

1 Monitoring migratory birds in stopover habitat: 2 assessing the value of extended duration audio 3 recording

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5 Running title: Monitor migratory birds with audio recording

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11 12 **ABSTRACT**

13 1. Because birds are frequently detected by sound, autonomous audio recorders (called automated
14 recording units or ARUs) are now an established tool in addition to in-person observations for
15 monitoring the status and trends of bird populations. ARUs have been evaluated and applied
16 during breeding seasons, and to monitor the nocturnal flight calls of migrating birds. However,
17 birds behave differently during migration stopover than during the breeding season. Here we
18 present a method for using ARUs to monitor land birds in migration stopover habitat.

19 2. We conducted in-person point counts next to continuously recording ARUs, and compared
20 estimates of the number of species detected and focal species relative abundance from point
21 counts and ARUs. We used a desk-based audio bird survey method for processing audio
22 recordings, which does not require automated species identification algorithms. We tested two

23 methods of using extended duration ARU recording: surveying consecutive minutes, and
24 surveying randomly selected minutes.

25 3. Desk-based surveys using randomly selected minutes from extended duration ARU recordings
26 performed similarly to point counts, and better than desk-based surveys using consecutive
27 minutes from ARU recordings. Surveying randomly selected minutes from ARUs provided
28 estimates of relative abundance that were strongly correlated with estimates from point counts,
29 and successfully showed the increase in abundance associated with migration timing. Randomly
30 selected minutes also provided estimates of the number of species present that were comparable
31 to estimates from point counts.

32 4. ARUs are an effective way to track migration timing and intensity in remote or seasonally
33 inaccessible migration stopover habitats. We recommend that desk-based surveys use randomly
34 sampled minutes from extended duration ARU recordings, rather than using consecutive
35 minutes from recordings. Our methods can be immediately applied by researchers with the
36 skills to conduct point counts, with no additional expertise necessary in automated species
37 identification algorithms.

38 **Keywords**

39 autonomous audio recording, bird survey, migration, stopover habitat, passive acoustic monitoring,
40 point count, relative abundance

41

42 **1 | INTRODUCTION**

43 Conserving bird populations requires knowledge of bird distribution and habitat use at all stages
44 of their life cycle, including during breeding, migration, and non-breeding periods (Sherry & Holmes,
45 1995) . Monitoring birds' habitat use during migration is a necessary component of conservation plans
46 for migratory birds. Historically, researchers have primarily relied on in-person observations including
47 mist-netting (Peach, Buckland & Baillie, 1996) and point counts (Ralph, Droege & Sauer, 1995) for
48 migration monitoring, but because birds are frequently detected by sound, audio recording technology
49 offers opportunities to expand monitoring techniques. Here we present a method for using audio
50 recorders to monitor birds in migration stopover habitat during spring migration.

51 Figuring out how to best monitor bird abundance and diversity in remote habitat is a current
52 challenge. The climate in high latitude continental regions increases the challenges associated with
53 accessing remote areas during spring migration. Significant annual snow accumulation, followed by
54 rapid melting as temperature increases, makes unpaved roads impassable for several weeks each spring
55 in much of northern North America, typically during the same time period when migrant bird species
56 begin to arrive in the region. Developing survey monitoring protocols that can be implemented despite
57 poor traveling conditions is a way to fill in gaps in knowledge of northern forest birds, and birds in
58 similarly remote habitats.

59 Autonomous recording units (ARUs) are programmable audio recorders that
60 can be deployed in the field for long time periods to efficiently maximize the spatial and temporal
61 extent of monitoring. Passive acoustic monitoring is widely used in ecology to monitor and study
62 vocalizing organisms; ARUs have been deployed to study bats (Tuneu-Corral et al., 2020), whales
63 (Baumgartner et al., 2019), invertebrates (Penone et al., 2013), amphibians (Dutilleux & Curé, 2020)

64 and birds (Shonfield & Bayne, 2017). ARUs are also used to evaluate the success of conservation
65 programs (Shonfield & Bayne, 2017). Current challenges for implementing passive acoustic
66 monitoring include the availability of reference sound libraries, minimizing errors in species
67 identification, and determining the relationship between acoustic index values and their associated real-
68 world underlying parameters (Gibb, Browning, Glover-Kapfer & Jones, 2019).

