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Using microphone arrays to investigate microhabitat selection by declining breeding birds

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Understanding the microhabitat preferences of animals can help managers to develop better conservation and recovery strategies, but is challenging. Traditional methods are limited by cost, accuracy, and human resources. In this study, we investigated avian microhabitat preferences using microphone arrays that are capable of accurately localizing vocalizing birds. Our objective was to identify the microhabitat associations of two common species in steep population decline, the Boreal Chickadee *Poecile hudsonicus* and the Cape May Warbler *Setophaga tigrina*. We deployed 68 eight-channel arrays at random locations in Labrador, Canada during the 2016 avian breeding season. We 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. We also characterized the microhabitat at randomly determined control locations. Results show that Boreal Chickadees select trees with greater diameter-at-breast-height that are surrounded by greater stem density. We did not find evidence that Cape May Warblers exhibit microhabitat selection during song production. The study shows that microphone arrays are an effective tool for identifying preferred microhabitat that could be incorporated into future conservation or recovery strategies.

Keywords: acoustic localization, acoustic monitoring, birdsong, conservation, habitat

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 body size, that limit dispersal. At finer spatial scales, individuals select locations for home ranges based on general habitat characteristics, such as a densely vegetated coniferous forest. At the final scale, individuals select specific microhabitat (e.g., individual trees) for engaging in daily activities, such as singing, nesting, or foraging (Johnson 1980, Hutto 1985, Block & Brennan 1993, Jones 2001). For example, Acadian Flycatchers *Empidonax virescens* in southeastern USA inhabit swampy woodland habitat, and then 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 & Cooper 1998, Allen *et al.* 2017).

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 to balance competing objectives such as maximizing timber harvest, minimizing risk to wildlife, and fostering post-harvest habitat restoration (Brown *et al.* 2004, Kilgore & 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 & Stouffer 2013, Nemes & Islam 2017). Without identifying and quantifying the microhabitat, researchers can only assume that resident animals use each element within the general habitat equally. It is therefore 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 (Martin & Geupel 1993, Bibby *et al.* 2000, Nemes & 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 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 synchronized acoustic recording units distributed in a location where individuals are expected to vocalize. Because sound travels at a slow and predictable rate through air (approximately 343 ms^{-1}), 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 among 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 kilometres 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 eight-microphone cable-free array into a single backpack and to set it up in the field in under one hour. Microphone arrays record vocalizations passively, thus removing the need to capture animals and minimizing observer effects on avian behaviour and habitat choice (Mech & Barber 2002, Lee & 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). Microphone arrays may therefore increase accuracy and reduce the time investment associated with studying microhabitat selection. Yet most studies involving microphone arrays to date 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 & Vehrencamp 2008; inter-individual spacing in male American Bullfrogs *Rana catesbeiana* and Greater Sage Grouse *Centrocercus urophasianus,* Bates *et al.* 2010, Patricelli & Krakauer 2010). Very few studies have used microphone array technology to identify and characterize microhabitat preferences (for an exception, see Wilson & Bayne 2018).

In this study, we used microphone arrays in the boreal forest of Labrador, Canada to test for microhabitat selection by Boreal Chickadees *Poecile hudsonicus* and Cape May Warblers *Setophaga tigrina*, two common species in steep population decline according to the USGS North American Breeding Bird Survey 1966–2015 report (Sauer *et al.* 2017). The Boreal Shield Ecozone is approximately 1.8 million km^2 (approximately 18% of Canada's landmass), is 88% forested, and thus provides substantial habitat for breeding birds. Yet, most 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). We therefore conducted our study in Labrador to expand coverage of the Boreal Shield Ecozone.

Using audio recordings from microphone arrays deployed in 2016, we estimated the locations of Boreal Chickadee call perches and Cape May Warbler song perches. Then, in 2017, we returned to the study site and characterized the microhabitat at the exact points where the focal species had vocalized the previous year, as well as at a matching set of random control points at the same general location. Our 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 Boreal Chickadee call perches and Cape May Warbler song perches.

