by hyper-abundant moose affect songbirds more dramatically as grassland dominates (Rae et al., 2014).

Looking to historical breeding bird surveys, we can see how YBFL, BAWW and BHVI were distributed on North Mountain in the past. Breeding bird survey (BBS) counts occurred at North Mountain starting in 1967. Despite gaps from 1974 to 1995, BBS data show that overall, BHVI and BAWW populations have grown while YBFL have declined since the 1960s. It should be noted that more BAWW may have been observed as a result of changes in observer detection as the surveyors across the years were different people (D. McCorquodale, Cape Breton University, pers. *comm*., December, 2017). It is anticipated that data collected on BAWW abundance is underestimated during the mid-1990s to 2002 (D. McCorquodale, Cape Breton University, pers. comm., December, 2017).

A more detailed habitat analysis is required to understand which areas YBFL, BAWW, and BHVI prefer. Appropriate variables may include the amount and composition of multiple habitat types, rather than associations between only woodland and grassland. There is also a need for a more comprehensive review of how forest songbird productivity is influenced by fragmentation, further delving into the implications of behaviour such as the pairing status of BAWWin North Mountain rather than occupancy.

2.5.5 Selected Species

YBFL, BHVI, and BAWW were among the 20 most observed species during the breeding season (2014-2015) on North Mountain by BSC (2015). These species were not correlated with either treed or grassland habitat types (Campbell, 2015). There are several reasons why BSC might have found no forest association with forest birds, two of which are: i) high variability in territory placement in patchy boreal habitat, and ii) variation in abundance of species at breeding grounds due to factors during their migration or in wintering habitat (Rappole and McDonald, 1994). Other reasons may be that a 5 min single visit is not long enough to capture all the species present, especially for less-conspicuous species (Petit et al., 1995). However, there is no indication in the literature that YBFL, BHVI, or BAWW have low detection rates. Overall it is difficult to predict habitat preferences for habitat generalists compared to those with specific niches (Dettmers et al., 2002). Seemingly, forest birds should be associated with forest but the wide range of factors, including predation and competition, make it difficult to isolate the effect of forest indices on bird distribution (Bucklin et al., 2015).

2.5.5.1 Yellow-bellied flycatcher

YBFLs breed throughout most of Canada, though they were the last discovered flycatcher due to their drab appearance and highly concealed nests (Gross and Lowther, 2001). The boreal forest songbird modelling project in Alberta found high densities of YBFL in closed-canopy young or mixed forest, and open mature mixed-wood (Boreal Avian Modelling Project, 2015). In lower densities, YBFLs preferred closed mature forest types. YBFL prefer to stay away from edges but may adapt to use strips of riparian forest as narrow as 60 m following clear-cuts (Darveau et al., 1995). YBFLs commonly breed near streams and in alder thickets (Gross and Lowther, 2001). This flycatcher seems to require an element of saturated landscape, such as poorly drained soils or wetlands, at the borders of their territory, as well as at least 50% conifer cover within (Gross and Lowther, 2001). YBFL show high site fidelity to their small territories, returning to past nest sites for several years, laying their eggs on dark vegetation (Gross and Lowther, 2001).

In the breeding season, YBFL males arrive on Cape Breton in early June (Sullivan et al., 2009). Species distribution maps show that a smaller part (11-30%) of the landscape is suitable habitat on North Mountain, while other proximate areas have 81-100% suitable habitat (Boreal Avian Modelling Project, 2015). These birds remain relatively unaffected by the impacts of forestry, since their habitat is often in forest types unfit for harvest (Gross and Lowther, 2001).

2.5.5.2 Blue-headed vireo

The generalist habitat preferences of BHVI makes predicting their breeding requirements difficult; single-visit point-counts showing presence and absence are likely unable to capture actual area-use. BHVI may be found at high elevations and in mid-late successional forests with well-developed understories, small clearings, and saturated zones (Morton and James, 2014). BHVIs use alder regrowth as part of their breeding habitat and as a result, populations may increase in areas experiencing regrowth following logging practices (Morton and James, 2014). However, their breeding range is known to be sensitive to logging disturbance as they require mature continuous forest types (Morton and James, 2014). Areas dominated by old-growth forests explain why breeding densities are relatively high, 0.76-1.00 males per ha (Boreal Avian Modelling Project, 2015). In northern Cape Breton, species distribution maps indicate 51-80% habitat suitability in this part of the island (Boreal Avian Modelling Project, 2015).

2.5.5.3 Black-and-white warbler

BAWWs use both open and closed canopy forest and nest at the base of trees, shrubs, or low branches. These warblers are somewhat resilient to forest fragmentation and use edge habitat when interior forest is not available (Rudnicki and Hunter, 1993). Yet conclusions about their adaptability to landscape change are inconsistent. Adults and young use habitat differently: BAWW fledglings consistently use large openings such as clear-cuts within hardwood forests whereas adults do not (Streby et al., 2011). This may indicate that fledglings use moose-browsed grasslands. Many factors, including a suite of interspecies interactions, reproductive biology, and climate factors, influence BAWW habitat use during the breeding season (Dalley, 2003).

In their northern breeding range, BAWW will use mid-successional forests but prefer mature forests with openings under the canopy cover and swamps (Kricher, 2014). A population in Texas showed strong association with “increasing numbers of tree species, vegetation height, percent canopy closure, percent of sapling hardwoods, large tree density, and number of shrub species” (Conner et al., 1983, p.44). Potentially their choice for diverse vegetation reflects their diverse foraging skills, as insect diversity is likely to be higher when multiple tree species co-habit an area. BAWWs forage on the inner branches and at the trunks of trees but are overall generalist foragers because they will glean insects off twigs, 90% of the time in one study (Paszkowski et al., 2004) but rarely catch them in the air (Kricher, 2014). These warblers also have adapted to nest in diverse places including moss or at the base of shrubs or small trees, and in twigs above wet or dry small clearings (Rudnicky and Hunter, 1993). Seemingly, BAWW are better adapted to changes in forest structure compared to other forest songbirds such as BTBW.

Where mature forest is present, BAWWs may avoid edges, choosing interior areas (Kricher, 2014). As little interior forest is present on North Mountain, BAWWs have made use of small forest fragments (Campbell, 2015) which appear on several point-count locations primarily composed of grassland. BAWWs on North Mountain are establishing territories in poorer quality habitat than individuals in interior forest. In one study, there were higher densities of BAWW territories (territory size = 2-6 ha) in highly fragmented habitat than in the nearby interior forest (Paszkowski et al., 2004; Kricher, 2014). Yet fledgling success was higher for territories in interior forest compared to territories in fragmented habitat. Therefore, breeding success may be affected by pairs in poorer-quality habitat (Van Horne, 1983). Although BAWW reproductive success may be lowered in fragmented habitat, the species still is seemingly adaptable as the resources of disturbed landscapes still support adult survival, as indicated by their site fidelity in fragmented habitat (Paszkowski et al., 2004).

BAWWs using the moose-browsed grassland in North Mountain are not only affected by disturbance from moose, but the site quality is also compounded by noise pollution. Following July 1, 2017 the Cabot Trail was fully re-surfaced adjacent to the North Mountain study area (C. D'Orsay, Parks Canada, *pers. comm.,* July 6 2017). The timing of road construction on the first week of July is during the nestling period, since BAWWs first arrive in Northern Cape Breton in late May (Sullivan et al., 2009). Therefore, intensive construction could have potentially caused adult BAWW to abandon their nests. Although songbirds such as golden-cheeked warbler seemed unaffected by road noise (Lackey et al., 2011) others including male ovenbirds had lower pairing success in areas close to noise pollution (Habib et al., 2007).

CHAPTER 3 METHODS

3.1 Overview: Methods of Sampling Breeding Birds and their Habitat

There are many methods of monitoring breeding birds and their habitats depending on the research question, the species of interest, and the corresponding scale of analysis. Many indices of breeding birds, such as walking transects, territory mapping, and nest monitoring, inform the type of habitat data being collected including home-range-level cover types (*e.g.* tree, grass), territory-level horizontal and vertical vegetation structure or foraging characteristics, and nest-site vegetation (e.g. height categories, species-level identification) (Bibby et al., 2000).

Often a researcher will use point-counts to obtain information data about the abundance and diversity of birds, especially for noticeable species with modest territories (Toms et al., 2006). Some point-count protocols have been established for almost a century (Bart et al., 1995). For example, the North American Breeding Bird Survey assesses coarse-level avian abundance along roadsides. Other long-term monitoring projects, such as the Atlas Bird Survey, cover large areas and data are collected not only about abundance and diversity but also signs that confirm breeding success. One Atlas index of breeding is food-carrying and this behaviour is widely used instead of intensive nest monitoring. In some cases, this index produces similar estimates of breeding when compared to known nest sites (Vickery et al., 1992; Morgan et al., 2010; Corbani et al., 2014).

To obtain a thorough perspective of a songbird population, it is appropriate to approach avian and habitat sampling through a variety of levels (landscape, territory/community, and nest site). This is crucial in the context of bird-habitat studies because "what you find depends on where you look" (Cunningham and Johnson, 2016). The appropriate uses, including benefits, and where relevant, limitations, are described below.

3.1.1 Landscape Level

The diversity of breeding songbirds is more often determined by habitat at landscape levels (>1 km) than by the habitat composition of their defended territory (0.5-8 ha approximately) (Collins, 2014; Drapeau et al., 2016). This is also the level at which ecosystem shifts, such as a transition from forest to grassland, may be examined, and how the amounts, configurations, and edges of these cover types affect birds (Villard and Metzger, 2014). Birds are primarily affected by landscape patch configuration if more than 20% of their habitat is considered fragmented (Villard and Metzger, 2014). In cases where landscape patchiness is high, the layout of patches can alleviate some detrimental impacts associated with habitat loss (Villard and Metzger, 2014).

3.1.2 Territory/ Community Level

When studying bird-habitat relationships, working at a territory level, often 0.5-8.0 ha for songbirds or at a home-range level of 4-12 ha (Collins, 2004), allows researchers to collect local vegetation data, in addition to conducting standard point-counts. This contributes to a better understanding of food availability and reproductive success. When assessing how well a species is thriving in a disturbed area, researchers may use the density of male songbird territories as an indicator of species habitat preferences (Whitaker, Taylor, Warkentin, 2008). Higher densities of males in an area may indicate favourable vegetation characteristics and lower densities as less favourable habitat, intuitively (Whitaker, Taylor, Warkentin, 2008). However, the reality may be the exact opposite according to Van Horne (1983), who states there will not be a higher density of birds in superior habitat "unless territory size is treated as a sampling unit, not individual species" (p.4). If a density estimate is based on counting the number of singing males at each point-count, as is widespread practice (Bibby et al., 2000), the researcher is likely to arrive at misleading conclusions. This is because, first, unpaired males often have smaller, more tightly-packed territories than paired males and second, unpaired 'floater' males sing more than paired males (Byers et al., 2015).

Observing reproductive activity also often requires territory mapping and the banding of birds to keep track of individuals (Vickery et al., 1992), thus demanding resources and expertise beyond the scope of this project. Territory mapping may indicate habitat quality more accurately than using fitness parameters (Perot and Villard, 2009); however, Bibby et al. (2000) state that territory mapping remains an intensive method yielding diminishing returns relative to observer effort. The method is also criticized for ignoring pre-breeding or non-territorial habitat use within the larger home range (Whitaker and Warkentin, 2010). In continuous grasslands, territory mapping and indirect measures of reproductive success resulted in similar findings to nest searching (Vickery et al., 1992). However, grassland amongst patchy forest, as in some herbivore-browsed ecosystems, makes this difficult (Cox, 1960).

3.1.3 Nest-site level

The nest-site level presents difficulties for obtaining songbird data, as finding enough nests for a reasonable sample size is time-consuming (Collins, 2004). finding nests is not always necessary; one study that sampled the site characteristics of 0.04 ha nest sites and non-nest sites within a single BAWW territory found slope to be the only habitat difference (p=0.003) (Collins, 2004). For species with a wide range of nesting habitat researchers may make inferences from habitat data collected at a territory level. Species with more specific nest requirements, such as woodpeckers, vegetation data may be collected at the nest-site level. Overall, questions concerning the breeding success of birds best operate with a nest-site component; however, field season logistics often prevent researchers from finding nests and indirect indices of breeding success such as pairing status are used instead (Thompson, 2007).

The methods for this project include point-counts and song recordings of BAWW to determine pairing status. BSC monitored 100 points in the North Mountain savannah to determine the proportion of grassland, forest, and scrub habitat at each point location in 2014-2015 (Campbell, 2015). The field methods used in this project are a continuation of BSC's work and aim to further explore the inconsistent findings regarding the high proportion of non-forested-habitat use by forest generalist species.

3.2 Study-Area

The study was conducted on the highland plateau of North Mountain (46°48'29.4"N; 60°41'16.1"W) (*Figure* 1), one of the areas most heavily browsed by moose within CBHNP. As such, many studies have occurred on North Mountain regarding spruce budworm and moose-browsing vegetation dynamics as well as BSC work (Smith et al., 2010; BSC, 2014; BSC, 2015; Franklin et al., 2015). The moose-browsed savannah is highly diverse. In some areas, wide-open fields contain scattered snags and low shrubs, which have avoided being browsed by snow cover (Franklin et al., 2016). In other areas, cover types dramatically change from grass to valleys dominated by bracken fern. Severely browsed balsam fir and white birch are prominent and downed deadwood is common, although covered by graminoids (Franklin et al., 2016).

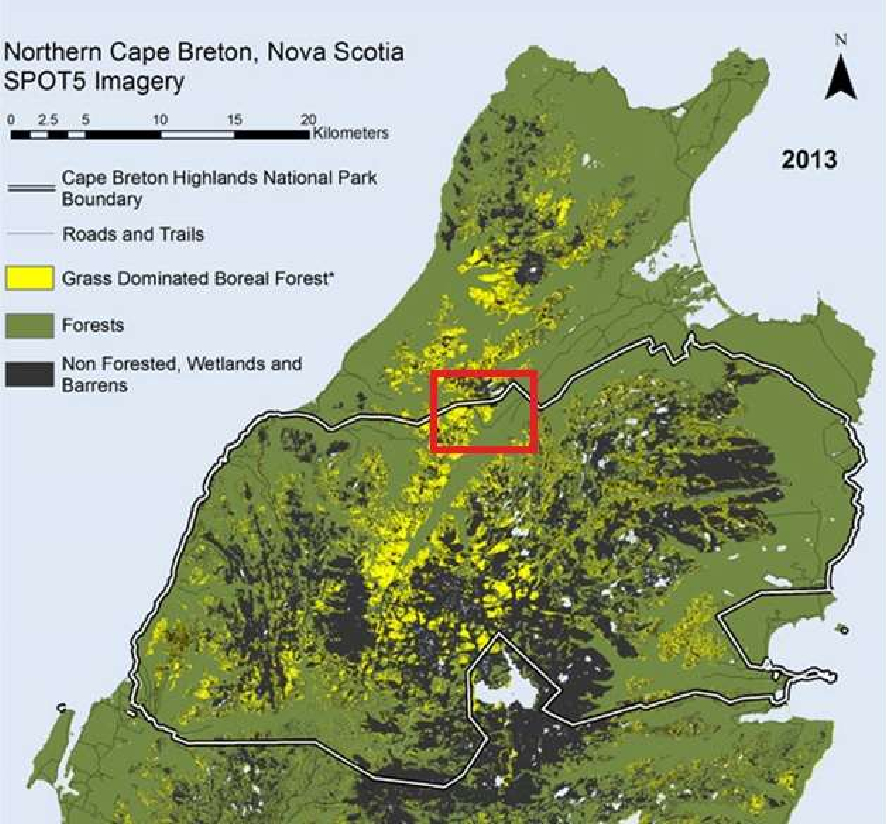


Figure 1 North Mountain (shown in red box) on Cape Breton Island. Cover types were identified using Spot5 Imagery: grasslands, forests, and non-forested areas. The image was accessed from Smith et al. (2015) CBHNP Moose Management Plan.

3.3 Field Methods of Data Collection

3.3.1 Point-counts

Two trained observers with more than five years of birding experience each completed three visits to 55 point-count locations, chosen by systematic random sampling, between sunrise and 10 am. BSC point-count standards were improved upon by altering the survey time length from six to ten min, using a range-finder to ensure that birds were within a fixed radius of 140 m and increasing the number of site visits to each point from one visit to three. Repeated counts allowed for more confidence in species detectability and observer bias.

Observers were randomly assigned to a group of points by their letter name (A2, A3, A4) rather than by individual points for the ease of logistics and improved efficiency. Advanced planning ensured that the same person did not complete all three sampling events at each point-count location. Safety, weather, and wildlife avoidance occasionally dictated the presence of both observers at a point location, but only one observer completed the count. The following methods were adopted from the Rocky Mountain Bird Observatory protocols (Hanni et al., 2009). Upon arrival at the point location, observers waited two min before starting each survey to reduce the disruption to birds that may have been caused as a result of the observer(s) being present. Using a timing device set for 10 min, observers recorded all bird species seen and heard using standard four-letter codes. Observers recorded how each bird was initially observed with the following codes: V=visual, C=calling, S=singing, D= drumming, F=Flyover, or O=other aural (*e.g.* wing beats). Flocks of birds were recorded as a group observation with the number of individuals listed under frequency. At each point-count, surveys were carried out only under certain weather conditions and the weather codes were captured accordingly to descriptions provided by Hanni et al. (2009) (see *Table* 1).

Table 1 Weather conditions for cloud and wind adhered to for point-count protocol- as taken from The Rocky Mountain Bird Observatory (Hanni et al., 2009).

Cloud Cover		Wind	
Observed	Score	Observed	Score
0-15%	0	Less than 1.6 km/hr; smoke rises vertically	0
16-50%	1	1.6-4.8 km/hr; smoke drift shows wind direction	1
51-75%	2	6.4-11.3 km/hr; leaves rustle, wind is felt on face	2
76-100%	3	12.9-19.3 km/hr; leaves, small twigs in motion	3
fog /drizzle	4	20.9-28.9 km/hr; raises dust, leaves, branches	4

We followed distance sampling methods of empirical collection (Thomas et al., 2002), but not for the common purpose of estimating density. Instead, this project calculated the distance to each individual bird to ensure it was within the 150 m radius of the count location through the use of a Nikon Aculon range-finder. The exact radial horizontal distance from observer to the bird was recorded. In instances of observing flocks, we took one distance for the group to represent all individuals. Birds that were flushed immediately prior to observer arrival at the point locations had their distances estimated from point centre. Customary practices were followed for distance sampling, such as the importance of looking up and staying at the point location. In instances without a clear line of sight, an object easily sighted would be used to calculate a range with the distance to the bird sighting being subsequently added or subtracted to provide an appropriate final range estimate (Sagebrush Songbird Monitoring Protocol, 2016). We confirmed species identifications after the point-count was completed when necessary.

