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9 **Using microphone arrays to investigate microhabitat selection by declining breeding birds**

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18 Understanding the microhabitat preferences of animals can help managers to develop better
19 conservation and recovery strategies, but is challenging. Traditional methods are limited by cost,
20 accuracy, and human resources. In this study, we investigated avian microhabitat preferences
21 using microphone arrays that are capable of accurately localizing vocalizing birds. Our objective
22 was to identify the microhabitat associations of two common species in steep population decline,
23 the Boreal Chickadee *Poecile hudsonicus* and the Cape May Warbler *Setophaga tigrina*. We
24 deployed 68 eight-channel arrays at random locations in Labrador, Canada during the 2016 avian
25 breeding season. We returned in 2017 to the 18 array locations where the target species had been
26 detected the previous year and characterized the microhabitat at the exact locations where they
27 had been detected. We also characterized the microhabitat at randomly determined control
28 locations. Results show that Boreal Chickadees select trees with greater diameter-at-breast-
29 height that are surrounded by greater stem density. We did not find evidence that Cape May
30 Warblers exhibit microhabitat selection during song production. The study shows that
31 microphone arrays are an effective tool for identifying preferred microhabitat that could be
32 incorporated into future conservation or recovery strategies.

33

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

35 In birds and other taxa, habitat selection is viewed as a hierarchical, decision-making process that
36 occurs at several spatial scales (McGarigal *et al.* 2016). At the first and broadest scale, avian
37 species are restricted to a geographic range based on physiological constraints, such as
38 thermoregulation and metabolic rate, and morphological constraints, such as wing-shape and
39 body size, that limit dispersal. At finer spatial scales, individuals select locations for home ranges
40 based on general habitat characteristics, such as a densely vegetated coniferous forest. At the
41 final scale, individuals select specific microhabitat (e.g., individual trees) for engaging in daily
42 activities, such as singing, nesting, or foraging (Johnson 1980, Hutto 1985, Block & Brennan
43 1993, Jones 2001). For example, Acadian Flycatchers *Empidonax virescens* in southeastern USA
44 inhabit swampy woodland habitat, and then select Nuttall's Oak *Quercus nuttallii* and
45 Possumhaw Holly *Ilex decidua* trees for nesting sites more often than would be expected by
46 chance based on the abundance of these tree species (Wilson & Cooper 1998, Allen *et al.* 2017).

47 Biologists and government agencies can develop better conservation and recovery
48 strategies by identifying and preserving a species' preferred microhabitat, particularly if it is
49 associated with increased survival and reproduction (Jones 2001). Furthermore, models including
50 microhabitat and general habitat variables are often better at predicting avian community metrics
51 such as presence, abundance, and diversity (e.g., McDermott *et al.* 2011) than models produced
52 at only one spatial scale. Incorporating microhabitat information can also assist managers to
53 balance competing objectives such as maximizing timber harvest, minimizing risk to wildlife,
54 and fostering post-harvest habitat restoration (Brown *et al.* 2004, Kilgore & Blinn 2004). The
55 techniques used by managers can dramatically influence several microhabitat characteristics
56 important for birds, such as retaining a large volume of coarse woody debris and snags used for
57 nesting and foraging (Riffell *et al.* 2011).

58 Identifying microhabitat selected by wildlife can be challenging and time-consuming
59 (Bibby *et al.* 2000, Stratford & Stouffer 2013, Nemes & Islam 2017). Without identifying and
60 quantifying the microhabitat, researchers can only assume that resident animals use each element
61 within the general habitat equally. It is therefore crucial to establish the microhabitat selected
62 relative to its availability in the broader environment, and relative to the availability of
63 alternatives (Jones 2001). Most studies involve searching for and following marked individuals
64 to determine territory boundaries and features used for singing and/or nesting, and then
65 measuring the vegetation characteristics of those features (Martin & Geupel 1993, Bibby *et al.*
66 2000, Nemes & Islam 2017). Other studies link telemetry locations to associated vegetation (e.g.,
67 Patten *et al.* 2005, Hansbauer *et al.* 2010). Both approaches are labour-intensive and limit the
68 number of individuals sampled and the spatial extent over which one can infer relationships.