69 Point-count surveys are the most commonly used bird monitoring protocol for long-term study
70 sites (Ralph, Droege, & Sauer, 1995; Rosenstock, Anderson, Giesen, Leukering & Carter, 2002), but
71 ARUs are now viewed as a viable supplement to point-counts, especially during the breeding season
72 when birds vocalize frequently (Furnas & Callas, 2015; Klingbeil & Willig, 2015; Shonfield & Bayne,
73 2017; Darras et al., 2018; Darras et al., 2019). Many researchers have compared ARUs and point
74 counts in terms of their estimates of species richness and relative abundance or occupancy (Haselmayer
75 & Quinn, 2000; Campbell & Francis, 2011; Tegeler, Morrison & Szewczak, 2012; La & Nudds, 2016),
76 including in temperate forest (Klingbeil & Willig, 2015). However, none of these studies (including the
77 23 studies reviewed in Darras et al.'s (2018) meta-analysis) compared point counts and ARUs during
78 migration. Birds behave and vocalize differently during migration than during the breeding season
79 (Morse, 1991; Rappole & Warner, 1976). Testing and refining migration-specific monitoring techniques
80 for ARUs is therefore necessary to understand how data from ARUs compare to data from in-person
81 observations.

82 ARUs are currently used during migration to record the flight calls of nocturnally migrating
83 species. They are deployed to track the abundance of migrants as they move through an area, and can
84 provide helpful information about migratory flyway locations, migration phenology, and relative
85 abundance (Sanders & Mennill, 2014; Evans & Rosenburg, 2000). Understanding how migrating birds
86 use migratory stopover habitat is a different challenge, and requires different methods. Determining

87 how birds are distributed in stopover habitat, the relative abundance and species richness of birds in
88 such habitat, and the timing of arrival and departure from the stopover area are all important research
89 questions for applied conservation.

90 To take advantage of the large volume of data generated by continuously recording ARUs,
91 researchers are actively developing methods for automated identification of vocalizing organisms
92 (Salamon et al., 2016; Gibb, Browning, Glover-Kapfer & Jones, 2019). In contrast, we present a
93 method that can be implemented by anyone with the skills to conduct point counts, that does not rely
94 on machine learning for species identification and data processing. Because applications of ARUs in
95 migration stopover habitat have been under-explored in the literature thus far, we demonstrated and
96 assessed an immediately applicable monitoring technique.

97 We compared data from ARU surveys to in-person point count surveys during spring migration
98 in the northern Great Lakes region of the United States. Our goal was to understand how ARUs could
99 be applied to monitor diurnal stopover habitat use during migration by examining whether ARUs could
100 provide estimates of relative abundance and number of species that are comparable to estimates from
101 in-person surveys. We asked the following questions. 1) What are the differences between the number
102 of species detected using point counts and using ARUs? 2) Can ARUs give estimates of relative
103 abundance for focal species that are correlated with estimates of relative abundance from point counts?
104 3) Can randomly sampling from extended duration audio recordings provide better estimates of focal
105 species abundance or the number of species detected than consecutive minutes of audio recording?

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108 **2 | MATERIALS AND METHODS**

109 We conducted in-person point counts alongside continuously recording ARUs on the southern
110 shore of Lake Superior during two months at the start of spring migration. We compared both raw data
111 and model-based estimates of the number of species detected and focal species abundance from point
112 counts and ARUs.

113 **2.1 | Study site**

114 We conducted field work in a 2.7 km² area on the Point Abbaye peninsula in Baraga County,
115 Michigan, USA (Fig. 1). Surveys took place from 2 April to 22 May 2019, and were conducted daily
116 unless prevented by weather conditions. Field work was designed to coincide with the arrival and peak
117 abundance of early season migrating birds. Point Abbaye juts into the southern part of Lake Superior
118 and comprises the western border of Keweenaw Bay. Habitat included forested wetland, upland
119 hardwood, and hardwood forest disturbed by recent logging activity. We selected survey sites randomly
120 across the study area. All spatial analyses were done in the R programming language using the 'rgdal',
121 'geosphere', 'rgeos', 'sp', 'mapproj', and 'spatstat' packages (Baddeley, Rubak, & Turner, 2015; Bivand,
122 Keitt, & Rowlingson, 2018; Bivand & Lewin-Koh, 2019; Bivand & Rundel, 2018; Bivand, Pebesma, &
123 Gomez-Rubio, 2013; Hijmans, 2019; Pebesma & Bivand, 2005; R Core Team, 2020). We conducted a
124 pilot study in 2018 to test our protocols and evaluate the accessibility of our randomly selected survey
125 locations. See Appendix A for details about pilot year surveys, and survey site and date selection.