Additional protocols adopted from Hanni et al. (2009)

- Observers paused at point-counts in the case of road noise and resumed counts when noise at ceased.
- Observers refrained from wearing hats, sunglasses, or bright clothing while conducting point-counts to reduce influencing bird behaviour
- Observers paid special attention when conducting point-counts to avoid missing window species, which are defined as common species often heard through.
- Observers conducted point-counts from anywhere within a 25 m radius of the point centre.

3.3.2 BAWW Song Recording & Territory Mapping

The objective of mapping BAWW territories was to determine the proportion of different song modes for individual males attempting to breed on North Mountain. Initial searching for BAWW males occurred informally while walking between point-count location. Any BAWW seen or heard were marked with coordinates and revisited after point-counts were completed. Unlike traditional territory mapping where the observer walks in systematic transects (Bibby, 2000), visits to territories involved covering a 150 m radius area from the last observation of a male. Once visual or auditory confirmation was obtained, male movements were tracked with the least amount of disruption through means such as keeping greater than 50 m away. Observers followed individual males, creating multiple GPS waypoints around their estimated defended area. Upon subsequent visits, additional GPS waypoints were added and over time the centre of each male's territory was confirmed.

The edges of territories were more difficult to define, especially in territories with dense alder thickets where the male was seen singing on the top of a shrub or a tree on one or two occasions. However, in these cases, the males were consistently heard and their approximate location could be inferred based on their song. Consequently, this project offers no exact territory size estimates, partially since territory mapping tending to underestimate size (Anich et al. 2009). The aim was to determine the approximate centre of each territory necessary for vegetation sampling. By collecting vegetation data within a 100 m radius from the point centre, the data collected confidently demonstrate that each territory overlaps significantly with the vegetation survey. It is possible that a portion of the vegetation survey does not overlap the full territory area, since territories may be different shapes. However, the small portions that do not overlap are biologically irrelevant, as they would likely be encompassed in the larger home-range area.

A territory was perceived to be abandoned in cases where there was no sign of BAWWs after three separate visits. Observers attempted to visit each territory more than four times to ensure that the male was consistently present in each area. Based on the selected time of survey, this project assumed that by the end of the first week of June, most BAWW males should have set up territories. However, the presence of a female singing on high perches and territorial disputes with other males were also used as confirmation.

Two methods were used to record the songs of male BAWWs. Throughout the first two weeks, observers attempted to witness BAWW foraging, and marked additional territory GPS waypoints while recording male songs using a handheld Zoom H4N recorder. For the second two weeks of June, a tripod was placed at the estimated centre of each territory and observers recorded between 30 and 120 min of audio feed per visit. To obtain clear recordings, the Zoom H4N recorder was set to a consistent 80 to 100 mic input volume. The recorder was set up in the estimated centre of the territory, and then in random placements within 100 m radius of the centre point location for subsequent recordings, although care was taken not to disturb any vegetation and remain at least 200 m away from any roads. Variance in the amount of time recorded was due to weather, wildlife, and simultaneously completing point-counts during the recording time.

3.3.3 Field-based Vegetation Sampling

Vegetation sampling occurred in mid-August after birds had fledged to minimize nesting disruption. While sampling vegetation, observers were careful to avoid disturbing and trampling sensitive bog and fen habitats in the area. A group of 11 observers sampled vegetation in groups of four to five at both local (2 m x 2 m plots) and neighbourhood (100 m radius) levels. Often vegetation data collected at a micro level is most relevant around an identified nest, enabling nest-site characteristics to be ascertained. However, the vegetation data collected in this project, in accordance with Rae et al. (2014), similarly attempted to link moose-browsed vegetation to avian presence.

Two distinguishing habitat variables between the territories of paired and unpaired BAWW are plant species richness and slope (Paszkowski et al., 2004). Our study site is composed of similarly sloped terrain, but there were some occurrences of steep slopes at the edges of roads. The slope of a landscape affects breeding success because ground-nesting birds benefit from building their nests on higher ground as it protects the young from flooding (Paszkowski et al., 2004). However, it was not anticipated that vegetation richness would explain the difference in territories, as the boreal forest in Cape Breton has limited richness in tree species.

Vegetation sampling for this project used a similar approach to that of Rae et al. (2014) who assessed the relative abundance of each cover type by height intervals. The local-level vegetation protocol involved setting up 2 m x 2 m plots at a randomly selected distances between 1 to 20 m, and at a cardinal direction (one technician spins compass continually until the second technician orders them to stop) from the point centre of each territory. In total, between three and eleven observers completed three 2 m x 2 m plots for each point. For each plot, the observers estimated and described the cover types present (shrub, scrub etc.) and the proportion of each cover type within the plot for each vegetation height category (Rae et al., 2014) (see Table 2). Heights of trees and shrubs were determined with metre sticks. Overhanging branches from larger trees were individually counted at the height of the branch included within the plot.

Table 2 Categorical representation of cover type proportion and vegetation height as part of the local-level vegetation sampling protocol adopted from Rae et al. (2014).

Levels of Cover Type Representation	Vegetation Height Categories
0 = 0%	1= 0.0-0.50 m
1 = 0-25%	2= 0.51-1.0 m
2 = 26-50%	3= 1.01-2.0 m
3 = 51-75%	4= 2.01-5.0 m
4 = 76-100%	5 = >5.01 m

Neighbourhood-level vegetation was also sampled at a 100 m radius (31416 m^2) from the centre of each territory by estimating the percentage of shrub, treed, saturated, and scrub (fern, grass areas as categorized by Campbell, 2015) within the radius without an assigned height category. Observers used a rangefinder to mark 100 m from point centre in all cardinal directions when carrying out their assessment of neighbourhood-level habitat types. Lastly, special habitat features such as slope, aspect, presence of big trees, and sapsucker holes were also measured. In each territory, one observer was assigned to search the 100 m radius from point centre for trees with yellow-bellied sapsucker holes, which are a BAWW forage quality indicator. The number of trees with sapsucker holes was recorded as well as the number of big trees, defined as greater than 60 cm diameter at breast height (dbh), in each territory. Slope and aspect were measured with a compass equipped with a clinometer from point centre in a random direction by a single observer.

3.3.4 Spatial forest data acquisition & conversion of point-count data

This project sought to study the finding that BSC research showed no association to treed areas for selected forest birds using local-level vegetation data (100 m radius from point-count centre) on North Mountain. The aim was to understand whether that initial finding was due to an inadequate level of analysis. Literature shows that typically local-level (100-200 m) habitat information does not predict the distribution of generalist species (Cunningham and Johnson, 2016). Furthermore, with point locations a mere 300 m apart, a local-scale was appropriate. Local-level approaches are useful in patchy habitat where we expect tree cover and composition will differ significantly. As such, we used remote sensing data to describe the patchiness of the forests on North Mountain.

All spatial data were processed using ArcMap (ESRI) ™ software. Vector data were acquired for each point-count location, as generated by Cape Breton Highlands National Park. The 100 point-count locations were given to BSC for its 2014 and 2015 studies on changes in bird species diversity since the creation of grassland habitat. This study took a subset of 55 points chosen through systematic random sampling in 2017 by lead researcher M.A. and visualized the point-counts in ArcMap. A separate database spreadsheet was created for each of the three selected species, which indicated whether the species was present or absent on North Mountain. Data from three years of surveying were compiled, including the 2014 and 2015 BSC work and this study's 2017 point-count field data. Therefore, there were four indices of selected species presence and absence data: 2014, 2015, 2017, and total with all years combined. This study did not calculate individual species detectability and instead addressed observer bias in the point-count design. In the context of understanding habitat relationships, without factoring in rare species and avoiding the assumption that a high density of a species equals habitat preference, simple presence and absence data were used.

To describe forest loss in components of North Mountain, the SPOT5 imagery, colour pansharp at 2.5 m resolution, August 2013, Boreal Forest Mask, was used due to its high resolution which was conducive to characterizing a highly patchy habitat (CBHNP, 2015). The Boreal Forest Mask was developed by CBHNP in response to a need to better represent newly created grassland areas, which were highly underrepresented in the spatial data of the park. The process of creating the mask involved isolating boreal forest from Acadian forest, separating out barren and wetland areas, and classifying (and ground-checking) all other areas as grassland (see CBHNP, 2015). Effort was made to ensure that small (< 1 ha) treed patches were included, as these areas are important to forest birds (Schlossberg and King, 2008). This project acquired and used the SPOT5 imagery file for North Mountain area from CBHNP. Although SPOT5 imagery was generated in 2013, the imagery is sufficiently accurate for the purposes of this project, since vegetation changes from moose browsing are decadal in timeline at the very least. The received file was converted to a grid format using an ArcMap tool. The classification for all habitat types was turned off except for boreal treed/alder in order to characterize the forest in the study site.

We included alder thickets as part of our definition of forest due to the lack of diversity in shrubs due to moose browsing at our study site. The management context by CBHNP staff also influenced our decision; past work by BSC had concentrated on understanding how the extent of boreal forest loss had affected birds. Note: there was no Acadian forest was present in the study area.

To define the spatial boundary around each point location (as in the Boreal Avian Modelling Project, 2012), a 140-m radius buffer was applied with a geoprocessing tool. After the buffers were in place, we isolated the SPOT5 forest data within the buffered boundaries by using an 'intersect' geoprocessing tool to intersect the values within, which were then exported to create a new layer. Using this layer, new attributes were created by adding new fields to the data attributes and running a tool to calculate area geometries. With these fields in place, we were able to develop three indices of forest: mean patch size, total number of patches, and total forested area. The forest indices output data were then combined with the presence and absence bird data in the previously established database spreadsheet.

3.4 Analysis

3.4.1 Song Analysis

Song data were analyzed to determine whether there were differences in song modes and singing rates of paired vs unpaired male BAWW. Lead researcher M.A. made spectrograms of each vocalization using Song Scape, a program produced by Wildlife Acoustics.™ Each A and B song were distinguished using these spectrograms. The number of each song type per visit was compiled. The total of A and B songs sung for each territory was summarized for all visits with territories separated into two groups: i) confirmed paired; and ii) considered unpaired, based on the absence of a female having been observed. To compare song modes between paired and unpaired BAWW, the number of 5-min intervals was counted in which the bird sang. Next, the song data were analyzed by song mode in each 5-min interval (adapted from Staicer et al., 2006); mode is defined as the sequential strings of the various A and B type songs. To compare singing modes, each bird's singing was separated into 5-min intervals and then classified as: i) mostly serial mode, or ii) mostly repeat mode. Repeat mode is a string of mostly A songs, while serial mode is comprised of both A and B songs, being defined as a string containing more than two B songs.

Fisher's Exact Probability Test (2 x 2) was employed to determine if proportions of A and B songs, repeat and serial mode in i) total season and ii) early vs late season, were significantly different between individual paired versus unpaired males (McDonald, 2014). For both analyses, $p < 0.05$ was used with Bonferroni correction for small sample sizes ($p<0.00183$), where appropriate and indicated by an asterisk in tables.

Both singing rates and song types were used to confirm pairing status, as in Harris and Reed (2002). Singing rates were calculated by creating a chart with the i) territory name, ii) date, and iii) number of intervals sung. Next, a column was filled to indicate whether the bird sang mostly in repeat or serial mode during that interval. For example, if there was a single B song and 40 A songs in five minutes, the interval was recorded as repeat mode. Summary statistics were calculated for paired and unpaired territories, which were unequal in size. To compare the means between total paired and unpaired, the number of intervals with repeat mode or serial mode singing was counted and reported as percentages of the total intervals with any singing. Averages and standard deviations were reported for serial- and repeat-mode intervals for territories.

3.4.2 Territory Vegetation Analysis

For local data we summed the values for each cover type and then took the average to obtain one value for each height category. Neighborhood data was not summarized, and input as raw values. Habitat variables were moderately normal according to probability plots (*i.e.*, for each variable, only the distribution for sub-group 'paired' or 'unpaired' were non-normal, never both). Therefore, this project assumed normality since one-way ANOVAs are less rigid with this assumption (McDonald, 2014). A visual assessment of box-plots was used to determine equal variance. After performing exploratory statistics, the four habitat variables were divided, which exhibited more than three times the unequal variance from other habitat variables, and a further Welche's ANOVA was performed (MacDonald, 2014). Differences in other habitat variables were assessed by one-way ANOVA. Since habitat variables exhibited high multicollinearity, we were unable to use MANOVA (McDonald, 2014). Statistical significance was determined at $p < 0.05$.

CHAPTER 4 Differences in Song and Territory Habitat for Paired versus Unpaired Black-and-white Warblers Inhabiting the Moose-browsed Grasslands of Cape Breton Highlands National Park

4.1 Introduction

Assessments of pairing status of male songbirds can yield valuable insights into habitat quality, including habitat degradation. For forest birds in disturbed habitats, we can draw conclusions about their thresholds for territory requirements by their successful acquisition of mates. One valuable tool to infer pairing status is the types of songs males sing during the breeding season (Staicer, 1989; Bourque and Villard, 2001; Harris and Reed, 2002; Staicer et al., 2006),
Male birds sing complex or multiple song types for various purposes (Byers et al., 2015). Song studies typically focus on male bird song which is far more frequent, and on species with complex songs such as warblers (Kroodsma, 2004). A male bird's repertoire may be sung to defend his territory from other males (Byers et al., 2015). Males may increase their repertoire and change features of their songs based on neighbouring males, with song-sharing and counter-singing on the breeding grounds (Woodward, 1998).

In addition to song complexity, the frequency of singing is also postulated to indicate that a male has acquired a mate. Overall, unpaired birds sing more than paired birds (Byers et al., 2015). Singing rates are influenced by any combination of time of day, proximity to the nest (Weary et al., 1994), the quality of territory habitat (Manica et al., 2014), and proximity to a neighbour (Morse, 1967). For example, a male may sing less not because he has a mate, but because his territory is isolated from neighbours (Morse 1967). Singing rates may be associated with the ability of a male to successfully rear young, there is no confirmation of female preference for high-singing males. Females may rate males on how well he sings, or how complex the song is. How well a bird sings his ‘performance song’ varies by age. Older males sing with more consistency and sometimes complexity, supporting the theory that experienced males have higher breeding success (Byers et al., 2015).

Natural and experimental behavioural studies show that, in many cases, song types indicate whether a male is mated (Kroodsma et al., 1989; Staicer 1989, 1996; Spector 1991). A combination of singing frequency and song type accurately advertises pairing status in a variety of warblers including Grace’s Warbler *(Setophaga graciae*) (Staicer, 1989), Adelaide’s Warbler

(Setophaga adelaidae) (Staicer, 1996), American Redstart (AMRE) (*Setophaga ruticilla*) (Staicer et al., 2006), and Black-and-white warbler (BAWW) (Tyler, 1953; Woodward, 1998; C. Staicer, pers. *comm*. November 20, 2016).

For BAWW, the frequency of song types sung changes after finding a mate. BAWW sing two main song types; type-A songs are the typical "squeaky wheel" song while type-B songs are longer and move downward in pitch. The seasonal timing of these songs may also differ with type-A songs sung repeatedly (repeat mode) more in the early season prior to mating, while a combination of type-A and type-B songs (serial mode) are typically sung in late spring once the male has found a female (Spector, 1992). Unlike other warblers, there is no evidence of song-mode use differentiating between the bird's position in its territory, the presence of females, nor as a mechanism in territorial disputes for BAWW (Spector, 1992).

BAWW prefer mature or mid-aged mixedwood forest, but tolerate swamps and shrubbery (Kricher, 2014) although birds in these latter habitat types can be associated with lower breeding success (Paszkowski et al., 2004) due to higher nest predation in edge habitats. There may be a positive relationship between patchy habitat and higher numbers of unpaired birds (Paszkowski et al., 2004; Staicer et al., 2006) and song-use (Perez-Granados et al., 2016). Most research specifically linking pairing status to song was published over half a century ago (Tyler, 1953).

There is a need for studies investigating the link between foraging resources in territories and male song attributes (Manica et al., 2014). Campbell (2015) conducted avian point counts on North Mountain in the boreal forest of Cape Breton, where moose (*A. a. andersoni*) browsing and spruce budworm (*Choristoneura fumiferana*) have reduced most of the woodland to scrub and grassland (Franklin et al., 2015). They found that BAWW were curiously dispersed amongst the grass-tree mosaic with no preference for treed areas (Campbell, 2015). Our study examined a BAWW population on the moose-browsed grassland of Cape Breton Highlands National Park (CBHNP) for an assessment of habitat quality and its influence on pairing status.

Our objective was to find out whether paired males sang consistently differently than unpaired males, and furthermore, whether there were differences in habitat features within the territory boundaries of paired and unpaired BAWW. We hypothesized that the moose-browsed grassland of North Mountain is a habitat sink, hosting primarily unpaired BAWW males. Based on other

Parulidae research on early-morning singing (compared to dawn song), we predicted: i) unpaired males to sing > 90% in repeat-mode (Morse, 1976; Lein, 1978); ii) paired males to sing in serial mode more than unpaired males in late season; and iii) unpaired males to sing more overall than paired males. We expected pairing status could be inferred by the proportions of singing modes in early and late seasons. In response to suggestions for research on the habitat characteristics of BAWW territories in fragmented habitat (Kricher, 2014), we predicted higher proportions of shrub for unpaired birds and steeper slopes for paired birds.

4.2 Methods

4.2.1 Study Site

The study was conducted on the highland plateau of North Mountain (46°48'29.4"N; 60°41'16.1"W), one of the areas heavily browsed by moose within CBHNP (*Figure* 1). Vegetation dynamics after a spruce budworm outbreak, moose browsing and bird populations have been studies in this area (MacLean, 1988; Campbell, 2014; Campbell, 2015; Franklin et al., 2015). The savannah is highly diverse. In some areas, wide-open grass areas (*Calamagrostis* dominated) contain scattered snags and low shrubs (primarily *Alnus incana*), which have avoided being browsed by snow cover (Franklin et al., 2016). In other areas, cover types dramatically change from grass to valleys dominated by bracken fern (*Pteridium aquilinum*). Severely browsed balsam fir *(Abies balsamea)* and white birch *(Betula papyrifera)* are prominent and downed deadwood is common, although covered by graminoids (Franklin et al., 2015).