69 Microphone arrays allow researchers to localize vocalizing animals with sub-metre
70 accuracy and are thus a promising new technique for studying acoustic and spatial behaviour
71 (Barker *et al.* 2009). Microphone arrays consist of three or more synchronized acoustic recording
72 units distributed in a location where individuals are expected to vocalize. Because sound travels
73 at a slow and predictable rate through air (approximately 343 ms^{-1}), an animal's acoustic signal
74 will reach each microphone at a slightly different time, depending on where the animal is in
75 relation to each microphone. The location of the vocalizing animal can be determined by
76 measuring the time-of-arrival differences of the sound among the microphones in the array, and
77 then applying a tri-lateralization technique to those values (e.g., Wilson *et al.* 2014). Unlike older
78 microphone arrays, which required kilometres of cable and several days to set up (Mennill *et al.*
79 2006), modern microphone arrays use commercially available wireless acoustic recording units
80 that are easy to transport and set up. For example, Mennill *et al.* (2012) were able to fit an entire

81 eight-microphone cable-free array into a single backpack and to set it up in the field in under one
82 hour. Microphone arrays record vocalizations passively, thus removing the need to capture
83 animals and minimizing observer effects on avian behaviour and habitat choice (Mech & Barber
84 2002, Lee & Marsden 2008). Having multiple systems deployed simultaneously and recording
85 continuously, or scheduled to record for long periods of time, can increase the likelihood of
86 detecting rare species (Blumstein *et al.* 2011). Microphone arrays may therefore increase
87 accuracy and reduce the time investment associated with studying microhabitat selection. Yet
88 most studies involving microphone arrays to date have been proof-of-concept studies, with only
89 a few studies applying the technology to biological questions (e.g., duetting behaviour in Rufous-
90 and-white Wrens *Thryophilus rufalbus*, Mennill *et al.* 2006, Mennill & Vehrencamp 2008; inter-
91 individual spacing in male American Bullfrogs *Rana catesbeiana* and Greater Sage Grouse
92 *Centrocercus urophasianus*, Bates *et al.* 2010, Patricelli & Krakauer 2010). Very few studies
93 have used microphone array technology to identify and characterize microhabitat preferences
94 (for an exception, see Wilson & Bayne 2018).

95 In this study, we used microphone arrays in the boreal forest of Labrador, Canada to test
96 for microhabitat selection by Boreal Chickadees *Poecile hudsonicus* and Cape May Warblers
97 *Setophaga tigrina*, two common species in steep population decline according to the USGS
98 North American Breeding Bird Survey 1966–2015 report (Sauer *et al.* 2017). The Boreal Shield
99 Ecozone is approximately 1.8 million km² (approximately 18% of Canada’s landmass), is 88%
100 forested, and thus provides substantial habitat for breeding birds. Yet, most bird surveys within
101 this ecozone, including the USGS North American Breeding Bird Survey, have been conducted
102 in southern Ontario and Quebec, with poor coverage outside these regions (Downes *et al.* 2011).
103 We therefore conducted our study in Labrador to expand coverage of the Boreal Shield Ecozone.

104 Using audio recordings from microphone arrays deployed in 2016, we estimated the
105 locations of Boreal Chickadee call perches and Cape May Warbler song perches. Then, in 2017,
106 we returned to the study site and characterized the microhabitat at the exact points where the
107 focal species had vocalized the previous year, as well as at a matching set of random control
108 points at the same general location. Our objectives were to (1) demonstrate that microphone
109 arrays are a feasible and practical method for studying microhabitat selection in birds, and (2)
110 determine and describe the microhabitat characteristics of Boreal Chickadee call perches and
111 Cape May Warbler song perches.

