Using microphone arrays and a new localization workflow to determine critical habitat and microhabitat of landbirds in a boreal forest ecosystem

by

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Abstract

Biodiversity is declining rapidly among North American landbirds. While population decreases are most evident in species at risk, steep declines in common avian species have also been observed and shown to have significant economic and ecological impacts. Basic data on distributions and habitat preferences are lacking for many species. Traditional methods used to obtain this information are limited by cost, accuracy, and human resources. Furthermore, traditional methods have a limited capacity to accurately estimate metrics such as population density and microhabitat selectively. Recently, microphone arrays have become a more affordable, portable, and capable method of obtaining this data. I deployed 110 microphone arrays in the Labrador portion of the Boreal Shield Ecozone. My objectives were to (1) demonstrate a new localization workflow using microphone arrays, (2) determine the relationships between habitat characteristics and avian community parameters, and (3) identify microhabitat features associated with two common species in steep decline, the Boreal Chickadee (*Poecile hudsonicus*) and the Cape May Warbler (*Setophaga tigrina*).

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CHAPTER 1: General introduction

1.1 Status of North American Landbirds

Biodiversity among North American landbirds has declined significantly in the last 40 years (Şekercioğlu et al. 2004; Berlanga et al. 2010; Downes et al. 2011). Partners in Flight, a tri-national North American initiative for the conservation of birds, states that 86 of the 448 species assessed are at high risk of becoming extinct, with 22 species expected to lose 50% of their current population in the next 40 years (Rosenberg et al. 2016). Additionally, the abundance of landbirds in North America has declined by approximately 1.5 billion individuals (or 9%) since 1970 (Rosenberg et al. 2016). For example, 35% of the 450 bird species that are found in Canada have declined in number by at least 25% since the 1970s (Government of Canada 2014), and 46 of the 269 landbird species that breed in Canada have declined by more than 50% in number (Berlanga et al. 2010; Downes et al. 2011). Currently, the Committee on the Status of Endangered Wildlife in Canada has designated 58 landbird species as being at risk under the categories of endangered, threatened, or special concern (COSEWIC 2018).

These declines in abundance are attributed to a number of factors. Partners in Flight lists several large-scale threats to bird populations, including urbanization, tropical deforestation, climate change, agricultural land conversion, and energy and resource extraction (Rosenberg et al. 2016). For example, although North American forest cover has remained stable over the last 20 years (Keenan et al. 2015), a long-term study using high-resolution satellite imagery found that there was a global net loss of 1.5 million km^2

of forest from 2000 to 2012 (Hansen et al. 2013). Across the tropics, 2101 km^2/year were lost during this period, with half of this loss occurring in the rainforests of South America (Hansen et al. 2013). The latter region is of particular importance to Partners in Flight because approximately 30% of the species on the initiatives' "watch list" and list of "common species in steep decline" are migratory species that breed in Canada and/or the United States, but that rely on South American forests during the boreal winter (Rosenberg et al. 2016). The watch list identifies the species that are at the highest risk of extinction in North America and of the greatest conservation concern at the continental scale. The list of common species in steep decline includes species that are still abundant, but that have experienced long-term declines in number (Rosenberg et al. 2016).

Habitat change and habitat loss are also widespread on the avian breeding grounds in Canada. The boreal forest is rapidly changing in North America and Eurasia (Bradshaw et al. 2009; Gauthier et al. 2015). The boreal forest is a key resource for the Canadian economy because paper and lumber are among the largest national exports. They are linked to the annual harvest of approximately 780,000 ha of the 347 million ha of total forested area in Canada (Gauthier et al. 2015; NRCan 2017). Between 2015 and 2016, a further 34,000 ha (< 0.1%) of forest was converted to another land type (*e.g.*, agricultural land) and 19 million ha (5.0%) were lost due to insects, fire, and disease (NRCan 2017). Within the Boreal Plains ecozone, approximately 75% of forested habitat has been converted to agricultural land since the 1900s (Hobson and Bayne 2000). Given that approximately 60% of Canada's landbirds and 50% of North American warbler species breed within the boreal forest of Canada (Downes et al. 2011), it is clear that the boreal

forest is of critical importance for maintaining the survival and reproduction of landbird populations.

The loss of landbird resident and migrant species (Şekercioğlu et al. 2004; Berlanga et al. 2010; Downes et al. 2011) has substantial ecological and economic impacts. For example, landbirds save the Canadian forestry industry an estimated $5.4 billion per year by consuming pests (Mols and Visser 2002; Classen et al. 2014; Wells et al. 2014). Birds also facilitate ecosystem processes (Whelan et al. 2008; Sekercioğlu et al. 2016), such as seed dispersal (Şekercioğlu et al. 2004; Garcia et al. 2010; Garcia and Martinez 2012), pollination (Anderson et al., 2006), and nutrient decomposition (De Vault et al. 2003). Similarly, they are the foundation for recreational activities, with 4.8 million Canadians having spent $537 million on birding in 2012 alone (FPTGC 2014). Conserving landbirds is therefore important for our ecosystems and our economy. They also have significant cultural and symbolic importance, and are often central figures in heraldry, religion, and mythology (Cocker and Tipling 2013).

Legislation, such as Canada's *Species at Risk Act* (S.C. 2002, c. 29), provides a framework for conserving landbirds. Yet implementing recovery strategies is often hindered by an inability to identify critical habitat and distribution patterns for individual species. Currently, there are several techniques researchers can use to obtain this information. The most common method has been the point count technique, in which individual birds are included in counts if they are seen or heard (Blumstein et al. 2011; Mennill et al. 2012; Venier et al. 2012). Despite its widespread use, however, point

counts are subject to several biases (Digby et al. 2013; Klingbeil and Willig 2015). For example, the ability to detect and classify vocalizations *in situ* varies widely with observer skill (Hobson et al. 2002; Hutto and Stutzman 2009). It is also often not possible to know how far away a detected bird is, or whether the same individual or multiple individuals are being detected. Furthermore, point counts are typically only 5-10 min in length, and are often conducted only during the early morning when birds are most active. Consequently, point counts often fail to detect less common or less vocal species (Hobson et al. 2002; Bas et al. 2008). The reliability of detecting vocalizations at a given distance also varies among species, populations, vocalization types, habitat types, and weather conditions (Johnson 2008; Yip et al. 2017).

In an attempt to address some of these limitations, several variations of the traditional point count method have been developed. For example, distance sampling (Buckland et al. 2001), double-observed surveys (Nichols et al. 2000), MacKinnon lists (MacKinnon and Phillips 1993), spot mapping (Schwab et al. 2006), and removal surveys (Farnsworth et al. 2002) incorporate species-specific detection probabilities to estimate density and abundance. Forcey et al. (2006) sampled across 6 different habitats and found considerable variation in detection probability (59.8% to 84.2%) using a double-observer method. O'Dea et al. (2002) compared the MacKinnon list method to traditional point counts and found that both methods had equivalent estimates of species richness, but that MacKinnon lists overestimated species abundance, lacked a sampling protocol, and required considerably more time for both field collection and data entry. Furthermore, all five of these methods rely on several indirect assumptions. For example, they assume that

individuals are not double-counted during surveys, that individuals are accurately assigned to being within or outside a set survey boundary, and that the observer does not affect the distribution of individuals (Murray et al. 2011; Reidy et al. 2011). Yet, these assumptions are often violated or untested (Murray et al. 2011; Reidy et al. 2011). For example, the presence of human observers has been shown to affect the natural behaviour and habitat choice of birds (Mech and Barber 2002; Lee and Marsden 2008).

1.2 Acoustic Monitoring

Acoustic monitoring, which is based on audio recorders placed in the environment to passively record species-specific sounds, is a new technique that overcomes many of the limitations of point counts (Blumstein et al. 2011; Mennill et al. 2012). Virtually all landbirds regularly produce species-specific vocalizations, especially during the breeding season, and, therefore, monitoring these vocalizations can be a reliable way of determining whether a particular species is present at a given location. Unlike humans, recorders are ideal for detecting rare species because they can operate continuously for long periods of time, at night, and at multiple locations simultaneously (Hutto and Stutzman 2009; Klingbeil and Willig 2015).

In addition to determining species presence, audio recording units can be used as part of a microphone array to localize vocalizing animals in 2-dimensional or 3-dimensional space (Blumstein et al. 2011). This can allow researchers to distinguish among spatially separated individuals (*e.g.*, those living in adjacent territories), and to identify and characterize preferred microhabitats, such as singing posts and nesting sites.

This allows researchers to study microhabitat use in the absence of obscuring or confounding observer effects. Additionally, birds are known to vocalize at species-specific rates (Emlen 1972). By calculating the area over which vocalizations are detected, vocalization density can be calculated and used as a proxy for population density (Marques et al. 2013). This information can be incorporated into population monitoring protocols, which is useful for developing conservation decisions about land management.

Localization requires multiple microphones to be distributed throughout the environment at a high enough density that vocalizations from target species are detected at three or more microphone locations. Because sound travels at a constant and predictable speed, it will arrive at each microphone at a slightly different time. These time-of-arrival differences among microphones can be measured from audio recordings using various techniques, such as spectrogram or waveform cross-correlation, and trilateralization can then be used to calculate the origin of the sound in 2-dimensional or 3-dimensional space (Wilson et al. 2014).

There are several factors that affect detection and localization accuracy of sound in a microphone array. Detection and localization accuracy are significantly better when the total number of microphones and microphone density are higher (Patricelli and Krakauer 2010; Mennill et al. 2006; Mennill et al. 2012), when signals are produced within the area bound by the array (McGregor et al. 1997; Bower and Clark 2005), when signals are produced in open versus densely foliated habitat (McGregor et al. 1997;

Mennill et al. 2012), and when signals contain frequency modulation (McGregor et al. 1997). Therefore, the detection capability and accuracy of microphone arrays can vary according to array configuration, habitat, and target species.

Despite these limitations, previous studies and reviews have indicated that microphone arrays are an effective tool for surveying wildlife populations (Blumstein et al. 2011; Shonfield and Bayne 2017), though there are still several challenges remaining. First, a reliable and automated method for species recognition has yet to be developed (Blumestein et al. 2011). Software programs exist, but are often not commercially available or have been developed for particular taxa and cannot be applied to data that contain several types of vocalizations from multiple taxa. Second, there is currently no framework or workflow that is capable of processing large volumes of audio recordings efficiently. Existing procedures involve one or more manual steps, such as processing each vocalization individually to determine time-of-arrival differences (*e.g.*, Sound Finder, Wilson et al. 2014). Manual steps in the processing of individual vocalizations limits the number of localizations that can be processed in a single study to a few hundred or, possibly, a few thousand.

In this study, I used the cable-free microphone array technology described by Mennill et al. (2012) to assess habitat and microhabitat use of landbirds at a local scale in central Labrador, Canada, regardless of their current population or conservation status. I conducted the study in Labrador because 15 of its 102 native species are at risk (Mactavish et al. 2016; NLFLR 2017; Appendix 1). Within the Boreal Shield Ecozone in

Labrador, there have been significant declines in bird species that occupy open and shrub/early successional habitats, including those listed as “not at risk” (Downes et al. 2011). The Labrador portion of the Boreal Shield Ecozone is also under-represented in national bird surveys (Downes et al. 2011). The majority of surveys in this ecozone were conducted in southern Ontario and Quebec, with poor coverage outside of these regions (Downes et al. 2011). Finally, Labrador is subject to intense development. In particular, logging, hydroelectric power generation (*e.g.*, the Lower Churchill Project), and mining are significant sources of human disturbance (Roberts et al. 2006). Therefore, studies on the avian communities in this region, and subsequent monitoring of these communities, are important for understanding the impact of these disturbances. The study area I sampled included 88 sites across the 2016 and 2017 avian breeding seasons, and encompassed a 50 x 50 km area in Labrador that was south of Grand Lake, north of the Churchill River, and west of Goose Bay and Lake Melville.

1.3 Study Objectives

The first objective, detailed in the second chapter, was to determine whether or not microphone arrays are a practical tool for characterizing avian communities. I introduce and explain the methodology of a new, automated localization workflow that is capable of processing millions of vocalizations from thousands of hours of recordings. I test the accuracy of this workflow using speaker playbacks broadcasted from known locations to determine if this localization procedure is as accurate as previous procedures that required manual oversight. Included in the chapter are the number of vocalizations

recorded, the amount of time required to detect, identify, and localize the vocalizations, and the accuracy of localization.

The second objective, detailed in the third chapter, was to determine the relationships between habitat characteristics and avian community parameters (*i.e.* species richness, composition, and the presence/absence of individual species). I also compared my results to those observed previously in other locations across North America. Changes in avian community parameters are influenced by several habitat characteristics, such as mean tree height, stem density, canopy cover (MacArthur and MacArthur 1961; MacArthur et al. 1962; Lee and Rotenberry 2005; McElhinny et al. 2005; Lemaître et al. 2012), and vegetative species richness (Lee and Rotenberry 2005). I use the microphone array data to develop explanatory models that identify the habitat characteristics that are associated with avian species richness, avian species composition, and the presence/absence of each avian species across the study area. Finally, using a subset of 20 arrays that were deployed in the same locations in both 2016 and 2017, I calculated the similarity of species compositions between two consecutive breeding seasons.

The third objective, detailed in the fourth chapter, was to determine if birds vocalized selectively from particular types of song perches. The chapter focused on the microhabitat selection of Boreal Chickadee (*Poecile hudsonicus*) and Cape May Warbler (*Setophaga tigrina*), which are two common species experiencing steep population declines across their range (Rosenberg et al. 2016; Sauer et al. 2017). Using the

localization data provided by the microphone arrays, I tested whether the microhabitat characteristics of singing locations differed in structure from locations selected at random from within the same general habitat. The ability to localize singing birds over long periods of time across broad geographic regions makes this approach useful for understanding the habitat and microhabitat requirements of birds. If these species were listed under the *Species at Risk Act* (S.C. 2002, c. 29), this information would be valuable for conservation efforts because recovery documents and conservation strategies require data on critical habitat and microhabitat used during the breeding phase.

1.4 Co-authorship Statement

I conducted this research independently, but with contributions made from Dr. David Wilson, my graduate supervisor. In particular, he aided with the initial research proposal, preparation of manuscripts, and several practical aspects of the thesis (*e.g.*, equipment maintenance). I was responsible for the majority of the study design, but was in direct consultation with David Wilson. It is worth noting that I used the microphone array set-up described by Mennill et al. (2012), of which David Wilson was a co-author. I completed the data collection with the assistance of David Wilson, Bronwen Hennigar (MSc student in the Wilson lab), and Mohammad Fahmy (Honours student in the Wilson lab).

William Balsom wrote and developed the custom localization program used throughout the thesis and described in detail in chapter 2 (co-author of any manuscript derived from that chapter). I completed the data analyses and interpretation with guidance

from David Wilson, and I wrote the manuscripts that constitute the chapters of this thesis (chapter 2-4). I made revisions to these manuscripts based on the recommendations of David Wilson (co-author of those manuscripts), as well as comments provided by my committee members (Dr. Ian Warkentin and Dr. Yolanda Wiersma). As the chapters of this thesis are written as manuscripts to be submitted for publication as separate entities, there is some necessary repetition of material between the general introduction and manuscript chapters.

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CHAPTER 2: A new method for studying avian communities using microphone arrays and acoustic localization

Abstract: There are several methods for obtaining information about the distribution, abundance, and habitat requirements of individual species within an avian community. However, many of these methods are limited by cost, accuracy, and human resources. Microphone arrays are an emerging technique used to obtain avian community data. Despite recent advances in hardware, such as cable-free arrays, the workflow options for processing large volumes of audio recordings and performing localization algorithms on large datasets are still lacking. In this study, I describe a new custom localization program and fully automated workflow. I then use the workflow to detect and localize songs from a largely understudied avian community from the boreal forest in Labrador, Canada. Using this new method, I was able to process, detect, and accurately localize millions of detections from thousands of hours of audio with only 325 h of processing time. This technique is easy to use, requires minimal manual inspection, and the code is free, using software that is available to most institutions and laboratories.

2.1 Introduction

Identifying the presence or absence of bird species across several locations is an important first step to understanding the distribution, abundance, and habitat requirements of individual species within an avian community. There are several direct observation techniques used to survey and monitor birds, such as point counts, spot mapping, and radio telemetry, but these methods are often limited because they require highly trained

personnel whose presence on the ground has been shown to affect natural avian behaviour and habitat choice (*e.g.*, Mech and Barber 2002; Lee and Marsden 2008). Additionally, there are often limitations to the timing and duration of observations. For example, most observations are conducted during the early morning, thus excluding or otherwise underrepresenting nocturnal species and species that are most active during the day.

Acoustic monitoring involves the use of one or more passive acoustic recording units that are used in place of a human observer. This technology mitigates several biases associated with other monitoring methods. In particular, point counts are associated with observer bias because the ability to detect and classify vocalizations in situ varies with observer skill (Hobson et al. 2002; Hutto and Stutzman 2009). Acoustic recording units provide permanent archives of recordings that can be inspected repeatedly to confirm species identity. Acoustic recording units have also been shown to be more robust than human-observer methods to variations in vocalizations of individual species, habitat type, and weather, which obscure aural detection and species identification (Hobson et al. 2002; Blumstein et al. 2011).

Microphone arrays are an emerging technique in which three or more passive acoustic recording units are synchronized and dispersed in an animal's environment. This technique has been used to study the vocal and spatial behaviour of several taxa (Mennill and Vehrencamp 2008; Krakauer et al. 2009; Bates et al. 2010; Harris et al. 2016) and to survey bird species abundance, richness, and composition (Hobson et al. 2002; Acevedo and Villanueva-Rivera 2006; Celis-Murillo et al., 2009, 2012). The primary advantage of

using a microphone array over point count method is the ability to localize individual vocalizations in space (Blumstein et al. 2011). Since sound travels at a predictable rate through the air, the time required for an acoustic signal produced by an animal to reach each microphone in the array will differ slightly. It is therefore possible to determine the location of the signal using the time-of-arrival differences among the microphones in the array. There are several approaches for determining time-of-arrival differences, including spectrogram and waveform cross-correlation. Trilateralization algorithms can then be applied to the time-of-arrival differences to calculate the spatial origin of the signal (Wilson et al. 2014). With localization, the sampling area can be standardized and set to a small enough area that all vocalizations produced within it are detected. This, in theory, mitigates the effects of habitat, weather, species, and bird behaviour on the probability of detection and inclusion in the sample. Additionally, since the array is spatially explicit, and since birds tend to vocalize at species-specific rates, it is possible to calculate song density, which is the number of songs per unit of area per unit time (Stevenson et al. 2015). Song density should correlate with animal densities, and, so, can be used as a consistent and reliable metric to be compared among sites, regions, years, and studies (Stevenson et al. 2015).

A significant challenge to using microphone arrays is that the recordings from each microphone must be synchronized. If they are not, the time-of-arrival differences and the localizations derived from them will be inaccurate. The traditional method of synchronizing a microphone array was to connect the microphones to a central recording device via long cables (Mennill et al. 2012). Deploying these arrays took large teams of

researchers multiple days to set up (*e.g.* Fitzsimmons et al. 2008, Mennill and Vehrencamp 2008). The transportation and deployment time of these systems limited the number of arrays that could be established in a single study and often did not allow for arrays to be treated as the unit of replication (Mennill et al. 2012).