4.2.2 Territory mapping

We first delineated the territories of nine male BAWWs on North Mountain, using territory mapping methods for continuous grasslands (Vickery et al., 1992; Perot and Villard, 2009). The locations of any BAWW seen or heard on point counts were marked with coordinates and then males were found again several hours later following the completion of point counts. Unlike traditional territory mapping where the observer walks in systematic transects (Bibby et al., 2000), our visits to territories involved covering a 150 m radius around each observation (sight or sound) of a male. We tracked male movements with the least amount of disruption (minimal playbacks - used only as last resort after losing track of the bird) and created multiple GPS points around their estimated defended area. Upon subsequent visits, we added additional GPS points and over time confirmed each male's general territory. The edges of territories were more difficult to define, especially in territories with dense alder thickets where the male was seen singing on the top of a shrub or tree on one or two occasions - although in these cases the males were consistently heard and we inferred their approximate location based on their song. Consequently, we offer no exact territory size estimates, being cognizant that territory mapping tends to underestimate territory extent (Anich et al., 2009).

We attempted to visit territories more than four times to ensure it was occupied by a male bird. By the end of the first week of June, most BAWW males should have set up territories - although the presence of a female singing on high perches and territorial disputes with other males were also used as confirmation.

4.2.3 Song recording

Recording the early-morning songs of BAWW males involved two methods. Throughout the first two weeks we attempted to observe pairs, foraging behaviours, and mark additional territory GPS points while recording songs using a handheld Zoom H4N recorder. For the second two weeks of June, we used a tripod placed at the centre of each territory and recorded between 30 and 120 min per visit. For most of our recordings we did not maintain visual contact, as the recorder was left on a tripod. We recorded early-morning songs because there are higher levels of extra-pair copulations before sunrise and during the dawn song, which add further layers of complexity in defining a bird as paired or unpaired and rendering it more difficult to compare differences in song modes (Staicer et al., 2006).

To obtain clear recordings, we set the Zoom H4N recorder to a consistent high microphone level. We set up the recorder in our estimated centre of the territory, then in random placements within 100 m radius of the point centre for subsequent recordings and >200 m from the road. Variance in the amount of recording time resulted from adverse weather, wildlife interference (*i.e.* bears, moose, coyotes) and simultaneously completing point counts during the recording time. We used unequal sampling periods of 10-60 min per observation, consistent with other song-type studies (e.g. Kroodsma et al., 1978).

There are potentially confounding effects when considering the movements and interactions between males sharing territory boundaries. However, all recordings were deemed independent since we recorded adjacent territories on different days to ensure that males were not influencing neighbouring birds' songs when we placed and retrieved the H4N recorder. Territories were also a minimum of 150 m apart, but to ensure independence, males were observed concurrently by two observers. Since BAWW territories may be as small as 2 ha (Kricher, 2014) two males may share a territory boundary, but we are confident there are two separate territories. Furthermore, both males were observed simultaneously in these adjacent territories, confirming separation of territories. The range of the H4N for songbirds ranges from a maximum of 50-150 m away, such that it is unlikely that adjacent male’s songs were recorded in the neighboring territory.

4.2.4 Vegetation sampling

Vegetation sampling occurred in mid-August after birds had fledged, minimizing disruption. Observers sampled vegetation in groups of 4-5 people at both local (2 m x 2 m plots) and neighbourhood (100 m radius) level. Although vegetation data collected at a micro-scale is more relevant to ascertain nest-site characteristics, we collected vegetation in accordance with Rae et al (2014) which also assessed the impact of moose browsing on birds.

The only distinguishing habitat variables between the territories of paired and unpaired BAWW reported in the literature were plant species richness and slope (Paszkowski et al., 2004). In Cape Breton's boreal forest, there are few tree species to begin with, so we would not expect tree richness to explain differences. Therefore, we used an approach similar to that of Rae et al. (2014 assessing the relative abundance of each cover type by height intervals. The local-level vegetation protocol involved setting up 2 m x 2 m plots at a random distance (assigned a random number between 1 and 20 m) and cardinal direction (one person spins compass continually until the second person orders them to stop) from point centre of each territory. In total, between 3 and 11 observers completed three 2 x 2 m plots for each point. For each plot, the observer estimated the cover types (shrub, non-coniferous trees, and coniferous trees) and the proportion of each cover type in the plot: 0 (0% cover), 1 (1-25%), 2 (26-50%), 3 (51-75%), 4 (76-100%) for each vegetation height category (1 = 0-0.5 m, 2 = 0.5-1 m, 3 = 1-2 m, 4 = 2-5 m, 5 = >5 m. Heights of trees and shrubs were determined with metre sticks. Overhanging branches from larger trees were counted at the height of the branch within the plot, not the tree.

Neighbourhood-level vegetation was also sampled from a 100 m radius from the centre of territories: % shrub, forest, scrub (fern, grass) without height categories, as well as the presence of landscape saturated by water. Observers used a rangefinder to mark 100 m from point centre in all cardinal directions, to assess habitat types. Lastly, special habitat features such as slope, aspect, presence of big trees, and Yellow-bellied Sapsucker holes were measured. In each territory, one observer was designated to search the 100 m radius from point centre for trees with yellow-bellied sapsucker holes which are a BAWW forage quality index. The number of trees with sapsucker holes was recorded as well as the number of big trees (>60 dbh) in each territory. Slope and aspect were determined by a single observer with a compass clinometer from point centre in a random direction.

4.2.5 Song Analysis

We analyzed each recording from BAWW territories using the Wildlife Acoustics program “Song scope” (Wildlife Acoustics, 2018). Using this software, it was possible to distinguish between A and B songs using the spectrogram, with the numbers of each song type per visit compiled into a Microsoft Excel™ spreadsheet. We summarized the total A and B songs sung for each territory for all visits with territories separated into two groups: i) confirmed paired; and ii) unpaired based on the absence of a female having been observed. To compare song modes between paired and unpaired BAWW, we counted the number of 5 min intervals in which the bird sang. Next, we analyzed song data by song mode in each 5 min interval (adapted from Staicer et al., 2006), mode being the sequential strings of the various A and B type songs. To compare singing modes, we separated 5 min time intervals of each bird's singing into i) mostly (over 50%) serial mode or ii) mostly repeat mode. Repeat mode is a string of mostly A-songs, while serial mode is comprised of both A + B songs, being defined as a string containing > 2 B songs).

Fisher’s Exact Probability Test (2 x 2) was employed to determine if proportions of A and B songs, repeat and serial mode in i) total season and ii) early vs late season were significantly different between individual paired vs. unpaired males. For both analyses, we used $p < 0.05$ with Bonferroni correction for small sample sizes ($p<0.00183$), where appropriate, indicated by an asterisk.

As justified by Harris and Reed (2002), we used both singing rates and song types to confirm pairing status. We calculated singing rates by creating a chart with the i) territory name, ii) date, and iii) number of time-intervals sung. Next, we filled in a column indicating whether the bird sang mostly in repeat or serial mode during that time-interval (for example if there was a single B-song, and 40 A-songs in five min, we recorded this time-interval as repeat mode). We then calculated summary statistics for paired and unpaired territories, which were unequal in size. To compare the means between total paired and unpaired, we summed the number of time-intervals with repeat mode and then with serial mode and reported these as percentages. We reported the averages and standard deviations for serial and repeat mode time-intervals for paired and unpaired territories.

4.2.6 Vegetation Analysis

We examined probability plots to test for normality before employing a one-way ANOVA, in which the assumption of normal distribution is not rigid (McDonald, 2014). Most variables were normally distributed according to probability plots (*i.e.* for each variable, only the distribution for sub-group ‘paired’ or ‘unpaired’ were non-normal, never both). We used Levene's test to determine that almost all variables exhibited equal variance, as required in the assumptions of one-way ANOVA. For the variable summed-height shrub the variance was unequal therefore we used Welches ANOVA. Since habitat variables exhibited high multicollinearity, we were unable to use MANOVA (McDonald, 2014). Statistical significance was determined at $p < 0.05$ (McDonald, 2014). For variables with significantly different means, we used Fisher’s Exact Probability Test to determine differences between individual territories (rather than just paired and unpaired groups; McDonald, 2014).

4.3 Results

Overall, we found that song modes and types were not useful in reliably distinguishing the pairing status of BAWW. Paired birds sang less (regardless of song mode) than unpaired males on average. Our results show little support for the use of song types and modes in differentiating BAWW male pairing status.

4.3.1 Proportion of paired / unpaired territories

We observed six territories with bachelor males and three territories with pairs. One unpaired male abandoned his territory and was removed from the analysis after >3 visits with zero songs. We recorded audio for a total of 31.68 h from nine territorial males with a median sampling duration of 50 min. We confirmed a bird as paired over multiple observations of a male and female closely foraging together, male displays, and soft call notes between the two.

4.3.2 Detectability

Singing rates (% singing rate= total number of time-intervals sung / total time-intervals sampled) varied widely across males in both paired (range 0.07-0.66%) and unpaired territories (0.15-0.67%; *Table 3*). Two paired males P1 (0.07 %) and P2 (0.16%) had low singing rates compared to unpaired males UN3 (0.67%), UN2 (0.5%), and UN1 (0.36%). However, this trend was not consistent for paired male P3 or unpaired male UN5 (0.66%, 0.15%). On average, paired males (29.6%, median 16%) sang less than unpaired males (40%, median 36%). There was a difference of 10% between the averages and 20% between the medians of paired vs. unpaired males. Unpaired males were not consistently easy to differentiate from paired males based on their singing rates.

Table 3 Singing rates by time-interval (% singing rate= total number of time-intervals sung / total time-intervals sampled) for each territory.

Territory	Singing Rate (%)
P3	0.66
P1	0.07
P2	0.16
UN1	0.36
UN3	0.67
UN2	0.5
UN5	0.15
UN4	0.32

4.3.3 Song Modes

4.3.3.1 Total season

As expected, we found that for total season (month of June) paired birds sang, on average, in repeat mode less (6.3 ±2.9 intervals) than unpaired (10.6 intervals ±4.3) males. However, there was no difference in serial mode singing between paired (8.0 intervals ±3.3) and unpaired (7.8 ±5.3).

When comparing differences between individuals, we found more significant differences between unpaired vs unpaired males than between paired vs unpaired males- contrary to our hypothesis. When assessing differences in the proportion of repeat and serial mode singing between individual males, there were no significant differences between paired and paired males (p> 0.064), there were more (five out of ten) significant differences between unpaired males than differences between paired vs unpaired males (three out of fifteen) (*Table 4*).

Table 4 Total-season differences (significant (alpha level =0.05) with Bonferroni correction = 0.0018) in proportion of serial / repeat mode singing organized by paired (P) vs unpaired (UP) males. Asterisk indicates relationships also observed in late season only.

Unpaired (UP) vs. Paired (P)	*p*-value	Unpaired vs. Unpaired	*p*-value
UN1 vs P3	0.00122*	UN3 vs UN1	0.00039*
UN2 vs P3	0.00000545*	UN3 vs UN2	0.0000000631*
UN2 vs P1	0.00153*	UN4 vs UN2	0.000000601*
		UN4 vs UN1	0.00092*
		UN5 vs UN2	0.00021*

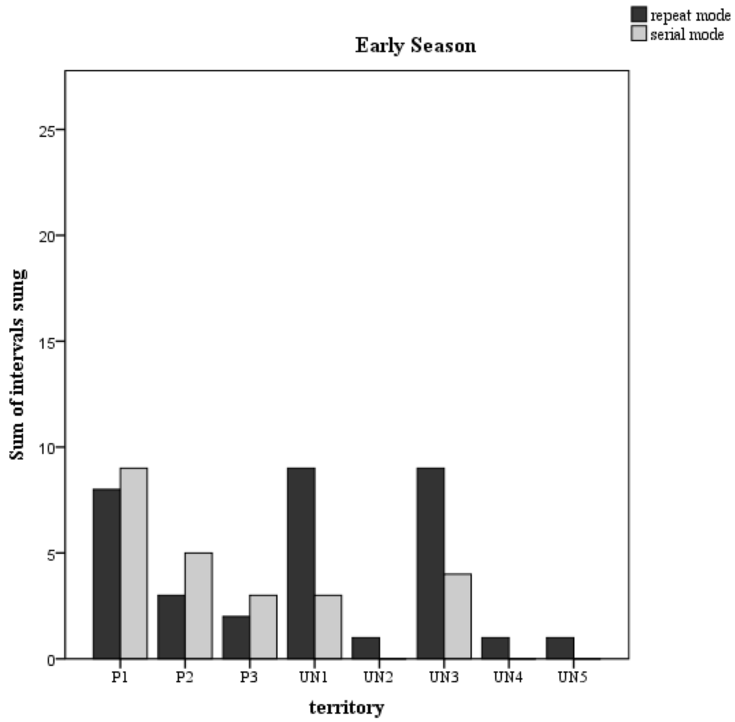
4.3.3.2 Early vs. Late season

On average, we found relatively equal frequency of repeat mode singing (4.2 intervals for paired, 4.3 intervals for unpaired) by BAWW males in early season (June 1-15, 2017). There were less 5 min intervals sung on average sung in serial-mode between paired males (sung 5.6) and unpaired males (sung 1.4). In the late season (June 16-30, 2017), unpaired males sang on average more regardless of singing mode, (6.4 intervals in repeat, 6.4 intervals in serial) than paired males (2 intervals in repeat, 2.3 intervals in serial).

There were no differences (p>0.16) between any individuals' (regardless of pairing status) song-mode for early season; however, by late season songs became more variable, with six differences between unpaired vs unpaired males (*Table 5*). Although there were differences between individual unpaired males, there were only three differences observed (*Table 5)* between unpaired and paired males, demonstrating singing-mode trends are inconsistent between paired males and between unpaired males (*Figure* 2).

Table 5 Singing modes of unpaired vs. paired birds for late season. Frequency of singing mode differences observed in late season, but not evident in pooled early and late season (total season) marked **

Paired (P) vs. Unpaired (UP)	*p*-value	Unpaired vs. Unpaired	*p*-value
P3 vs. UN2	0.00001	UN3 vs. UN1	4.06-E08
P1 vs. UN3**	0.00023	UN2 vs. UN3	2.70-E10
P3 vs. UN1	0.00058	UN2 vs. UN4	2.66-E10
		UN2 vs. UN5	0.00005
		UN5 vs. UN1**	0.00126
		UN4 vs. UN1	0.00071
3 significant /15 total		6 significant / 10 total	



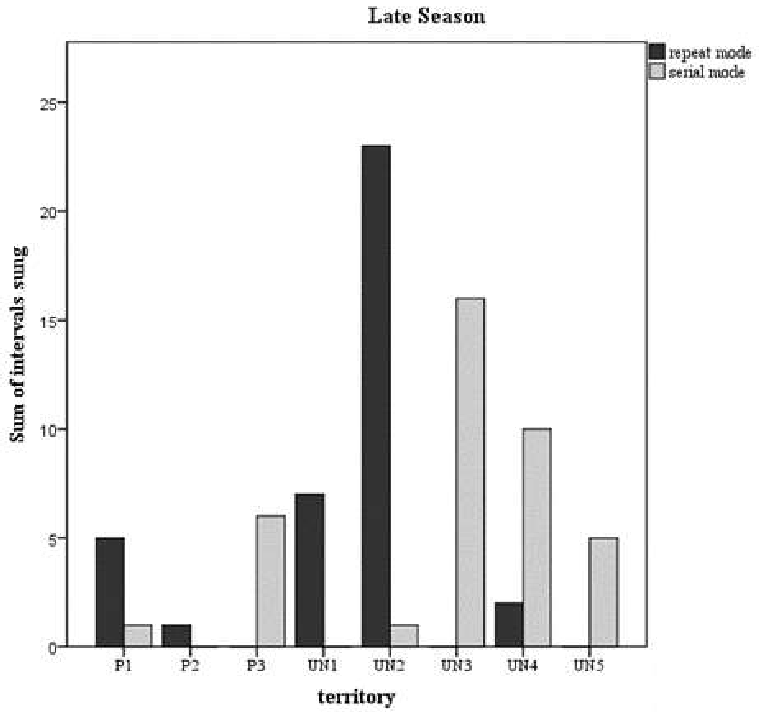


Figure 2 Comparison of repeat and serial mode singing for BAWW males in early (top) and late (bottom) season. Territories with 'P' indicate paired, and 'UN' indicate unpaired males.

Increased recording time exhibited a weak positive relationship with increased singing time-intervals (*Figure 3*). We tested this effect to determine the potentially confounding effect of unequal sampling periods affecting results. There were uneven sampling periods due to field logistics and discovering territories at various times within the month. The relationship between total time recorded and the probability of bird singing was relatively weak (Linear Regression, R^2=0.060). However, indicative that the length of sampling period is somewhat important.

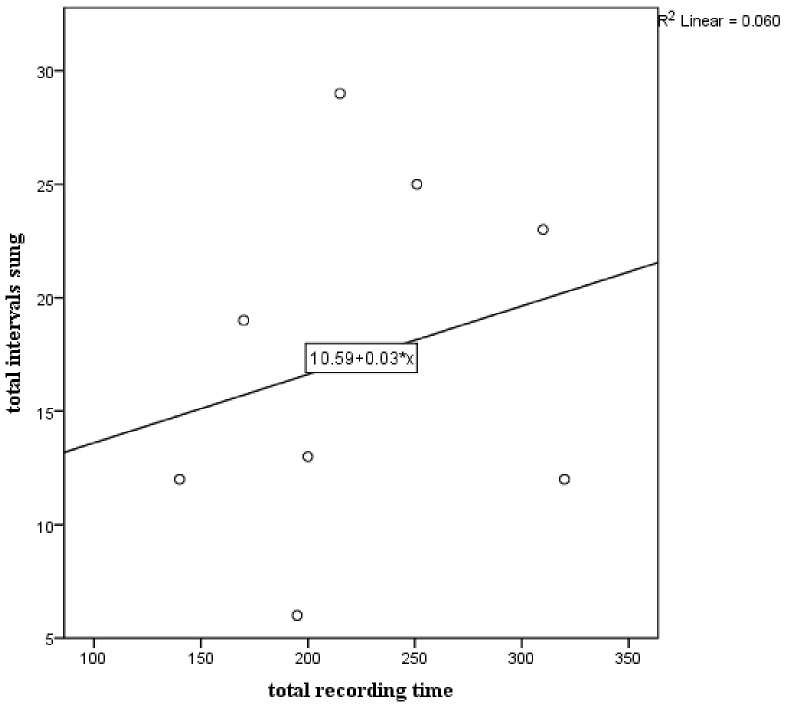


Figure 3 Relationship between the number of 5 min time intervals with singing to the total time recorded.