METHODS

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 annual population decline rates of 4.4% in Nova Scotia and 5.2% 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 & Latta 1998), and which spends the winter in parts of the southern USA, South America, and the Caribbean, including Puerto Rico and the Virgin Islands. In summer, it is a Spruce Budworm specialist whose abundance increases with outbreaks of Spruce Budworm *Choristoneura fumiferana* (Baltz & Latta 1998). The North American Bird Conservation Initiative identifies Cape May Warbler as a “common bird in steep decline” (NABCI 2014), and the USGS North American Breeding Bird Survey 1966–2015 report indicates that North American populations have declined by 2.5% annually, amounting to a 72% population decline, from approximately 25 million to seven million individuals, since the mid-1960s (Sauer *et al.* 2017).

Array deployment

We deployed 68 microphone arrays in a 50 x 50 km area (centred at 53°25’01” N, 60°30’07” W) between North West River and Happy Valley-Goose Bay in Labrador, Canada during our study species' 2016 breeding season (15 May to 15 July). Sites were selected at random, but with the constraints that they were within 1 km of road or trail access, a minimum distance of 100 m from roads, and a minimum distance of 500 m from each other. We 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. As per Wilson and Mennill (2011), we separated sites by a minimum of 500 m because this reduced the risk of detecting the same birds at multiple sites, since both species maintain relatively small territories (approximately 5 ha for Boreal Chickadee, Ficken *et al.* 1996; < 1 ha for Cape May Warbler, Baltz & Latta 1998). 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) 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) placed approximately 1.35 m above the ground, and a second external omnidirectional microphone (model: SMM-A2, frequency range: 50–20000 Hz ± 10 dB) 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; Wildlife Acoustics, Concord, MA, USA). The position of each microphone was determined using a survey-grade GNSS with 10-cm accuracy (model: 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 four arrays (i.e., 16 recorders), and two arrays were relocated each day throughout the season.

We recorded weather variables by placing a portable weather station (model: Kestrel 5500 Weather Meter; KestrelMeters.com, Boothwyn, PA, USA) in the middle of every other array. Because two arrays were deployed at any given time, and because one of them always included a weather station, we 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) and wind speed (± 0.1 km/h). Temperature, in particular, affects the speed of sound and is required for sound localization. Wind exceeding approximately 15 km/h can also affect the signal-to-noise ratio and thus the probability of detecting signals (D. Wilson unpubl. data). However, wind speeds at microphone array locations were always low (mean ± SD: 0.8 ± 1.7 km/h; range: 0.0–12.2 km/h) and thus were not considered further.

Acoustic analysis

To identify and localize Cape May Warblers, we used the song as described in the Birds of North America species account (Baltz & Latta 1998; Fig. 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). We used the "chick-a-dee" call to identify and localize Boreal Chickadees (Fig. 1) because it is produced in a variety of contexts. The call is 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). We therefore concluded that this call would be an appropriate signal for identifying microhabitat use on the breeding grounds.

We recorded 1632 h of 8-channel audio. 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). We used the following settings within *Kaleidoscope*: FFT window size = 256 points (5.33 ms), frequency range of potential signals = 2000–10 000 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 detection (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 cluster to which it was assigned. The analysis ran on a desktop computer (iMac, 32 GHz Intel Core i5, 16 GB RAM) and took approximately 25 h to process.

We estimated detection error by using Audacity software (Audacity® software is copyright © 1999–2019 Audacity Team. The name Audacity® is a registered trademark of Dominic Mazzoni) to manually review and annotate all boreal bird vocalizations contained in one of our 2-h audio recordings. We then processed that same audio file in Kaleidoscope using the same detection settings used in our study. Kaleidoscope detected 2513 vocalizations, including all of the 2379 vocalizations that we had scored manually, plus 134 faint vocalizations that we had missed during the manual review. Kaleidoscope did not detect any sounds from non-avian sources. Therefore, at the detection step, the false negative (i.e., avian vocalizations that were not detected) and false positive error rates (i.e., non-avian sounds that were detected) were both zero, which agrees with other, more comprehensive tests of Kaleidoscope's detection accuracy (e.g., Siracusa *et al*. 2019). We note that the much larger dataset in our study (i.e., 1632 h) did contain some non-avian detections (e.g., bears, squirrels, sirens), but these were less than 1% of all detections.