During the last decade, cable-free microphone arrays have been developed for studying species in terrestrial communities (Ali et al. 2009; Thompson et al. 2009; Collier et al. 2010; Blumstein et al. 2011; Mennill et al. 2012; Stevenson et al. 2015). These arrays comprise commercially available recorders that synchronize with each other using self-generated radio signals (Burt and Vehrencamp 2005) or a common GPS time source (*e.g.*, Mennill et al. 2012). Because these systems are cable-free, they can be deployed in the field more easily and more quickly than their cable-based counterparts. For example, Mennill et al. (2012) were able to fit an entire 8-microphone cable-free array into a single backpack, and to set it up in the field, covering an area of approximately 0.25 ha, in under 1 h.

Despite these advances in hardware, software options for detecting and localizing signals from large volumes of recordings are lacking. Software programs exist for isolating vocalizations/sounds, assigning species labels to the vocalizations, and then performing spectrogram or waveform cross-correlation. Examples include ISHMAEL, which was developed by the Cooperative Institute for Marine Resources Studies (CIMRS) bioacoustics lab at Oregon State University (Mellinger et al. 2017), XBAT, which was developed by the Cornell Lab of Ornithology (Mills and Figueroa 2005), and

Sound Finder, which was developed by Wilson et al. (2014). However, these software programs often require one or more manual steps, such as building species-specific recognizers for detecting vocalizations or processing each vocalization individually to determine time-of-arrival differences prior to localization. Additionally, no software of which I am aware is able to process large volumes of audio data efficiently. For example, ISHMAEL requires approximately 1 h to process 1 h of audio recordings. As a result, most studies involving the technology have been proof-of-concept studies or have involved a maximum of a few hundred detections, which significantly reduces the temporal and/or spatial coverage of such studies (Bower and Clark 2005; Mennill et al. 2012; Spillman et al. 2015; Stepanian et al. 2016).

To alleviate the deficiencies of previous software, my objectives in this study were to (1) develop a workflow that can automatically detect and localize animal sounds recorded with a microphone array; (2) show that the workflow can handle large datasets (*i.e.*, thousands of hours of audio recordings); and (3) quantify the accuracy of localizations using a series of playbacks broadcasted from known locations. To address objectives 2 and 3, I deployed 110 microphone arrays in forest stands of eastern Labrador, Canada.

2.2 Methods

2.2.1 Signal processing workflow

The software and workflow used for processing vocalizations involves three steps: detection, identification, and localization. The first two steps utilize *Kaleidoscope*

software (Version 4.3.2, Wildlife Acoustics, Concord, MA, USA). The third step is accomplished using a custom program written in MATLAB (Version 6.1, The MathWorks, Natick, MA).

2.2.1.1 Detecting vocalizations

Kaleidoscope software automatically detects vocalizations from a collection of long audio recordings. The vocalizations can be comprised of "phrases" that contain "syllables" (Catchpole and Slater 2008) that are above the threshold of background noise and within a user-defined minimum and maximum frequency range and duration. The background noise is determined by an algorithm that estimates the ambient level of background energy through a rolling average of power levels going back in time by the user-specified maximum duration of potential signals. *Kaleidoscope* generates a detection list text file with one row for each detection and columns describing the structure of the detection (minimum, maximum, and mean frequency) and its position within the raw recording (time of onset and duration).

Kaleidoscope uses a cluster analysis to group together detections with similar acoustic structure. The program calculates the distance of each detection to the centroid of the nearest cluster in multi-dimensional space. If a vocalization is within a user-defined distance from that centroid (a value between 0 and 2, where 0 excludes all detections and 2 includes all detections), then the vocalization is assigned to that cluster. The user can preview the vocalizations in clusters and rename clusters to match the species they represent.

2.2.1.2 Localizing vocalizations

Vocalizations are localized automatically using a custom program written in MATLAB (SoundScope; Balsom et al., in prep). The following input files are required for localization: (1) the detection list text file produced by *Kaleidoscope*, (2) a text file listing the date and start time of each raw audio recording, (3) a text file listing which audio files were produced from the same array during the same time period, (4) the audio files containing the detections, (5) a text file containing GPS coordinates of each microphone in each array, and (6) a text file containing temperature data corresponding to the times and dates of the recordings.

Each detection is localized in two steps. First, the program identifies the channel in which the detection has the maximum signal-to-noise ratio ("reference channel"), applies a bandpass filter based on *Kaleidoscope's* determination of the minimum and maximum frequencies of the detection, and then uses pair-wise waveform cross-correlations to measure when the signal was detected in each channel relative to when it was detected in the reference channel. The result of this step is a vector with the observed time-of-arrival differences. Second, the program produces a three-dimensional lattice, with 2-m resolution, over a simulation of the study site. The study site is defined by the most northern, eastern, western, and southern microphone coordinates, and by the minimum and maximum heights of each of the microphones. A 100-m buffer is added to each side of the simulated study site, and a 10-m buffer above and below the site. Most avian acoustic signals produced beyond this buffer could not be detected by three or more

microphones, and, so, could not be localized using this method. For each vertex in the lattice, the program calculates the time it would take for the vocalization to travel to each microphone, based on the known temperature and derived speed of sound. The vertex that minimizes the difference between the observed and theoretical time-of-arrival differences is selected by the program as the most likely origin of the vocalization. This process is then repeated 100 times, with a new smaller study area centred on the estimated origin of the vocalization from the previous iteration (dimensions equal to the spatial resolution of the previous iteration), and a progressively finer lattice resolution. For each vocalization, the program produces a unitless error value, which is the sum of absolute differences between the theoretical time-of-arrival differences of the final estimated origin and the original observed time-of-arrival differences (hereon in, "localization error value"). This error term is not a direct measure of geographic error, but, rather, a measure of model fit. As there are multiple factors that influence localization, it is possible for a vocalization to be localized to its true spatial origin with perfect accuracy, but to still have a high localization error value.

2.2.2 Microphone array deployment

In order to test the accuracy of the workflow and its ability to handle large data, I deployed microphone arrays at 110 sites in Labrador, Canada during the 2016 and 2017 avian breeding seasons. The sites were distributed across a 50 x 50 km area of Labrador that is south of Grand Lake, north of the Churchill River, and west of Goose Bay and Lake Melville (central UTM: 20U 666550 m E, 5921190 m N; Chapter 3, Figure 3.1). During 2016 (16 May – 10 July), arrays were deployed at 68 sites. During 2017 (17 May

– 30 June), arrays were deployed at 42 sites, including 22 at new locations and 20 at locations from the previous season.

The locations of sites were selected at random, but with the constraints that they were within 1 km of road access and a minimum distance of 500 m from each other. I chose a maximum distance from road access of 1 km because hiking beyond this distance through dense forest while carrying a microphone array would have been difficult and would have reduced our sample size. I chose to separate sites by a minimum of 500 m because this reduced the risk of detecting the same birds at multiple sites (Wilson and Mennill 2011). GPS coordinates for sites were generated using a random integer set generator that creates non-repeating integers within confined boundaries (RANDOM.org). These random coordinates were then plotted on 1:50,000 scale topographic maps (National Topographic System, Series A771, Edition 4MCE, Map13 F/7 - 13 F/10) and discarded if they violated the inclusion criteria or were within a delineated swamp, bog, or water body.

Each array consisted of four audio recorders (Model SM3, Wildlife Acoustics, Concord, MA, USA) that were placed at the corners of a 40 m X 40 m square, and which provided complete coverage of an area of approximately 0.15 ha. Field equipment consisted of 16 recorders (*i.e.*, 4 arrays) in 2016 and 8 recorders (*i.e.*, 2 arrays) in 2017. Each recorder was fitted with a Garmin SM3 GPS that was used to provide a standard GPS time source to synchronize the recorders within an array to within 1 ms of each other. Recorders were attached to trees using two drywall screws (Figure 2.1). Each

recorder had two channels: one built-in microphone (pick-up pattern: omnidirectional; frequency response: 50–20,000 Hz, ± 10 dB; Wildlife Acoustics, Concord, MA, USA) was positioned approximately 1 m above the ground, and a second microphone (model: SMM-A2; pick-up pattern: omnidirectional; frequency response: 50–20,000 Hz, ± 10 dB) was positioned in the canopy approximately 2 to 3 m above the first using an extendable painter's pole with a hook at the end (Figure 2.2). A wire hook attached to the external microphone was hooked over a tree branch to fasten the microphone in place. Both microphones were oriented to point towards the middle of the array. Microphone positions were determined with a survey-grade Global Navigation Satellite System (GNSS; Geo7X, Trimble, Sunnyvale, CA, USA) with 10-cm accuracy (Figure 2.3).

Each array fit into a pair of backpacks and could be set up by a team of two people. On a typical day, the research team (2 to 4 people) could take down, relocate, and set up two microphone arrays. After arriving at a target location, the average set-up time for a microphone array, including the time required to position the microphones, was less than 1 h. After setting up an array, each recorder was programmed to record continuously until stopped, and to create a new stereo sound file every 2 h throughout this time (WAVE format, 24 kHz sampling rate, 16-bit amplitude encoding). All arrays were left recording for a minimum of 24 h, beginning 2 h after the initial setup to minimize disturbance effects associated with setup. During periods of heavy rain, the arrays were left in place for at least one day after the rain had stopped.

2.2.3 Localization accuracy

To determine the localization accuracy of the microphone arrays, I performed speaker playbacks at 8 microphone arrays. A tonal frequency up-sweep stimulus (200 ms in length, increasing logarithmically from 0.5 to 2.5 kHz) was played 9 to 15 times from a 12.7-cm loudspeaker (5 watts, Model No 7-100, Pignose Ind., Las Vegas, NV, USA) placed facing upwards in the approximate centre of the array. The amplitude of the stimulus was 90 dB sound pressure level, as measured at 1 m from the speaker with a sound level meter (c-weighing, fast-response). The position of the loudspeaker was recorded using the Trimble Geo 7x GNSS. These coordinates were used as the "true" location of the sound. The stimuli were localized in MATLAB to obtain estimates of the location using the procedure described above (section 2.2.1.2).

Although the localization program is capable of producing location estimates in three-dimensional space, we found an unexpectedly high amount of localization error in the vertical z-dimension. Error values were significantly reduced and location estimates were more accurate when localizing sounds in two-dimensional space. Location estimates were, on average, 4.00 m (±9.32 m, standard deviation) farther from the true location when localized in three-dimensional space. Therefore, localization accuracy was defined as the two-dimensional distance between the location of the loudspeaker, as estimated by the localization program, and the location of the loudspeaker, as determined by the GNSS. Localization accuracy was compared to the localization error values produced by the localization program.

2.2.4 Avian community data analysis

An initial run of the detection and clustering process was performed in *Kaleidoscope* on a subset of 14 randomly selected 2-h audio files recorded from the 2016 dataset. Recordings were analyzed using the following settings: fast Fourier transformation (FFT) window size = 256 points (5.33 ms); frequency range of potential signals = 2000–10000 Hz; duration of potential signals = 0.1–4.0 s; maximum inter-syllable gap = 0.35 s. Settings used during the clustering process included: maximum distance from the cluster centre = 2.0; maximum states = 12; maximum distance to cluster centre for building clusters = 0.5; maximum clusters created = 500. This produced 36,416 detections and 201 clusters. The detections within the clusters were manually inspected and 56 of these clusters were renamed to reflect the species they represented. Species identities were determined by listening to recordings of vocalizations and viewing their associated spectrograms, and then comparing these to the species accounts on the Birds of North American website (Rodewald 2015). The remaining clusters contained multiple species vocalizing and thus were not renamed, but, instead, retained the default label, as recommended by the program instructions. The cluster information stored in the metadata file was then applied to the full 2016 and 2017 datasets. This eliminated the need to manually assign detections to species.

In the full dataset (110 microphone array samples), I detected 4,879,624 vocalizations (2016 = 2,734,885; 2017 = 2,144,739) from 32 species of birds from 5862.6 h of audio. All detections were localized in MATLAB using the procedure described

above (section 2.2.1.2). The resulting dataset included several duplicated detections (same vocalization in multiple channels), detections of non-avian, non-target sounds (*e.g.*, mosquitoes, squirrels, vehicles), and detections with large localization error values.

I used the "rgeos" package (Bivand and Rundel 2017) in R (Version 3.0.1; R Core Team, Boston, MA, USA) to identify those detections contained within the bounds of the microphone array (most northern, eastern, western, and southern microphone coordinates), plus a 5-m buffer on each side of the array. Based on this, the dataset was reduced to 1,928,312 detections. I further reduced the data to include only those detections with a localization error value ≤ 0.02, which corresponds to a localization accuracy of 3.55 m or better for 90% of detections (see Results). A total of 470,761 detections met this criterion. For sites that were sampled in both years, only the data from 2017 were included (with the exception of one array in 2017 which had no species present), which allowed for a relatively equal number of sampling sites in the two years (2016 = 48 sites, 2017 = 40 sites). Additionally, I removed all duplicate and non-target detections, which reduced the number of detections to 59,155. I manually reviewed the classifications of the remaining detections to confirm the species assignment was correct, though this step is not a necessary part of the basic detection/localization process.

2.3 Results

2.3.1 Efficiency of localization workflow

Using the final version of the analytical approach detailed above, and once sufficiently trained with the software programs, the complete signal processing workflow,

including the optional manual review of detections to confirm correct species assignment, required approximately 325 h, or 41 days (assuming an 8-h workday). Detecting vocalizations within Kaleidoscope, including the initial training step, required approximately 25 h. With a standard computer (iMac, 32 GHz Intel Core i5, 16 GB RAM) using parallel processing across 4 processors, localizing the nearly 5 million detections (0.5-2.0 s in length) required approximately 140 h. However, the localization process was fully automated and required only 5-10 min to set up. Manually inspecting the detections to confirm species identification required 160 h.

2.3.2 Localization accuracy

The average localization accuracy for the speaker playbacks (*i.e.*, distance between their true location and the location estimated by the localization program) was 3.08 m (n = 160 sounds). I found that 17.5% of the stimuli were localized to within 1 m of their true location, and 87.5% to within 5 m of their true location. I found that 12.5% of stimuli had a localization accuracy of at least 5 m (Figure 2.4). I was able to determine that 90% of stimuli that were localized with a localization error value of 0.02 or less were within 3.55 m of their true locations (Table 2.1). Comparing this to natural bird vocalizations recorded with my arrays, 867,970 vocalizations in 2016 (31.7% of all vocalizations recorded in 2016) and 585,576 vocalizations in 2017 (27.3 %) had a localization error value of 0.02 or less.

2.4 Discussion

Multiple studies have argued that acoustic monitoring is preferred over traditional observer-based methods for monitoring avian communities because recording units detect continuously (Acevedo et al. 2009; Blumstein et al. 2011). Extending the approach to microphone arrays can yield even more insight by permitting the localization of individuals. Although hardware obstacles associated with microphone arrays have been overcome, software obstacles have not. Most studies involve only a few dozen or few hundred sounds, yet leaving multiple recorders recording for many days can yield millions of detections. I developed a system that is able to process, detect, and localize millions of detections from thousands of hours of audio in a timely fashion.

Generating location estimates for a larger number of detections can be an expensive and time-consuming process. The localization procedure used in this study employed *Kaleidoscope* and MATLAB software. Currently, the localization algorithm written in MATLAB is in the process of being translated to be able to run in R (Balsom et al., in prep). As it is presented here, though, the initial cost of these software programs may limit the accessibility of this workflow to some laboratories. *Kaleidoscope* is currently $1500 USD and MATLAB is currently $500 USD for an educational license, plus both products require an annual software maintenance fee. However, the main advantage of the procedure is that the vocalization detection and localization steps were fully automated and significantly reduced the time spent manually processing data. Once the input files were formatted, the custom program built in MATLAB was able to localize

each detection in approximately 400 ms, allowing for a large dataset (*ca.*, 5 million vocalizations) to be processed in approximately 6 days.

I was able to produce accurate location estimates with a high level of confidence based on sounds broadcasted from within the array (mean: 3.08 m, 95% confidence interval: 2.59-3.56 m). These results are comparable with a previous study using the same array configuration that reported an average location accuracy of 1.87 m for sounds produced within the array and 10.22 m for sound produced outside the array (Mennill et al. 2012). Other studies have had better accuracy (*i.e.*, McGregor et al. 1997; Patricelli and Krakauer 2010), but these studies had significantly higher microphone densities and/or occurred in areas with less dense vegetation (*i.e.*, open fields). The distribution of localization accuracies was also similar to those found in a previous study. Wilson et al. (2014) broadcasted 76 natural sounds from 5 species (3 bird and 2 frog vocalizations) from a loudspeaker in 38 different microphone arrays and used Sound Finder software to localize the sounds in two-dimensional space. They were able to localize 24% of sounds to within 1 m of the actual location and 74% of sounds to within 10 m (Wilson et al. 2014). My ground truth experiment, which involved 160 sounds broadcasted in 8 arrays, had comparable accuracy; approximately 18% of sounds were localized to within 1 m and 97% of sounds were localized to within 10 m (Figure 2.4).

There were at least four sources of potential measurement error associated with localization in this study. First, the accuracy of localization is highly dependent on the accuracy of the measured positions of each microphone in the array. The global

positioning system used, while more accurate than a conventional GPS, had an average horizontal accuracy of 0.34 m, but ranged from 0.1 m to 1.2 m. However, this is a significant improvement from studies using a very similar microphone array configuration that reported an average microphone position error of greater than 1 m (*i.e.*, Mennill et al. 2006; Mennill et al. 2012; Wilson et al. 2014). Second, the position of the second (external) microphone of the acoustic recorder for each corner of the array was assumed to be directly above the first (built-in) microphone and thus occupying the same position on the horizontal plane. Deviations from this assumption likely occurred and affected the quality of localizations, as placement of the external microphone was never perfect and depended on the availability of branches. Third, the waveform cross-correlation procedure depends on a high signal-to-noise ratio. While limited, a number of locations were situated in locations where natural noise (*e.g.*, wind, running water, creaking trees) and anthropogenic noise (*i.e.*, vehicle traffic) were apparent in recordings. Similarly, low signal-to-noise ratios can also be present when there is more than one signal being produced at a given point in time. There were several instances when two or more birds vocalized from different locations within the array, which produced high localization error values. An alternative to waveform cross-correlation is spectrogram cross-correlation, which can better align signals recorded in noisy environments (Bower and Clark 2005; Zollinger et al. 2012). Waveform cross-correlation has superior temporal resolution when the signal can be distinguished from the background noise, while spectrogram cross-correlation is computationally more demanding and requires more time to process (Zollinger et al. 2012; Wilson et al. 2014).

There are many methods available to researchers for studying and monitoring avian communities. The utility and feasibility of each method depends on the research question being asked, the time and financial resources available, and the quality of data needed. Point counts are perhaps the most common method to determine species richness, species diversity, and the abundance of avian species (Blumstein et al. 2011; Mennill et al. 2012; Venier et al. 2012). However, acoustic monitoring provides permanent records of bird vocalizations and removes the observer effect and other biases associated with methods such as point counts. This permits researchers to use a dataset acquired from a few field seasons to address multiple research topics, such as variation in song structure, inter-year and/or inter-season variation in song production, and presence/absence patterns of individual species. Furthermore, a recent review found that acoustic recorders often performed equal to or better than point counts when estimating species richness, abundance, and composition (Shonfield and Bayne 2017). These results could be obtained with one or two acoustic recorders placed in several locations across a landscape. However, microphone arrays and localization permit researchers to answer questions that require the investigator to determine the spatial relationships among individuals or between individuals and other aspects of their environment. Examples of previous studies employing this technology include determining the distance between duetting partners in rufous-and-white wrens, *Thryothorus rufalbus* (Mennill et al. 2006; Mennill and Vehrencamp 2008), and the inter-individual spacing of chorusing male frogs (Bates et al. 2010). Spatial information can also be used to estimate density of individuals within the environment by calculating the area over which vocalizations are detected (*i.e.*, Dawson and Efford 2009; Marques et al. 2013). I believe that this type of research can be

incorporated into monitoring programs to better understand how individuals within a bird community utilize the structures (*e.g.*, trees, shrubs) within their environment, as well as to estimate population density.