4.3.4 Song Types

The proportion of song types differed amongst all combinations of individual unpaired males, as such our results show we cannot then differentiate pairing status based on song type (as we hoped there would be the most differences between paired and unpaired males). There were ten out of ten differences of unpaired vs. unpaired males and one out of three differences between paired and paired males, relative to six out of 15 possible differences between unpaired and paired males. The number of B-songs increased in late season for UN3-UN5 and P3; however, for P1 and P2, most B-songs were sung in the early season. There was no clear trend between the proportion of A and B song types between paired and unpaired males. Note the asynchrony in timing of our visits to territories (*Figure 4)*; this allowed us to better interpret the accuracy of our assessments in pairing status. Although song modes are more reliable indices of breeding, we justified our examination of song types because there were no consistent relationships in song modes across all paired vs. all unpaired males.

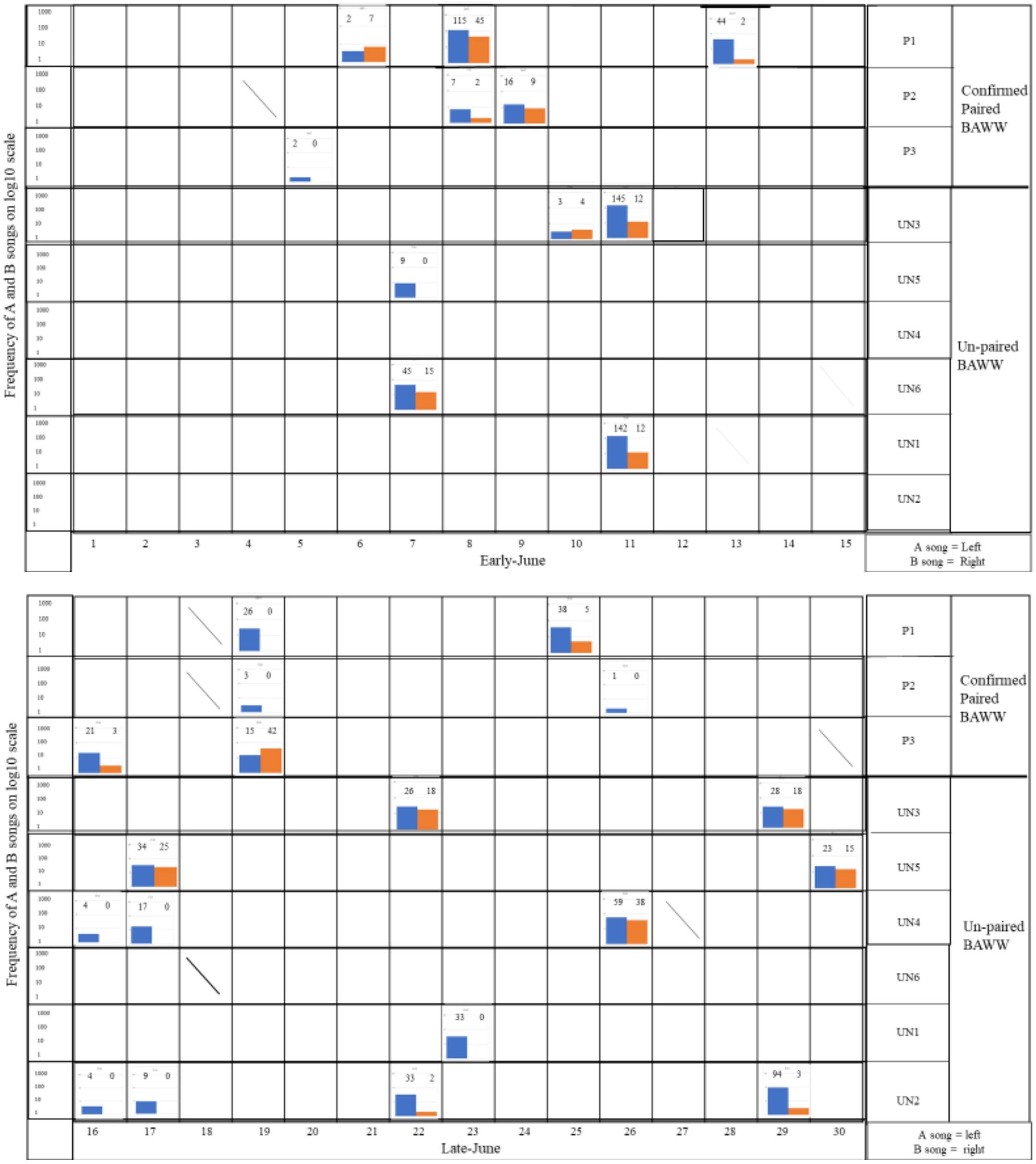


Figure 4 Total frequency of song types (A-songs in blue, B-songs in orange) per recording for paired and unpaired BAWW males throughout early (June 1-15, 2017) and late (June 16-30, 2017) season. Days with blank squares indicated no sampling and days with a slash line represented a sampled day with 0 songs recorded. Recording times per visit vary from 5 to 120 min and number of song types are graphed on a $\log_{10}$ scale. Blank days are left to show asynchrony in timing of visits and observing territories Note: UN2, UN4 were not found until late season (therefore blank for early season).

4.3.5 Vegetation Comparison

4.3.5.1 Compare means of habitat variables

There were no significant differences in habitat variables between paired and unpaired male territories. Shrub (summed-height) was the only variable close to being different (Welches ANOVA p=0.057*) between paired and unpaired BAWW territories (see *Table 6*).

Table 6 Comparison of means using one-way ANOVA for all habitat variables except summed-height shrub (Welches ANOVA) for paired vs. unpaired BAWW males.

Habitat Variables	*p*-value
summed-height treed	0.851
neighbourhood-level forest	0.606
aspect	0.968
local-level 0.5-1 m height	0.35
local-level 1-2 m height	0.684
local-level 2-5 m height	1
local-level 5 m + height	0.937
big trees	0.566
sapsucker holes	0.503
neighbourhood-level scrub	1.00
slope	0.209
neighbourhood-level saturated	0.34
summed-height shrub (Welche)	0.057

4.4 Discussion

Our most significant finding was that, contrary to the literature, paired and unpaired BAWW males display no consistent patterns in their proportions of repeat and serial mode singing. Individual males, whether paired or unpaired, vary widely. As such, our data on BAWW do not support the hypothesis that pairing status can be determined from song modes due to the high variation within paired and unpaired male songs. With regard to habitat differences, we found weak support (p=0.057) of greater proportions of shrubs in unpaired male territories compared to paired males.

We expected, and found, more unpaired than paired males on North Mountain, potentially because of low forest cover. This proportion is consistent with the findings of Paszkowski et al. (2004) who reported seven unpaired territories and three paired territories in fragmented shrubby habitat. Higher numbers of bachelor birds in poorer quality patchy habitat have been observed in other studies as well (Staicer et al., 2006). This study contributes to the call from Kricher (2014) for more studies linking territory information in disturbed forested habitat - our results show pairing success rates of 33% in a fragmented landscape.

Time within the breeding season did not appear to influence singing modes between paired and unpaired males. We expected paired BAWW to sing in serial mode more than unpaired birds in late season, as identified in the literature (Tyler, 1953). Instead, there was no significant difference between song-mode singing; unpaired males sang more regardless of mode type. In the early season, paired males sang more serial time-intervals than unpaired males, but not in the late season. Examining differences in singing modes between individuals, there were only three cases of significant differences between paired and unpaired territories. As such, our results do not support Spector's (1992) statement that males sing more in serial mode after pairing than unpaired males. These results may be explained by asynchrony of breeding events between different males which obscured our ability to define one general ‘late’ season for all birds. In other words, our delineation on June 15th between early and late season may be inaccurate for a male if he finds a mate only on June 14.th However, according to Kricher et al. (2014), males found mates soon after arriving on breeding grounds. Since males arrive onto Cape Breton Island at the end of May, it seems highly likely that males with a decent chance of mating would have succeeded within two weeks after arrival.

Unpaired birds did not sing in repeat-mode >90% of the time, contrary to expectations. There was wide variation in repeat mode singing between unpaired birds. For two territories, there was >90% repeat-mode singing, but the other three territories did not fit this pattern. Staicer et al. (2006) found that when AMRE males sang >90% of the time in repeat mode, there was a high probability they were unpaired. Still, our data support smaller differences in repeat-mode singing between paired and unpaired males singing. We found that unpaired birds sang in repeat mode on average more time-intervals than paired birds.

Males in early season may only be temporarily unpaired, but by late season males will either have a mate or remain bachelors for the season. As such, we expected the differences in repeat-mode singing to be even greater than during early season. Our results indeed showed that unpaired males sang more than paired birds in repeat mode on average in late season, but they also sang more in serial mode. One explanation for this could be that unpaired males in other warblers use B-songs as territorial songs in confrontation with other males. Although this has not been confirmed for BAWW, this is feasible based on several other warblers exhibiting this behaviour (Spector, 1992). It is possible that paired males lost a mate in early season and began to sing more in repeat mode to find a new mate in late season. Regardless of potentially lost mates, other warblers showed a resurgence of repeat-mode singing in late season (Kroodsma, 1989) although this has not been reported in the literature for BAWW specifically.

As hypothesized, singing rates overall were higher for unpaired males which attempt to attract females throughout the breeding season, whereas paired males are occupied by nest building and foraging for the female so they spent less time singing. The pattern of higher singing rates for unpaired males was inconsistent, only true between two paired males which sang less than three unpaired males. Still, the differences between the median of paired and unpaired males showed that unpaired males sang 20% more than paired; this is similar to the 25% difference reported by Foote et al. (2017). These findings are important in representing Breeding Bird Survey data accurately when reproductive rates are likely overestimated in surveys since a higher proportion of unpaired males are detected (Foote et al., 2017).

Singing rate results must be interpreted cautiously due to the complex role of extra-pair copulations. For single-brood BAWW, high singing rates among early-season males are not honest indicators of pairing status, as many may soon find a mate, whereas males with high singing rates in late season are more likely floater males, since paired males often sing less. Still the complexity deepens; female hooded warblers (*Setophaga citrina*) with mates with low singing rates engaged in extra-pair copulations with males of neighbouring territories who had higher singing rates (Chivers et al., 2008). Since unpaired males have higher singing rates, the paired female would be less likely to engage in extra-pair copulation with a paired neighbouring male, thus choosing floater males with inherently higher singing rates. Likely this is due to females choosing single males for extra-pair copulations.

Another potentially confounding variable is that paired and unpaired males use different amounts of their territory, affecting the average distance from the recording device. Paired males use almost 50% less of their territory than unpaired males (Collins, 2004) which could explain instances of the recorder picking up fewer songs at known paired territories. The literature states that paired males in general sing less (Byers et al., 2015), and the recorder placement could have been out of the range to record them (recorder is able to pick up BAWW songs up to approximately 70 m therefore covering a large portion of territory), especially since the male spends more time mate-guarding and near the nest (Collins, 2004). Temperature and forage availability are also known to affect singing rates (Gil and Gahr, 2002), but this was beyond the scope of our study.

4.4.1 Song types

There is no clear trend between the proportion of A and B songs between paired and unpaired males in our results. BAWW are expected to sing fewer repeat-mode A songs in late season after pairing (Tyler, 1953 in Spector, 1992). Although 'less' is undefined for BAWW, in other warblers it is a 44-50% drop in A-songs (Lein, 1978; Morse, 1966). In our study, we had three territories with visually confirmed pairs; however, the first observations of these males occurred in the presence of their mate, precluding opportunities to assess any declines in A-songs.

The use of B-songs varies between warbler species. Although B-songs are used in territorial defence by some warblers, we observed male BAWW singing alarm calls rather than B-songs on occasions of aggressive interactions with conspecific males. During foraging, we observed communication calls between male and female that were low chips – rather than the B-songs used to communicate between males and females in other warblers (Spector, 1992).

4.4.2 Territory habitat

Although our results showed that there were no statistically significant differences in habitat variables between paired and unpaired territories, the summed height of shrubs were somewhat different. We found that the individual-plot heights of shrubs were not different, consistent with Morse (1977), but total amounts of shrubs at the micro-level (4 m² plot) were almost different ($p = 0.057$) between the two groups. Typically, choosiness for local- or micro-level habitat features is more often associated with nest specialists such as woodpeckers (Betts et al., 2006); however, lower rates of breeding success are typical for dense shrubby habitat compared to mid-aged mixedwood for BAWW (Paszkowski et al., 2004). Therefore, it is reasonable to find differences in shrubs between paired and unpaired birds, although our study does not attempt to be predictive considering our modest sample size.

It is somewhat unsurprising that there are no differences in the proportion of scrub, shrub, and forest at the 100 m level because BSC did not find differences even between presence and absence, nor did Paszkowski et al. (2004) in a similar study comparing BAWW territories. Consequently, it would be even more unlikely to find differences between paired and unpaired BAWW territories. Other habitat variables suggested to be important in BAWW territory selection included slope (steeper slopes protect nest sites from floods), and the presence of many big trees, which may provide better forage for this bark-gleaning species. However, we did not observe differences in slope as in other studies (Collins, 2004). Furthermore, the role of big trees may be more significant in landscapes with more competition and less food availability. On North Mountain, the high insect availability within alder thickets may mean less dependence on large trees for foraging. In a similarly disturbed forest with willow and alder thickets, Paszkowski et al. (2004) found that only 30% of BAWW were observed foraging on large trees.

4.4.3 Study limitations

Although our sample size of territories was small, Spector (1992) poses that a sample of 10 individuals would be enough for meaningful song comparisons as long as the time of day of recordings remained constant, as well as maintaining sight of the male during recordings to interpret the social situation of his singing. This is further supported by Staicer et al (2006) using a sample of 10 for intensive song study of AMRE. Yet the power of our analysis would have increased had we obtained a larger sample size. The influence of individual variation was persistent at the small scale we used, and patterns would be more discernable with a larger sample.

We can be confident that our recordings are not a result of an individual singing louder or quieter while in the same geographical place. Most evidence shows that warblers sing about the same loudness unless they are doing low-frequency call notes (like BAWW) between mates (Spector, 1992). Their normal high-pitched calls would be absorbed by vegetation, and instead mediumpitched call notes are used between males communicating with females on a ground nest (Spector, 1992). This explains why we picked up few call notes on recordings. Detectability could be affected by the fact that our H4N recorders were not tracking the bird; rather, they were placed within the territory for most of our recordings. As a result, the recorder could have picked up fewer songs due to placement, thus reducing our sample size. By using a tripod set up in different places within the birds' territory, we ran the risk of getting fewer recordings, but there was less bias from observer presence; maintaining visual contact with the bird would have resulted in confounding effects.

Asynchrony of timing of pairing and re-pairing somewhat affects our ability to detect differences in the proportions of song mode use between paired and unpaired birds in early and late season. This was shown by Staicer et al., (2006): "different arrival times of males and high rates of nest predation, after which females sometimes disappeared or, in rare cases, changed mates. Thus, at any given time, neighboring males often were in different breeding stages. Males who lost their mates sang at high rates, similar to males before they were paired" (p.447).

4.4.5 Future Research

Our research provides novel natural history observations and identifies patterns in song behaviour between paired and unpaired males of a relatively unstudied species. Improvements for future studies could involve capturing a more representative sample of song types to obtain an estimate of breeding density. We suggest that half of the entire North Mountain site (20 km^2 total) should be searched exhaustively and territories mapped for all BAWW to obtain an estimate of territory density. The distances between territories affect the amount and type of singing. In areas with closely packed territories, males may attempt to sing longer sections of song phrases to differentiate from neighbouring males (Goretskaia, 2013). Since BAWW territory sizes are variable, it is difficult to ascertain whether North Mountain territories were dense. In our study, having multiple objectives of conducting simultaneous point counts while searching for BAWW constrained our ability to map all territories at the site.

4.5 Conclusion

Our study shows that forest fragments on North Mountain provide adequate habitat to host BAWWs. However, many of these territory-holders appear to be unpaired, perhaps indicating that the grassland may be a habitat sink. The data do not show that females assess territories based on habitat features because there were no strong differences in habitat between territories regardless of the presence of a mate. Moreover, it may be male quality that is being selected for rather than territory habitat. A male bird may remain unpaired due to aspects of his song and fitness qualities, although two of our unpaired territories were found mid-season by which point females could have been nesting, causing them to be overlooked.

We found singing rates to be higher for unpaired males, supporting the hypothesis that unpaired males disproportionately are recorded on bird surveys. Overall, our results do not support the use of song types/modes for detecting pairing status of BAWW. Yet our study provided valuable updates regarding song-use by BAWW, such as their seemingly inconsistent use of repeat and serial mode songs regardless of pairing status. In addition, we suggest that B-songs (by extension serial-mode singing) are used more than previously thought by unpaired males, potentially showing the prevalence of alternative song uses between mates.

CHAPTER 5 Does Local-level Forest Cover and Composition Explain Songbird Distribution in the Moose-browsed Grassland of Cape Breton Highlands National Park?

5.1 Introduction

The amount and configuration of forest habitat as it may influence the distribution of songbirds remains a controversial topic in ornithology (Schlossberg and King, 2009). The effects of habitat isolation and patch size become more relevant in cases where there is less than approximately 30% habitat left, in addition to the general habitat loss (Andrén, 1994; Villard et al., 1999; Lee et al., 2002; Villard and Metzger, 2014). Patch ecology that uses variables such as the number of patches or patch size to predict species occurrences was originally developed for agricultural land management, but it has been criticized (Prugh et al., 2008) for being overly simplistic, using artificial spatial units (Schlossberg and King, 2009), even though the opposite has also been found (Lee et al., 2002). Overall, the relative influence of forest amount and composition affects forest songbird distribution inconsistently amongst individuals of the same species, and between species.

Ecological classifications of interior, specialist or generalist birds are often used to categorize the niches of forest birds and use habitat differently, therefore are distributed over the landscape differently. Specialist forest birds may distribute themselves in relation to micro-level (1-50 m) factors such as a single tree (Toenies et al., 2018), while generalist forest birds often select for habitat at neighbourhood (400 m +) or landscape (1-2 km) scales (Winiarski et al., 2017). Our observations of songbird habitat preferences on the level of analysis that we choose, often resulting in contrasting answers. For instance, forest songbirds may prefer forest at a landscape level but not a local level because they “use both edge and interior woodland features and benefit from both the better cover of dense woodlands and greater invertebrate prey density at edges” (Cunningham and Johnson, 2016).

Researchers use local-level approaches to examine the effects of edge and competition in bird-habitat relationships (Desrochers et al., 2010). Forests fragmented by anthropogenic (e.g. forestry) or natural (e.g. herbivory, insects) causes contain more edges. The increased light and complex vegetation structure of edge habitat support more species, but also lead to higher predation rates on adult and young birds (Fink et al., 2006). Competition among forest-associated songbirds also occurs in fragmented or edge habitats in landscapes where there is little remaining forest cover.