112

113 **METHODS**

114 **Target species**

115 The Boreal Chickadee is a small (10 g) year-round resident of the boreal forest (Ficken *et al.*
116 1996). The IUCN lists Boreal Chickadees as being of least concern in terms of conservation
117 status, but populations are declining in several portions of their range throughout the USA and
118 Canada. The USGS North American Breeding Bird Survey 1966–2015 report indicates annual
119 population decline rates of 4.4% in Nova Scotia and 5.2% in New Brunswick, Canada (Sauer *et*
120 *al.* 2017). Data specific to Newfoundland and Labrador do not exist, as these regions are not
121 included in the USGS North American Breeding Bird Survey (Sauer *et al.* 2017). In 2007, the
122 Boreal Chickadee was placed on the National Audubon Society’s “Top 10 Common Birds in
123 Decline” list, with a reported 73% population decline from 19.5 million to 5.2 million
124 individuals since the mid-1960s (Brennan 2007, Butcher 2007).

125 The Cape May Warbler is a small (10 g) Neotropical migrant that breeds extensively in
126 the Canadian boreal forest during the summer (Baltz & Latta 1998), and which spends the winter

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

135

136 **Array deployment**

137 We deployed 68 microphone arrays in a 50 x 50 km area (centred at 53°25'01” N, 60°30'07” W)
138 between North West River and Happy Valley-Goose Bay in Labrador, Canada during our study
139 species' 2016 breeding season (15 May to 15 July). Sites were selected at random, but with the
140 constraints that they were within 1 km of road or trail access, a minimum distance of 100 m from
141 roads, and a minimum distance of 500 m from each other. We chose a maximum distance from
142 road access of 1 km because hiking beyond this distance through dense forest while carrying a
143 microphone array would have been difficult and would have reduced our sample size. As per
144 Wilson and Mennill (2011), we separated sites by a minimum of 500 m because this reduced the
145 risk of detecting the same birds at multiple sites, since both species maintain relatively small
146 territories (approximately 5 ha for Boreal Chickadee, Ficken *et al.* 1996; < 1 ha for Cape May
147 Warbler, Baltz & Latta 1998). GPS coordinates for sites were generated using a random integer
148 set generator that creates non-repeating integers within confined boundaries (RANDOM.org).
149 These random coordinates were then plotted on 1:50,000 scale topographic maps (National

150 Topographic System, Series A771, Edition 4MCE, Map13 F/7 - 13 F/10) and discarded if they
151 violated the inclusion criteria or were within a delineated swamp, bog, or water body.

152 Each array consisted of four audio recorders (model: SM3; Wildlife Acoustics, Concord,
153 MA, USA) attached to trees in a 40 x 40 m square that encompassed approximately 0.15 ha.
154 Each recorder had two channels: a built-in omnidirectional microphone (frequency range:
155 50–20000 Hz \pm 10 dB) placed approximately 1.35 m above the ground, and a second external
156 omnidirectional microphone (model: SMM-A2, frequency range: 50–20000 Hz \pm 10 dB)
157 positioned in the forest canopy approximately 2 to 3 m above the first. All microphones were
158 pointed towards the centre of the array. As a requirement of localization (Mennill *et al.* 2012),
159 recorders were synchronized to within 1 ms of each other by connecting them to external GPS
160 units (model: Garmin SM3 GPS; Wildlife Acoustics, Concord, MA, USA). The position of each
161 microphone was determined using a survey-grade GNSS with 10-cm accuracy (model: Geo7X;
162 Trimble, Sunnyvale, CA, USA). Each recorder was programmed to record continuously until
163 stopped, and to create a new stereo sound file every 2 h throughout this time (WAVE format, 24
164 kHz sampling rate, 16-bit amplitude encoding). Each array recorded for 24 h, beginning 2 h after
165 setup to minimize disturbance effects associated with setup. The array was left recording for an
166 additional day if it rained on the first day. Field equipment included four arrays (i.e., 16
167 recorders), and two arrays were relocated each day throughout the season.