All vocalizations detected by Kaleidoscope were localized using a custom MATLAB program (Mathworks; Natick, MA, USA). For each detection, the program identified the channel in which the vocalization had the highest signal-to-noise ratio ("reference channel"). It bandpass-filtered the vocalization using the minimum and maximum frequencies provided by

Kaleidoscope to maximize the signal-to-noise ratio, and then used pairwise 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 confidence of the estimated location. Based on a ground-truthing experiment in which we broadcast 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 (J.P. Ethier unpubl. data). We reduced our overall dataset to include only those vocalizations produced within the array with a localization error value of 0.01 or less (22 519 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, we relied on 2-dimensional estimates of location for this study.

We manually inspected all remaining detections in Kaleidoscope to correct false positive classifications (i.e., detections labeled by Kaleidoscope as a target species but actually belonging to a non-target species) and false negative classifications (i.e., detections belonging to a target species but labelled by Kaleidoscope as a non-target species). Kaleidoscope incorrectly labelled 25 of the 22 519 total detections as Boreal Chickadee (i.e., false positive error = 0.1%), and incorrectly labeled 232 of the 308 Boreal Chickadee vocalizations as a different species (i.e., false negative error = 75.3%). Kaleidoscope incorrectly labelled four of the 22 519 total detections as Cape May Warbler (i.e., false positive error < 0.1%), and incorrectly labeled 10 of the 56 Cape May Warbler vocalizations as a different species (i.e., false negative error = 17.9%). Reviewing the 22 519 vocalizations and correcting the classification errors required 160 h.

Microhabitat characterization

In 2017, we returned to the 18 array locations where either Boreal Chickadee (13 array locations) or Cape May Warbler (eight 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 we measured (see below) are structural traits that change very little between consecutive years unless significantly altered or disturbed (e.g., by logging or forest fire).

For each array and for each species, our 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 randomly determined control sites from within the same array. Birds often produce several vocalizations from the same perch site, so we considered perch sites to be different only if they were separated by more than 3.59 m, which was the localization accuracy (95% confidence) of our system. If more than 12 perch sites existed within a given array for a given species, we selected 12 at random. If fewer than 12 existed, we 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. The number of randomly determined control sites in a given array matched the total number of perch sites (i.e., both species combined, or a maximum of 24 points) at that array (see Table 1).

We located perch sites and the randomly determined control sites by converting their UTM coordinates to waypoints on the Trimble Geo 7x. We 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 a site was not within 2 m of a tree trunk (24 of 73 perch sites for Boreal Chickadee, 11 of 34 perch sites for Cape May Warbler, 65 of 143 randomly determined control sites), we could not assign it to a particular tree with confidence and we therefore eliminated the site 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). These exclusions explain why the final number of randomly determined control sites does not always match the total number of perch sites in a given array (Table 1). Although it never occurred, if a perch site and a control site had been located in the same tree, then a new randomly determined control site would have been created and used in its place. Shrubs were not excluded, but all perches were nevertheless found in Balsam Fir *Abies balsamea*, Black Spruce *Picea mariana*, or White Birch *Betula papyrifera*.

For each perch site and control site, we 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 (stems/m^2; Avery & Burkhart 2015). Canopy cover was measured using a densiometer (Model-A, convex) held while facing north. Diameter-at-breast-height (DBH; tree diameter at a height of 1.35 m) was measured using a standard diameter tape. We also noted the status of each tree as living or dead; we considered a tree to be living if > 75% of its branches had green needles/leaves.

Statistical analysis

We used generalized linear mixed models to test whether microhabitat characteristics at a given site predicted site type (perch site versus random control site). DBH, canopy cover, and stem density were included as fixed-effect variables, and array number as a random-effect variable to control for the nonindependence among sites within a given array. Site type was included as the dependent variable and was modelled using adaptive Gauss-Hermite quadrature and a binomial distribution (1 = perch site; 0 = random control site). Separate models were used for Boreal Chickadee and Cape May Warbler, and each included only those arrays in which the focal species was present. In three arrays, both species were present, so the same set of random control sites from those arrays was included in both analyses (Table 1). Analyses were conducted in R (R Core Team 2018) using the lme4 package (Bates *et al.* 2015). Due to the relatively small sample sizes, we considered fixed effect variables to be statistically significant when $P \leq 0.05$, and to be a statistical trend when $0.05 < P \leq 0.1$.