Large-mammal herbivory such as that of moose (*Alces alces*) is one cause of forest loss and fragmentation, sometimes creating large open areas devoid of trees and affecting the distribution of forest birds (Campbell, 2015). In areas with hyperabundant moose, such as in Newfoundland (Rae et al., 2014) and Northern Cape Breton Island (Franklin, 2013), browsing of shrubs and trees converts the boreal forest to savannah-type grasslands (Franklin et al., 2015). Despite these drastic ecosystem shifts, three forest songbirds - Blue-headed Vireo (BHVI) (*Vireo solitarius*), Yellow-bellied (YBFL) (*Empidonax flaviventris*), and Black-and-white Warbler (BAWW) (*Mniotilta varia*) - appear surprisingly unaffected by the moose-induced habitat changes (Rae et al., 2014; Campbell, 2015).

The general breeding grounds of YBFL are typically coniferous forest and treed peatlands (Gross and Lowther, 2011). In a study of thresholds to forest disturbance, YBFL showed tolerance for only patch cutting or single tree removal – and a sensitivity and avoidance of large open areas (Guenette and Villard, 2005). As this species primarily forages for insects in the air, it is possible that YBFL are adapted to open areas- often found along the edges of bogs, in the shrub-peat interface. Open areas may also be used as a nest site, YBFL nest at the base of tree roots or amongst moss, horizontal logs (Gross & Lowther, 2011).

BHVI are associated with mixedwood forests, or hemlock stands (Toenies et al., 2018) and often forage within the mid-canopy. Apart from requiring a shrub or tree in which to build their nests, they have, relative to cavity nesters, no specific requirements for nest sites. BHVI are less sensitive to intensive silviculture treatments such as conifer plantations and intensive patch cuts (Guenette and Villard, 2005), which is consistent with their choice of territories (3 ha) to include some open areas, usually wetlands in addition to forests. BHVI do not prefer edge but may be forced into these marginal areas due to the shortage of forest. With an already low breeding rate, they could be even more affected by increased nest predation and edge habitat.

BAWW are defined in many ways from forest specialists (Campbell, 2015), generalists (Rae et al., 2014), and in some texts they are referred to as a shrubland species (Schlossberg and King, 2008) or forest edge species (Toenies et al., 2018), and their breeding habitat ranges widely from dense shrubs to open young-to-mid-aged mixedwood. This diversity may stem from their ability to forage and nest non-specifically; however, the literature shows higher breeding rates in areas with mid-aged, less fragmented mixedwood over thickets (Paszowski et al., 2004). There is doubt about whether BAWW even respond to habitat at a local level (Rae et al., 2014), with one study showing that they select habitat mostly at a broad level (Desrochers et al., 2010).

In this study we focus on the relationships between forest variables and the presence or absence (P/A) of forest songbirds BAWW, BHVI, and YBFL within a moose-browsed landscape on North Mountain (approximately 20 ha) of Cape Breton Highlands National Park (CBHNP). The understanding of these selected species as forest birds is currently at odds with recent evidence showing no association to forest at a local (100 m) level (Campbell, 2015). Our objectives were to test for differences in forest patch size, the number of forested patches, and sum treed area at a 140 m (6.15 ha) level, between selected forest bird P/A. We hypothesize that the inclusion of these composition variables and larger level of analysis will produce strong relationships between selected species P/A and forest parameters. Our hope is to better understand the distribution of these forest birds relative to the diversity of available habitat and provide insights about boreal songbird resiliency to moose-browsing in CBHNP.

5.2 Methods

5.2.1 Study Area

The study was conducted on the highland plateau of North Mountain (46°48'29.4"N; 60°41'16.1"W), which is heavily browsed by moose within CBHNP. Many studies have occurred on North Mountain regarding spruce budworm (*Choristoneura fumiferana*) and moose-browsing vegetation dynamics as well as Bird Studies Canada (BSC) work (Campbell, 2014; Campbell, 2015; Franklin et al., 2015). The moose-browsed savannah is highly diverse. In some areas, wide-open fields contain scattered snags and low shrubs, which have avoided becoming browsed by snow cover in winter (Franklin et al., 205). In other areas, cover types dramatically change from grass to valleys dominated by bracken fern. Severely browsed balsam fir (*Abies balsamea)* and white birch (*Betula papyrifera*) are prominent and downed deadwood is common, although covered by graminoids (Franklin et al., 2015).

5.2.2 Data collection

5.2.2.3 Point counts

One-hundred point locations were systematically placed 300 m apart on North Mountain avoiding Acadian Forest and non-forest categories (i.e. barrens and bogs) for BSC in their 2014 and 2015 studies on changes in bird species diversity since the creation of grassland habitat (*Figure* 5). The average proportion of forest surrounding each point location was 18% (±0.17) with an average of 66% grassland (± 0.24) (Campbell, 2015). We used a subset of 55 points chosen through systematic random sampling. Early morning (dawn to 10 am) counts by competent birders who could identify birds by song and call. We used 10-minute counts and used a rangefinder to ensure birds were within a 150 m radius of point centre. Each point was visited three times from June 1- July 2. The 10-minute (versus 6-minute by BSC), three visits (versus one by BSC) and use of a rangefinder gave a good representation of spatial use by the three species.

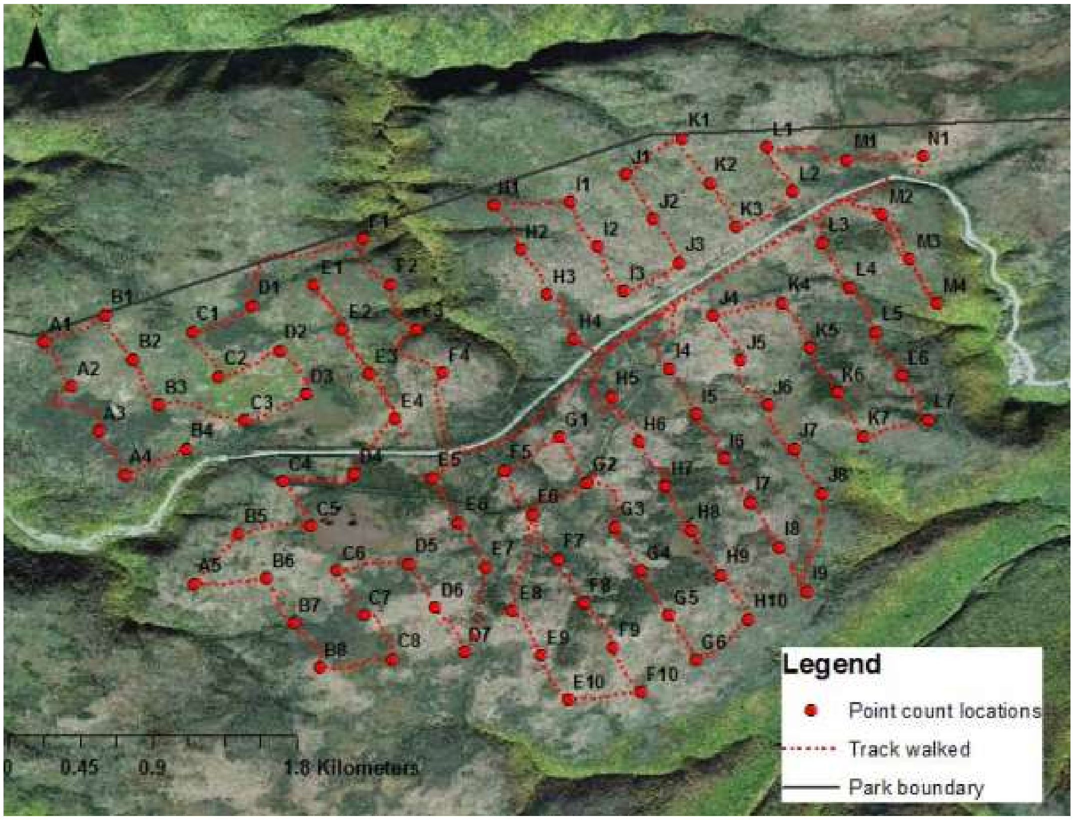


Figure 5 Total point count locations on North Mountain visited by BSC in 2014 and 2015. Selected species were first observed to be un-associated with forest cover in 2015; the basis of our study.

A separate P/A database was created for each of the three selected bird species (BHVI, YBFL and BAWW) on North Mountain. Data from three years of surveying were compiled, including the 2014 and 2015 BSC work and this study's 2017 point-count field data. Therefore, there were four surveys P/A data for the selected species: 2014, 2015, 2017, and all years combined. This study did not calculate individual species' detectability and instead addressed observer bias in the point-count design. In the context of understanding habitat relationships, without factoring in rare species and avoiding the assumption that a high density of a species equals habitat preference, simple P/A data were used.

5.2.2.4 Spatial forest data acquisition and conversion of point-count data

To describe the forested components of North Mountain, the SPOT5 imagery, colour pansharp at 2.5 m resolution, August 2013, Boreal Forest Mask, was used due to its high resolution which was conducive to characterizing a highly patchy habitat (CBHNP, 2015). The Boreal Forest Mask was developed by CBHNP in response to a need to better represent newly created grassland areas, which were highly underrepresented in the spatial data of the park. Effort was made to ensure that small (< 1 ha) forest patches were included, as these areas are important to forest birds (Schlossberg and King, 2008). Variables such as alders and scrub were correlated, so categories of habitat remained as treed (including alders) and non-treed (including scrub). Wetlands and barrens were not included as they were unaffected by moose browsing, except for some alder thickets which could be classified as swamps.

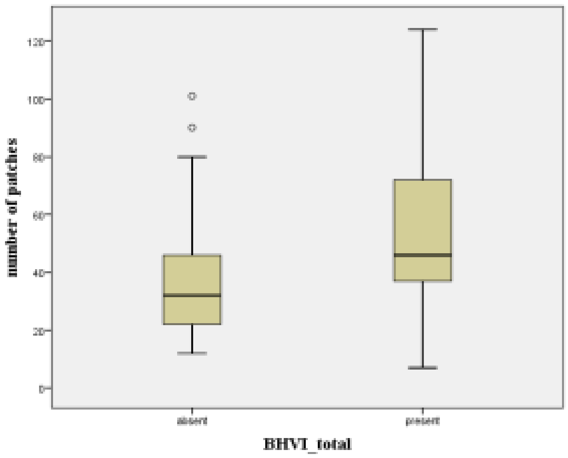
To define the spatial boundary around each point location (as in the Boreal Avian Modelling Project, 2012), a 140 m radius buffer (6.15 ha, within the range of a territory size) was applied with a geoprocessing tool. After the buffers were in place, we isolated the SPOT5 forest data within the buffered boundaries by using an 'intersect' geoprocessing tool to connect the values within, which were next exported to create a new layer. Using this layer, new attributes were created by adding new fields to the data attributes and running a tool to calculate area geometries. With these fields in place, we were able to develop three indices of forest using the tool calculate geometry in Arc-map: mean patch size, total number of patches, and total forested area. The forest indices output data were combined with the P/A bird data in the previously established database. All point locations surveyed on North Mountain contained at least some treed area within the 140 m (6.15 ha) radius of the habitat analysis.

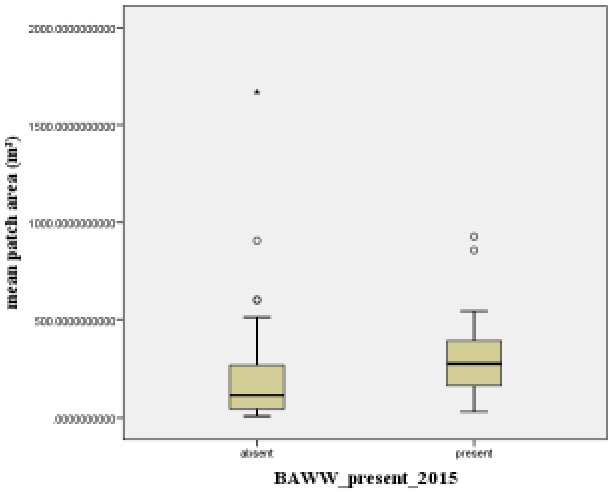
5.2.3 Analysis

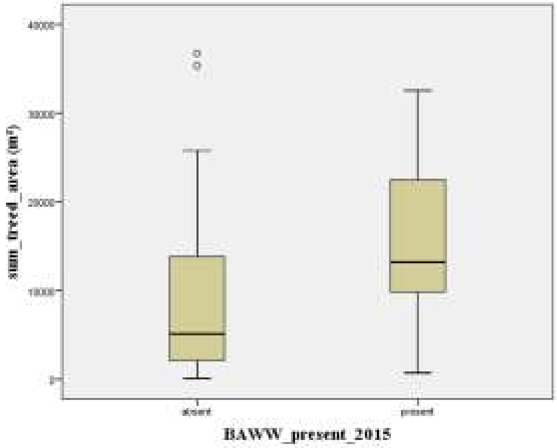
Relationships between bird P/A and habitat variables were assessed non-parametrically using the Mann-Whitney U test (hereafter referred to as Mann-Whitney U test) (McDonald, 2014). As the data were non-normally distributed and the sample size was small, this test was appropriate. The assumption of random sampling was met by using systematic random-sampling methods to choose point locations (from the previous 100) throughout the North Mountain study site. Vegetation and avian data collected at point locations were assumed to be independent due to the 300 m distance between points. The assumption of independence of avian data was addressed by following, in part, the Rocky Mountain Bird Observatory point-count protocols. Vegetation data were also deemed independent because of the consistently heterogeneous landscape of North Mountain. Histograms were compared between P/A for each independent forest variable, and it was observed that the shapes were all dissimilar, supporting the choice of the Mann-Whitney mean ranks rather than median ranks. We reported all differences as significant at an alpha level of 0.05. To compare differences between the number of years a selected species was present and forest variables, we used a one-way ANOVA, and reported significant differences also at an alpha level of 0.05.

5.3 Results

Overall, there were three differences between indices of BAWW presence (2015, total) and forest variables (mean patch area, sum treed area, and number of patches) and four significant differences between indices of BHVI presence (2014, total) and forest variables (mean patch area, sum treed area, and number of patches). Forest variables did not explain any differences between YBFL P/A. Boxplots (see *Figure 6*) show the distribution of data for all significant combinations of variables for BHVI and BAWW, but not for YBFL. Overall there were six outliers for BHVI and seven outliers for BAWW.


number of patches
120
100
80
60
40
20
0
absent
present
BHVI_total


mean patch area (m²)
2000.0000000000
1500.0000000000
1000.0000000000
500.0000000000
.0000000000
absent
present
BAWW_present_2015


sum_treed_area (m²)
40000
30000
20000
10000
0
absent
present
BAWW_present_2015

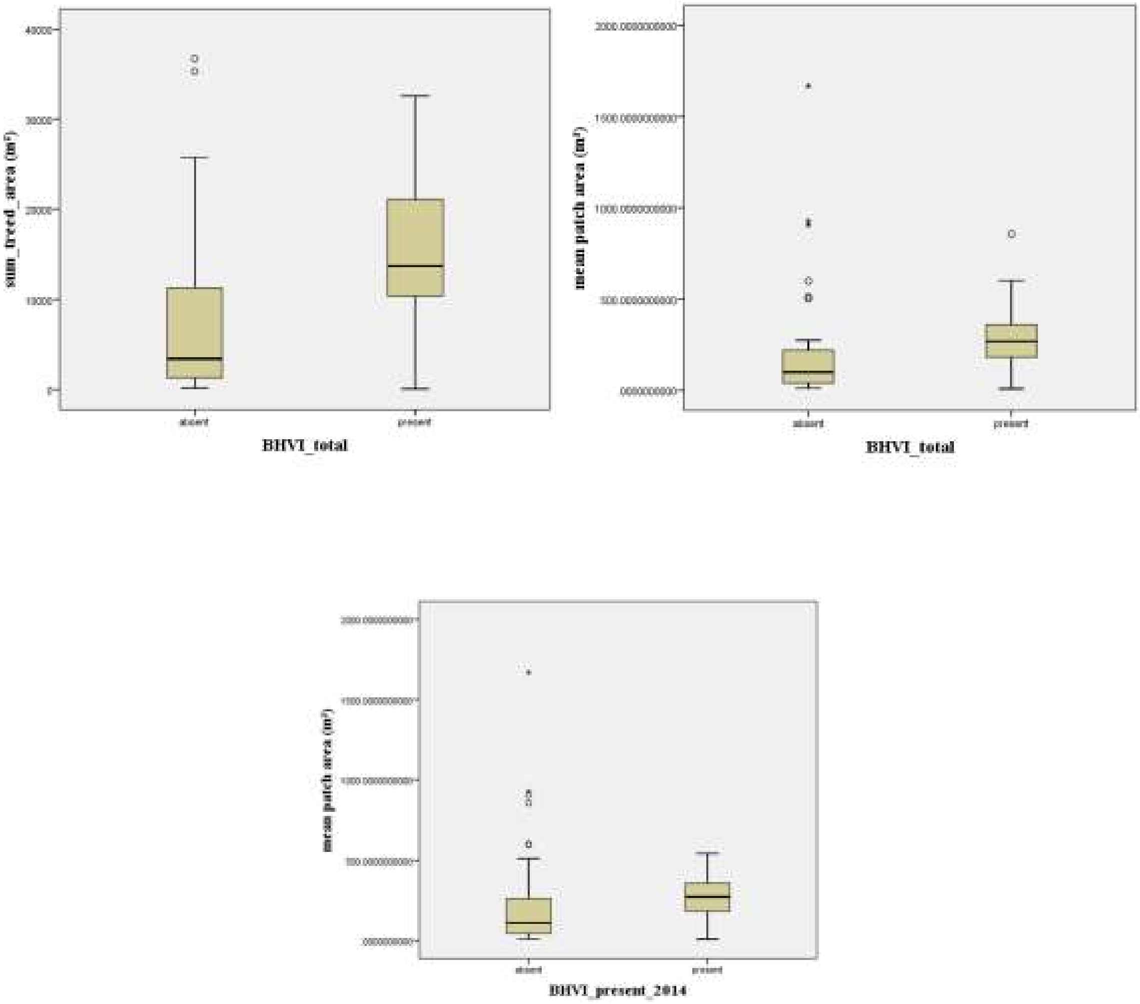


Figure 6 Box-Plots showing only significant relationships between habitat variables ‘number of treed patches,’‘mean patch area’ and total treed area between P/A data for BAWW and BHVI. Boxplots only show significant factors (p>0.05).