168 We recorded weather variables by placing a portable weather station (model: Kestrel
169 5500 Weather Meter; KestrelMeters.com, Boothwyn, PA, USA) in the middle of every other
170 array. Because two arrays were deployed at any given time, and because one of them always
171 included a weather station, we had continuous weather data for the general vicinity of each array.
172 The weather stations sampled at 20-min intervals throughout the field season. They recorded a

173 suite of weather variables, including temperature (± 0.1 °C) and wind speed (± 0.1 km/h).
174 Temperature, in particular, affects the speed of sound and is required for sound localization.
175 Wind exceeding approximately 15 km/h can also affect the signal-to-noise ratio and thus the
176 probability of detecting signals (D. Wilson unpubl. data). However, wind speeds at microphone
177 array locations were always low (mean \pm SD: 0.8 ± 1.7 km/h; range: 0.0–12.2 km/h) and thus
178 were not considered further.

179

180 **Acoustic analysis**

181 To identify and localize Cape May Warblers, we used the song as described in the Birds of North
182 America species account (Baltz & Latta 1998; Fig. 1). The Boreal Chickadee does not have a
183 true song, but does produce up to 13 different calls, including gargles, chirps, and cackles
184 (Ficken *et al.* 1996). We used the “chick-a-dee” call to identify and localize Boreal Chickadees
185 (Fig. 1) because it is produced in a variety of contexts. The call is used to locate mates during
186 foraging and nest cavity excavation, and to signal to a mate that the bird has returned to the nest
187 site with food (McLaren 1976). We therefore concluded that this call would be an appropriate
188 signal for identifying microhabitat use on the breeding grounds.

189 We recorded 1632 h of 8-channel audio. Following the field season, avian vocalizations
190 were automatically detected and grouped into clusters of similar sounds using Kaleidoscope
191 software (version 4.3.2; Wildlife Acoustics, Concord, MA, USA). We used the following
192 settings within *Kaleidoscope*: FFT window size = 256 points (5.33 ms), frequency range of
193 potential signals = 2000–10 000 Hz, duration of potential signals = 0.1–4.0 s, maximum inter-
194 syllable gap = 0.35 s. Settings used during the clustering process included: maximum distance
195 from the cluster centre = 2.0, maximum states = 12, maximum distance to cluster centre for

196 building clusters = 0.5, maximum clusters created = 500. Kaleidoscope generated a detection list
197 text file with one row for each detection (2 734 885 detections in total) and columns describing
198 the structure of the detection (duration, minimum frequency, maximum frequency, mean
199 frequency), its position within the raw recording, and the cluster to which it was assigned. The
200 analysis ran on a desktop computer (iMac, 32 GHz Intel Core i5, 16 GB RAM) and took
201 approximately 25 h to process.

202 We estimated detection error by using Audacity software (Audacity® software is
203 copyright © 1999–2019 Audacity Team. The name Audacity® is a registered trademark of
204 Dominic Mazzoni) to manually review and annotate all boreal bird vocalizations contained in
205 one of our 2-h audio recordings. We then processed that same audio file in Kaleidoscope using
206 the same detection settings used in our study. Kaleidoscope detected 2513 vocalizations,
207 including all of the 2379 vocalizations that we had scored manually, plus 134 faint vocalizations
208 that we had missed during the manual review. Kaleidoscope did not detect any sounds from non-
209 avian sources. Therefore, at the detection step, the false negative (i.e., avian vocalizations that
210 were not detected) and false positive error rates (i.e., non-avian sounds that were detected) were
211 both zero, which agrees with other, more comprehensive tests of Kaleidoscope's detection
212 accuracy (e.g., Siracusa *et al.* 2019). We note that the much larger dataset in our study (i.e., 1632
213 h) did contain some non-avian detections (e.g., bears, squirrels, sirens), but these were less than
214 1% of all detections.