In conclusion, I have provided a new analytical approach to accurately determine the location of individuals using acoustic localization. It is the first to be able to handle a large volume of data while maintaining comparable accuracy with other systems developed in recent years. The sound detection, species identifications, and localization procedures are almost fully automated and require minimal manual inspection. The code is free and uses software that is available to most institutions and laboratories. I also demonstrated that this workflow can be combined with recent advances in microphone array hardware (Mennill et al. 2012) to efficiently and accurately survey avian communities. Overall, the acoustic monitoring and localization methods specified here provide powerful tools for researchers to study animal behaviour and ecology.

Figure 2.1: The audio recorder (Model SM3, Wildlife Acoustics, Concord, MA, USA) used for the microphone array, and the Garmin SM3 GPS (black disc above recorder) that was used to provide a standard time source to synchronize the recorders.

Figure 2.2: The external microphone was extended 2 to 3 m above each audio recorder using a modified hook on a painter's pole.

Figure 2.3: The survey-grade GNSS (Geo7X, Trimble, Sunnyvale, CA, USA) with 10-cm accuracy used to determine the location of each microphone in the array.

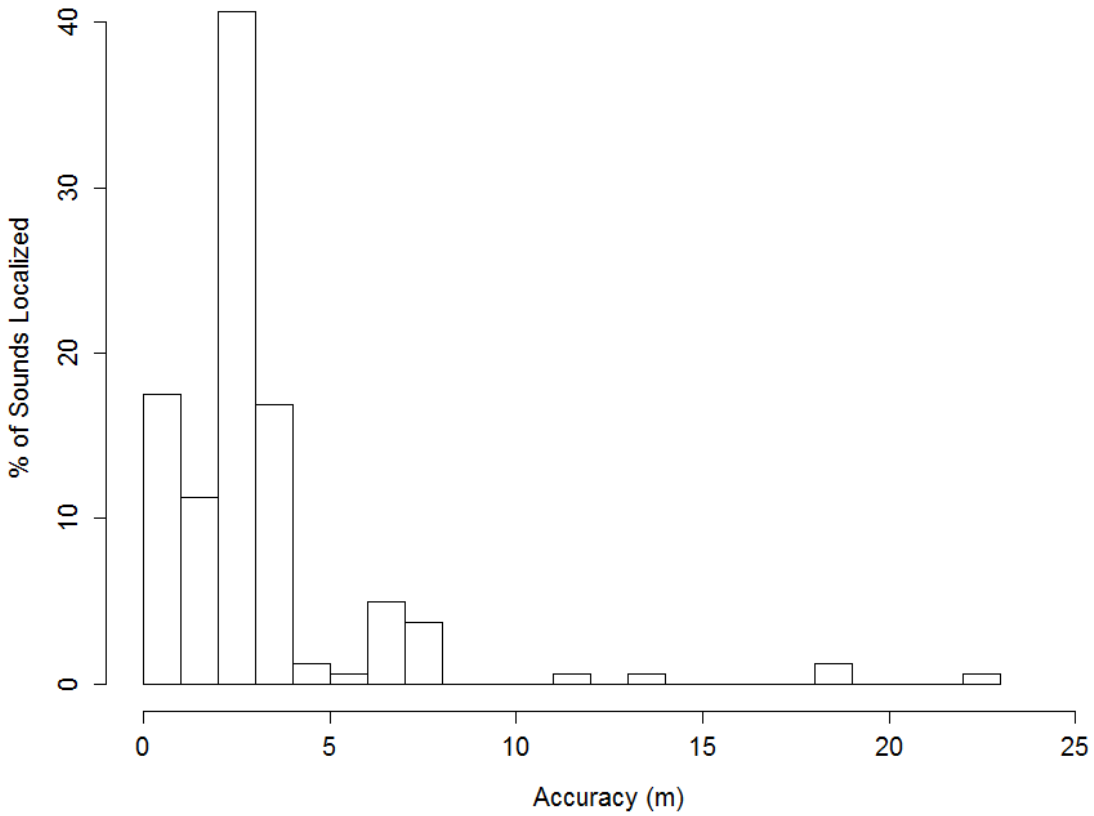

Figure 2.4: The localization accuracy of broadcasted sounds that were localized using a custom MATLAB program. Localization accuracy is the difference between the location of the vocalization, as estimated by the custom MATLAB program, and the true location, as determined by the Trimble GNSS. Data are based on 160 frequency upsweeps broadcasted from within 8 microphone arrays.

Table 2.1: Results of the ground truthing experiment that demonstrate the relationship between localization error, as calculated by the localization program, and localization accuracy.

Localization		Localization accuracy (m)				
error value	N	50%	75%	90%	95%	100%
< 0.01	80	2.012	3.157	3.427	3.591	4.719
< 0.02	144	2.365	3.038	3.550	6.665	13.951
< 0.03	152	2.358	3.160	4.719	6.773	18.255
All	160	2.392	3.240	6.684	7.416	22.814

Notes: Localization accuracy is the difference between the origin of the upsweep stimulus, as estimated by the custom MATLAB localization program, and the true origin of the stimulus, as determined by the Trimble GNSS. Shown for each localization error value are five common percentiles of localization accuracy. As an example of how to interpret this table, 95% of localizations with an error value between 0 and 0.01 have a localization accuracy of 3.591 m or less, whereas 95% of localizations with a localization error value between 0 and 0.02 have a localization accuracy of 6.665 m or less.

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CHAPTER 3: The influence of the physical structure and floristics of habitat on a boreal forest bird community

Abstract: Studies conducted at regional and continental scales have found that avian richness, composition, and abundance, as well as the presence or absence of a particular species, are associated with variation in the physical structure of the vegetation and composition of vegetative species (floristics) within broad habitat types. The relative contribution of physical structure and floristics is contested, and relationships between these variables and community parameters are often species-specific. Relatively less research has been conducted at the local scale. In this study, I used 110 microphone arrays deployed during two breeding seasons to survey an avian community in a 50 x 50 km region of the boreal forest in Labrador, Canada. The three main objectives were (1) to determine the relationships between avian species richness and the physical structure and floristic composition of the habitat, (2) to determine if the relationships between the avian community and either physical structure or floristics are species-specific, and (3) to investigate the spatial and temporal patterns of the avian community composition. I found that physical structure and floristics were not related to avian species richness, though richness was associated with weather. Relationships were species-specific, with both physical structure and floristics being poor predictors of presence for the majority of species. Avian species composition was also similar among three categorical forest types identified at the study area, but different between the two consecutive breeding seasons. Collectively, these results indicate the importance of considering species individually and as a community as a whole, since different patterns emerge at different levels of analysis.

3.1 Introduction

Avian community characteristics, such as species richness, species diversity, and composition are influenced by several environmental factors, including habitat characteristics, weather patterns, and species interactions. Many studies have shown that the physical structure of habitat best describes avian assemblages among broad habitat classifications (*e.g.,* grassland, deciduous forest, coniferous forest), whereas the composition of vegetative species (*i.e.,* floristics) best describes avian assemblages within habitat classifications (Rotenberry 1985; Lee and Rotenberry 2005). However, there is evidence that both physical structure and floristics influence bird assemblages at both spatial scales and that their relative influences are species-specific, particularly in regions where habitat is relatively homogeneous (*e.g.,* Schmiegelow and Mönkkönen 2002; Lemaître et al. 2012). Furthermore, avian assemblages are influenced by abiotic factors, such as local weather conditions. Interannual variation in bird abundance and composition among breeding seasons is driven indirectly by variation in temperature and rainfall, which affects the distribution and availability of food, resources, and shelter for birds across the landscape (Sparks et al. 2002; Şekercioğlu et al. 2012; Grima et al. 2017). It is therefore important to look not only at the relationship between habitat and avian communities, but also at how that changes over time and in relation to abiotic factors, such as weather.

Several metrics have been proposed for studying the general habitat of birds (Jones 2001; McElhinny et al. 2005). Changes in avian composition, abundance, and presence/absence patterns across a landscape have been shown to be correlated with

aspects of physical structure, including foliage height diversity, mean tree height, stem density, and canopy cover (MacArthur and MacArthur 1961; MacArthur et al. 1962; Lee and Rotenberry 2005; McElhinny et al. 2005; Lemaître et al. 2012), as well as with aspects of floristics, including the richness and diversity of vegetative species (Gillespie and Walter 2001; Poulsen 2002; Lee and Rotenberry 2005) and the densities of particular tree species (Willson and Comet 1996; Thompson et al. 1999). These relationships are often complex, and the direction of any correlation is often specific to an avian species, population, or foraging guild. The majority of these findings have been based on studies conducted at large spatial scales and across several environmental gradients throughout North America (MacArthur et al. 1962; Willson and Comet 1996; Thompson et al. 1999; Lee and Rotenberry 2005; Lamaitre et al. 2012) and Europe (Honkanen et al. 2010; Poulsen 2002). Relatively few studies have investigated if these bird-habitat relationships persist at the local or stand scale (Rotenberry 1985; Berg 1997; Seavy and Alexander 2011) and how local weather conditions might influence these relationships.

The boreal forest is an excellent region to investigate bird-habitat relationships. The Boreal Shield Ecozone in Canada is an important breeding location for more than 240 North American bird species (Blancher and Wells 2005; Downes et al. 2011). However, the majority of surveys in this ecozone have been conducted in southern Ontario and Quebec, with poor coverage outside these regions in areas such as Labrador (Downes et al. 2011). Therefore, this region provides a pertinent place to test whether relationships that might be evident based on data collected in Ontario and Quebec hold true in places such as Labrador, where forests reflect different aspects of the ecozone.

I used microphone arrays comprised of 4 synchronized recorders to study the bird-habitat relationships of the local avian community within a 50 x 50 km area in Labrador, Canada. Multiple factors, including weather, species, and an individual's behaviour, affect the range over which a species' song can be heard (Hobson et al. 2002; Blumstein et al. 2011). Therefore, using a single recorder to determine presence/absence can introduce significant error in determining whether or not a species is present. The microphone array allows researchers to standardize the sampling area by considering only those vocalizations produced within a defined area that is close enough to the microphones to ensure birds are detected. Since each bird species produces a unique vocalization, and vocalizes regularly during the breeding season, audio recordings from their environment can be a reliable method of determining which species are present (Blumstein et al. 2011). By surveying the bird species recorded within arrays, I was able to correlate species richness and presence with the physical structure and floristics of the habitat associated with those locations.

In this chapter, I had three main objectives. First, I determined the relationships between avian species richness and three environmental factors, including weather and the physical structure and floristics of the habitat. Consistent with previous studies mentioned above, I hypothesized that local species richness would be significantly correlated with changes in physical structure, floristics, and weather characteristics. Second, I investigated the patterns of the avian community composition among three categorical forest types and between two consecutive breeding seasons. Since many bird

species show site fidelity to particular breeding locations (Schlossberg 2009), I predicted that the species composition would not be significantly different between breeding seasons. Conversely, I predicted that species composition would differ among forest types, since each type differs in physical structure and floristics characteristics. Third, I determined if the relationships between the avian community and either physical structure or floristics were species-specific. Based on previous findings within the boreal forest (Seavy and Alexander 2011; Lemaître et al. 2012), and that each bird species differs in its food and shelter requirements (Johnson 1980), I hypothesized that the contributions of physical structure and floristics would vary among species. I have presented the relationships of presence/absence with physical structure and floristics characteristics for the avian community as a whole, but also for each species.

3.2 Methods

3.2.1 Study area

The study focused on a 50 x 50 km area (centred at 666550 m E, 5921190 m N, UTM Zone 20U), with sites distributed north and west of Happy Valley – Goose Bay, Newfoundland and Labrador, Canada (Figure 3.1). Houses and cottages are distributed sparsely throughout the entire area, but most of the human population is concentrated in the towns of Happy Valley-Goose Bay to the south, and North West River and Sheshatshiu to the north. The study area falls within the provincial Forest Management District 19A, which is approximately 2.27 million hectares (Forsyth et al. 2003), or approximately 0.5% of the 552 million-ha boreal forest in Canada. The area has a history of logging and other disturbances, including natural wildfire, drought, and disease. The

most recent large-scale burns occurred in 1972, 1985, and 1994 (Simon and Schwab 2005). Most notably, a large portion of the study area (approximately 34,000 ha) was burned by wildfire in 1985 (Notzl et al. 2013; Figure 3.1). During the same years, several portions of the forest were clearcut (Simon and Schwab 2005).

Forest stands in the area are dominated by black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). Other species in the upper canopy, in order of decreasing prevalence within study sites, are tamarack (*Larix laricina*), white birch (*Betula papyrifera*), heart-shape birch (*Betula cordifolia*), and trembling aspen (*Populus tremuloides*). The woody vegetation in the understory includes speckled alder (*Alnus incana*), American mountain-ash (*Sorbus americana*), squashberry (*Viburnum edule*), willow (*Salix* spp.), serviceberry (*Amelanchier* spp.), and skunk currant (*Ribes glandulosum*). The most common ericaceous species in the understory are Labrador tea (*Rhododendron groenlandicum*), sheep laurel (*Kalmia angustifolia*), swamp laurel (*Kalmia polifolia*), and leatherleaf (*Chamaedaphne calyculata*).

3.2.2 Microphone arrays

Between 16 May and 10 July of the 2016 avian breeding season, I deployed eight-channel (four-recorder) microphone arrays at 68 different locations for a minimum 24 h each. During the 2017 avian breeding season, I deployed microphone arrays between 17 May and 30 June at 42 locations, including 22 new locations and 20 locations sampled during 2016 to allow for analyses of temporal species similarity. All locations that were resampled in 2017 were sampled within 3 Julian days of when they were sampled in

2016. Locations were selected at random, but with the constraints that they were within 1 km of road access and a minimum distance of 500 m from each other. I chose a maximum distance from road access of 1 km because hiking beyond this distance through dense forest while carrying a microphone array would have been difficult and would have reduced our sample size. I chose to separate sites by a minimum of 500 m because this reduced the risk of detecting the same birds at multiple sites (Wilson and Mennill 2011). GPS coordinates for locations were generated using a random integer set generator that creates non-repeating integers within confined boundaries (RANDOM.org). These random coordinates were then plotted on 1:50,000 scale topographic maps (National Topographic System, Series A771, Edition 4 MCE, Map 13 F/7 – 13 F/10) and discarded if they violated the inclusion criteria or were within a delineated swamp, bog, or water body based on provincial forest inventory maps.

Each array consisted of four digital audio recorders (Model SM3, Wildlife Acoustics, Concord, MA, USA) that were placed at the corners of an approximately 40 m X 40 m square. Each recorder had two channels: one built-in omnidirectional microphone (frequency response: 20–20,000 Hz ± 10 dB) was positioned approximately 1 m above the ground, and a second external omnidirectional microphone (model: SMM-A2; frequency response: 20–20,000 Hz ±10 dB) was positioned in the canopy approximately 2 to 3 m above the first. All microphones were pointed towards the centre of the array. Each recorder was programmed to record continuously and to produce a new stereo audio file for each 2 h time block (WAVE format, 24 kHz sampling rate, 16-bit amplitude

encoding). All arrays were left recording for a minimum of 24 h, beginning 2 h after setup to minimize potential disturbance effects associated with setup. At any given time, two arrays were deployed and recording during 2016, whereas one array was deployed and recording at any given time during 2017.

I recorded weather variables by placing a Kestrel 5500 portable weather station in the middle of every second array during 2016 and at every array during 2017. Arrays were always deployed in pairs within a few kilometers (1-4 km) of each other during 2016, so weather conditions should have been sufficiently similar between the sites to justify obtaining weather data from only one of them. These devices provided weather data at 20-min intervals throughout the field season, including temperature (± 0.1 °C), wind speed (± 0.1 km/h), relative humidity (± 0.1%), and barometric pressure (± 0.1 mb). Temperature, in particular, affects the speed of sound and was required for the sound localization process. Wind can also affect the signal-to-noise ratio and thus the probability of detecting distant signals. However, wind speeds at microphone array locations were always low (mean = 0.75 km/h, standard deviation = 1.65 km/h, minimum = 0.00 km/h, maximum = 12.24 km/h) and thus were not considered further. Since precipitation can affect avian vocal activity and the signal-to-noise ratio on recordings, I supplemented these data with precipitation data for Happy Valley-Goose Bay, Labrador, which I obtained from the Environment and Climate Change Canada weather website. If the first 24 h of recording included more than 10 mm of rain, I left the array recording for an additional 24 h after the rainfall had decreased to below the threshold, and then used only the audio recordings from the final 24 h period in subsequent acoustic analyses.

3.2.3 General habitat characterization

The general habitat was characterized at each array by assessing vegetation cover at 5 standardized habitat sampling points, including midway between each pair of recorders and in the centre of the array. At each point, I measured canopy cover (%) with a spherical densiometer held pointing north. I determined stem density by holding a 2-m pole horizontally and then counting the number of trees touched by the pole while making a full rotation (Avery and Burkhart 2015). The standard definition of a tree in monitoring protocols is any woody species with a height exceeding 2 m and a diameter at breast height (DBH) exceeding 4 cm (EMAN 2004). However, with several locations being dominated by wetlands with stunted tree growth, I defined a "tree" as any woody species with a minimum height of 1.5 m and a minimum DBH of 1 cm. The number of trees was divided by the area of the circle [$\pi(2)^2$] to determine stem density in trees/m^2 (Avery and Burkhart 2015). Using a standard diameter tape, I measured the diameter at breast height of the three trees nearest to the sampling point. I determined vegetative species richness within the array by recording the total number of species of trees, shrubs, and ericaceous plants encountered within the array while walking among habitat sampling points (approximately 1 h of effort). I found that the ground layer among arrays was consistently a combination of sphagnum moss and lichen, and thus omitted it from further consideration. I calculated the mean value for each structural habitat characteristic (DBH, stem density, canopy cover) from among the 5 habitat sampling points.

Although all locations were dominated by black spruce and balsam fir, I identified three distinct forest types within the general coniferous forest habitat type on the basis of species that were secondarily dominant (*i.e.*, > 5% but < 50% of stems). The "spruce/fir type" contained only black spruce and balsam fir in the canopy layer, or also contained a smaller portion (≤ 20% of stems) of jack pine (*Pinus banksiana*). The "birch/poplar type" was distinguished by the secondary prominence of birch and/or poplar species in the canopy layer. The "tamarack type" was distinguished by secondary prominence of tamarack in the canopy layer. Locations with tamarack appeared to have greater ericaceous plant species richness when compared to the other forest types.

3.2.4 Acoustic analysis

3.2.4.1 Detecting vocalizations

I used Kaleidoscope software (Version 4.3.2, Wildlife Acoustics, Concord, MA, USA) to automatically detect avian vocalizations and to group them into clusters of similar sounds. The settings used in the program included: maximum distance from the cluster centre = 2.0, fast-Fourier transform size = 256 points (5.33 ms), maximum number of states = 12, maximum distance to cluster centre for building clusters = 0.5, and maximum clusters created = 500. These settings ensure that all detections are assigned to a cluster. The clusters approximate species, but, sometimes, multiple clusters were associated with a single species. I therefore inspected sample detections from each cluster and manually renamed clusters according to the species they represented. Species identities were determined by listening to recordings of vocalizations and reviewing their

associated spectrograms, and comparing these to the species accounts on the Birds of North American website (Rodewald 2015).