RESULTS

After removing sites that were not located within 2 m of a tree trunk, our final analysis included microhabitat measurements at 150 sites distributed across 18 array locations (Boreal Chickadee: 49 sites across 13 arrays; Cape May Warbler: 23 sites across eight arrays; random control: 78 sites across 18 arrays; Table 1). Stem density was negatively correlated with DBH (n = 150, Spearman’s *rho* = -0.29, $P < 0.001$) and positively correlated with canopy cover (n = 150, Spearman’s *rho* = 0.20, $P = 0.014$); DBH and canopy cover were not correlated (n = 150, Spearman's *rho* = 0.07, $P =0.392$). Although some of the predictor variables were intercorrelated, the correlations were relatively weak (i.e., |Spearman's *rho*| < 0.5), so we retained all three of the microhabitat variables in the statistical models (Hinkle *et al.* 2002). Furthermore, variance inflation factors were all less than 1.3 (Tables 2 & 3), indicating that our data did not have problems associated with multicollinearity (Zuur *et al*. 2015).

Boreal Chickadees exhibited microhabitat selectivity. DBH and stem density were significant predictors of site type (Table 2). Compared to randomly determined control sites from within the same array, they vocalized from sites with greater stem density and from trees with greater DBH (Fig. 2). Canopy cover was not a significant predictor of site type (Table 2).

Cape May Warblers did not exhibit microhabitat selectivity. DBH, stem density, and canopy cover were not associated with perch type (Table 3).

DISCUSSION

During the breeding season, Boreal Chickadees and Cape May Warblers preferentially occupy spruce-fir dominated forests (Ficken *et al.* 1996, Baltz & Latta 1998) and follow key food resources across local and regional scales (Morse 1978, Root 1988). 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 & Latta 1998). Here, using microphone array technology, we show that Boreal Chickadees further select call perches in larger trees that are surrounded by greater stem density. These microhabitat characteristics differ from the microhabitat characteristics of sites selected at random from within the same general location.We did not find evidence that Cape May Warblers exhibit microhabitat selectivity.

The Boreal Chickadee is a year-round resident of the boreal forest and demonstrates limited dispersal behaviour related to food distribution (Root 1988). Flocks congregate preferentially in mature stands in the winter, but birds occupy both young and mature forest stands during the breeding season, with a preference for forests containing spruce and fir tree species (Hadley & Desrochers 2008). However, there is evidence that Boreal Chickadees prefer to feed from larger trees 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 & Rice 1982) and non-breeding seasons (Gayk & Lindsay 2012). Vassallo and Rice (1982) demonstrated that Boreal Chickadees feed in the upper and outer portions of trees, independent of tree height, whereas Black-capped Chickadees feed in the lower half and inner portions of trees and use a wider variety of tree species (i.e., deciduous and coniferous trees, Vassallo & Rice 1982). Gayk and Lindsay (2012) showed that, during the winter in Michigan, USA, Boreal Chickadees feed exclusively within conifer species and spend significantly more time foraging in the top 3 m of trees, as compared to Black-capped Chickadees.

In this study, we found that Boreal Chickadees vocalized from large trees that are surrounded by high stem density. 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 select older trees when feeding and storing food, and that they mostly ignore trees less than 6 m in height for these activities.

Information on general habitat selection of Cape May Warblers during the breeding season has been collected in Ontario, Canada and Maine, USA, but is lacking for most of its breeding range, including in Labrador (Baltz & Latta 1998). The species occupies coniferous habitats with spruce (*Picea* sp.) and Balsam Fir of medium- to old-age (50+ years), where Spruce Budworm infestations tend to occur (Baltz & Latta 1998). In Quebec, Canada, Cape May Warblers preferentially use 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 Warblers. 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 & Latta 1998). Nests are typically concealed near the trunk near the top of the tree (MacArthur 1958). During the breeding season, males sing from approximately 2 m below the top of the tree (Kendeigh 1947).