Mann-Whitney tests showed three differences between the mean ranks of BAWW P/A for all three forest indices; however, these differences were not consistent between years (*see Table 7*). P/A data for BAWW collected in 2015 shows a significant (*p*=0.033) positive relationship to the forest variables *sum treed area*, and *mean patch area.* Areas with BAWW present were more likely to have more forest coverage (*sum treed area*) (15,029 m²) than areas with BAWW absent (9,200 m²). There were also larger treed patches (326 m²) associated with BAWW presence rather than absence (233 m²). The number of treed patches were not related to BAWW P/A in the 2015 data; however, there was a significant (*p*=0.016) positive relationship when P/A data were summed for all years (BAWW total). There were more forest patches in areas where BAWW were present (50) than absent (32). On point count locations with BAWW present, the range of sum treed areas was from 6 m^2 to 32553 m^2, the mean patch areas from 9 m^2 to 926 m^2, and the number of forest patches from 7 to 124.

One third of possible relationships between BHVI and forest variables were significant (see *Table* 7). BHVI were more likely to be present in areas with large patches of forest in two of the four indices of P/A: `*BHVI 2014*` where there was a significant difference (p=0.006) between points with BHVI present (278 m^2) compared to absent (251 m^2); and `*BHVI total*` with significantly (p <0.05) larger patches of forest on points with BHVI (303 m^2) compared to without (230 m^2). BHVI presence (*BHVI total*) was also positively associated with increased forest cover (p=0.001) when comparing presence (15,187 m^2) and absence (8,039 m^2). There were significantly higher numbers of forest patches (p=0.018) on points with BHVI observed (56) versus not observed (39). There were no significant relationships ($p \geq 0.107$) for BHVI P/A data collected in 2017 or 2015. On point count locations with BHVI present the range of sum treed areas was from 6 m^2 to 32553 m^2, the mean patch areas from 9 m^2 to 856 m^2, and the number of forest patches from 7 to 124.

There were no significant relationships (p≥ 0.078) between YBFL P/A and forest variables. YBFL were seemingly distributed on North Mountain with no discernable preference for forest patch size. All selected forest birds exhibited high year-to-year variability. None of the species showed a positive relationship to any of the forest variables for all years. The range extended from 6 m^2 to 32553 m^2 of sum treed areas, 9 m^2 to 926 m^2 mean patch forested areas, and 7 to 99 forest patches on count locations with YBFL present.

Table 7 Mean, standard error (SE) for forest variables: number of forest patches, mean forest patch area, and sum treed area. Sample size (n) listed for species P/A for 2014, 2015, 2017, and total. Results of the Mann Whitney U test are listed under p-value (asymp. Sig. (2-tailed)). Significant (alpha level =0.05) variables are denoted with an asterisk.

			Number of Patches	**Mean Patch Area**	**Sum Treed Area**
	Mean		45.93	258.5 m^2	10819.15 m^2
	SE		3.7	41.1	1326
	n				
Indices of P/A	**0**	**1**	**(*p*-value)**	**(*p*-value)**	**(*p*-value)**
BAWW_2014	46	8	0.387	0.306	0.233
BAWW 2015	39	15	0.292	0.046*	0.033*
BAWW 2017	23	31	0.186	0.306	0.181
BAWW total	13	41	0.016*	0.279	0.142
YBFL 2014	45	9	0.515	0.291	0.291
YBFL 2015	46	8	0.688	0.119	0.355
YBFL 2017	32	22	0.603	0.078	0.238
YBFL total	24	30	0.979	0.243	0.465
BHVI 2014	39	15	0.306	0.05*	0.087
BHVI 2015	50	4	0.186	0.306	0.165
BHVI 2017	45	9	0.464	0.167	0.107
BHVI total	33	21	0.018*	0.006*	0.001*

Overall, seven out of 36 comparisons of forest associations and bird P/A were significant (*Table* 7). Next, we tested the relationship between forest variables and the number of years: 0 (absent all 3 years), 1 (present in 1 year), 2 (present in 2 years), 3 (present in 2014, 2015, and 2017).

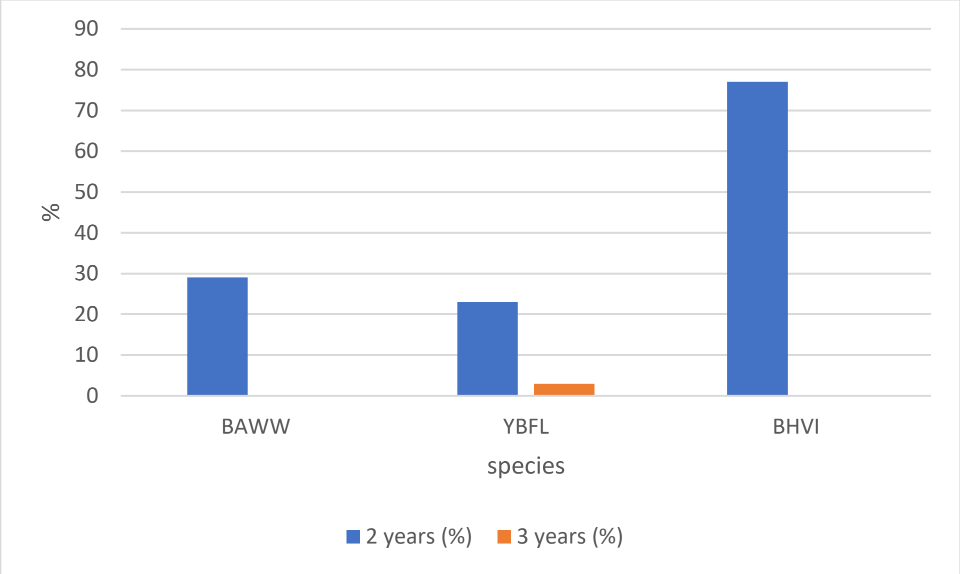


Figure 7 Species re-occurrence: total point locations with selected species observed in two and three years.

As shown in *Figure 7,* the selected species, although not necessarily individuals, appeared to show little site fidelity for more than two years, as demonstrated by the lack of observations of BAWW and BHVI at points for 3 years.

For BAWW, the only significant difference was between '# years observed' and '% treed' (p=0.011) For BHVI, year explained significant differences for two habitat variables: 'number of patches' (p=0.029), and '% treed' (p=0.014). For YBFL, there were no differences between the treed variables and year categories.

5.4 Discussion

We found that occupied habitats were, for the most part, not more forested than unoccupied sites, which was contrary to our hypothesis. Our results show that the composition and amount of forest was not consistently associated with the distribution of YBFL, BAWW, or BHVI although the relationship between forest variables and BHVI and BAWW was positive in seven instances overall, with larger patches and more continuous forest. Reasons for the inconsistent relationship between P/A and forest variables may differ for each species. In BHVI and BAWW, known forest associates, their apparent indifference to metrics of forest habitat may result from an inadequate scale of analysis or inadequate distance between point locations. On the other hand, YBFL, although a forest associate, can tolerate open areas and primarily utilize alder thickets (not mixedwood areas), in which case our broad definition of forest was not specific enough to identify patterns in their distribution. Results are discussed in the context of each individual species biology, year effects, non-habitat variables, spatial-level, study limitations, and future research.

One explanation is that remnant forest on North Mountain was perceived to be of relatively uniform habitat quality to each bird, in each 6.15 ha site (6 ha is within the size range of a songbird territory). Other studies in CBHNP showed that selected species also showed no preference for varying metrics of forest habitat even throughout the somewhat more in-tact forests of nearby French Mountain (*i.e.* less moose-browsing), suggesting that the amount of forest, although differing across sites, was equally preferable (Campbell (2015). Despite the classification of these species as forest species, BAWW and YBFL appear to accept a wide range of tree cover in their respective habitats.

5.4.1 BAWW

We found only three significant relationships, out of a possible twelve, between BAWW distribution and forest variables, indicating that BAWW somewhat prefer more forest cover, larger forest patches, and a higher number of forest patches. However, the high year-to-year variation in these results suggests that forest cover or composition exerts a low pressure on BAWW habitat selection at a local level.

One consideration in interpreting our results may be that, in some cases, BAWW choose habitat at a community level rather than local level (Rae et al., 2014). As the community level implies roughly a 0.5-1 km² area, BAWW choosing ideal habitat on North Mountain must not have prioritized forest cover since the area is equally dominated by grass and ferns. Our inclusion of forest composition variables and increased spatial level to 6.15 ha (compared to BSC habitat analysis) was still perhaps not enough to identify the habitat preferences of BAWW. Yet the short 300 m distance between point locations constrained our ability to broaden the scale of analysis. Furthermore, other studies using coarse-level habitat data found no relationships between BAWW and forest cover (Trzcinski et al., 1999).

Another cause for BAWW indifference to the forest variables we measured could be that the birds are using the remnant isolated single trees, snags, and horizontal logs, throughout the grassland, as shelter and nesting locations (Kricher, 2014; Boreal Avian Modelling Project, 2015). These types of trees would have been unaccounted for in the analysis since only tree patches larger than 2.5 m x 2.5 m (pixel size) would have been included in the classification of forest. BAWW may use these single trees as habitat in cases where forest patches are inundated with territories. Perhaps there is simply just *enough* trees, which explains the lack of association between forest variables and BAWW P/A. Most literature associates BAWW with forests, so individuals using mostly open habitat may be unpaired males that are more likely to populate poorer quality habitat. It is logical to think that most BAWW observed on point locations were coming from alder and treed edges, but it is important to note that BAWW must also be using grassland since several occupied sites contained very little trees.

With fewer trees from which to glean insects, BAWW could have adapted to forage using their less common aerial insectivore-type methods. For example, we observed BAWW hawking insects in the air on several occasions throughout open bog habitat on North Mountain. Hawking is not likely the preferred method of foraging; Paszkowski (2014) confirmed that BAWW gleaned insects off bark 80% of the time. Early-regeneration forests have high nutrient availability through increased plant productivity, increasing insect productivity for this warbler to hunt (Gower et al. 1996), but mature forest also has immense availability of bark upon which to search. In general, bark foragers such as BAWW have a wider range of habitat available to them, making it more difficult to determine their preferences (Blake and Hoppes, 1986). Our findings of BAWW distribution further support BAWW foraging in open grasslands.

5.4.2 BHVI

All our observations of BHVI occurred in mixedwood forest patches bordering alder thickets, consistent with Zimmerling et al. (2017). Therefore, it is unsurprisingly that of the three bird species, BHVI showed the strongest relationship (four differences out of 12) to the forest variables we measured. BHVI glean insects off branches and twigs, primarily in the mid-canopy and seem to be using small remnant patches of forest on North Mountain. Of the three indices of forest habitat, BHVI are most influenced by the size of forest patches, with larger forest patches more likely to host BHVI in two of the four years. There is little indication that BHVI are using the fern and grass-dominated savannah. In support of their strong forest association, BHVI were also the least abundant of the three bird species on the surveyed plots, occurring on only nine of the 55 point-locations. Low BHVI abundance may be influenced by a high proportion of the remnant areas being alder thickets, for which BHVI show a low preference.

With such strong reliance on trees for habitat, we expected BHVI to be consistently associated with forest variables. However, this was not the case, and the roles of BHVI song volume, territory size, and association with open wetlands may explain the variation in our results. As BHVI use open wetlands at the edge of their territories (Morton and James, 2014), we must not assume that ideal habitat can be simplified to forest. BHVI also have a relatively wide-ranging territory size, which could exceed the spatial boundary of 6.15 ha in our analysis. Effort was made to ensure that individuals were visually located on point-counts or by attempting to locate the distance of songs with range-finder, but the loud projecting song of the BHVI could have resulted in the distance being underestimated, and it is possible BHVI observed by sound may have been outside of the 150 m range.

5.4.3 YBFL

Landscape-level habitat choice (Taylor and Krawchuk, 2005), competition, and selection for non-forested resources offer potential explanations for the lack of relationship between YBFL and local-level forest metrics. We know forests (often edges and steep slopes in mixedwood areas) are an important component of YBFL habitat, offering perches for foraging and gleaning insects off branches. However, their seeming indifference to forest at a local level suggests that the species must tolerate low levels of (a significant portion of point locations contain less than 50% forest), further supported by their use of open bogs (Gross and Lowther, 2011), or accept a wide range in the amount and composition of forest in their habitat. Selection for non-forest resources such as small, not large open areas (Blake and Hoppes, 1987; Guenette and Villard, 2005) and wetlands may be equally as important as forest. Open grasslands support a high abundance of insects that YBFL could benefit from using aerial insectivore techniques while open bogs provide nesting habitat in sphagnum or at the base of tree roots. However, flycatchers do not seem to choose territorial habitat based predominantly on the highest abundance of arthropods and insects (Mäntylä et al., 2015).

YBFL observed on points with a high proportion of grassland may be unpaired individuals in poorer quality habitat. Despite gaps in our knowledge of this elusive flycatcher's habitat preferences, wetlands combined with interior dense forest seem to be ideal habitat (Gross and Lowther, 2011). It is possible that unpaired YBFL are being forced to use less forest and more open grassland in response to competition with Alder Flycatchers, of which we observed many in alders on North Mountain.

5.4.4 Level of spatial analysis

Coarser-level data may be sufficient in analysis of relatively homogeneous ecosystems, but our study shows the importance of representing the finer-level configuration and composition of forest patches. It is well known that in an area devoid of continuous good habitat, smaller patches and linear fragments may be used more (Villard et al., 2014); e.g., fence rows used to delineate agricultural fields are still useful to birds despite their width of only a few metres in some cases (Haas, 1995).

The local-level scale of analysis may not have provided the range of vegetation diversity necessary to distinguish differences in forest habitat required for generalist birds. Although there were point locations on North Mountain almost devoid of forest, others had over 60% woodland cover, and most points had a mixture of forested and open areas. At a community- or landscape-level scale of analysis, it may be more feasible to identify the thresholds of habitat preferences. Undoubtedly there is no consensus about which spatial level best shows differences but using the boundaries of a defended territory would be a more accurate approach. The time and resource constraints of our project prevented mapping territories.

There is also the possibility that the distribution of the three species was in part due to positive spatial autocorrelation (Betts et al., 2006), in that similar forest indices may exist closer together. However, while at larger scales the North Mountain landscape was mostly open grassland, at a micro-level it was highly diverse throughout its entirety, suggesting autocorrelation effects would be minimal compared to studies set in a continuous grassland bordering a continuous forest, where points next to one another would be more likely to be the same.

5.4.5 Multiple factors and year-to-year effects

We found that the variable *year* explained the variation in two of the forest variables, number of patches and total forest cover. Factors which may affect the changing abundance of YBFL, BHVI, and BAWW arriving on North Mountain include low site fidelity, or high diversity in the amount of tree cover individual birds select for. Villard et al. (1999) also found there was high year-to-year variation when testing relationships between forest birds and forest cover and composition (Villard et al., 1999), especially in edge habitats. Relationships between species presence and forest community structure make avian conservation and restoration decisions somewhat difficult as there is such high year-to-year variability – especially for species such as BAWW which have low site fidelity. Often the behaviour of moving to different areas each year to breed is more common in landscapes with high levels of predation (Fink et al., 2006). Furthermore, marginal habitat may also have higher mortality rates and contribute to the high year-to-year variation in individual usage (Thompson et al., 2002). Landscapes that experience disproportionately strong predation or mortality are often areas with large amounts of edge habitat, such as in North Mountain.

Factors other than cover and composition of associated vegetation may dictate the distribution of selected songbirds. Heikkinen et al. (2004) asserted that most patterns of species variation in a landscape are complex and interconnected amongst multiple variables; it is possible we found inconsistent relationships between selected species and forest habitat due to a combination of variables. We justified our focus on forest cover and composition because it is the forest which has been in decline because of moose, and their extensive browsing is expected to continue.

We found that our three forest-bird species did not consistently prefer areas with more forest. The findings are consistent with those of Schlossberg et al. (2010), where only half of the shrub-associated bird species showed a significant preference for greater shrub cover, suggesting there may be a threshold of minimum forest cover required. For BAWW that nest on the ground, fern- and grass-covered local landscapes may provide adequate food and nesting habitat, although our data also show a higher number of unpaired birds in these areas (M. Alexander, unpublished data, Chapter 4 in this thesis). Rigid human-constructed concepts about a species ‘preferred’ habitat become obsolete when researchers consider the other factors affecting its distribution such as sexual selection, competition, and song (Corbani et al., 2014).

5.4.6 Forest cover and composition

BHVI (total) and BAWW (2015) were associated to forest cover out of the eight possible indices of presence (year), showing weak support about whether these species select for forest cover at the local level. Winiarski et al (2017) found that forest cover at a landscape level can be a better predictor of presence than local-level forest indices, but other studies show landscape-level analysis (10 km x 10 km) similarly fail to predict species presence (Trzcinski et al., 1999). Our results demonstrate that the most important forest variable in determining BHVI and BAWW distribution was mean patch size. In recent decades there have been continued arguments regarding the value of habitat composition in explaining species distribution. Patch area is at times an important predictor of forest birds, as in our study (Lee et al., 2002). However, in cases where there is a high amount of edge habitat, the manner remnant habitat is arranged on the landscape becomes more important (Villard and Metzger, 2014).

5.4.7 Study limitations

Observer effects, such as disturbance and detection, are critical to consider when interpreting results. Effects such as walking through an area only two times can cause territory establishment to be disturbed, resulting in fewer territories occurring in disturbed areas (Bötsch et al., 2017). As point locations were visited on three separate occasions in 2017, there is a possibility that observer presence had a disproportionate effect on whether the selected species was observed, compared to 2014 and 2015 counts, which were only visited once. Since species detectability was addressed using rangefinders to ensure that birds were within the radius of observation, we are confident in the reliability of our point-count data – visiting each count three times made it more likely that we observed true presence in these habitats (species detectability rates were high).

Future studies should include alternative classification of forest, mapping territories as the natural spatial unit of the analysis and determining the nesting success (instead of pairing) of selected species. Our study defined forest as alder and treed, consistent with past studies in the park (e.g. BSC, and Boreal Forest Mask spatial project by CBHNP); however, classifying alder thickets as separate forest types could help researchers better understand the preferences of selected species. Future studies may also obtain a more accurate understanding of habitat choice from mapping territories of these species and using territory boundaries as the spatial unit of habitat analysis rather than using P/A data surrounding a point-count location. Future research determining the breeding success of these species would help assess whether YBFL, BAWW, and BHVI on North Mountain are mostly bachelors in marginal habitat, or breeding individuals adapting to forage and nest in more open areas.

5.5 Conclusion

The weak association of selected species to forest habitat metrics suggests that YBFL, BHVI, and BAWW may be adapting to crossing or utilizing large open grasslands, supported by the notion that they already cross inhospitable habitat during migration (Bélisle et al., 2001). At the landscape level, despite the extreme transformation to grassland, North Mountain retains adequate forest in the surrounding area to support populations of YBFL and BAWW. CBHNP managers should not be concerned about the effect of moose browse on YBFL or BAWW populations, since the amount of habitat must decline below approximately one third (at a spatial unit of analysis of 2000 m radius) before the species declines. On the North Mountain plateau, the minimum threshold of forest habitat may not have been exceeded, although there is uncertainty about whether the rule of one third habitat decline is useful at our local level.