Detected vocalizations were localized using a custom MATLAB program, which is described in Chapter 2. First, the program identified the channel with the maximum signal-to-noise ratio ("reference channel"). Second, it bandpass filtered (a set minimum and maximum frequency) the detection to remove frequencies above and below the target signal (*e.g.*, wind noise). Third, the program conducted pair-wise waveform cross-correlations to measure the time-of-arrival differences of the signal between the reference channel and the other 7 channels in the array. Finally, using the time-of-arrival differences for each vocalization, combined with information about temperature and the locations of the microphones, the program produced UTM coordinates in two- and three-dimensions, and a localization error value that reflects the certainty of the estimated location (see chapter 2 for details of the localization algorithm).

3.2.4.2 Dataset filtering

I applied a number of exclusion criteria to the initial dataset. Previous studies (*e.g.*, Mennill et al. 2012; Wilson et al. 2014) demonstrated that localization becomes less reliable when analysing sounds produced outside the array. Additionally, I wanted to limit the sampling area to that which was assessed for general habitat characteristics. Using the "rgeos" package (Bivand and Rundel 2017) in R (Version 3.0.1; R Core Team, Boston, MA, USA), I created a 2-dimensional spatial polygon of the array based on the UTM coordinates of the array microphones. I then determined the minimum distance of each

localized vocalization from the edge of the polygon (0 m if inside the polygon). The list of vocalizations was reduced to include only those that originated from inside the microphone array or from within 5 m of its edge. This filtering step reduced the number of vocalizations considered for statistical analysis by approximately 60% (from 4,879,624 to 1,928,312). This reduction is substantial, but not surprising. Based on localization estimates in this study, and on previous research (*e.g.*, Dawson and Efford 2009), microphones can detect birds that are up to 90 m away. Therefore, the vast majority of the active "listening" space of the array fell outside my target area for habitat analyses.

I further reduced the dataset to include only those vocalizations that occurred during the targeted 24-h period of the recordings and that had a localization error value of 0.02 or less, which reduced the dataset from 1,928,312 to 470,761 vocalizations (*i.e.*, to 10% of the original). I considered these localizations to be accurate because, based on a "ground-truthing" speaker playback experiment, 90% of vocalizations with an error value ≤ 0.02 are within 3.55 m of their true locations (see Chapter 2). This error value strikes a balance between including vocalizations that are localized with a relatively high accuracy and retaining a large enough dataset that still reflects the local avian community. Next, although the localization procedure relies on vocalizations being detected in multiple channels, it is necessary to remove duplicate detections when counting the number of vocalizations produced. Whenever the same species was detected in multiple channels within 250 ms of each other, I retained only the first instance of the vocalization. This reduced the dataset from 470,761 to 89,242 vocalizations (*i.e.*, to 2% of the original). Finally, I excluded vocalizations produced by non-target sources, such as red squirrels

(*Tamiasciurus hudsonicus*) and humans, which reduced the dataset from 89,242 to 49,155 vocalizations (*i.e.*, to 1% of the original).

3.2.5 Statistical analysis

All statistical analyses were performed in R (Version 3.0.1; R Core Team, Boston, MA, USA). For all analyses, data from the 2016 and 2017 breeding seasons were combined. After the dataset filtering, 2 array sites from the 2017 breeding season yielded no detections, and thus were removed from analysis. For sites that were sampled in both years, only data from 2017 were included in statistical models, in order to yield a similar number of samples from each year (2016 = 48 sites, 2017 = 40 sites). All descriptive statistics are mean ± standard deviation, unless stated otherwise.

3.2.5.1 Avian community

To give a general overview of the avian community of the study area, I calculated the proportion of the 88 sites where bird species were present. The naming conventions of the species followed the American Ornithological Society's checklist (Chesser et al. 2018; see Appendix 2 for species codes and common and scientific names).

3.2.5.2 Species richness

I investigated the relationship between avian species richness and several environmental variables. Species richness was the total number of species detected at a site during a 24-h sampling period. First, I used a general linear model to determine if species richness was related to habitat characteristics. The predictor variables in this

model were 3 physical structure variables, including mean canopy cover (%), mean stem density (stems/m^2), and mean DBH (cm), as well as the floristic variable, vegetative species richness. Second, I used a general linear model to determine if species richness was associated with mean daily temperature and Julian date. Although these two predictor variables were correlated (Pearson's $r = 0.673$, n = 88, $p < 0.001$), the variance inflation factor was 1.83, which was lower than values typically associated with multicollinearity (Quinn and Keough 2002). For each location, mean daily temperature was calculated as the mean value recorded by the portable weather station at 20-min intervals across the 24-h recording session. Third, to determine if species richness was consistent at a given location between breeding seasons, I compared species richness between the 20 locations sampled in both 2016 and 2017 using a paired-samples t-test. Finally, I used a single-factor ANOVA to determine if avian species richness was related to forest type, using the Tukey multiple comparison of means with 95% family-wise confidence level for post-hoc tests.

3.2.5.3 Species-specific presence

I used logistic models to test for a relationship between habitat characteristics and the presence/absence of each species that was present in at least 10% of the array sites (*i.e.*, ≥ 9 of 88 sites). As predictor variables, I included 3 physical structure variables (mean canopy cover, mean stem density, and mean DBH) and 1 floristic variable (vegetative species richness).

The three forest types represent categorical variation within the natural boreal forest. These categories are associated with floristics, but the classifications were subjective and based on personal observation. Therefore, I decided to record the forest type and address it through a separate set of analyses. I conducted a series of analyses using contingency tables and chi-square tests of independence to determine if the forest type was associated with the proportion of array locations where a given species was detected. The analysis was restricted to 14 species that met the assumptions of the test (*i.e.,* 80% of expected cell counts should be 5 or more), as per Quinn and Keough (2002).

3.2.5.4 Spatial and temporal species composition

I used the Sorensen index (C_S), which is widely used in pair-wise comparisons (Sorensen 1948; Southwood and Henderson 2000; Lennon et al. 2001; Magurran 2004) to compare the species composition in a given location from one forest type to the species composition in a given location from another forest type. The index is defined as the proportion of species that are present at both locations in a pairwise comparison:

$$C_S = \frac{2a}{2a + b + c}$$

where *a* is the number species found at both locations, *b* is the number of species found at the first location and not the second, and *c* is the number of species found at the second location but not the first. C_S values near 1 indicate that the two locations are very similar in species composition, whereas C_S values near 0 indicate that the two locations are very different. I randomly selected 24 array locations from each forest type (n = 72). To compare the average similarities in avian composition among the birch/poplar, spruce/fir,

and tamarack forest types, I calculated C_S between all possible combinations of array locations for each pair of forest types. For example, I compared each of the 24 locations of the birch/poplar type to each of the 24 locations of the tamarack type, which resulted in 576 C_S values. I then calculated the mean of these C_S values to quantify the average (± standard deviation) similarity for the two forest types.

Rather than using a different index, I adjusted the variables of the Sorensen index to calculate temporal species similarity (C_t) for each of the 20 arrays that were deployed in the same locations in both 2016 and 2017. Temporal species similarity at a given site was defined as the proportion of species that were present at the location at both time points (Magurran 2004):

$$C_t = \frac{2a}{2a + b + c}$$

where a = number of species found at both points in time, b = number of species at time point 1 but not time point 2, and c = number of species at time point 2 but not time point 1. C_t was calculated separately for each of the 20 array sites sampled in both 2016 and 2017, and then averaged among the 20 sites.

3.3 Results

3.3.1 Avian community

Based on the 59,155 detections that comprised my final dataset, I detected 32 species across the 88 microphone array sites (Figure 3.2). The three most common species, as determined by the proportion of sites in which they were present, were Ruby-

crowned Kinglet, Dark-eyed Junco, and Yellow-rumped Warbler (Figure 3.2). The majority of species (22 species or 69%) were present at fewer than half of the sites. Common Nighthawk, a species-at-risk in Newfoundland and Labrador, was detected at a single site, and was the only species-at-risk detected in this study.

3.3.2 Species richness

Habitat characteristics, including mean canopy cover, mean stem density, mean DBH, and vegetative species richness, did not predict avian species richness ($F_{4,83} = 1.19$, $p = 0.321$, adjusted $R^2 = 0.01$). However, avian species richness was associated with mean daily temperature and Julian date ($F_{2,85} = 8.19$, $p < 0.001$, adjusted $R^2 = 0.14$; Table 3.1). When controlling for Julian date, species richness increased significantly with increasing mean daily temperature. In contrast, after controlling for the effects of mean daily temperature, species richness did not change with changes in Julian date (Table 3.1).

Species richness was compared among 20 locations sampled in both 2016 and 2017 (Table 3.2). Overall, species richness was significantly higher in 2016 (9.60 ± 2.64 species) than in 2017 (6.75 ± 4.02 species; 95% CI of mean difference = 1.42–4.28 species; paired *t*-test: $t_{19} = 4.18$, $p < 0.001$). I also found that species richness was significantly associated with forest type ($F_{2,85} = 3.30$, $p = 0.042$, adjusted $R^2 = 0.05$; Figure 3.3). Post-hoc pairwise comparisons showed that mean species richness was significantly higher in the birch/poplar type (9.12 ± 3.50 species) than in the spruce/fir type (7.17 ± 3.45 species, $p = 0.048$), but not significantly different than in the tamarack type (7.50 ±

2.50 species, $p = 0.153$). Avian species richness did not differ between the spruce/fir and tamarack types ($p = 0.925$).

3.3.3 Species-specific presence

I tested the relationship between the presence of each species and habitat characteristics (Table 3.3). For Black-throated Green Warbler, Cape May Warbler, and Magnolia Warbler, the logistic models had a McFadden R^2 greater than 0.2, indicating an excellent model fit (McFadden 1974). For the majority of species, however, the general habitat characteristics were not significant predictors of presence versus absence.

When controlling for other variables, increases in mean stem density, mean DBH, and vegetative species richness were each associated with increased probability of Black-throated Green Warbler presence (Table 3.3). Stem density was positively associated with Boreal Chickadee presence, canopy cover was positively associated with Cape May Warbler presence, and vegetative species richness was positively associated with Magnolia Warbler and Yellow-bellied Flycatcher presence (Table 3.3).

I tested the relationship between the presence of each species and forest type (Table 3.4). Black-throated Green Warbler and Cape May Warbler were more likely to occupy the birch/poplar type than the other forest types. Orange-crowned Warbler and White-throated Sparrow were more likely to occupy the tamarack type than the other forest types. American Robin was less likely to occupy the spruce/fir type and more likely to occupy the birch/poplar type (Table 3.5).

3.3.4 Spatial and temporal species composition

Avian species composition was similar among the three forest types (Table 3.6). Birch/poplar and tamarack stands were the most similar (mean $C_S = 0.50 \pm 0.157$), whereas spruce/fir and tamarack stands were the least similar (mean $C_S = 0.46 \pm 0.191$). These values indicate a moderate level of similarity among forest types, with nearly 50% of species being found in both forest types on average in pair-wise comparisons. Some species were absent from select forest types (Table 3.6). Bohemian Waxwing and Common Raven were absent from birch/poplar arrays, whereas Alder Flycatcher, Brown Creeper, Magnolia Warbler and Northern Waterthrush were absent from tamarack stands. American Crow, Winter Wren, and Canada Goose were absent from both birch/poplar and tamarack stands, but present in spruce/fir stands. However, the absences of these 9 species from these forest types may be coincidental because each species was present in only 1 to 3 locations overall.

When comparing locations sampled in both 2016 and 2017, the mean temporal species similarity was 0.52 ± 0.23 (range: 0.00–0.84; Table 3.2). Therefore, depending on the array, the composition of the avian communities ranged from very similar between years to complete species replacement.

3.4 Discussion

I found that physical structure (DBH, canopy cover, stem density) and floristic (vegetative species richness) variables were not significant predictors of avian species richness. However, these variables, singly or in combination, were significant predictors of presence for a number of species inhabiting the boreal forest. Species composition ranged widely between 2016 and 2017 in locations that were sampled in both years.

3.4.1 Avian community

The 32 species observed in this study have been documented previously to be present in the area by previous researchers, local land managers, and the conservation authority in Happy Valley-Goose Bay (Simon and Schwab 2005; HVGB 2010). The three most prevalent species – Ruby-crowned Kinglet, Dark-eyed Junco, Yellow-rumped Warbler – are forest generalist species, which are common and widespread throughout the coniferous and mixedwood habitats during the breeding season (Whitaker and Montevecchi 1999; Drapeau et al. 2000). The Common Nighthawk was the only species-at-risk of the 15 thought to be in Newfoundland and Labrador, and it was detected at only a single microphone array site (NLFLR 2017). However, it is notable that Common Nighthawk was observed at this site in both 2016 and 2017, suggesting that this site is used consistently by this species.

3.4.2 Species richness

It is generally accepted that avian species richness increases with habitat diversity, which includes increased variation in both habitat structure and vegetative species

composition (Whittaker et al. 2001). While this concept is usually applied at spatial scales that incorporate several broad habitat types (*e.g.*, forest, grassland, wetland), it can also be applied at a finer scale, such as within a single habitat type (*e.g.*, coniferous forest). In North America and Europe, differences in avian assemblages at the regional scale are known to be associated with differences in the physical structure and floristics of forests (Rotenberry 1985; Warren et al. 2005). Several studies have shown a relation between avian species richness within a single forested habitat type and the DBH, stem density, and canopy cover of those habitats (*i.e.,* Berg 1997; Warren et al. 2005; Deppe and Rotenberry 2008; Lemaître et al. 2012). However, these findings were conducted within more heterogeneous habitats and across larger spatial extents *(i.e.*, ≥ 100 x 100 km) than this study. For example, Deppe and Rotenberry (2008) correlated species richness with canopy cover and stem density at temporary stop-over sites in Mexico, and sampled locations across a wide environmental gradient that ranged from densely vegetated dunes and thickets to relatively open and sparsely vegetated mangroves. Additionally, the three physical structure characteristics (DBH, stem density, and canopy cover) that I considered are closely related to stand age, which correlates with the number of avian species in the boreal forest region (McCarthy and Weetman 2006; Thompson et al. 1999). I found that avian species richness was not correlated with DBH, tree height, or stem density. This is consistent with previous studies (Rotenberry 1985; Lee and Rotenberry, 2005) that found that physical structure characteristics better explain differences in avian assemblages between, rather than within, broad habitat classifications. Therefore, my data provides further support that variation in the physical structure of the habitat accounts for a relatively small proportion of the variation in species richness at fine spatial scales.

A strong, positive correlation between vegetative species richness and avian species richness has been demonstrated previously at the landscape scale (*i.e.*, James and Wamer 1982; Currie 1991; Tews et al. 2004). However, even at finer spatial scales, having a greater diversity of tree species increases the number of niches that different species can exploit for foraging, nesting, and shelter (Lee and Rotenberry 2005). For example, within 1-km^2 plots, Gillespie and Walter (2001) and Poulsen (2002) both found that both the number of bird species and the number of individuals of each species were positively correlated with the number of tree species. However, these studies were conducted in areas of high avian and vegetative species richness and diversity. For example, in the Gillespie and Walter (2001) study, which was conducted in Costa Rica and Nicaragua, mean forest bird richness was 22 ± 8.40 species (range = 12-35), and mean woody vegetation richness was 41.14 ± 9.19 species (range = 27-54). I found that vegetative species richness was not a significant predictor of avian species richness. This may be due to the lack of variation in vegetative species richness among locations where arrays were deployed (mean vegetative species richness = 4.84 ± 1.40). The vast majority of sites (approximately 98%) were dominated by black spruce and/or balsam fir. Greater than 70% of the canopy layer composition was comprised of these two tree species (JP Ethier, personal observation). Small differences in the compositions of the shrub and ericaceous herb layers were noted among locations, but the locations predominantly contained speckled alder and Labrador tea. This vegetative species composition is indicative of the spruce-moss domain of Quebec (412,400 km^2) and District 19A of Labrador (22,700 km^2), which constitute a large portion of the boreal forest

(approximately 8% of the 5,520,000 km^2; Robitaille and Saucier 1998; Forsyth et al. 2003).

Avian species richness was positively correlated with mean daily temperature after controlling for Julian date. DesGranges and LeBlanc (2012) conducted a similar study in the Quebec-Labrador Peninsula region of the Canadian boreal forest and also found that species richness was significantly correlated with temperature. At larger spatial scales, such as among different climatic zones, this pattern is explained by the species-energy theory (Wright 1983), which states that warmer temperatures allow for increased vegetative growth and therefore more food for primary and secondary consumers, such as birds. However, this is not likely the primary driver of the relationship at the small spatial scale used in my study. Another possibility is that a portion of avian species was present within arrays, but remained silent and thus undetected on cooler days. However, given that I recorded vocalizations over a 24-h period, this is unlikely, as individuals tend to produce thousands of vocalizations over a single day (Catchpole and Slater 2008). More realistically, the relationship between temperature and avian species richness is probably due to variation in the arrival dates of the various bird species, since departure and arrival dates are known to be affected by weather variables, such as precipitation, wind, and temperature (Sparks et al. 2002; Deppe et al. 2015). My data suggest that some migrant species were absent from the study area at the beginning of the study period (May) when temperatures were cooler, and that, as the study progressed towards late June/early July, temperatures increased and more species arrived.

Previous studies have shown that habitat floristics can affect avian assemblages at various scales (Rotenberry 1985; Lee and Rotenberry 2005; Hewson et al. 2011; DesGranges and LeBlanc 2012; Lemaître et al. 2012), and that this is especially true when comparing assemblages within a single, broad habitat type. By including forest type in my analyses, I found that avian species richness was higher in locations within the birch/poplar type, as compared to in the spruce/fir type. There is some evidence that mixed-wood forest stands (those than contain coniferous and deciduous tree species) support a higher diversity of food sources, particularly arthropods, and potential nest sites (Work et al. 2004; Buddle et al. 2006), which may contribute to higher avian species richness (Hobson and Bayne, 2000).

3.4.3 Species-specific presence

For the majority of species, the physical structure and floristics of the habitat were not significant predictors of presence/absence. This is consistent with previous studies (*i.e.*, Rotenberry 1985; Lee and Rotenberry 2005; Seavy and Alexander 2011; Lemaître et al. 2012) that found that both the physical structure and floristics of a habitat are potentially important when considering species individually, but that each species responds differently to variation in habitat characteristics. Therefore, some species show little or no response to variation in physical structure and floristics.

The relationship between forest type and presence was species-specific, with some species appearing to have a preference for specific forest types. For example, American Robin, Black-throated Green Warbler, and Cape May Warbler were present in a higher

proportion of birch/poplar stands than in any other forest type. This may be driven by the increased diversity of food resources in stands with a deciduous component. Conversely, Orange-crowned Warbler and White-throated Sparrow were present in the highest proportion of locations within tamarack stands. These species tend to be associated with deciduous or mixed-wood habitats that are shrubby with low growth and numerous openings in the vegetation, or near the edges of these habitats (Falls and Kopachena 2010; Gilbert et al. 2010). Many of the tamarack stands were in close proximity to more open areas, such as wetlands or riparian habitat with small streams, which may have met the habitat requirements of these species.

Overall, my findings suggest that, at the local scale, the composition of avian assemblages in my study area is influenced predominantly by factors other than the habitat characteristics measured in this study. Several non-habitat factors affect habitat selection in birds, including competition (Jaakkonen et al. 2015), conspecific and heterospecific attraction (Forsman et al. 1998; Parejo et al. 2005; Campomizzi et al. 2008), and physiological constraints (Block and Brennan 1993; Jones 2001). Alternatively, it may be that, as Niemi et al. (1998) state, there is an "overabundance of suitable sites" within my study area. The authors specified that, while some locations are avoided, the majority of habitat is viewed as being of equivalent quality and thus equally exploited.