In the current study, we did not find any evidence that Cape May Warblers exhibit microhabitat selectivity during song production, though our sample size for this analysis (*n* = 23 perch sites across eight arrays) was small. In a study conducted in parallel to this one, we showed that, across 88 sites, Cape May Warblers were more likely to be found in conifer stands with greater mean canopy cover (J.P. Ethier unpubl. data). Given this previous finding, and the small sample size associated with the current study, future research on microhabitat selectivity in Cape May Warbler is needed.

Using microphone arrays to characterize microhabitat selection has several advantages over traditional methods that involve searching for and visually detecting individuals. First, traditional methods can introduce bias because the observer's presence influences the birds' behaviour (Mech & Barber 2002, Lee & Marsden 2008). By passively recording vocalizations, the risk of microphone arrays affecting natural behaviour is greatly reduced. Second, microphone arrays can be placed in locations where direct observation and tracking of individuals would be inefficient or otherwise challenging, such as in wetlands or densely vegetated habitats. Third, microphone arrays provide permanent archives of recordings that can be inspected to address additional research topics, such as changes of microhabitat use across the breeding season. Fourth, microphone arrays can be more efficient than direct observation. In our study, we monitored 68 locations for a minimum of one day each, and our study species were vocally active for approximately 17 h per day. Setting up and taking down each array took a team of two people 2 h, manually inspecting the acoustic detections took a single person in the lab an additional 160 h, and making a return trip to each array location to measure microhabitat took approximately 40 minutes per array. Our microphone array approach therefore required approximately 477 person-hours. Obtaining the same spatial and temporal coverage of these sites using direct observation would have required 1156 person-hours, assuming that the observer would not need to make a return trip to measure microhabitat (i.e., 2.4 times longer). Given the low detection rates of our two species, and of rare species more generally, the increased efficiency of microphone arrays could facilitate research on these animals that would not be feasible using direct observation alone.

Although microphone arrays offer many advantages for characterizing microhabitat preferences, there are also several ways that this approach can be improved. First, 50 of our 68 arrays did not detect the target species, so future researchers may consider using point counts, playbacks, or observations from local birders (e.g., https://ebird.org) to pre-screen potential sites before setting up an array. Second, the approach could be improved by continuing to improve hardware and software. For example, microphone locations could be measured more accurately using better GNSS technology or total surveying stations, and recording channels could be synchronized more accurately using self-generated radio signals or interconnecting cables (Blumstein *et al*. 2011, Mennill *et al*. 2012). Vocalizations could also be detected, categorized, and localized more accurately using improved software solutions (e.g., Blumstein *et al*. 2011, Mennill *et al*. 2012, Knight *et al*. 2019). For example, although Kaleidoscope had negligible detection error (0%) and false positive classification error (≤ 0.1%), its rate of false negative classification error was high (75.3% for Boreal Chickadee, 17.9% for Cape May Warbler), and we consequently had to invest 160 h to correct the errors (note, however, that we did not tailor Kaleidoscope's classifier to the two target species because our study was part of a broader study that required us to assign all detections to all species in the community). Third, arrays could be deployed in different configurations to increase the information obtained. We attempted to localize birds in three-dimensional space, but the short trees at our study site restricted microphone separation and, consequently, localization accuracy in the vertical dimension. Future studies could rectify this by deploying arrays in regions with taller trees. Alternatively, if two-dimensional localization is sufficient, then the second microphone on each recorder could be displaced horizontally to expand spatial coverage on the horizontal plane. In summary, there are multiple ways to improve the overall workflow of using microphone arrays to study microhabitat preference.

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 in particular. Based on our findings, conserving mature spruce-fir dominated forest would likely benefit Boreal Chickadees, since they vocalize preferentially from trees with greater DBH (i.e., larger trees) that are surrounded by high stem density. 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 Boreal Chickadee and Cape May Warbler should include additional aspects of bird ecology that are known to impact habitat and microhabitat preferences, including species interactions (Campomizzi *et al.* 2008), sources of disturbance (Zabala *et al.* 2012), and habitat and microhabitat features not measured in the current study, such as the number and DBH of standing dead trees and the abundance of course woody debris (Drapeau *et al.* 2000; Riffell *et al.* 2011).