126 **2.2 | Automated recording units**

127 Birds were recorded using three SWIFT bioacoustic recorder rugged units (Cornell Lab of
128 Ornithology, Ithaca, NY, USA), and one AudioMoth bioacoustic recorder that was housed in a thin
129 plastic bag for light weather proofing (Hill et al., 2018; Open Acoustic Devices, Southampton, UK).
130 SWIFT units used a built in PUI Audio brand omni-directional microphone. The AudioMoth unit used

131 an analog microelectro-mechanical systems (MEMS) microphone. We refer to both the SWIFT and
132 AudioMoth units as “automated recording units” (ARUs). ARUs recorded at a sampling rate of 48 kHz
133 and saved recordings as uncompressed .WAV files. The signal to noise ratio reported by device
134 manufacturers is approximately 58 dB for the SWIFT units, and approximately 44 dB for the
135 AudioMoth unit.

136 **2.4 | Field survey methods**

137 ARUs recorded continuously for five hours each day, beginning within 10 minutes of local
138 sunrise time (United States Naval Observatory, 2016). ARUs were attached to trees less than 0.6 m in
139 diameter, and were placed 1.5–2 m above the ground (Darras et al., 2018). The SWIFT omni-
140 directional microphones were always oriented downward to prevent precipitation landing directly on
141 the microphone. After the five hour recording period ended each day, ARUs were moved to new
142 locations for the next day’s samples, thereby rotating the ARU and point count samples through all 18
143 survey locations approximately every five days. The sampling order for the points was chosen
144 randomly.

145 Point counts were conducted daily next to each ARU during the five hour recording period.
146 Point counts involved recording all birds seen and heard at an unlimited distance during a stationary,
147 10-minute count. We did not survey in high wind or heavy precipitation. See Appendix A for detailed
148 point count protocols.

149 **2.5 | Desk-based audio surveys**

150 We conducted desk-based audio bird surveys by listening to ARU recordings played through
151 headphones on a laptop computer in the lab after the end of the field season. We tested three types of
152 desk-based audio surveys: 1) we listened to a recording of the 10 consecutive minutes during which the

153 in-person point count was conducted; 2) we listened to 24 minutes selected randomly from the five
154 hour recording duration; 3) we sampled a subset of 10 of the 24 random minutes (without listening to
155 those minutes again). Our goal was to compare each of these desk-based ARU survey methods to in-
156 person point count observations.

157 For each audio file, the desk-based survey technician noted the identity of each bird species that
158 vocalized, the type of vocalization, and the 30-second time intervals in which each species vocalized.
159 Detailed protocols for completing desk-based audio surveys can be found in Appendix A, and a
160 completed data sheet from a desk-based survey is shown in Fig. S6. We sampled 24 random minutes
161 from each ARU on each day because we wanted at least 20 minutes without anthropogenic disturbance.
162 After discarding randomly selected minutes that contained a human voice, we were ultimately able to
163 use data from 22 randomly selected minutes from each ARU on each survey day (i.e. we never had to
164 discard more than two of the 24 randomly selected minutes because of human voices).

165 **2.6 | Indices for observed number of species and relative abundance**

166 We summed the number of unique species detected (S) separately using each survey type: 10-
167 minute, in-person point counts (S_p); 10 consecutive minute ARU surveys (S_{10C}); 10 random minute
168 ARU surveys (S_{10R}); and 22 random minute ARU surveys (S_{22R}) (Box 1). We calculated a value of S for
169 each individual survey on each day, resulting in three or four values of S for each survey type on each
170 day.

171 We created an index of daily relative abundance (A) for two focal species (*Regulus satrapa*
172 (Golden-crowned Kinglet) and *Troglodytes hiemalis* (Winter Wren)) using each survey type (Box 1).
173 Our relative abundance indices were: the mean observed number of individuals per point count (A_p);
174 the proportion of 30-second intervals with a vocalization calculated by surveying n minutes in sections

175 of 10 consecutive minutes (A_{nC}); the proportion of 30-second intervals with a vocalization calculated by
176 surveying n minutes in sections of one minute chosen randomly from the five hour survey window
177 (A_{nR}). To reduce the number of zero abundance counts in our data, we calculated relative abundance
178 indices by grouping all surveys of each type for each day, so there was a single value for each
179 abundance index on each day. Note that while April 16th and 17th data appear on plots and in results,
180 ARU malfunctions on those dates made the number of sampled minutes n different for those two dates
181 for some of our abundance indices. See Appendix A for detailed discussion of sample size on these
182 dates.

183 **2.7 | Statistical Analysis**

184 **2.7.1 | Observed number of species**

185 To determine whether the survey type (S_{10C} , S_{10R} , S_{22R}) significantly influenced the number of
186 species detected, we modeled the number of species detected using a generalized linear mixed model
187 (GLMM) with a Poisson error distribution and log link function, using the ‘lme4’ package in R (Bates,
188 Maechler, Bolker, & Walker, 2015; R Core Team, 2020). Our fixed effects were survey type, day of
189 year, a second degree polynomial term for day of year, wind, rain, noise, and interaction terms for day
190 of year x survey type, and survey type x rain. We also used day of year as a random effect; we collected
191 up to four samples of each of four survey types per day, and new birds potentially arrived daily during
192 the study period, so we expected that the number of species detected by all surveys on each day would
193 be strongly correlated, regardless of survey location or survey type. More information about our
194 GLMM can be found in Appendix A.