3.4.4 Spatial and temporal species composition

The temporal species similarity values were highly variable among sites, ranging from 0.00 to 0.84 among the 20 locations sampled in both years. Some of this variation may be attributed to the observation that species richness at these locations was generally lower during 2017 in comparison to 2016 (Table 3.2). If a small number of species are present in the first year but do not return the next year, this will increase the temporal species turnover value, even if there are no new species that are present only in the second year. These results may also indicate that individuals and species are not consistently occupying particular patches or territories within the overall area between consecutive years. As the area of the microphone array is relatively small, individuals may have returned in 2017 to locations adjacent to the array site but just outside the area of detection. It is also possible that errors in detecting vocalizations and assigning them to species may have reduced temporal species similarity. Whatever the reason, my results are consistent with the meta-analysis by Schlossberg (2009), which found that 64% of adult migratory forest birds do not return to the same location between breeding seasons.

Differences in weather patterns and the arrival dates of individual species potentially influenced the differences in avian species composition observed between years. Wiley and Richards (1982) found that there was a positive correlation between temperature, the number of vocalizations, and the detectability of birds, as individuals were more likely to sing in warmer temperatures. Previous studies have also found that there is a negative relationship between temperature and date of arrival of migratory species, with species arriving on breeding sites earlier when spring temperatures are

warmer (Sparks et al. 2002). I noted a strong positive relationship between mean daily temperature and species richness. I also observed that snow in the forest persisted on the ground for a longer period into the breeding season in 2017 (JP Ethier, personal observation), and that the daily mean temperature (averaged over 24 h) in 2017 was 3.5ºC (±4.8 SD) cooler compared to in 2016 when comparing the same Julian dates (17 May and 30 June). It is possible that the birds were less vocal in 2017 due to cooler temperatures, as compared to 2016. It may also be possible that migration in 2017 was delayed one or two weeks. E-bird checklists (ebird.org) for Happy Valley-Goose Bay for these years support this argument. Several migratory warbler species (*e.g.*, Black-throated Green Warbler, Magnolia Warbler, Orange-crowned Warbler, Tennessee Warbler) were first recorded on the checklist approximately one week later in 2017, as compared to 2016. Since locations were sampled within a few days (Julian date) of each other in 2016 and 2017 in my study, daily temperature, through its effects on arrival dates, is likely the primary cause for differences in species richness and composition between breeding seasons.

There were relatively small differences in species composition between forest types. Most species detected in the study area were found in at least one location within each forest type. The primary difference was the proportion of sites in which each species was present, which I discussed when interpreting the species-specific models. That a handful of species were absent from certain forest types is likely coincidental. For example, Winter Wren was absent from birch/poplar and tamarack locations. However, this species was found in only one location in the study, and this location happened to be

spruce/fir. Furthermore, Winter Wrens are known to nest and forage near water and are associated with mature forest habitats that include large trees and components of dead wood in the form of both standing dead trees and downed woody debris (Hejl et al. 2002). These features, while not formally recorded, were most associated with birch/poplar locations and not spruce/fir locations (Ethier, personal observation).

3.4.5 Considerations and implications

There are some limitations to the scope of my study. My findings are likely only applicable to the general area in which the study took place (*i.e.*, the boreal forest of Labrador), as wildlife-habitat relationships inferred from relatively small spatial extents have limited transferability (Tuanmu et al. 2011). Regardless, such relationships are important for making local land-use decisions and are often necessary for establishing conservation efforts to protect habitat critical for survival and reproduction (Morrison et al. 2006). Furthermore, in this study, inferences based on statistical analysis could only be made for species that were adequately abundant. However, the most common species are generally those with the fewest constraints on habitat selectivity, such as generalists, which are the least likely to show significant effects. This presents a potential problem, as those species that are of the greatest interest to conservation efforts are usually uncommon or rare (Cunningham and Lindenmayer 2005).

I only considered a small subset of physical structure and floristic variables that have previously been used to study bird-habitat relationships. Commonly used variables include percent cover of each vegetative species (Gillespie and Walter 2001; Poulsen

2002; Lee and Rotenberry 2005; DesGranges and LeBlanc 2012), the number and percent cover of vegetative strata/height classes (Hobson and Schieck 1999; Deppe and Rotenberry 2008), total vegetative volume (Lewis and Starzomski 2015), and the number and DBH of snags/standing dead trees and downed woody debris (Imbeau et al. 1999; Drapeau et al. 2000). Incorporating these habitat variables may explain more variation in species richness and species-specific presence. Future studies should also include distances to landscape features such as wetlands, waterbodies, and anthropogenic structures (*e.g.*, roads, powerlines), as these features have the potential to significantly influence avian assemblages (*e.g.*, Summers et al. 2011; Zlonis et al. 2017).

It is important to collect data about habitat selection by common species, since many rare species were once abundant. Indeed, conservation organizations, such as Partners in Flight, emphasize that prevention is more feasible and affordable than recovery (Rosenberg et al. 2016), and consequently stress the importance of researching and monitoring all species in order to keep "common birds common". My findings provide a knowledge base for resource managers within the eastern boreal region of Labrador for determining which environmental characteristics are associated with species richness, presence, and composition. I found that DBH, canopy cover, stem density, and vegetative species richness were poor predictors of avian species richness, yet were significant predictors of presence for several individual avian species. These results indicate the importance of considering species individually and as a community as a whole, since different patterns emerge at different levels of analysis.

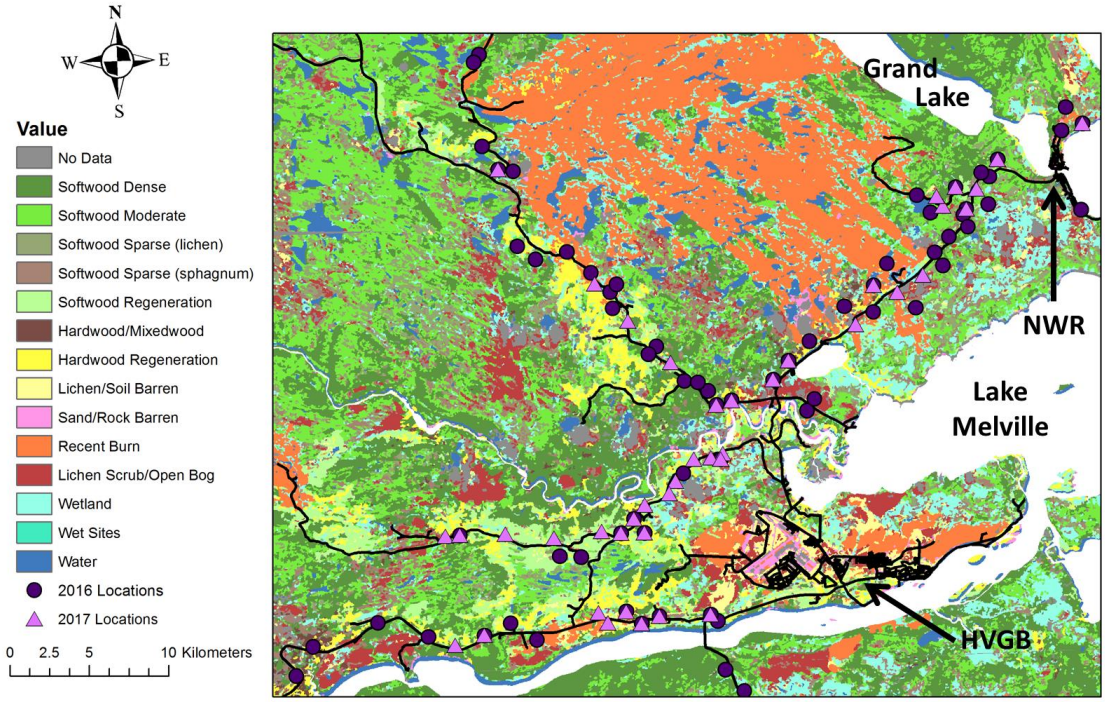

Figure 3.1: Map of 110 sites near North West River (NWR) and Happy-Valley-Goose Bay (HVGB), Labrador, where aspects of the avian community were compared to the physical structure and floristics of the habitat. Sites were sampled during the 2016 (n = 68, depicted by circles) and 2017 (n = 42, depicted by triangles) avian breeding seasons (May-July). Note: some points overlap because 20 locations from 2016 were resampled in 2017. The large area identified as "recent burn" (orange) represents the 1985 wildfire that destroyed 340 km^2. Base map provided by Nature Conservancy of Canada and Memorial University. Original figure is in colour.

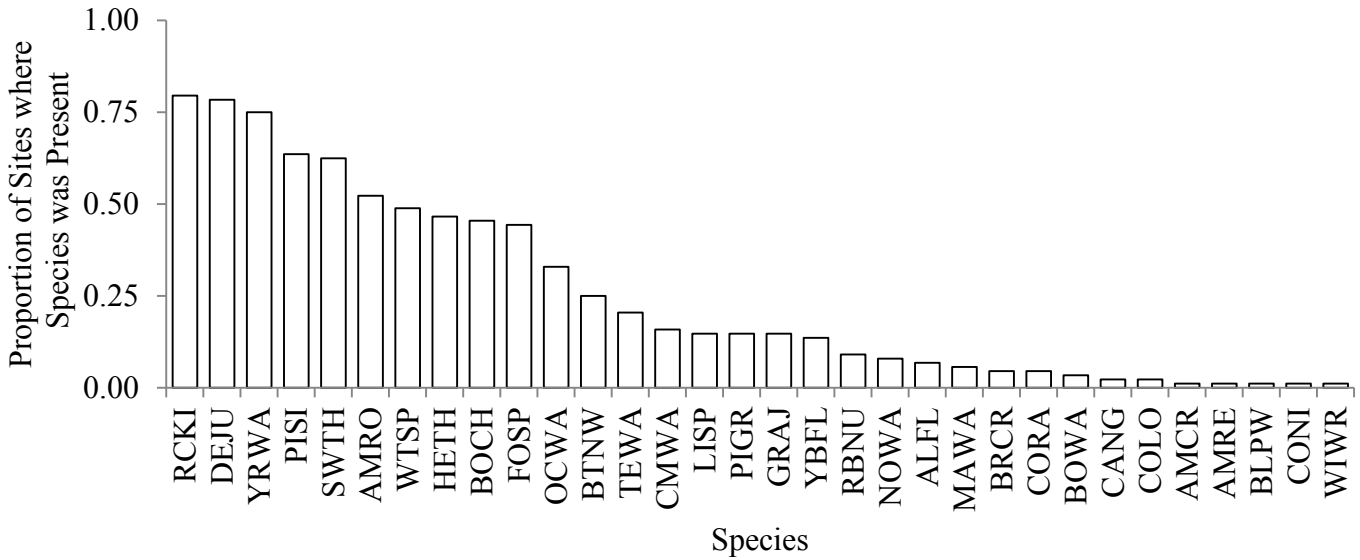

Figure 3.2: The proportion of 88 sites sampled in Labrador, Canada where bird species were present. Sites were sampled during the 2016 (N = 48) and 2017 (N = 40) avian breeding seasons. Species codes: ALFL = Alder Flycatcher (*Empidonax alnorum*), AMCR = American Crow (*Corvus brachyrhynchos*), AMRE = American Redstart (*Setophaga ruticilla*), AMRO = American Robin (*Turdus migratorius*), BLPW = Blackpoll Warbler (*Setophaga striata*), BOCH = Boreal Chickadee (*Poecile hudsonicus*), BOWA = Bohemian Waxwing (*Bombycilla garrulus*), BRCR = Brown Creeper (*Certhia americana*), BTNW = Black-throated Green Warbler (*Setophaga virens*), CANG = Canada Goose (*Branta canadensis*), CMWA = Cape May Warbler (*Setophaga tigrina*), COLO = Common Loon (*Gavia immer*), CONI = Common Nighthawk (*Chordeiles minor*), CORA = Common Raven (*Corvus corax*), DEJU = Dark-eyed Junco (*Junco hyemalis*), FOSP = Fox Sparrow (*Passerella iliaca*), GRAJ = Grey Jay (*Perisoreus canadensis*), HETH = Hermit Thrush (*Catharus guttatus*), LISP = Lincoln's Sparrow (*Melospiza lincolnii*), MAWA = Magnolia Warbler (*Setophaga magnolia*), NOWA = Northern Waterthrush (*Parkesia noveboracensis*), OCWA = Orange-crowned Warbler (*Oreothlypis celata*), PIGR = Pine Grosbeak (*Pinicola enucleator*), PISI = Pine Siskin (*Spinus pinus*), RBNU = Red-breasted Nuthatch (*Sitta canadensis*), RCKI = Ruby-crowned Kinglet (*Regulus calendula*), SWTH = Swainson's Thrush (*Catharus ustulatus*), TEWA = Tennessee Warbler (*Oreothlypis peregrina*), WIWR = Winter Wren (*Troglodytes hiemalis*), WTSP = White-throated Sparrow (*Zonotrichia albicollis*), YBFL = Yellow-bellied Flycatcher (*Empidonax flaviventris*), YRWA = Yellow-rumped Warbler (*Setophaga coronata*).

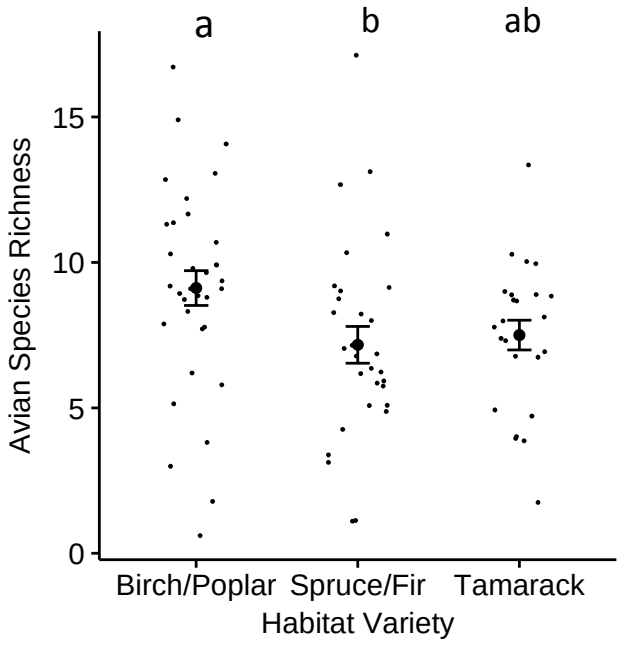

Figure 3.3: Avian species richness by forest type across 88 sites sampled in the 2016 and 2017 avian breeding seasons in Labrador, Canada. Open circles show avian species richness at each array. Filled circles with error bars show the mean (± standard error) avian species richness for a given forest type. All forest types were dominated by black spruce and/or balsam fir. The Birch/Poplar type also included birch and/or aspen (n = 34), and the Tamarack type also included tamarack (n = 24). The Spruce/Fir type included only spruce and fir (n = 30). Forest types with the same lowercase letter are statistically indistinguishable (Tukey multiple comparison of means; $\alpha = 0.05$).

Table 3.1: Summary of the general linear model of avian species richness regressed against mean daily temperature (°C) and Julian date across 88 sites in Labrador, Canada during the 2016 and 2017 avian breeding seasons. Statistically significant ($\alpha = 0.05$) variables are shown in bold.

Variable	Estimate	Standard Error	*t* value	*p* value
Intercept	2.34	4.54	0.52	0.608
Mean Daily Temperature	**0.25**	**0.10**	**2.54**	**0.013**
Julian Date	0.02	0.03	0.62	0.635

Overall model: $F_{2,85} = 8.19$, $p < 0.001$, adjusted $R^2 = 0.14$

Table 3.2: Avian species that were present in 2016 and 2017 for 20 arrays sampled in both years in Labrador, Canada. The temporal species similarity (C_t) was calculated between years. The array labels (*e.g.*, 'A003/A074') refer to the array numbers used at the same geographic location in 2016 and 2017.

Array	Species in 2016	Species in 2017	Similarity (C_t)
A003/A074	5: DEJU, FOSP, PISI, RCKI, YRWA	3: BOCH, HETH, WTSP	0.00
A004/A075	7: BOCH, DEJU, HETH, OCWA, PISI, RCKI, SWTH	4: AMRO, HETH, RCKI, SWTH	0.55
A005/A076	7: AMRO, BOCH, FOSP, HETH, OCWA, PISI, RCKI	6: AMRO, BOCH, DEJU, HETH, RCKI, SWTH	0.62
A006/A077	7: BLPA, BOCH, DEJU, HETH, OCWA, RCKI, WTSP	5: BOCH, CMWA, PIGR, RCKI, WTSP	0.50
A008/A078	8: BOCH, DEJU, HETH, PISI, RCKI, GRJA, WTSP, YRWA	1: RCKI	0.22
A011/A079	10: AMRO, BOCH, DEJU, FOSP, HETH, OCWA, PISI, RCKI, WTSP, YRWA	9: AMRO, BOCH, CORA, DEJU, FOSP, OCWA, PISI, WTSP, YRWA	0.84
A012/A080	7: AMRO, DEJU, FOSP, HETH, OCWA, PISI, WTSP	8: AMRO, BOCH, CORA, DEJU, PIGR, PISI, RCKI, YRWA	0.53
A014/A081	7: BOCH, CMWA, DEJU, FOSP, RCKI, SWTH, YRWA	2: BOCH, RCKI	0.44
A015/A082	11: BOCH, FOSP, HETH, MAWA, NOWA, PIGR, PISI, RBNU, RCKI, SWTH, YRWA	6: AMRO, DEJU, HETH, PISI, RCKI, WTSP	0.35
A033/A096	8: DEJU, FOSP, HETH, PISI, RCKI, SWTH, WTSP, YRWA	7: AMRO, DEJU, HETH, PISI, RCKI, SWTH, WTSP	0.80
A034/A097	11: AMRE, BTNW, BLPA, BOCH, CMWA, DEJU, FOSP, NOWA, RCKI, WTSP, YRWA	8: BTNW, BOCH, CMWA, DEJU, PISI, SWTH, WTSP, YRWA	0.63
A037/A098	12: AMRO, BTNW, BOCH, CMWA, DEJU, LISP, PISI, RCKI, SWTH, WIWR, YBFL, YRWA	17: ALFL, AMRO, BTNW, BOCH, BRCR, CMWA, DEJU, FOSP, MAWA, PIGR, PISI, RCKI, SWTH, GRAJ, WIWR, YBFL, YRWA	0.76

Table 3.2 (Continued):

Arrays	Species in 2016	Species in 2017	Similarity (C_t)
A038/A099	13: AMRE, CMWA, DEJU, FOSP, HETH, MAWA, NOWA, OCWA, PISI, SWTH, TEWA, WTSP, YRWA	13: ALFL, AMRO, DEJU, FOSP, HETH, MAWA, NOWA, PIGR, RCKI, SWTH, WTSP, YBFL, YRWA	0.62
A040/A100	12: AMRO, BLPW, BOCH, CMWA, CORA, DEJU, FOSP, HETH, RCKI, SWTH, WTSP, YRWA	9: DEJU, HETH, LISP, OCWA, PIGR, PISI, RCKI, SWTH, WTSP	0.48
A043/A104	15: AMRO, BOCH, BRCR, DEJU, FOSP, NOWA, OCWA, PISI, RBNU, RCKI, TEWA, GRAJ, WTSP, YBFL, YRWA	9: AMRO, BTNW, BOCH, DEJU, RCKI, SWTH, TEWA, YBFL, YRWA	0.58
A044/A105	8: BTNW, BOCH, DEJU, PISI, RCKI, SWTH, YBFL, YRWA	4: AMRO, DEJU, SWTH, YBFL	0.50
A055/A109	12: AMRO, DEJU, FOSP, HETH, OCWA, PISI, RCKI, SWTH, GRAJ, WTSP, YBFL, YRWA	9: AMRO, BOCH, DEJU, FOSP, HETH, SWTH, WTSP, YBFL, YRWA	0.76
A062/A110	11: ALFL, AMRO, CONI, DEJU, FOSP, PISI, RCKI, SWTH, TEWA, WTSP, YRWA	6: ALFL, AMRO, CMWA, CONI, FOSP, TEWA	0.59
A063/A111	9: DEJU, FOSP, HETH, OCWA, PISI, RCKI, SWTH, WTSP, YRWA	0	0.00
A067/A112	12: AMRO, BTNW, BOCH, BRCR, DEJU, FOSP, PISI, RCKI, SWTH, TEWA, WTSP, YRWA	9: BOCH, CMWA, DEJU, NOWA, PISI, RCKI, SWTH, YBFL, YRWA	0.57

Species codes: ALFL = Alder Flycatcher, AMCR = American Crow, AMRE = American Redstart, AMRO = American Robin, BLPW = Blackpoll Warbler, BOCH = Boreal Chickadee, BOWA = Bohemian Waxwing, BRCR = Brown Creeper, BTNW = Black-throated Green Warbler, CANG = Canada Goose, CMWA = Cape May Warbler, COLO = Common Loon, CONI = Common Nighthawk, CORA = Common Raven, DEJU = Dark-eyed Junco, FOSP = Fox Sparrow, GRAJ = Grey Jay, HETH = Hermit Thrush, LISP = Lincoln's Sparrow, MAWA = Magnolia Warbler, NOWA = Northern Waterthrush, OCWA = Orange-crowned Warbler, PIGR = Pine Grosbeak, PISI = Pine Siskin, RBNU = Red-breasted Nuthatch, RCKI = Ruby-crowned Kinglet, SWTH = Swainson's Thrush, TEWA = Tennessee Warbler, WIWR = Winter Wren, WTSP = White-throated Sparrow, YBFL = Yellow-bellied Flycatcher, YRWA = Yellow-rumped Warbler

Table 3.3: Regression coefficients and pseudo R^2 of logistic regression models comparing presence/absence versus habitat characteristics for 21 bird species across 88 sites. Only those species that were present in at least 10% of the sites (*i.e.*, ≥ 9 of 88 sites) were analysed. Values in bold indicate significance using log-likelihood statistics ($\alpha = 0.05$). Pseudo R^2 calculated using McFadden (1974).