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Table 1. The number of Boreal Chickadee call perches, Cape May Warbler song perches, and randomly determined control sites in each microphone array (*n* = 18). Perches for a given species were separated by more than 3.59 m. Perches and control sites that were not within 2 m of a tree trunk were not included.

	Boreal Chickadee	Cape May Warbler	Control
A003	5	0	4
A004	8	0	6
A005	2	0	4
A006	4	0	2
A008	7	0	9
A011	0	1	1
A012	0	1	1
A014	3	5	8
A015	9	0	7
A033	1	3	3
A034	0	4	5
A037	0	2	1
A038	0	1	1
A040	2	6	9
A043	2	0	6
A044	3	0	5
A063	2	0	2
A067	1	0	4

Total	49	23	78

Table 2. Relationship between microhabitat and site type for Boreal Chickadee at 13 microphone array locations in Labrador, Canada. Site type (perch site (*n* = 49) versus random control site (*n* = 69)) was the dependent variable and was modeled with a generalized linear mixed-effects model (adaptive Gauss-Hermite quadrature, binomial distribution, logit link). Fixed effects include diameter-at-breast-height (DBH) of the focal tree, as well as the surrounding stem density and canopy cover; their estimates are on a log-odds scale and are shown relative to the random control site level. SE = standard error; VIF = variance inflation factor.

Fixed Effect	Estimate ± SE	*z*	*P*	VIF
DBH	0.07 ± 0.04	1.99	0.047	1.14
Stem Density	1.13 ± 0.47	2.41	0.016	1.15
Canopy Cover	0.00 ± 0.01	0.03	0.978	1.04

Random effect of array number: variance < 0.01, standard deviation < 0.01

Table 3. Relationship between microhabitat and site type for Cape May Warbler at eight microphone array locations in Labrador, Canada. Site type (perch site ($n = 23$) versus random control site ($n = 29$)) was the dependent variable and was modeled with a generalized linear mixed-effects model (adaptive Gauss-Hermite quadrature, binomial distribution, logit link). Fixed effects include diameter-at-breast-height (DBH) of the focal tree, as well as the surrounding stem density and canopy cover; their estimates are on a log-odds scale and are shown relative to the random control site level. SE = standard error; VIF = variance inflation factor.

Fixed Effect	Estimate ± SE	z	p	VIF
DBH	0.03 ± 0.08	0.33	0.743	1.06
Stem Density	-0.29 ± 0.82	-0.35	0.726	1.25
Canopy Cover	0.01 ± 0.01	0.82	0.410	1.26