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

219 Kaleidoscope to maximize the signal-to-noise ratio, and then used pairwise waveform cross-
220 correlations to measure the time-of-arrival differences of the vocalization between the reference
221 channel and each of the other channels in the array. Using these time-of-arrival differences, the
222 known locations of the microphones, and the temperature at the time of recording, the program
223 estimated the two-dimensional location from which the sound originated (UTM coordinates). It
224 also provided an error value that reflects the confidence of the estimated location. Based on a
225 ground-truthing experiment in which we broadcast frequency upsweeps through a speaker from
226 known locations inside microphone arrays, 95% of localizations with an error value of 0.01 (a
227 unitless measure of confidence) or less are within 3.59 m of their true locations in 2-dimensional
228 space (J.P. Ethier unpubl. data). We reduced our overall dataset to include only those
229 vocalizations produced within the array with a localization error value of 0.01 or less (22 519
230 vocalizations). The program can also estimate locations in 3-dimensions, but the ground-truthing
231 experiment showed the three-dimensional localization to be inaccurate in the vertical dimension
232 (i.e., elevation). Thus, we relied on 2-dimensional estimates of location for this study.

233 We manually inspected all remaining detections in Kaleidoscope to correct false positive
234 classifications (i.e., detections labeled by Kaleidoscope as a target species but actually belonging
235 to a non-target species) and false negative classifications (i.e., detections belonging to a target
236 species but labelled by Kaleidoscope as a non-target species). Kaleidoscope incorrectly labelled
237 25 of the 22 519 total detections as Boreal Chickadee (i.e., false positive error = 0.1%), and
238 incorrectly labeled 232 of the 308 Boreal Chickadee vocalizations as a different species (i.e.,
239 false negative error = 75.3%). Kaleidoscope incorrectly labelled four of the 22 519 total
240 detections as Cape May Warbler (i.e., false positive error < 0.1%), and incorrectly labeled 10 of

241 the 56 Cape May Warbler vocalizations as a different species (i.e., false negative error = 17.9%).
242 Reviewing the 22 519 vocalizations and correcting the classification errors required 160 h.

243

244 **Microhabitat characterization**

245 In 2017, we returned to the 18 array locations where either Boreal Chickadee (13 array locations)
246 or Cape May Warbler (eight array locations) had been detected in 2016. Localizing vocalizations
247 required several weeks of processing and therefore it was not possible to return to locations
248 during the same breeding season. However, the microhabitat features that we measured (see
249 below) are structural traits that change very little between consecutive years unless significantly
250 altered or disturbed (e.g., by logging or forest fire).

251 For each array and for each species, our goal was to characterize the microhabitat of up to
252 12 different estimated perch locations from the previous year (hereafter referred to as "perch
253 sites"), and to compare the microhabitat characteristics of those perch sites to the microhabitat of
254 randomly determined control sites from within the same array. Birds often produce several
255 vocalizations from the same perch site, so we considered perch sites to be different only if they
256 were separated by more than 3.59 m, which was the localization accuracy (95% confidence) of
257 our system. If more than 12 perch sites existed within a given array for a given species, we
258 selected 12 at random. If fewer than 12 existed, we used all of the available perch sites. Random
259 sites were determined using a random number generator (RANDOM.org) to produce a northern
260 offset (between 0 and 40 m) and an eastern offset (between 0 and 40 m) from the southwest
261 corner of the array. The number of randomly determined control sites in a given array matched
262 the total number of perch sites (i.e., both species combined, or a maximum of 24 points) at that
263 array (see Table 1).

264 We located perch sites and the randomly determined control sites by converting their
265 UTM coordinates to waypoints on the Trimble Geo 7x. We then used the built-in navigation
266 software, which gives a real-time estimate of location after base-station correction (Goose Bay
267 base station, which was within 25 km of all locations), to find the sites within the arrays. If a site
268 was not within 2 m of a tree trunk (24 of 73 perch sites for Boreal Chickadee, 11 of 34 perch
269 sites for Cape May Warbler, 65 of 143 randomly determined control sites), we could not assign it
270 to a particular tree with confidence and we therefore eliminated the site from further
271 consideration. A tree was defined as any woody stemmed species with a diameter greater than or
272 equal to 1 cm, with viable perching locations (i.e., branches, limbs). These exclusions explain
273 why the final number of randomly determined control sites does not always match the total
274 number of perch sites in a given array (Table 1). Although it never occurred, if a perch site and a
275 control site had been located in the same tree, then a new randomly determined control site
276 would have been created and used in its place. Shrubs were not excluded, but all perches were
277 nevertheless found in Balsam Fir *Abies balsamea*, Black Spruce *Picea mariana*, or White Birch
278 *Betula papyrifera*.