Species	Mean Canopy Cover	Mean Stem Density	Mean DBH	Vegetative Species Richness	Pseudo R^2
American Robin	-0.01	-0.46	-0.02	0.05	0.02
Black-throated Green Warbler	0.01	**2.76**	**0.23**	**0.51**	0.22
Boreal Chickadee	0.00	**1.68**	0.00	-0.14	0.08
Cape May Warbler	**0.06**	1.01	-0.41	-0.19	0.24
Dark-eyed Junco	-0.01	-0.40	-0.02	0.25	0.04
Fox Sparrow	0.01	0.30	-0.01	-0.01	0.04
Gray Jay	0.00	0.93	-0.05	-0.09	0.03
Hermit Thrush	-0.02	1.13	-0.14	-0.10	0.11
Lincoln's Sparrow	0.01	-2.08	-0.34	0.16	0.18
Magnolia Warbler	0.07	-1.79	-0.05	**0.79**	0.24
Northern Waterthrush	0.03	0.01	0.07	0.17	0.08
Orange-crowned Warbler	0.00	-1.75	-0.20	0.36	0.16
Pine Grosbeak	0.02	-0.27	-0.01	0.21	0.03
Pine Siskin	0.02	0.82	-0.03	0.00	0.05
Red-breasted Nuthatch	0.03	0.52	0.16	-0.41	0.17
Ruby-crowned Kinglet	0.02	-0.25	-0.01	-0.15	0.03
Swainson's Thrush	0.00	1.15	0.07	0.32	0.07
Tennessee Warbler	0.03	-0.26	0.04	0.39	0.09
White-throated Sparrow	-0.02	-0.92	-0.17	0.07	0.17
Yellow-bellied Flycatcher	0.02	0.36	0.03	**0.48**	0.08
Yellow-rumped Warbler	-0.01	1.74	0.21	0.07	0.07

Table 3.4: The number of array locations, of the 24 sampled from each forest type, where a given species was present.

Species	Forest type		
	Birch/Poplar	Spruce/Fir	Tamarack
Alder Flycatcher	2	1	0
American Crow	0	1	0
American Robin	16	10	13
Black-throated Green Warbler	15	2	1
Bohemian Waxwing	0	1	1
Boreal Chickadee	14	13	8
Brown Creeper	1	2	0
Canada Goose	0	1	0
Cape May Warbler	8	2	1
Common Raven	0	2	2
Dark-eyed Junco	19	18	20
Fox Sparrow	13	9	8
Hermit Thrush	10	10	14
Lincoln's Sparrow	4	2	7
Magnolia Warbler	1	1	0
Northern Waterthrush	3	2	0
Orange-crowned Warbler	7	4	15
Pine Grosbeak	2	4	4
Pine Siskin	17	16	13
Red-breasted Nuthatch	2	4	1
Ruby-crowned Kinglet	20	18	20

Table 3.4 (Continued)

Species	Forest type		
	Birch/Poplar	Spruce/Fir	Tamarack
Swainson's Thrush	20	12	12
Tennessee Warbler	7	2	3
Whiskey Jack	4	4	1
White-throated Sparrow	8	9	19
Winter Wren	0	1	0
Yellow-bellied Flycatcher	7	2	1
Yellow-rumped Warbler	20	17	16

Table 3.5: Contingency tables showing the observed number (and expected number) of locations where a given species was present versus absent across three forest types. Each species was tested independently. Bold numbers indicate a statistically significant chi-square test of independence ($\alpha = 0.05$).

Species	Occupancy	Forest type			Chi-square	p-value
		Birch/Poplar	Spruce/Fir	Tamarack		
AMRO	Present	23 (17.8)	10 (15.7)	13 (12.5)	7.57	**0.023**
	Absent	11 (16.2)	20 (14.3)	11 (11.5)		
BTNW	Present	19 (8.5)	2 (7.5)	1 (6)	28.23	< **0.001**
	Absent	15 (25.5)	28 (22.5)	23 (18)		
BOCH	Present	19 (15.5)	13 (13.6)	8 (10.9)	2.97	0.227
	Absent	15 (18.5)	17 (16.4)	16 (13.1)		
CMWA	Present	11 (5.4)	2 (4.8)	1 (3.8)	11.26	**0.004**
	Absent	23 (28.6)	28 (25.2)	23 (20.2)		
DEJU	Present	25 (26.7)	24 (23.5)	20 (18.8)	0.87	0.648
	Absent	9 (7.3)	6 (6.5)	4 (5.2)		
FOSP	Present	18 (15.1)	13 (13.3)	8 (10.6)	2.21	0.331
	Absent	16 (18.9)	17 (16.7)	16 (13.4)		
HETH	Present	15 (15.8)	12 (14)	14 (11.2)	1.93	0.380
	Absent	19 (18.2)	18 (16)	10 (12.8)		
OCWA	Present	9 (11.2)	5 (9.9)	15 (7.9)	13.73	**0.001**
	Absent	25 (22.8)	25 (20.1)	9 (16.1)		
PISI	Present	22 (21.6)	21 (19.1)	13 (15.3)	1.47	0.479
	Absent	12 (12.4)	9 (10.9)	11 (8.7)		
RCKI	Present	28 (27)	22 (23.9)	20 (19.1)	1.09	0.581
	Absent	6 (7)	8 (6.1)	4 (4.9)		
SWTH	Present	26 (21.3)	17 (18.8)	12 (15)	4.87	0.088
	Absent	8 (12.8)	13 (11.3)	12 (9)		
TEWA	Present	10 (7)	5 (6.1)	3 (4.9)	2.87	0.238
	Absent	24 (27)	25 (23.9)	21 (19.1)		
WTSP	Present	12 (16.6)	12 (14.7)	19 (11.7)	12.27	**0.002**
	Absent	22 (17.4)	18 (15.3)	5 (12.3)		
YRWA	Present	27 (25.5)	23 (22.5)	16 (18)	1.29	0.526
	Absent	7 (8.5)	7 (7.5)	8 (6)		

Species codes: AMRO = American Robin, BTNW = Black-throated Green Warbler, BOCH = Boreal Chickadee, CMWA = Cape May Warbler, DEJU = Dark-eyed Junco, FOSP = Fox Sparrow, HETH = Hermit Thrush, OCWA = Orange-crowned Warbler, PISI = Pine Siskin, RCKI = Ruby-crowned Kinglet, SWTH = Swainson's Thrush, TEWA = Tennessee Warbler, WTSP = White-throated Sparrow, YRWA = Yellow-rumped Warbler.

Table 3.6: The number of shared and unshared avian species and corresponding Sorensen's index (mean $C_S \pm$ standard deviation) values in pairwise comparisons among 3 forest types across 72 arrays. For example, in the comparison of birch/poplar stands and tamarack stands, 19 species were present in both forest types, while 6 species were present in one type and not the other. All forest types were dominated by black spruce and/or fir. The Birch/Poplar type also included birch and/or aspen (n = 24), and the Tamarack type also included tamarack (n = 24). The Spruce/Fir type included only spruce, fir, or pine (n = 24).

Forest types	Species shared	Species not shared	Mean C_S
Birch/Poplar - Tamarack	19: AMRO, BTNW, BOCH, CMWA, DEJU, FOSP, GRAJ, HETH, LISP, OCWA, PIGR, PISI, RBNU, RCKI, SWTH, TEWA, WTSP, YBFL, YRWA	6: ALFL, BOWA, BRCR, CORA, MAWA, NOWA	0.496 ± 0.157
Birch/Poplar - Spruce/Fir	23: ALFL, AMRO, BTNW, BOCH, BRCR, CMWA, DEJU, FOSP, GRAJ, HETH, LISP, MAWA, NOWA, OCWA, PIGR, PISI, RBNU, RCKI, SWTH, TEWA, WTSP, YBFL, YRWA	5: AMCO, BOWA, CANG, CORA, WIWR	0.468 ± 0.187
Tamarack - Spruce/Fir	21: AMRO, BTNW, BOWA, BOCH, CMWA, CORA, DEJU, FOSP, GRAJ, HETH, LISP, OCWA, PIGR, PISI, RBNU, RCKI, SWTH, TEWA, WTSP, YBFL, YRWA	7: ALFL, AMRO, BRCR, CANG, MAWA, NOWA, WIWR	0.464 ± 0.191

Species codes: ALFL = Alder Flycatcher, AMCR = American Crow, AMRE = American Redstart, AMRO = American Robin, BLPW = Blackpoll Warbler, BOCH = Boreal Chickadee, BOWA = Bohemian Waxwing, BRCR = Brown Creeper, BTNW = Black-throated Green Warbler, CANG = Canada Goose, CMWA = Cape May Warbler, COLO = Common Loon, CONI = Common Nighthawk, CORA = Common Raven, DEJU = Dark-eyed Junco, FOSP = Fox Sparrow, GRAJ = Grey Jay, HETH = Hermit Thrush, LISP = Lincoln's Sparrow, MAWA = Magnolia Warbler, NOWA = Northern Waterthrush, OCWA = Orange-crowned Warbler, PIGR = Pine Grosbeak, PISI = Pine Siskin, RBNU = Red-breasted Nuthatch, RCKI = Ruby-crowned Kinglet, SWTH = Swainson's Thrush, TEWA = Tennessee Warbler, WIWR = Winter Wren, WTSP = White-throated Sparrow, YBFL = Yellow-bellied Flycatcher, YRWA = Yellow-rumped Warbler

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Chapter 4: Using microphone arrays to demonstrate microhabitat selectivity in two common avian species in steep decline: Boreal Chickadee and Cape May Warbler

Abstract: Understanding the microhabitat preferences of animals can help managers to develop better conservation and recovery strategies. However, identifying microhabitat preferences can be challenging. Traditional methods used to obtain this information are limited by cost, accuracy, and human resources. In this study, I investigated avian microhabitat preferences using microphone arrays that are capable of accurately localizing vocalizing birds. My objective was to identify the microhabitat characteristics associated with two common species in steep decline, the Boreal Chickadee (*Poecile hudsonicus*) and the Cape May Warbler (*Setophaga tigrina*). I deployed 68 eight-channel (four-recorder) arrays at random locations in Labrador, Canada during the 2016 avian breeding season. I returned in 2017 to the 18 array locations where the target species had been detected the previous year and characterized the microhabitat at the exact locations where they had been detected. I also characterized the microhabitat at a matching set of randomly determined control locations. Results show that Boreal Chickadees select trees with greater diameter-at-breast-height, and that Cape May Warblers select trees with greater canopy cover. These findings demonstrate microhabitat selectivity for these two species in steep decline.

4.1 Introduction

In birds and other taxa, habitat selection is viewed as a hierarchical, decision-making process that occurs at several spatial scales (McGarigal et al. 2016). At the first

and broadest scale, avian species are restricted to a geographic range based on physiological constraints, such as thermoregulation and metabolic rate, and morphological constraints, such as wing shape and size that limit the ability to disperse. At finer spatial scales, individuals select locations for home ranges based on general habitat characteristics of the environment, such as a densely vegetated coniferous forest. At the final scale, individuals select specific microhabitat (*e.g.*, specific trees) for engaging in daily activities, such as singing, nesting, or foraging (Johnson 1980; Hutto 1985; Block and Brennan 1993; Jones 2001). For example, Acadian Flycatchers (*Empidonax virescens*) in eastern Arkansas select Nuttall's oak (*Quercus nuttallii*) and possumhaw holly (*Ilex decidua*) trees for nesting sites more often than would be expected by chance based on the abundance of these tree species (Wilson and Cooper 1998).

Biologists and government agencies can develop better conservation and recovery strategies by identifying and preserving a species' preferred microhabitat, particularly if it is associated with increased survival and reproduction (Jones 2001). Furthermore, models including microhabitat and general habitat variables are often better at predicting avian community metrics, such as presence, abundance, and diversity (*e.g.*, McDermott et al. 2011), than models produced at only one spatial scale. Incorporating microhabitat information can also assist managers in balancing competing objectives, such as maximizing timber harvest, minimizing risk to wildlife, and fostering post-harvest restoration of the habitat back to its original state (Brown et al. 2004; Kilgore and Blinn 2004). The techniques used by managers can dramatically influence several microhabitat

characteristics important for birds, such as retaining a large volume of coarse woody debris and snags used for nesting and foraging (Riffell et al. 2011).

Identifying microhabitat selected by wildlife can be challenging and time-consuming (Bibby et al. 2000; Stratford and Stouffer 2013; Nemes and Islam 2017). Without identifying and quantifying the microhabitat, researchers can only assume that each element within the general habitat is used equally by an individual or species occupying that particular environment. Therefore, it is often crucial to establish the microhabitat selected relative to its availability in the broader environment, and relative to the availability of alternatives (Jones 2001). Most studies involve searching for and following marked individuals to determine territory boundaries and features used for singing and/or nesting, and then measuring the vegetation characteristics of those features at mapped locations determined from focal sampling (Martin and Geupel 1993; Bibby et al. 2000; Nemes and Islam 2017). Other studies link telemetry locations to associated vegetation (*e.g.*, Patten et al. 2005; Hansbauer et al. 2010). Both approaches are labour-intensive and limit the number of individuals that can be sampled and the spatial extent over which one can infer relationships.

Microphone arrays allow researchers to localize vocalizing animals with sub-metre accuracy and are thus a promising new technique for studying acoustic and spatial behaviour (Barker et al. 2009). Microphone arrays consist of three or more acoustic recording units distributed throughout a location where individuals are expected to vocalize. Since sound travels at a slow and predictable rate through air (approximately

343 m/s), an animal's acoustic signal will reach each microphone at a slightly different time, depending on where the animal is in relation to each microphone. The location of the vocalizing animal can be determined by measuring the time-of-arrival differences of the sound between the microphones in the array, and then applying a tri-lateralization technique to those values (*e.g.*, Wilson et al. 2014). Unlike older microphone arrays, which required kilometers of cable and several days to set up (Mennill et al. 2006), modern microphone arrays use commercially available wireless acoustic recording units that are easy to transport and set up. For example, Mennill et al. (2012) were able to fit an entire 8-microphone cable-free array into a single backpack and to set it up in the field in under an hour. Microphone arrays record vocalizations passively, thus removing the need to capture animals and minimizing observer effects on avian behaviour and habitat choice (Mech and Barber 2002; Lee and Marsden 2008). Having multiple systems deployed simultaneously and recording continuously, or scheduled to record for long periods of time, can increase the likelihood of detecting rare species (Blumstein et al. 2011). Therefore, microphone arrays may increase accuracy and decrease the time investments associated with studying microhabitat selection. Most studies involving microphone arrays have been proof-of-concept studies, with only a few studies applying the technology to biological questions (*e.g.*, duetting behaviour in Rufous-and-white Wrens, *Thryophilus rufalbus;* Mennill et al. 2006; Mennill and Vehrencamp 2008; inter-individual spacing in male American bullfrogs, *Rana catesbeiana*, and Greater Sage Grouse, *Centrocercus urophasianus;* Bates et al. 2010; Paticelli and Krakauer 2010). Very few studies have used microphone array technology to identify and characterize microhabitat preferences (e.g. Wilson and Bayne 2018).

In this study, I used microphone arrays in the boreal forest of Labrador, Canada to test for microhabitat selection in Boreal Chickadee (*Poecile hudsonicus*) and Cape May Warbler (*Setophaga tigrina*), two common species in steep decline according to the USGS North American Breeding Bird Survey 1966-2015 report (Sauer et al. 2017). I conducted this study in Labrador because the Boreal Shield Ecozone in Labrador is approximately 1.8 million km^2 (approximately 18% of Canada's landmass) and is 88% forested. Although the ecozone provides substantial habitat for breeding birds, the majority of bird surveys within this ecozone, including the USGS North American Breeding Bird Survey, have been conducted in southern Ontario and Quebec, with poor coverage outside these regions (Downes et al. 2011).

Using the audio recordings from microphone arrays, I estimated the locations of call perches of Boreal Chickadees and song perches of Cape May Warblers. I characterized the microhabitat at points where the focal species vocalized, as well as at a matching set of random control points at the same general location. My objectives were to (1) demonstrate that microphone arrays are a feasible and practical method for studying microhabitat selection in birds, and (2) determine and describe the microhabitat characteristics of the call and song perches selected by Boreal Chickadee and Cape May Warbler, respectively. I hypothesized that, if Boreal Chickadee and Cape May Warbler select perches non-randomly, then the microhabitat characteristics of those perches would differ from the characteristics of random points within the same general location.

4.2 Methods

4.2.1 Target species

The Boreal Chickadee is a small (10-g) year-round resident of the boreal forest (Ficken et al.1996). The IUCN lists boreal chickadees as being of least concern in terms of conservation status, but populations are declining in several portions of their range throughout the USA and Canada. The USGS North American Breeding Bird Survey 1966-2015 report indicates yearly declines of 4.35% in Nova Scotia and 5.24% in New Brunswick, Canada (Sauer et al. 2017). Data specific to Newfoundland and Labrador do not exist, as these regions are not included in the USGS North American Breeding Bird Survey (Sauer et al. 2017), In 2007, the Boreal Chickadee was placed on the National Audubon Society's "Top 10 Common Birds in Decline" list, with a reported 73% population decline from 19.5 million to 5.2 million individuals since the mid-1960s (Brennan 2007; Butcher 2007).