This study is an important contribution to improve our understanding of the complex role moose browsing plays in affecting the configuration and cover of forest and whether these changes affect insectivorous songbird habitat use. Our results seem to suggest a certain resilience of the selected bird species to the moose-browsed grassland, as indicated by their lack of consistent preference for forested areas at a local level. There is growing concern about the fate of boreal forest songbirds in areas dominated by grassland in the park. However, contrary to our hypothesis, there is no clear trend as to whether YBFL and BAWW will decline on North Mountain and similar habitats with less forested areas, and some indication BHVI are more reliant on forested habitats.

CHAPTER 6 CONCLUSION

Classifications of birds as forest species can bias our assumptions about their use of other habitats. All three species – YBFL, BHVI, and BAWW – are known forest birds, but their use of the grassland, ferns, snags, felled logs, and wetland habitats in North Mountain is important when considering their vulnerability to forest loss in CBHNP due to continued heavy moose browsing. We conceptualized the selected bird's potential adaptation to grassland by examining its effects on bird breeding success through an exploration of BAWW song types as indicative of breeding, and the distribution of BAWW, BHVI, and YBFL.

The level of spatial analysis of bird and habitat data can produce a wide range of different conclusions. For example, BAWW, BHVI, and YBFL may choose open habitat at a local level for the plentiful foraging opportunities but require forest at a home-range level for general cover from predators. Our research, which used local-level data (2.15 ha), contributes to the body of knowledge regarding the most appropriate level of analysis for explaining selected bird species distribution in patchy habitat. Our study allowed for a more complete understanding of the roles played by forest amount and composition at a local level in determining the distribution of three boreal songbirds. We found that of the three species, only BHVI showed a moderate association to forest, followed by BAWW, while YBFL appeared to choose habitat independent of the amount of forest.

We met our objective of determining whether the moose-browsed grassland mainly housed unpaired males and whether song could be used as a method of determining pairing status. Results showed about one third of BAWW were breeding pairs; that degree of breeding success in the most heavily browsed area of CBHNP suggests the species is likely adapting to and breeding even more successfully in other less-impacted areas. The insignificant differences in vegetation between paired and unpaired BAWW territories show that consideration should be made for alternative explanations of BAWW breeding success aside from forest habitat variables (*e.g.* the roles of male quality, song, territory size). Their adaptability in the face of habitat alterations suggests BAWW are at a low risk of population decline due to boreal forest loss produced by hyperabundant moose browsing. Although overall in areas with less shrubs and more grassland, the species will have less foraging and nesting opportunities.

The objective to update song-type use in BAWW was led to an unexpected conclusion: that song types did not differ between paired and unpaired birds, in contrast to past studies and theories. We suggest the novel idea that unpaired males sing more B-songs (serial-mode singing), which demonstrates the prevalence of alternative song uses between mates. To our knowledge, this may be the first evidence of equal B-song singing between paired and unpaired BAWW. Studies such as ours show the value of re-visiting and questioning past studies of song types. The study of song types in ornithology continues to produce contrasting evidence. To address this, song studies with larger sample sizes should be employed on North Mountain and elsewhere to further test the meaning of song types and expand the list of auditory cues for field technicians and avian consultants. Our hope is to move towards developing a protocol that will allow for the early identification of breeding status and enhance conservation protection for warblers.

Managers of CBHNP should be cognizant that there is evidence for YBFL, BHVI, BAWW survival in moose-browsed areas. It appears the survival of YBFL and BAWW is relatively high in North Mountain but low for BHVI. Despite relatively high occurrences of YBFL and BAWW throughout the grassland, it appears that many of these birds are without a mate (potentially indicating poorer quality habitat), as our results demonstrate for BAWW. We emphasize that future studies should examine the nesting and fledgling success of these species. Further studies should also include the tracking individuals to determine the role of factors outside of their breeding range in determining the presence of selected species, as well as mapping territories of each species to have a more precise understanding of habitat associations. Our results further support past studies by BSC in moose-browsed habitat on CBHNP and suggest that boreal forest decline on North Mountain has not exceeded a threshold where it can no longer support YBFL, BAWW, and BHVI.

The future of forest regeneration on North Mountain will affect the future of YBFL, BHVI, and BAWW breeding habitat. With moose population-limiting controls already in place, shrubs and trees are likely to continue regenerating, preventing the area from reverting completely to grassland. Nonetheless, it appears that the current amount of forest is still enough to provide habitat for the selected species. The distinct pathway of forest succession is unknown, but without moose, shrubs and trees are expected to return to the current grass-dominated areas. Although tree planting efforts by CBHNP staff have contributed to forest regeneration, the imminent spruce budworm outbreak may once again cause fir and spruce mortality in the park - boreal species will once again re-enter the flux of vegetation change – as is the nature of things.

Undoubtedly spruce budworm and moose play a crucial role shaping and maintaining habitat heterogeneity, and thereby indirectly impacting YBFL, BHVI, and BAWW distribution and breeding success on North Mountain. Although the patchy mosaic forests of North Mountain likely host individuals with poorer reproductive success, the moose-browed landscape supports a similar diversity of birds to surrounding forested areas (Campbell, 2015). It offers a myriad of microhabitats for diverse nesters and foragers such as YBFL and BAWW, which appear to have wide-ranging preferences for different proportions of forest, patch sizes, and number of forest patches. Although concerns regarding forest loss are well-founded for forest species such as Bicknell's thrush, the unique complexity of vegetation, snags, and minute tree-island composition of the grassland provide some alternative habitat for the three forest birds. Although it is not clear that *a change can do good* for all BAWW and BHVI, it seems very plausible for YBFL**.**

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APPENDIX A

Raw Data

Table A1 Summary table of total number of repeat and serial mode singing intervals (5-minute periods of >2 songs) between early and late season for all BAWW males.

Early season			Late season	
territory	repeat mode	serial mode	repeat mode	serial mode
P1	8	9	5	1
P2	3	5	1	0
P3	2	3	0	6
UN1	9	3	7	0
UN2	1	0	23	1
UN3	9	4	0	16
UN4	1	0	2	10
UN5	1	0	0	5

Table A2 Fischer Exact Probability Test results for BAWW song modes for early and late season

Territories	p value (E)	p value (L)
P2-P3	1	0.143
P2_P1	1	1
P2_UN1	0.167	1
P2_UN3	0.203	0.059
P2_UN4	0.444	0.231
P2_UN5	0.444	0.167
P2_UN2	0.444	1
UN2_P3	1	0.00001***
UN2_P1	1	0.366
UN1_UN2	1	1
UN2_UN3	1	2.70-E10***
UN2_UN4	1	2.66-E10***
UN2_UN5	1	0.00005***
UN5_P3	1	1
UN5_P1	1	0.015
UN5_UN1	1	0.00126**
UN5_UN3	1	1
UN5_UN4	1	1

UN4-P3	1		0.529
UN4_P1	1		0.013
UN4_UN1	1	0.00071**	
UN4_UN3	1		0.175
UN3_P3	0.326		1
UN3_P1	0.286	0.00023***	
UN3_UN1	1	4.06-E08***	
UN1_P3	0.28	0.00058**	
UN1_P1	0.251		0.462
P3_P1	1		0.015

Table A3 Neighbourhood-level (100-m radius) habitat data for BAWW territories

pairing status	territory	% shrub	% forest	% scrub	aspect	slope	% saturated	big trees	holes
Unpaired	BAWW11	3	2	2	95	20	1	1	2
Unpaired	BAWW11-3	2	1	2	216	4	0	0	0
Unpaired	BAWW0608	3	1	2	0	9	1	3	1
Unpaired	BAWW16	2	1	3	139	9	0	36	0
Unpaired	BAWW24	1	3	2	350	11	0	3	1
Unpaired	BAWW072	2	2	4	92	2	3	0	1
Paired	BAWWD5	3	1	4	98	3	4	6	0
Paired	BAWW042	3	2	3	129	5	1	0	0
Paired	BAWW053	3	3	2	210	4	1	0	5

Table A4 Local-level (2 m x 2 m plot) data of BAWW territories

date	territory	plot number	height category	% shrub	% deciduous	% conifer
16-Aug	BAWW D5	1	1	1	0	0
16-Aug	BAWW D5	1	2	0	0	0
16-Aug	BAWW D5	1	3	0	0	0
16-Aug	BAWW D5	1	4	0	0	0
16-Aug	BAWW D5	1	5	0	0	0
16-Aug	BAWW D5	2	1	1	0	1
16-Aug	BAWW D5	2	2	0	0	1
16-Aug	BAWW D5	2	3	0	0	0
16-Aug	BAWW D5	2	4	0	0	0
16-Aug	BAWW D5	2	5	0	0	0
16-Aug	BAWW D5	3	1	1	0	0

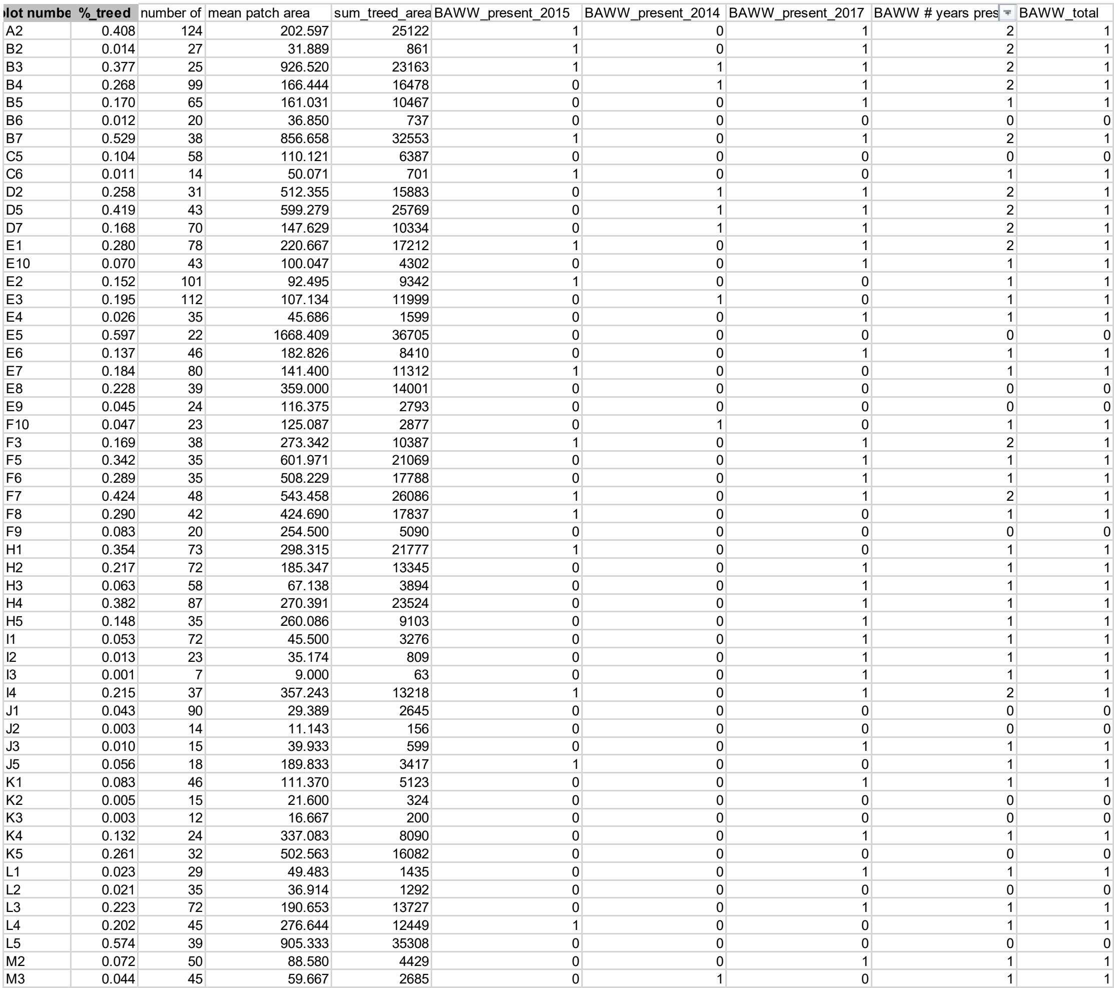
16-Aug	BAWW D5	3	2	0	0	0
16-Aug	BAWW D5	3	3	0	0	0
16-Aug	BAWW D5	3	4	0	0	0
16-Aug	BAWW D5	3	5	0	0	0
16-Aug	BAWW 072	1	1	2	0	1
16-Aug	BAWW 072	1	2	0	0	0
16-Aug	BAWW 072	1	3	0	0	0
16-Aug	BAWW 072	1	4	0	0	0
16-Aug	BAWW 072	1	5	0	0	1
16-Aug	BAWW 072	2	1	1	0	0
16-Aug	BAWW 072	2	2	1	0	1
16-Aug	BAWW 072	2	3	0	0	0
16-Aug	BAWW 072	2	4	0	0	0
16-Aug	BAWW 072	2	5	0	0	0
16-Aug	BAWW 072	3	1	1	0	0
16-Aug	BAWW 072	3	2	1	0	1
16-Aug	BAWW 072	3	3	0	0	1
16-Aug	BAWW 072	3	4	0	0	0
16-Aug	BAWW 072	3	5	0	0	0
16-Aug	BAWW0608	1	1	1	0	0
16-Aug	BAWW0608	1	2	1	0	0
16-Aug	BAWW0608	1	3	2	0	0
16-Aug	BAWW0608	1	4	0	0	0
16-Aug	BAWW0608	1	5	0	0	0
16-Aug	BAWW0608	2	1	1	0	0
16-Aug	BAWW0608	2	2	1	1	1
16-Aug	BAWW0608	2	3	0	0	0
16-Aug	BAWW0608	2	4	0	0	0
16-Aug	BAWW0608	2	5	0	0	1
16-Aug	BAWW0608	3	1	1	0	0
16-Aug	BAWW0608	3	2	0	0	1
16-Aug	BAWW0608	3	3	0	0	0
16-Aug	BAWW0608	3	4	0	0	0
16-Aug	BAWW0608	3	5	0	0	1
16-Aug	BAWW 053	1	1	0	0	0
16-Aug	BAWW 053	1	2	1	0	0

16-Aug	BAWW 053	1	3	0	0	0
16-Aug	BAWW 053	1	4	0	0	0
16-Aug	BAWW 053	1	5	0	1	0
16-Aug	BAWW 053	2	1	0	1	0
16-Aug	BAWW 053	2	2	0	0	0
16-Aug	BAWW 053	2	3	0	0	0
16-Aug	BAWW 053	2	4	0	0	0
16-Aug	BAWW 053	2	5	0	3	2
16-Aug	BAWW 053	3	1	1	0	0
16-Aug	BAWW 053	3	2	1	0	0
16-Aug	BAWW 053	3	3	2	0	0
16-Aug	BAWW 053	3	4	0	0	0
16-Aug	BAWW 053	3	5	0	1	0

Table A5 Number of years selected species were present at North Mountain (2014, 2015, 2017)

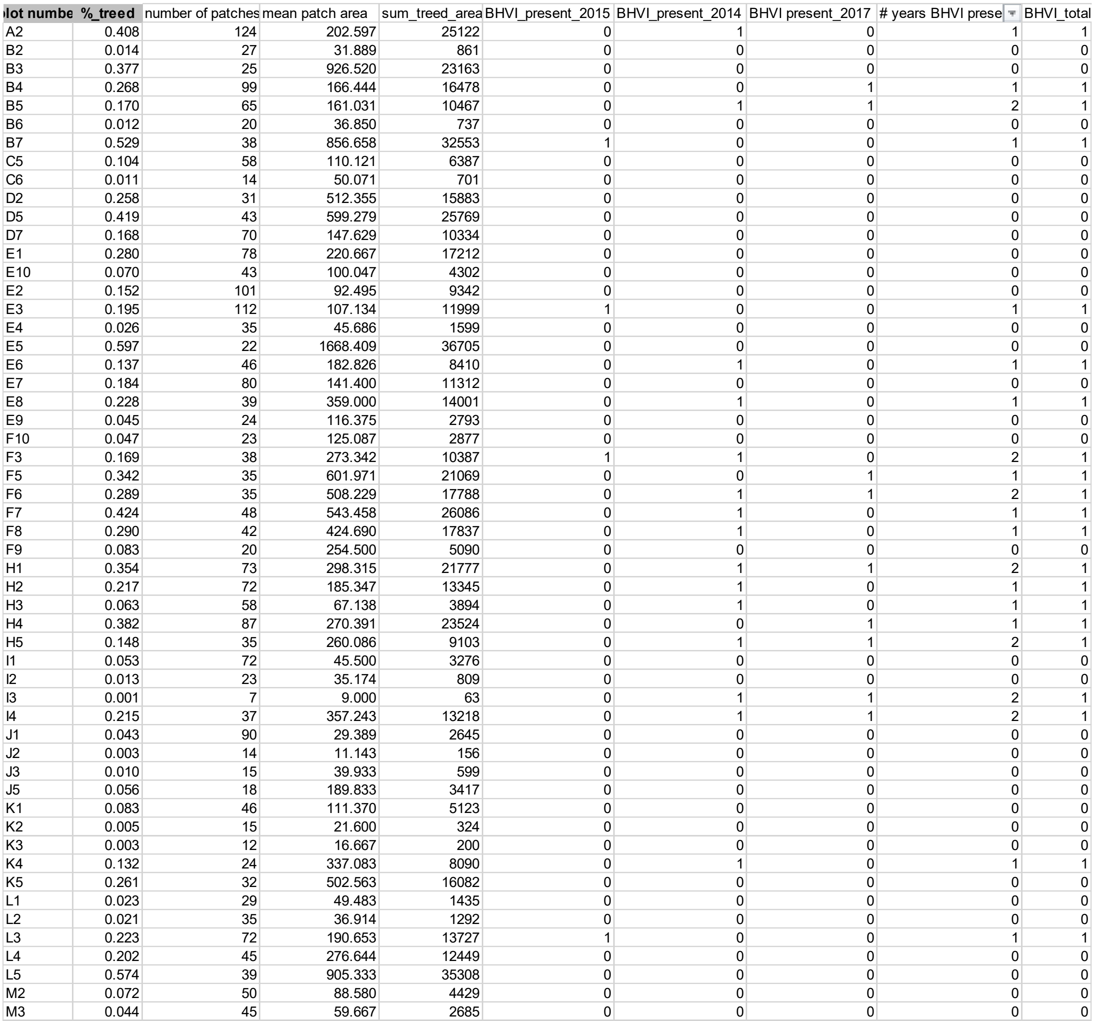
species	**2 years**	**3 years**
BAWW	12	0
YBFL	7	1
BHVI	7	0
Percentages		
	2 years (%)	3 years (%)
BAWW	29	0
YBFL	23	3
BHVI	77	0