279 For each perch site and control site, we measured stem density by holding a 2-m pole
280 horizontally, and then counting the number of trees touched by the pole while making a full
281 rotation. The number of trees was then divided by the area of the circle to determine stem density
282 (stems/m²; Avery & Burkhart 2015). Canopy cover was measured using a densiometer (Model-
283 A, convex) held while facing north. Diameter-at-breast-height (DBH; tree diameter at a height of
284 1.35 m) was measured using a standard diameter tape. We also noted the status of each tree as
285 living or dead; we considered a tree to be living if > 75% of its branches had green
286 needles/leaves.

287

288 **Statistical analysis**

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

301

302 **RESULTS**

303 After removing sites that were not located within 2 m of a tree trunk, our final analysis included
304 microhabitat measurements at 150 sites distributed across 18 array locations (Boreal Chickadee:
305 49 sites across 13 arrays; Cape May Warbler: 23 sites across eight arrays; random control: 78
306 sites across 18 arrays; Table 1). Stem density was negatively correlated with DBH ($n = 150$,
307 Spearman's $\rho = -0.29$, $P < 0.001$) and positively correlated with canopy cover ($n = 150$,
308 Spearman's $\rho = 0.20$, $P = 0.014$); DBH and canopy cover were not correlated ($n = 150$,
309 Spearman's $\rho = 0.07$, $P = 0.392$). Although some of the predictor variables were inter-

310 correlated, the correlations were relatively weak (i.e., |Spearman's ρ | < 0.5), so we retained all
311 three of the microhabitat variables in the statistical models (Hinkle *et al.* 2002). Furthermore,
312 variance inflation factors were all less than 1.3 (Tables 2 & 3), indicating that our data did not
313 have problems associated with multicollinearity (Zuur *et al.* 2015).

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

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

320

321 **DISCUSSION**

322 During the breeding season, Boreal Chickadees and Cape May Warblers preferentially occupy
323 spruce-fir dominated forests (Ficken *et al.* 1996, Baltz & Latta 1998) and follow key food
324 resources across local and regional scales (Morse 1978, Root 1988). The size and location of
325 individuals' territories within these broad-scale areas are influenced by the availability of trees
326 with soft heartwood for nest cavities for Boreal Chickadees (McLaren 1975), and by the number
327 of forest edges and the distribution of open patches for Cape May Warblers (Baltz & Latta
328 1998). Here, using microphone array technology, we show that Boreal Chickadees further select
329 call perches in larger trees that are surrounded by greater stem density. These microhabitat
330 characteristics differ from the microhabitat characteristics of sites selected at random from within
331 the same general location. We did not find evidence that Cape May Warblers exhibit microhabitat
332 selectivity.

333 The Boreal Chickadee is a year-round resident of the boreal forest and demonstrates
334 limited dispersal behaviour related to food distribution (Root 1988). Flocks congregate
335 preferentially in mature stands in the winter, but birds occupy both young and mature forest
336 stands during the breeding season, with a preference for forests containing spruce and fir tree
337 species (Hadley & Desrochers 2008). However, there is evidence that Boreal Chickadees prefer
338 to feed from larger trees during the breeding season (Haftorn 1974). Microhabitat selection for
339 nest sites, call perches, and foraging sites has been described for Boreal Chickadees in only a few
340 studies. Ficken *et al.* (1996) showed that Boreal Chickadee nest sites are most often near the
341 ground in dead tree stumps and rarely found at a height greater than 3 m above the ground. Other
342 studies have shown that, where sympatric, Boreal Chickadee and Black-capped Chickadee *P.*
343 *atricapillus* segregate when foraging during the breeding (Vassallo & Rice 1982) and non-
344 breeding seasons (Gayk & Lindsay 2012). Vassallo and Rice (1982) demonstrated that Boreal
345 Chickadees feed in the upper and outer portions of trees, independent of tree height, whereas
346 Black-capped Chickadees feed in the lower half and inner portions of trees and use a wider
347 variety of tree species (i.e., deciduous and coniferous trees, Vassallo & Rice 1982). Gayk and
348 Lindsay (2012) showed that, during the winter in Michigan, USA, Boreal Chickadees feed
349 exclusively within conifer species and spend significantly more time foraging in the top 3 m of
350 trees, as compared to Black-capped Chickadees.