The Cape May Warbler is a small (10-g) Neotropical migrant that breeds extensively in the Canadian boreal forest during the summer (Baltz and Latta 1998), and which spends the winter in portions of the southern United States, South America, and the Caribbean, including Puerto Rico and the Virgin Islands. In summer, it is a "spruce budworm specialist" since its abundance increases with outbreaks of spruce budworm, *Choristoneura fumiferana* (Baltz and Latta 1998). The North American Bird Conservation Initiative identifies Cape May Warbler as a "common bird in steep decline" (NABCI 2014). The USGS North American Breeding Bird Survey 1966-2015 report indicates that the North American populations have declined by 2.5% annually,

cumulating in a 72% population decline, from approximately 25 million to 7 million individuals, since the mid-1960s (Sauer et al. 2017).

4.2.2 Array deployment

I deployed 68 microphone arrays in a 50 x 50 km area between North West River and Happy Valley-Goose Bay in Labrador, Canada during the 2016 avian breeding season (15 May to 15 July; Figure 3.1). The locations of sites were selected at random, but with the constraints that they were within 1 km of road access and a minimum distance of 500 m from each other. I chose a maximum distance from road access of 1 km because hiking beyond this distance through dense forest while carrying a microphone array would have been difficult and would have reduced our sample size. I chose to separate sites by a minimum of 500 m because this reduced the risk of detecting the same birds at multiple sites (Wilson and Mennill 2011). GPS coordinates for sites were generated using a random integer set generator that creates non-repeating integers within confined boundaries (RANDOM.org). These random coordinates were then plotted on 1:50,000 scale topographic maps (National Topographic System, Series A771, Edition 4MCE, Map13 F/7 - 13 F/10) and discarded if they violated the inclusion criteria or were within a delineated swamp, bog, or water body.

Each array consisted of 4 SM3 audio recorders (Wildlife Acoustics, Concord, MA, USA) attached to trees in a 40 x 40 m square that encompassed approximately 0.15 ha. Each recorder had two channels: a built-in omnidirectional microphone (frequency range: 50–20000 Hz, ± 10 dB) was placed approximately 1.35 m above the ground, and a

second external omnidirectional microphone (model: SMM-A2; frequency range: 50–20000 Hz, ± 10 dB) was positioned in the forest canopy approximately 2 to 3 m above the first. All microphones were pointed towards the centre of the array. As a requirement of localization (Mennill et al. 2012), recorders were synchronized to within 1 ms of each other by connecting them to external GPS units (model: Garmin SM3 GPS). The position of each microphone was determined using a survey-grade GNSS with 10-cm accuracy (Geo7X, Trimble, Sunnyvale, CA, USA). Each recorder was programmed to record continuously until stopped, and to create a new stereo sound file every 2 h throughout this time (WAVE format, 24 kHz sampling rate, 16-bit amplitude encoding). Each array recorded for 24 h, beginning 2 h after setup to minimize disturbance effects associated with setup. The array was left recording for an additional day if it rained on the first day. Field equipment included 4 arrays (*i.e.*, 16 recorders), and 2 arrays were relocated each day throughout the season.

I recorded weather variables by placing a Kestrel 5500 portable weather station in the middle of every other array. Since two arrays were deployed at any given time, and since one of them always included a weather station, I had continuous weather data for the general vicinity of each array. The weather stations sampled at 20-min intervals throughout the field season. They recorded a suite of weather variables, including temperature (± 0.1 °C), wind speed (± 0.1 km/h), relative humidity (± 0.1%), and barometric pressure (± 0.1 mb). Temperature, in particular, affects the speed of sound and was required for sound localization. Wind can also affect the signal-to-noise ratio and

thus the probability of detecting signals. However, wind speeds at microphone array locations were always low (mean = 0.75 km/h, standard deviation = 1.65 km/h, minimum = 0.00 km/h, maximum = 12.24 km/h) and thus were not considered further. Humidity and barometric pressure have been found to have negligible effects on localization (Wölfel and McDonough 2009) and therefore were not considered further.

4.2.3 Acoustic analysis

I used the Cape May Warbler song, as described on the species' Birds of North America entry (Baltz and Latta 1998; Figure 4.1). The Boreal Chickadee does not have a true song, but does produce up to 13 different calls, including gargles, chirps, and cackles (Ficken et al. 1996). I used the "chick-a-dee" call to identify and localize boreal chickadees (Figure 4.1), since it is produced in a variety of contexts. This call can be used to locate mates during foraging and nest cavity excavation, and to signal to a mate that the bird has returned to the nest site with food (McLaren 1976). Therefore, I concluded that this call would be an appropriate signal for identifying microhabitat use on the breeding grounds.

I recorded over 3600 h of audio from 68 arrays. Following the field season, avian vocalizations were automatically detected and grouped into clusters of similar sounds using *Kaleidoscope* software (version 4.3.2, Wildlife Acoustics, Concord, MA, USA). I used the following settings within *Kaleidoscope*: FFT window size = 256 points (5.33 ms); frequency range of potential signals = 2000–10000 Hz; duration of potential signals

= 0.1–4.0 s; maximum inter-syllable gap = 0.35 s. Settings used during the clustering process included: maximum distance from the cluster centre = 2.0; maximum states = 12; maximum distance to cluster centre for building clusters = 0.5; maximum clusters created = 500. *Kaleidoscope* generated a detection list text file with one row for each vocalization (2,734,885 detections in total) and columns describing the structure of the detection (duration, minimum frequency, maximum frequency, mean frequency), its position within the raw recording, and the species to which it was assigned. The analysis ran on a desktop computer (iMac, 32 GHz Intel Core i5, 16GB RAM) and took approximately 25 h to process. Inspecting the resulting detections manually to confirm species identification required a further 160 h.

Vocalizations were localized using a custom MATLAB program (see details in chapter 2). For each detection, the program identified the channel in which the vocalization had the highest signal-to-noise ratio ("reference channel"). I bandpass filtered the vocalization using the minimum and maximum frequencies provided by Kaleidoscope to maximize the signal-to-noise ratio, and then used pair-wise waveform cross-correlations to measure the time-of-arrival differences of the vocalization between the reference channel and each of the other channels in the array. Using these time-of-arrival differences, the known locations of the microphones, and the temperature at the time of recording, the program estimated the two-dimensional location from which the sound originated (UTM coordinates). It also provided an error value that reflects the accuracy of the estimated location. Based on a ground-truthing experiment in which I

broadcasted frequency upsweeps through a speaker from known locations inside microphone arrays, 95% of localizations with an error value of 0.01 (a unitless measure of confidence) or less are within 3.59 m of their true locations in 2-dimensional space (see chapter 2). I reduced my overall dataset to include only those vocalizations produced within the array by Boreal Chickadees or Cape May Warblers (674 vocalizations), and only those with a localization error value of 0.01 or less (429 vocalizations). The program can also estimate locations in 3-dimensions, but the ground-truthing experiment showed the three-dimensional localization to be inaccurate in the vertical dimension *(i.e.,* elevation). Thus, I relied on 2-dimensional estimates of location for this study.

4.2.4 Microhabitat characterization

In 2017, I returned to 18 array locations where Boreal Chickadee (12 array locations) or Cape May Warbler (8 array locations) had been detected in 2016. Localizing vocalizations required several weeks of processing and therefore it was not possible to return to locations during the same breeding season. However, the microhabitat features that I measured (see below) are structural traits that, in all likelihood, change very little between consecutive years unless significantly altered or disturbed (i.e., logging, forest fire).

For each array and for each species, my goal was to characterize the microhabitat of up to 12 different estimated perch locations from the previous year (hereafter referred to as "perch sites"), and to compare the microhabitat characteristics of those perch sites to the microhabitat of an equal number of randomly determined control sites from within the

same array. Often several vocalizations were produced from each perch site. If both species occurred within an array, I used a separate set of random points for each species. Perch sites were considered different if they were separated by at least 1 m. If more than 12 perch sites existed within a given array for a given species, I selected 12 at random. If fewer than 12 existed, I used all of the available perch sites. Random sites were determined using a random number generator (RANDOM.org) to produce a northern offset (between 0 and 40 m) and an eastern offset (between 0 and 40 m) from the southwest corner of the array.

I located perch sites and the randomly determined control sites by converting their UTM coordinates to waypoints on the Trimble Geo 7x. I then used the built-in navigation software, which gives a real-time estimate of location after base-station correction (Goose Bay base station, which was within 25 km of all locations), to find the sites within the arrays. If no tree was within 2 m of a perch site, the location was considered an error and the site was eliminated from further consideration. A tree was defined as any woody stemmed species with a diameter greater than or equal to 1 cm, with viable perching locations (*i.e.*, branches, limbs). If no trees were within 2 m of a randomly determined control site, a new randomly determined site was created and used in its place to ensure that I had an equal number of perch sites and control sites for each species at each array. Shrubs were not excluded, however all perches were nonetheless found in balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), or birch trees (*Betula* sp.).

For each perch site and control site, I measured stem density by holding a 2-m pole horizontally, and then counting the number of trees touched by the pole while making a full rotation. The number of trees was then divided by the area of the circle to determine stem density as stems/m^2 (Avery and Burkhart 2015). Canopy cover was measured using a densiometer (Model-A, convex) held while facing north. Diameter-at-breast-height (tree diameter at the height of 1.35 m) was measured using a standard diameter tape. I also noted the status of each tree (living or dead). I consider a tree to be living if > 75% of its branches had green needles/leaves.

4.2.5 Statistical analysis

For each array and species, the mean diameter-at-breast height, mean stem density, and mean canopy cover were calculated from among all of the measured perch sites, and, separately, from among all of the measured control sites. I found that mean values did not meet the assumptions required for parametric tests (*i.e.*, normality, homogeneity of variance), so, for each species, I compared each microhabitat characteristic between perch sites and randomly determined control sites using paired Wilcoxon signed rank tests ($\alpha = 0.05$). Although I conducted three separate tests of the same general hypothesis for each species, I did not apply a correction for the associated inflation of experiment-wise type I error because the small sample sizes involved in the study ($n = 12$ for Boreal Chickadee; $n = 8$ for Cape May Warbler) would have led to an unacceptable increase in experiment-wise type II error (Freiman et al. 1978).

4.3 Results

Microhabitat was measured at 94 perch sites distributed across 18 array locations (Boreal Chickadee: 63 sites across 12 arrays; Cape May Warbler: 31 sites across 8 arrays), and at a matching set of 94 randomly selected sites from within those same array locations (Table 4.1). In all cases, focal trees were living and were either black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), or white birch (*Betula papyrifera*). Mean DBH was positively correlated with mean canopy cover (Spearman's *rho* = 0.32, *p* = 0.045, n = 40 sites, including 12 Boreal Chickadee perch sites, 8 Cape May Warbler perch sites, and 20 control sites) and negatively correlated with mean stem density (n = 40, Spearman's *rho* = -0.34, *p* = 0.032; Figure 4.2). Although these variables were inter-correlated, their relationships were relatively weak (*i.e.*, Spearman's *rho* < 0.5; Hinkle et al. 2002). Therefore, I analyzed each variable individually for my analysis of microhabitat selectivity rather than using a composite of the three variables.

Boreal Chickadees exhibited microhabitat selectivity (Figure 4.3). Compared to randomly determined sites from within the same array, they vocalized from trees with greater DBH ($W = 75$, $Z = 2.82$, $p = 0.002$, $n = 12$). Canopy cover ($W = 38$, $Z = -0.08$, $p = 0.970$, $n = 12$) and stem density ($W = 48$, $Z = 0.71$, $p = 0.519$, $n = 12$) of call perch sites did not differ significantly from those of randomly determined control sites from within the same array.

Cape May Warblers also demonstrated microhabitat selectivity (Figure 4.4). Canopy cover was significantly greater at song perch sites than at randomly determined

control sites (W = 33, Z = 2.10, p = 0.039, n = 8). Stem density (W = 20.5, Z = 0.35, p = 0.773, n = 8) and the DBH of trees (W = 29, Z = 1.54, p = 0.148, n = 8) did not differ significantly between song perch sites and randomly determined control sites.

4.4 Discussion

During the breeding season, Boreal Chickadees and Cape May Warblers preferentially occupy spruce-fir dominated forests (Ficken et al. 1996; Baltz and Latta 1998) and follow key food resources across local and regional scales (Root 1988; Morse 1978). The size and location of individuals' territories within these broad-scale areas are influenced by the availability of trees with soft heartwood for nest cavities for Boreal Chickadees (McLaren 1975), and by the number of forest edges and the distribution of open patches for Cape May Warblers (Baltz and Latta 1998). Here, using microphone array technology, I demonstrated that Boreal Chickadees and Cape May Warblers further select call and song perches within those territories based on microhabitat characteristics of individual trees or of the area immediately surrounding those trees. These microhabitat characteristics differ from the microhabitat characteristics of sites selected at random from within the same general location. Boreal Chickadees selected larger trees than expected by chance, whereas Cape May Warblers selected sites with greater canopy cover than expected by chance.

Boreal Chickadees are a year-round resident of the boreal forest and demonstrate limited dispersal behaviour related to food distribution (Root 1988). Flocks congregate preferentially in mature stands in the winter, but occupy both young and mature forest

stands during the breeding season, with a preference for forests containing spruce and fir tree species (Hadley and Desrochers 2008). However, there is evidence that Boreal Chickadees prefer to feed from larger trees when foraging during the breeding season (Haftorn 1974). Microhabitat selection for nest sites, call perches, and foraging sites has been described for Boreal Chickadees in only a few studies. Ficken et al. (1996) showed that Boreal Chickadee nest sites are most often near the ground in dead tree stumps and rarely found at a height greater than 3 m above the ground. Other studies have shown that, where sympatric, Boreal Chickadee and Black-capped Chickadee (*P. atricapillus*) segregate when foraging during the breeding (Vassallo and Rice 1982) and nonbreeding seasons (Gayk and Lindsay 2012). Vassallo and Rice (1982) demonstrated that Boreal Chickadees fed in the upper and outer portions of trees, independent of tree height, whereas Black-capped Chickadees fed in the lower half and inner portions of trees and utilized a wider variety of tree species (*i.e.,* deciduous and coniferous trees; Vassallo and Rice 1982). Gayk and Lindsay (2012) showed that, during the winter in Michigan, USA, Boreal Chickadees fed exclusively on conifer species and spent significantly more time foraging in the top 3 m of trees, as compared to Black-capped Chickadees.

I found that Boreal Chickadees in this study vocalized from large, living conifers. Given that the "chick-a-dee" call is produced by individuals communicating with mates when separated during foraging, it is likely that these vocalizations were from individuals establishing the location of a mate or advertising a foraging location, rather than from individuals engaged in activities at their nest site. In support of this, Haftorn (1974) noted that Boreal Chickadees during the summer in Alaska selected older trees when feeding

and storing food, and that they mostly ignored trees less than 6 m in height for these activities.

Information on general habitat selection of Cape May Warbler during the breeding season has been collected in Ontario, Canada and Maine, USA, but is lacking for the vast majority of its breeding range, including in Labrador (Baltz and Latta 1998). The species occupies coniferous habitats with spruce (*Picea* sp.) and balsam fir (*Abies balsamea*) of medium- to old-age (50+ years), where spruce budworm infestations tend to occur (Baltz and Latta 1998). In Quebec, Canada, Cape May Warblers preferentially used plantations of sparsely spaced 50+-year-old white spruce (*P. glauca*) with a canopy height of at least 10 m (DesGranges 1980). Microhabitat selection for nest sites, song perches, and foraging sites has also been studied in Cape May Warbler. They forage for invertebrates by gleaning, most often near the upper, outer portion of spruce and fir trees (MacArthur 1958). Nest sites are usually located in conifers in open parts of the forest or near the edge of forest patches (Baltz and Latta 1998). Nests are typically concealed near the trunk near the top of the tree (MacArthur 1958). During the breeding season, males sing at approximately 2 m below the top of the tree (Kendeigh 1947).

I found that Cape May Warblers sang from sites with greater canopy cover than the surrounding general habitat. Previously, I showed that, across 88 sites, Cape May Warblers were more likely to be found in habitats with greater mean canopy cover (Ethier, unpublished; see chapter 3). Since the hypothesized functions of birdsong are to repel competing males and attract and court females (Kroodsma and Byers 1991;

Catchpole and Slater 2008), individuals may sing from these locations to conceal their specific location, thereby preventing predation while advertising within a territory. There is some evidence from a field study on passerines that individuals increase song output when perched in concealed locations, likely limiting exposure to surprise attacks by predators and reducing predation risk (Campos et al. 2009). Alternatively, males may be signalling an appropriate location for a nest site that is well-concealed by the canopy, since Cape May Warblers are known to nest in the well-concealed, densely-foliated upper portions of spruce and fir trees (Baltz and Latta 1998).

This study is an initial, but important, step in using microphone arrays to demonstrate the microhabitat characteristics preferred by free-living birds in general, and by Boreal Chickadee and Cape May Warbler in particular. Based on my findings, conserving mature spruce-fir dominated forest would likely benefit these species, since Boreal Chickadees vocalize preferentially from trees with greater DBH, and Cape May Warblers vocalize preferentially from trees with greater canopy cover. However, it is also important to consider that the microhabitat selected in one context (*e.g.*, foraging) may differ from the microhabitat selected in another context (*e.g.*, nesting). Future research on these species should also include additional aspects of bird ecology, including species interactions (Campomizzi et al. 2008) and sources of disturbance (Zabala et al. 2012), which are known to impact habitat and microhabitat preferences. It is only when considering all aspects of a species' breeding ecology that sound conservation practices can be made.

Research on common species, such as Boreal Chickadee and Cape May Warbler, is necessary, as many rare species were once abundant. Conservation organizations, such as Partners in Flight, highlight the importance of studying and surveying all species in order to keep "common birds common," since prevention is more feasible and affordable than recovery (Rosenberg et al. 2016). I identified microhabitat preferences in a boreal forest for two common avian species in steep decline. Many recovery strategies focus on identifying and conserving critical habitat. For example, recovery strategies for Canada Warbler, *Cardellina canadensis*, and Prothonotary Warbler, *Protonotaria citrea*, both identify as a priority the need to determine critical habitat (Environment Canada 2011, 2016). My study suggests that not all parts of a habitat are used equally, and that conservation efforts may be improved by also considering critical microhabitat within a species' general habitat.

Table 4.1: The number of Boreal Chickadee call perches and Cape May Warbler song perches within each microphone array (n = 18). Different perches for a given species were separated by at least 1 m.