Random effect of array number: variance < 0.01, standard deviation < 0.01

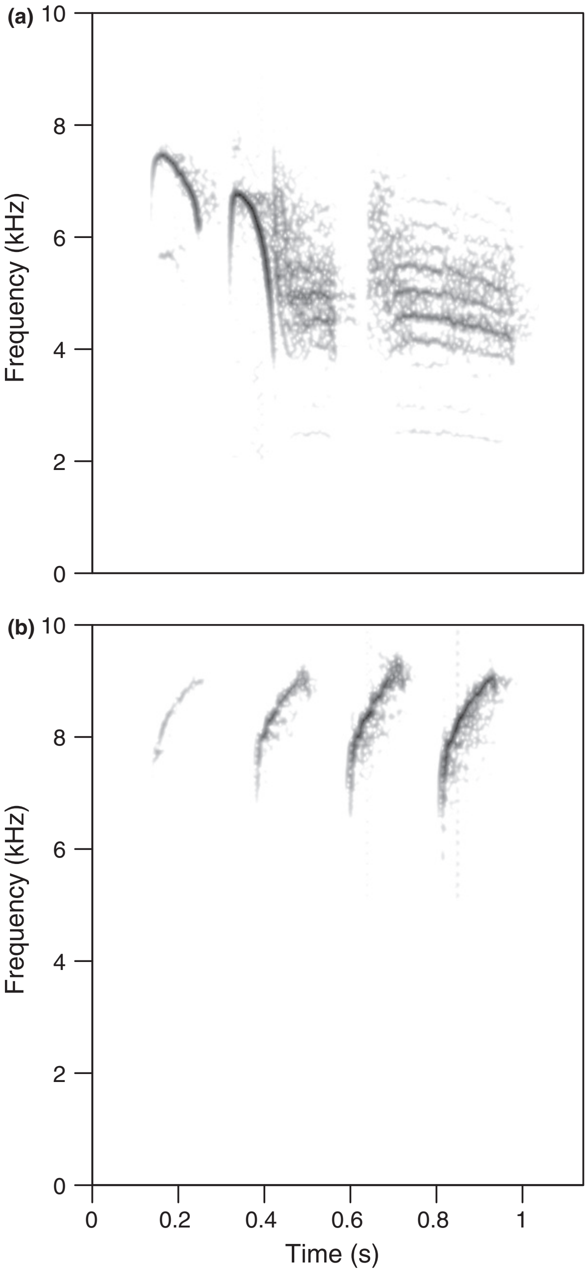

Figure 1. Spectrograms of the vocalizations used to detect and localize Boreal Chickadee and Cape May Warbler. We used a microphone array to record and localize these vocalizations so that we could characterize the microhabitat characteristics associated with vocalization perch sites. (A) The “chick-a-dee” call of the Boreal Chickadee. (B) The song of the Cape May Warbler, which is described as three to five “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.

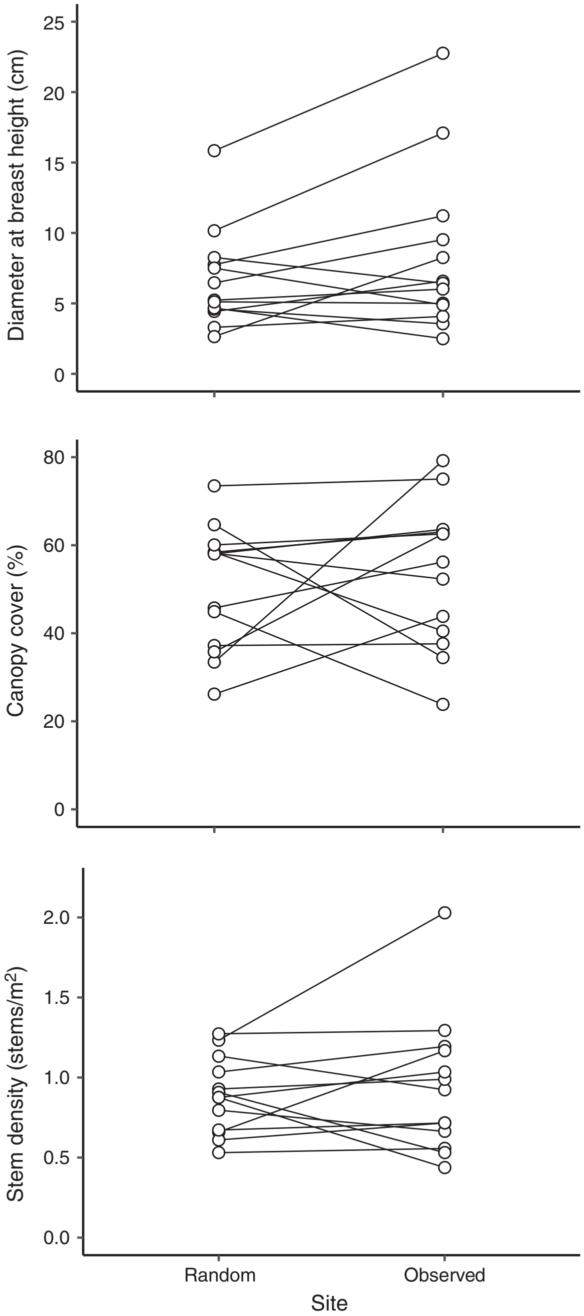

Figure 2. Microhabitat of call perch sites (*n* = 49) and randomly determined control sites (*n* = 69) for Boreal Chickadee at 13 array locations. To facilitate visualization, each point is an average of the raw measurements obtained from all sites (max = 12) of a given site type (perch versus control) at a given array. Furthermore, the independent variables (diameter at breast

height, canopy cover, and stem density) are shown on the y-axis and the dependent variable (site type) on the x-axis.