351 In this study, we found that Boreal Chickadees vocalized from large trees that are
352 surrounded by high stem density. Given that the “chick-a-dee” call is produced by individuals
353 communicating with mates when separated during foraging, it is likely that these vocalizations
354 were from individuals establishing the location of a mate or advertising a foraging location,
355 rather than from individuals engaged in activities at their nest site. In support of this, Haftorn

356 (1974) noted that Boreal Chickadees during the summer in Alaska select older trees when
357 feeding and storing food, and that they mostly ignore trees less than 6 m in height for these
358 activities.

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

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

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

400 Although microphone arrays offer many advantages for characterizing microhabitat
401 preferences, there are also several ways that this approach can be improved. First, 50 of our 68

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

424 This study is an initial, but important, step in using microphone arrays to demonstrate the
425 microhabitat characteristics preferred by free-living birds in general and by Boreal Chickadee in
426 particular. Based on our findings, conserving mature spruce-fir dominated forest would likely
427 benefit Boreal Chickadees, since they vocalize preferentially from trees with greater DBH (i.e.,
428 larger trees) that are surrounded by high stem density. However, it is also important to consider
429 that the microhabitat selected in one context (e.g., foraging) may differ from the microhabitat
430 selected in another context (e.g., nesting). Future research on Boreal Chickadee and Cape May
431 Warbler should include additional aspects of bird ecology that are known to impact habitat and
432 microhabitat preferences, including species interactions (Campomizzi *et al.* 2008), sources of
433 disturbance (Zabala *et al.* 2012), and habitat and microhabitat features not measured in the
434 current study, such as the number and DBH of standing dead trees and the abundance of course
435 woody debris (Drapeau *et al.* 2000; Riffell *et al.* 2011).

436

437

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- 589

590 **Table 1.** The number of Boreal Chickadee call perches, Cape May Warbler song perches, and
 591 randomly determined control sites in each microphone array ($n = 18$). Perches for a given species
 592 were separated by more than 3.59 m. Perches and control sites that were not within 2 m of a tree
 593 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
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594