	# of different perches	
Array Code	Boreal Chickadee	Cape May Warbler
A003	7	0
A004	10	0
A005	6	0
A006	4	0
A008	9	0
A014	4	5
A015	8	0
A033	1	5
A043	4	0
A044	5	0
A063	3	0
A067	5	0
A011	0	1
A012	0	1
A034	0	5
A037	0	2
A038	0	3
A040	0	9
Total	63	31

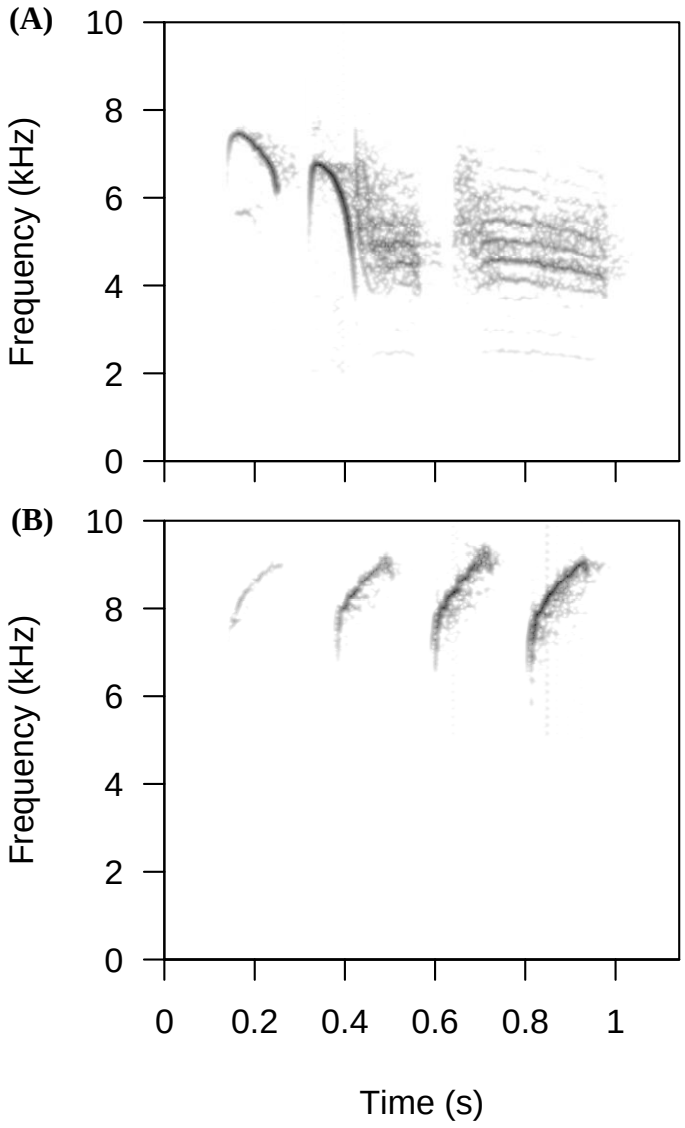

Figure 4.1: Spectrograms of the vocalizations used to detect and localize Boreal Chickadee and Cape May Warbler. I used a microphone array to record and localize these vocalizations so that I could characterize the microhabitat characteristics associated with vocalization perch sites. (A) The "chick-a-dee" call of the Boreal Chickadee. (B) The song of the Cape May Warbler, which is described as 3 to 5 "tseet" notes delivered with rising inflection (Baltz and Latta 1998). Spectrograms were generated with a 512-point fast Fourier transform, 90% overlap, and Hamming window. Temporal resolution is 2.1 ms, frequency resolution is 46.9 Hz, and the grayscale represents an amplitude range of 35 dB.

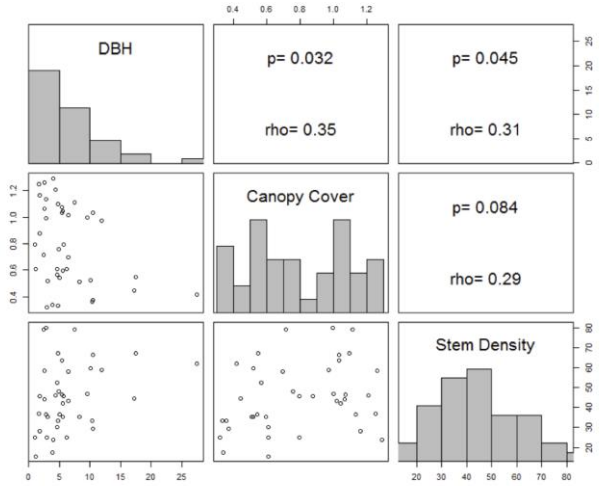

Figure 4.2: Diagnostic plots of 3 microhabitat variables associated with call and song perch sites used by Boreal Chickadees (n = 12 array locations) and Cape May Warblers (n = 8 array locations). Shown on the diagonal (top-bottom) are the mean diameter at breast height (cm), mean canopy cover (%), and mean stem density (stems/m^2). Above the diagonal are the Spearman correlation coefficients (rho) and associated p-values of pairwise comparisons of variables. Below the diagonal are scatterplots of pairwise comparisons of variables. Each point is an average of up to 12 perch sites at a given array for a given species, or an average of the same number of randomly determined control sites selected for that species from that same array.

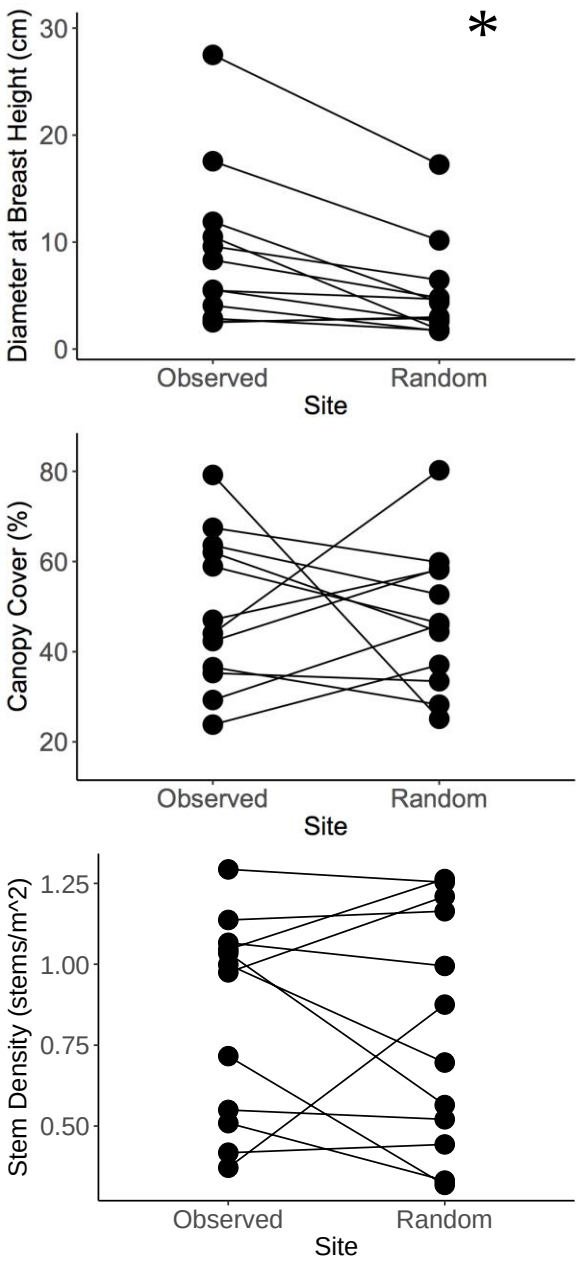

Figure 4.3: Pair-wise comparisons of the microhabitat of call perch sites and randomly determined control sites for Boreal Chickadee (n = 12 array locations). Shown are mean diameter at breast height (top), mean canopy cover (middle), and mean stem density (bottom). Each point is an average of up to 12 sites. Asterisks indicate a statistically significant difference between the observed perch sites and randomly determined control sites.

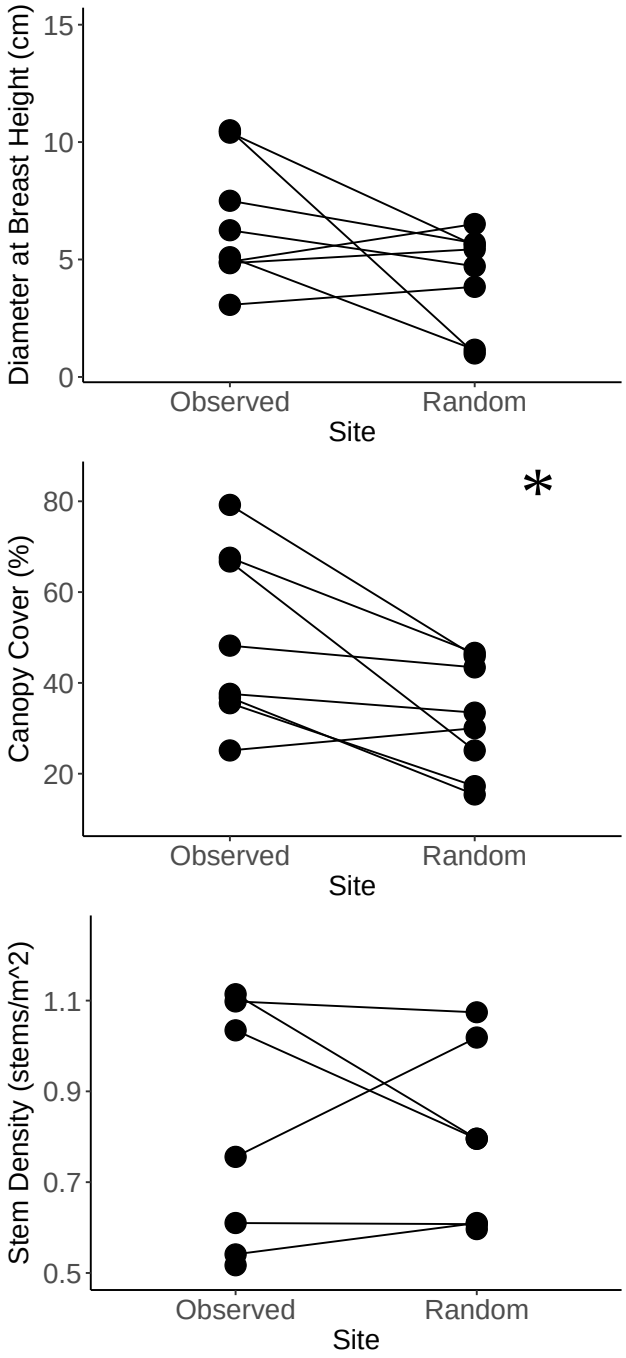

Figure 4.4: Pair-wise comparisons of the microhabitat of song perch sites and randomly determined control sites for Cape May Warbler (n = 8 array locations). Shown are mean diameter at breast height (top), mean canopy cover (middle), and mean stem density (bottom). Each point is an average of up to 12 sites. Asterisks indicate a statistically significant difference between the observed perch sites and randomly determined control sites.

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CHAPTER 5: Concluding discussion

5.1 Microphone arrays and acoustic monitoring

Microphone arrays are a powerful tool for studying animal behaviour and spatial ecology in a variety of taxa, including birds (Mennill et al. 2006; Mennill and Vehrencamp 2008; Paticelli and Krakauer 2010), amphibians (Bates et al. 2010), and mammals (Spillman et al. 2015). With acoustic recorders becoming more readily available and affordable, the applications for microphone arrays are rapidly expanding. Recently, microphone arrays have been used in innovative ways to study the impact of anthropogenic disturbance and habitat use (Shonfield and Bayne 2017a, 2017b; Yip et al. 2017). Previous studies have also shown that microphone arrays are a valuable tool for acoustic monitoring of avian communities. Shonfield and Bayne (2017b) recently reviewed several studies comparing human observers to acoustic recorders. They concluded that acoustic recorders often performed equal to or better than point counts when estimating avian species richness, abundance, and composition.

I used the cable-free microphone array technology described by Mennill et al. (2012). This technique enables researchers to record thousands of hours of audio and millions of vocalizations from several locations within the environment, and to localize the vocalizing individuals in 2- and 3-dimensional space. Currently, there are no commercially available software solutions for performing localizations on this volume of data. The localization workflow described in this thesis will thus allow future researchers to take full advantage of the recent advances in microphone array hardware. I have also

demonstrated how microphone arrays can be used to study avian community parameters (*i.e.*, species richness, composition, presence) and their relationships to habitat and microhabitat characteristics, with the ultimate goal of building bird-habitat models. Finally, I have provided a permanent archive of the audio recordings, which will be submitted to the Memorial University Library's digital repository. This archive will contain millions of acoustic signals from birds, but also from mammals, insects, and frogs, and will thus provide an important foundation for future research on conservation and spatial ecology. One such avenue would be to explore the influence of habitat characteristics on the density of each bird species. By localizing vocalizations and calculating the area over which they were detected, one can calculate the vocalization density of each species and use it as a proxy for population density, as in Marques et al. (2013).

5.2 Avian conservation, habitat relationships, and microhabitat selection

With the population declines and loss of biodiversity among North American landbirds over the last 40 years, both conservation organizations and government agencies have recognized the need for a greater understanding of the behaviour and ecology of birds (Downes et al. 2011; Rosenberg et al. 2016; COSEWIC 2018). In fact, the tri-national North American bird conservation initiative, Partners in Flight, has highlighted the importance of researching and monitoring all bird species, since even common species, such as Boreal Chickadee and Cape May Warbler, have shown steep population declines (Rosenberg et al. 2016; Sauer et al. 2017). Directly managing wildlife is challenging, and therefore it is often the habitat, or land, in which species reside that is

managed and conserved (Dale et al. 2000). In order for managers to make sound decisions, associations between avian communities and habitat must be established.

Several factors influence the distribution of birds in their environment, including the physical structure and floristics of the habitat (Rotenberry 1985; Lee and Rotenberry 2005), weather variables (Şekercioğlu et al. 2012; Grima et al. 2017), and community interactions (Johnson 1980; Morrison et al. 2006). The relative importance of each of these factors is contested and often depends on the spatial scale considered and the organism(s) being studied (Morrison et al. 2006).

I have shown that an avian community within the boreal forest of Labrador, Canada is influenced by variation in the physical structure and floristics of the habitat, as well as by mean daily temperature. Despite the habitat being relatively homogeneous, differences in avian species richness and composition were observed among three forest types. While species richness was observed to be higher in the birch/poplar type, I would caution against conserving this habitat at the expense of others, as some species (*e.g.*, Orange-crowned Warbler) displayed a preference (increased presence/decreased absence) for other types. Additionally, the influences of physical structure and floristics on presence were species-specific, which is consistent with previous studies in the boreal forest (Schmiegelow and Mönkkönen 2002; Lemaître et al. 2012). Finally, my results from studying the microhabitat selection of Boreal Chickadees and Cape May Warblers suggest that not all parts of a habitat are used equally. Therefore, I recommend that a variety of broad habitat types and forest types be conserved, as no one habitat variable

was found to be a definitive predictor of species richness or presence. Furthermore, I recommend that information about the microhabitat features (*e.g.*, trees, dead logs) used for nesting, foraging, and singing should be ascertained and incorporated into conservation and management strategies. For example, there is evidence in Cerulean Warblers (*Setophaga cerulea*) that microhabitat selected for singing is as important as nesting sites for successful reproduction (*i.e.*, Barg et al. 2006).

5.3 Scope and limitations

When considering the results of this study, it is important to consider that the research was conducted on an avian community during two consecutive avian breeding seasons (May-July) within a spruce/fir-dominated ecosystem with a recent history of disturbance, including natural forest fires and logging (Simon and Schwab 2005). There is substantial evidence to suggest that bird-habitat models perform poorly when applied beyond the scope in which they were developed (Block and Brennan 1993; Tuanmu et al. 2011). However, this does not mean that the results are inconsequential. Bird-habitat relationships are important for making local land-use decisions and are often necessary for establishing conservation efforts to protect habitat critical for survival and reproduction (Morrison et al. 2006). Thus, results of this study are intended to be used primarily by local land and resource managers.

Models correlating habitat characteristics to patterns of species-specific presence could only be made for those species that were sufficiently abundant (*i.e.*, found in $\geq$ 10% of microphone array locations). It also is possible that the relatively small number of

perch sites in the microhabitat analysis resulted in a failure to detect small effects. Small sample sizes are a common challenge in conservation-oriented studies, since the species being conserved tend to be quite rare.

5.4 Conclusion

Microphone arrays have proven to be a feasible method for obtaining habitat and microhabitat associations of boreal birds. Even when studying avian communities at the local scale in landscapes where the habitat is relatively homogeneous, there is variation in species richness and presence. Additionally, individuals appear to be selective of the microhabitat features used within the general habitat in which they reside. I encourage researchers to use the new procedures for processing acoustic data that I have outlined in this thesis, and to continue developing the overall approach. As stated by Shonfield and Bayne (2017b), it may be pertinent to combine human observer (*i.e.*, point counts) and acoustic monitoring techniques to get a better understanding of whether the two methods complement or contradict each other. Additional research should also be conducted to support the initial observations of this study and to build a greater understanding of spatial ecology and habitat use of birds.

5.5 References

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Appendix 1: Birds of Newfoundland and Labrador that are currently listed as species at risk according to Newfoundland and Labrador Fisheries and Land Resources (NLFLR, 2017). Species detected in this study are in bold.

Scientific Name	Common Name	Listed Status	Year of Listing
Bucephala islandica	Barrow's Goldeneye	Vulnerable	2000
Dolichonyx oryzivorus	Bobolink	Vulnerable	2015
Chaetura pelagica	Chimney Shift	Threatened	2007
Chordeiles minor	**Common Nighthawk**	Threatened	2007
Numenius borealis	Eskimo Curlew	Endangered	2000
Histrionicus histrionicus	Harlequin Duck	Vulnerable	2001
Pagophila eburnean	Ivory Duck	Endangered	2006
Catharus minimus	Gray-cheeked Thrush	Vulnerable	2005
Contous cooperi	Olive-sided Flycatcher	Threatened	2009
Falco peregrinus	Peregrine Falcon	Vulnerable	2007
Charadrius melodus melodus	Piping Plover	Endangered	2000
Loxia curvirostra percna	Red Crossbill	Endangered	2004
Calidris canutus rufa	Red Knot	Endangered	2007
Euphagus carolinus	Rusty Blackbird	Vulnerable	2007
Asio flammeus	Short-eared Owl	Vulnerable	2008

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Appendix 2: Bird species detected in this study, including scientific and common names and 4-letter alpha codes. Naming conventions follow the 58th supplement of the American Ornithological Society's checklist of North American birds (Chesser et al. 2017).

Scientific Name	Common Name	Alpha Code
Empidonax alnorum	Alder Flycatcher	ALFL
Corvus brachyrhynchos	American Crow	AMCR
Setophaga ruticilla	American Redstart	AMRE
Turdus migratorius	American Robin	AMRO
Setophaga striata	Blackpoll Warbler	BLPW
Setophaga virens	Black-throated Green Warbler	BTNW
Bombycilla garrulus	Bohemian Waxwing	BOWA
Poecile hudsonicus	Boreal Chickadee	BOCH
Certhia americana	Brown Creeper	BRCR
Branta canadensis	Canada Goose	CANG
Setophaga tigrina	Cape May Warbler	CMWA
Gavia immer	Common Loon	COLO
Chordeiles minor	Common Nighthawk	CONI
Corvus corax	Common Raven	CORA
Junco hyemalis	Dark-eyed Junco	DEJU
Passerella iliaca	Fox Sparrow	FOSP
Perisoreus canadensis	Grey Jay	GRAJ
Catharus guttatus	Hermit Thrush	HETH
Melospiza lincolnii	Lincoln's Sparrow	LISP
Setophaga magnolia	Magnolia Warbler	MAWA
Parkesia noveboracensis	Northern Waterthrush	NOWA
Oreothlypis celata	Orange-crowned Warbler	OCWA
Pinicola enucleator	Pine Grosbeak	PIGR
Spinus pinus	Pine Siskin	PISI
Sitta canadensis	Red-breasted Nuthatch	RBNU
Regulus calendula	Ruby-crowned Kinglet	RCKI
Catharus ustulatus	Swainson's Thrush	SWTH
Oreothlypis peregrina	Tennessee Warbler	TEWA
Zonotrichia albicollis	White-throated Sparrow	WTSP
Troglodytes hiemalis	Winter Wren	WIWR
Empidonax flaviventris	Yellow-bellied Flycatcher	YBFL
Setophaga coronata	Yellow-rumped Warbler	YRWA

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