Table A6 Forest variables and bird presence (1) and absence (0) at each point count location for BAWW



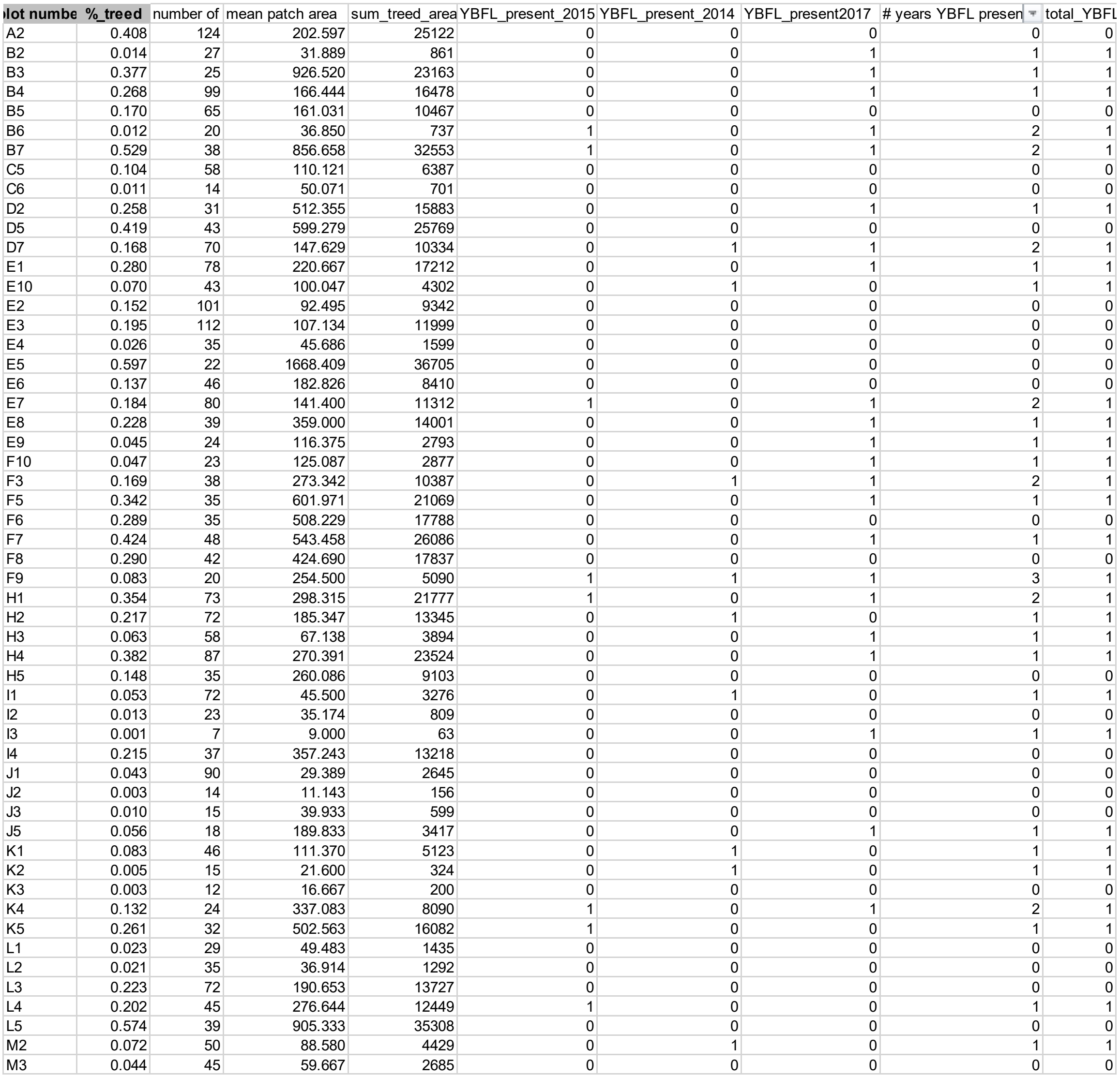
lot numbe	%_treed	number of	mean patch area	sum_treed_area	BAWW_present_2015	BAWW_present_2014	BAWW_present_2017	BAWW # years pres	BAWW_total
A2	0.408	124	202.597	25122	1	0	1	2	1
B2	0.014	27	31.889	861	1	0	1	2	1
B3	0.377	25	926.520	23163	1	1	1	2	1
B4	0.268	99	166.444	16478	0	1	1	2	1
B5	0.170	65	161.031	10467	0	0	1	1	1
B6	0.012	20	36.850	737	0	0	0	0	0
B7	0.529	38	856.658	32553	1	0	1	2	1
C5	0.104	58	110.121	6387	0	0	0	0	0
C6	0.011	14	50.071	701	1	0	0	1	1
D2	0.258	31	512.355	15883	0	1	1	2	1
D5	0.419	43	599.279	25769	0	1	1	2	1
D7	0.168	70	147.629	10334	0	1	1	2	1
E1	0.280	78	220.667	17212	1	0	1	2	1
E10	0.070	43	100.047	4302	0	0	1	1	1
E2	0.152	101	92.495	9342	1	0	0	1	1
E3	0.195	112	107.134	11999	0	1	0	1	1
E4	0.026	35	45.686	1599	0	0	1	1	1
E5	0.597	22	1668.409	36705	0	0	0	0	0
E6	0.137	46	182.826	8410	0	0	1	1	1
E7	0.184	80	141.400	11312	1	0	0	1	1
E8	0.228	39	359.000	14001	0	0	0	0	0
E9	0.045	24	116.375	2793	0	0	0	0	0
F10	0.047	23	125.087	2877	0	1	0	1	1
F3	0.169	38	273.342	10387	1	0	1	2	1
F5	0.342	35	601.971	21069	0	0	1	1	1
F6	0.289	35	508.229	17788	0	0	1	1	1
F7	0.424	48	543.458	26086	1	0	1	2	1
F8	0.290	42	424.690	17837	1	0	0	1	1
F9	0.083	20	254.500	5090	0	0	0	0	0
H1	0.354	73	298.315	21777	1	0	0	1	1
H2	0.217	72	185.347	13345	0	0	1	1	1
H3	0.063	58	67.138	3894	0	0	1	1	1
H4	0.382	87	270.391	23524	0	0	1	1	1
H5	0.148	35	260.086	9103	0	0	1	1	1
I1	0.053	72	45.500	3276	0	0	1	1	1
I2	0.013	23	35.174	809	0	0	1	1	1
I3	0.001	7	9.000	63	0	0	1	1	1
I4	0.215	37	357.243	13218	1	0	1	2	1
J1	0.043	90	29.389	2645	0	0	0	0	0
J2	0.003	14	11.143	156	0	0	0	0	0
J3	0.010	15	39.933	599	0	0	1	1	1
J5	0.056	18	189.833	3417	1	0	0	1	1
K1	0.083	46	111.370	5123	0	0	1	1	1
K2	0.005	15	21.600	324	0	0	0	0	0
K3	0.003	12	16.667	200	0	0	0	0	0
K4	0.132	24	337.083	8090	0	0	1	1	1
K5	0.261	32	502.563	16082	0	0	0	0	0
L1	0.023	29	49.483	1435	0	0	1	1	1
L2	0.021	35	36.914	1292	0	0	0	0	0
L3	0.223	72	190.653	13727	0	0	1	1	1
L4	0.202	45	276.644	12449	1	0	0	1	1
L5	0.574	39	905.333	35308	0	0	0	0	0
M2	0.072	50	88.580	4429	0	0	1	1	1
M3	0.044	45	59.667	2685	0	1	0	1	1

Table A7 Forest variables and bird presence (1) and absence (0) at each point count location for BHVI



lot numbe	%_treed	number of patches	mean patch area	sum_treed_area	BHVI_present_2015	BHVI_present_2014	BHVI present_2017	# years BHVI prese	BHVI_total
A2	0.408	124	202.597	25122	0	1	0	1	1
B2	0.014	27	31.889	861	0	0	0	0	0
B3	0.377	25	926.520	23163	0	0	0	0	0
B4	0.268	99	166.444	16478	0	0	1	1	1
B5	0.170	65	161.031	10467	0	1	1	2	1
B6	0.012	20	36.850	737	0	0	0	0	0
B7	0.529	38	856.658	32553	1	0	0	1	1
C5	0.104	58	110.121	6387	0	0	0	0	0
C6	0.011	14	50.071	701	0	0	0	0	0
D2	0.258	31	512.355	15883	0	0	0	0	0
D5	0.419	43	599.279	25769	0	0	0	0	0
D7	0.168	70	147.629	10334	0	0	0	0	0
E1	0.280	78	220.667	17212	0	0	0	0	0
E10	0.070	43	100.047	4302	0	0	0	0	0
E2	0.152	101	92.495	9342	0	0	0	0	0
E3	0.195	112	107.134	11999	1	0	0	1	1
E4	0.026	35	45.686	1599	0	0	0	0	0
E5	0.597	22	1668.409	36705	0	0	0	0	0
E6	0.137	46	182.826	8410	0	1	0	1	1
E7	0.184	80	141.400	11312	0	0	0	0	0
E8	0.228	39	359.000	14001	0	1	0	1	1
E9	0.045	24	116.375	2793	0	0	0	0	0
F10	0.047	23	125.087	2877	0	0	0	0	0
F3	0.169	38	273.342	10387	1	1	0	2	1
F5	0.342	35	601.971	21069	0	0	1	1	1
F6	0.289	35	508.229	17788	0	1	1	2	1
F7	0.424	48	543.458	26086	0	1	0	1	1
F8	0.290	42	424.690	17837	0	1	0	1	1
F9	0.083	20	254.500	5090	0	0	0	0	0
H1	0.354	73	298.315	21777	0	1	1	2	1
H2	0.217	72	185.347	13345	0	1	0	1	1
H3	0.063	58	67.138	3894	0	1	0	1	1
H4	0.382	87	270.391	23524	0	0	1	1	1
H5	0.148	35	260.086	9103	0	1	1	2	1
I1	0.053	72	45.500	3276	0	0	0	0	0
I2	0.013	23	35.174	809	0	0	0	0	0
I3	0.001	7	9.000	63	0	1	1	2	1
I4	0.215	37	357.243	13218	0	1	1	2	1
J1	0.043	90	29.389	2645	0	0	0	0	0
J2	0.003	14	11.143	156	0	0	0	0	0
J3	0.010	15	39.933	599	0	0	0	0	0
J5	0.056	18	189.833	3417	0	0	0	0	0
K1	0.083	46	111.370	5123	0	0	0	0	0
K2	0.005	15	21.600	324	0	0	0	0	0
K3	0.003	12	16.667	200	0	0	0	0	0
K4	0.132	24	337.083	8090	0	1	0	1	1
K5	0.261	32	502.563	16082	0	0	0	0	0
L1	0.023	29	49.483	1435	0	0	0	0	0
L2	0.021	35	36.914	1292	0	0	0	0	0
L3	0.223	72	190.653	13727	1	0	0	1	1
L4	0.202	45	276.644	12449	0	0	0	0	0
L5	0.574	39	905.333	35308	0	0	0	0	0
M2	0.072	50	88.580	4429	0	0	0	0	0
M3	0.044	45	59.667	2685	0	0	0	0	0

Table A8 Forest variables and bird presence (1) and absence (0) at each point count location for YBFL



lot numbe	%_treed	number of	mean patch area	sum_treed_area	YBFL_present_2015	YBFL_present_2014	YBFL_present2017	# years YBFL presen	total_YBFL
A2	0.408	124	202.597	25122	0	0	0	0	0
B2	0.014	27	31.889	861	0	0	1	1	1
B3	0.377	25	926.520	23163	0	0	1	1	1
B4	0.268	99	166.444	16478	0	0	1	1	1
B5	0.170	65	161.031	10467	0	0	0	0	0
B6	0.012	20	36.850	737	1	0	1	2	1
B7	0.529	38	856.658	32553	1	0	1	2	1
C5	0.104	58	110.121	6387	0	0	0	0	0
C6	0.011	14	50.071	701	0	0	0	0	0
D2	0.258	31	512.355	15883	0	0	1	1	1
D5	0.419	43	599.279	25769	0	0	0	0	0
D7	0.168	70	147.629	10334	0	1	1	2	1
E1	0.280	78	220.667	17212	0	0	1	1	1
E10	0.070	43	100.047	4302	0	1	0	1	1
E2	0.152	101	92.495	9342	0	0	0	0	0
E3	0.195	112	107.134	11999	0	0	0	0	0
E4	0.026	35	45.686	1599	0	0	0	0	0
E5	0.597	22	1668.409	36705	0	0	0	0	0
E6	0.137	46	182.826	8410	0	0	0	0	0
E7	0.184	80	141.400	11312	1	0	1	2	1
E8	0.228	39	359.000	14001	0	0	1	1	1
E9	0.045	24	116.375	2793	0	0	1	1	1
F10	0.047	23	125.087	2877	0	0	1	1	1
F3	0.169	38	273.342	10387	0	1	1	2	1
F5	0.342	35	601.971	21069	0	0	1	1	1
F6	0.289	35	508.229	17788	0	0	0	0	0
F7	0.424	48	543.458	26086	0	0	1	1	1
F8	0.290	42	424.690	17837	0	0	0	0	0
F9	0.083	20	254.500	5090	1	1	1	3	1
H1	0.354	73	298.315	21777	1	0	1	2	1
H2	0.217	72	185.347	13345	0	1	0	1	1
H3	0.063	58	67.138	3894	0	0	1	1	1
H4	0.382	87	270.391	23524	0	0	1	1	1
H5	0.148	35	260.086	9103	0	0	0	0	0
I1	0.053	72	45.500	3276	0	1	0	1	1
I2	0.013	23	35.174	809	0	0	0	0	0
I3	0.001	7	9.000	63	0	0	1	1	1
I4	0.215	37	357.243	13218	0	0	0	0	0
J1	0.043	90	29.389	2645	0	0	0	0	0
J2	0.003	14	11.143	156	0	0	0	0	0
J3	0.010	15	39.933	599	0	0	0	0	0
J5	0.056	18	189.833	3417	0	0	1	1	1
K1	0.083	46	111.370	5123	0	1	0	1	1
K2	0.005	15	21.600	324	0	1	0	1	1
K3	0.003	12	16.667	200	0	0	0	0	0
K4	0.132	24	337.083	8090	1	0	1	2	1
K5	0.261	32	502.563	16082	1	0	0	1	1
L1	0.023	29	49.483	1435	0	0	0	0	0
L2	0.021	35	36.914	1292	0	0	0	0	0
L3	0.223	72	190.653	13727	0	0	0	0	0
L4	0.202	45	276.644	12449	1	0	0	1	1
L5	0.574	39	905.333	35308	0	0	0	0	0
M2	0.072	50	88.580	4429	0	1	0	1	1
M3	0.044	45	59.667	2685	0	0	0	0	0

Table A9 Input for Mann-Whitney U Test

Forest Variables	Forest Bird Indices	N	Mean Rank	Sum of Ranks
	BAWW_present_2014			
number of patches	0	46	26.73	1229.5
	1	8	31.94	255.5
	Total	54		
mean patch area	0	46	26.59	1223
	1	8	32.75	262
	Total	54		
sum_treed_area	0	46	26.43	1216
	1	8	33.63	269
	Total	54		
	BAWW_present_2015			
number of patches	0	39	26.1	1018
	1	15	31.13	467
	Total	54		
mean patch area	0	39	24.85	969
	1	15	34.4	516
	Total	54		
sum_treed_area	0	39	24.67	962
	1	15	34.87	523
	Total	54		
	BAWW_present_2017			
number of patches	0	23	24.22	557
	1	31	29.94	928
	Total	54		
mean patch area	0	23	24.96	574
	1	31	29.39	911
	Total	54		
sum_treed_area	0	23	24.17	556
	1	31	29.97	929
	Total	54		
	BAWW_total			
number of patches	0	13	18.38	239

	1	41	30.39	1246
	Total	54		
mean patch area	0	13	23.38	304
	1	41	28.8	1181
	Total	54		
sum_treed_area	0	13	21.92	285
	1	41	29.27	1200
	Total	54		
	YBFL_present_2014			
number of patches	0	45	26.88	1209.5
	1	9	30.61	275.5
	Total	54		
mean patch area	0	45	28.51	1283
	1	9	22.44	202
	Total	54		
sum_treed_area	0	45	28.51	1283
	1	9	22.44	202
	Total	54		
	YBFL_present_2015			
number of patches	0	46	27.86	1281.5
	1	8	25.44	203.5
	Total	54		
mean patch area	0	46	26.11	1201
	1	8	35.5	284
	Total	54		
sum_treed_area	0	46	26.67	1227
	1	8	32.25	258
	Total	54		
	YBFL_present2017			
number of patches	0	32	28.42	909.5
	1	22	26.16	575.5
	Total	54		
mean patch area	0	32	24.38	780
	1	22	32.05	705
	Total	54		
sum_treed_area	0	32	25.41	813

	1	22	30.55	672
	Total	54		
	total_YBFL			
number of patches	0	24	27.44	658.5
	1	30	27.55	826.5
	Total	54		
mean patch area	0	24	24.71	593
	1	30	29.73	892
	Total	54		
sum_treed_area	0	24	25.75	618
	1	30	28.9	867
	Total	54		
	BHVI_present_2014			
number of patches	0	39	26.14	1019.5
	1	15	31.03	465.5
	Total	54		
mean patch area	0	39	24.9	971
	1	15	34.27	514
	Total	54		
sum_treed_area	0	39	25.23	984
	1	15	33.4	501
	Total	54		
	BHVI_present_2015			
number of patches	0	50	26.7	1335
	1	4	37.5	150
	Total	54		
mean patch area	0	50	26.88	1344
	1	4	35.25	141
	Total	54		
sum_treed_area	0	50	26.66	1333
	1	4	38	152
	Total	54		
	BHVI present_2017			
number of patches	0	45	26.8	1206
	1	9	31	279
	Total	54		

mean patch area	0	45	26.18	1178
	1	9	34.11	307
	Total	54		
sum_treed_area	0	45	25.96	1168
	1	9	35.22	317
	Total	54		
	BHVI_total			
number of patches	0	33	23.45	774
	1	21	33.86	711
	Total	54		
mean patch area	0	33	22.82	753
	1	21	34.86	732
	Total	54		
sum_treed_area	0	33	22.06	728
	1	21	36.05	757
	Total	54		