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

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

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

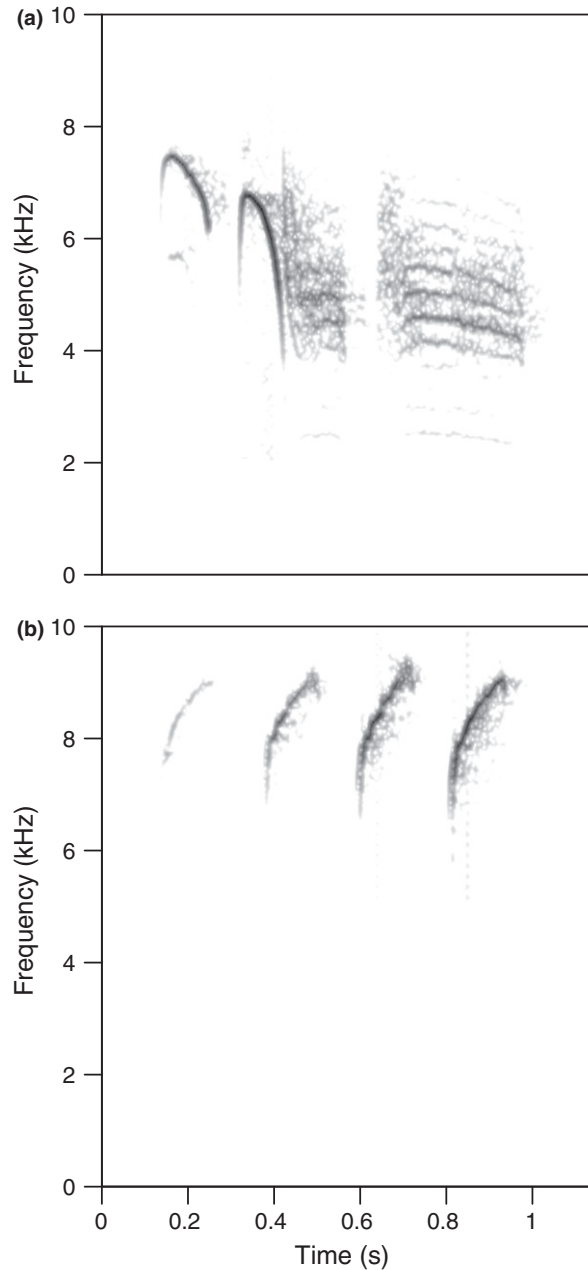
602

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

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

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

611



612

613 **Figure 1.** Spectrograms of the vocalizations used to detect and localize Boreal Chickadee and

614 Cape May Warbler. We used a microphone array to record and localize these vocalizations so

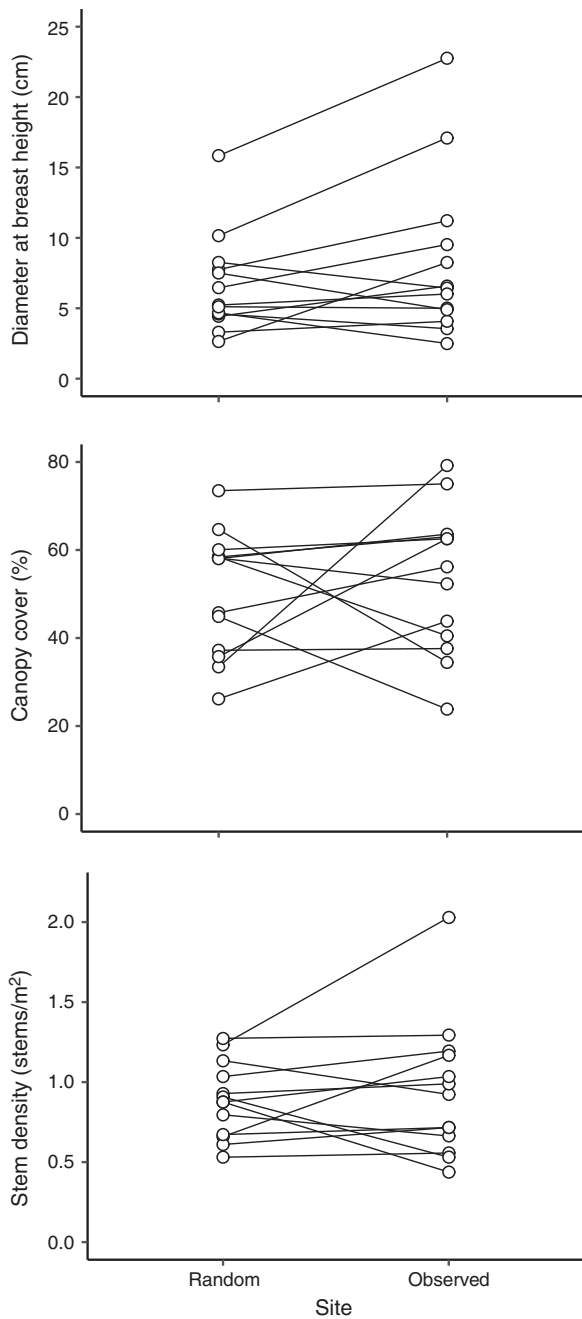
615 that we could characterize the microhabitat characteristics associated with vocalization perch

616 sites. (A) The “chick-a-dee” call of the Boreal Chickadee. (B) The song of the Cape May

617 Warbler, which is described as three to five “tseet” notes delivered with rising inflection (Baltz

618 and Latta 1998). Spectrograms were generated with a 512-point fast Fourier transform, 90%
619 overlap, and Hamming window. Temporal resolution is 2.1 ms, frequency resolution is 46.9 Hz,
620 and the grayscale represents an amplitude range of 35 dB.

621



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