195 **2.7.2 | Relative abundance**

196 We compared relative abundance estimates for our two focal species using data from A_p and
197 from each of the three desk-based audio survey types (A_{30C} , A_{30R} , A_{66R}). Winter Wrens were abundant in

198 the survey area, and vocalized frequently and loudly during early spring, representing a “best case”
199 scenario for detectability on ARU recordings. Golden-crowned Kinglets were abundant in the survey
200 area, but vocalized quietly (though regularly) during early spring, and so represent a greater challenge
201 for detection using ARUs.

202 We produced a total of eight relative abundance models, one using each of our four relative
203 abundance indices for each of our two focal species. For each relative abundance model, we fit
204 boosted regression trees (BRTs) (Elith, Leathwick, & Hastie, 2008; Friedman, 2001) using 200
205 iterations of five-fold temporal block cross validation, that used blocks of three consecutive days (Fig.
206 S3; Roberts et al., 2017). This resulted in a total of 1000 BRT fits per relative abundance model. We
207 generated predicted relative abundances by averaging predictions from the 1000 fits of each model. The
208 predictor variables in our model were day of year (continuous) and wind speed (categorical with three
209 levels representing Beaufort forces of 0-1, 2, or 3 or higher). We fit BRTs with the ‘gbm’ package in R
210 (Greenwell, Boehmke, Cunningham and GBM Developers, 2019; R Core Team, 2020). Details of
211 BRTs, including model tuning and control of overfitting are in Appendix A, and Figs. S4-S5.

212 We assessed the correlation between the observed data from our four abundance indices using
213 scatter plots and Spearman’s rank correlation coefficient. We also assessed correlation between the
214 predicted values from the BRT models trained using data from each of the four abundance indices. We
215 calculated Spearman’s rank correlation coefficient for all pairwise combinations of abundance indices,
216 with the exception A_{30R} and A_{66R} , since the data for A_{30R} is a sub-sample of A_{66R} data.

217 **3 | RESULTS**

218 Between 2 April and 22 May, 2019, we were able to survey on 37 days. During that time, we
219 conducted 137 in-person point counts. All four audio recorders experienced occasional malfunctions

220 that prevented us from recording the full five-hour survey window with some units on some days. One
221 SWIFT unit recorded 36 five-hour survey days, two SWIFT units recorded 35 five-hour survey days,
222 and the AudioMoth unit recorded 24 five-hour survey days, for a total of 650 hours recorded by ARUs.
223 Because of ARU malfunctions, on some days ARUs did not record the full five-hour period, but we
224 were able to manually turn on the units for the 10-minute period during the in-person point count.
225 Therefore, we recorded 130 10 consecutive minute periods with ARUs (during which a human observer
226 was present conducting a simultaneous point count) on 37 survey days, but only 124 periods of 22
227 randomly selected minutes on 36 survey days. A complete list of the species detected by each survey
228 method can be found in Table S1.

229 **3.1 | Observed number of species**

230 A chi-square ANOVA comparing our full model to a null model with survey type removed
231 showed that survey type (the S -index used) had a significant effect on the number of species detected
232 ($\chi^2_{9,21} = 247, p < 0.0001$). We detected a similar number of species using S_{10R} as we did using S_p (Fig. 2;
233 Table 1; change in the log of the number of species detected = -0.065, 95% CI [-0.2; 0.08], $p = 0.3888$).
234 Using S_{22R} , we detected significantly more species than by using S_p (Fig. 2; Table 1; change in the log
235 of the number of species detected = 0.305, 95% CI [0.17; 0.44], $p < 0.0001$). We detected fewer species
236 using S_{10C} than using S_p (Fig. 2; Table 1; change in the log of the number of species detected = -0.614,
237 95% CI [-0.78; -0.44], $p < 0.0001$). Listening to randomly selected rather than consecutive minutes
238 eliminated the gap in number of species detected between 10-minute point counts and 10-minute ARU
239 surveys (Fig. 2). Day of year had a significant effect on the number of species detected (Table 1), with
240 more species expected later in the migration season (Fig. 2).

241 Chi-square ANOVA showed that the overall effect of wind was not significant ($\chi^2_{19, 21} = 1.44$, $p =$
242 0.48), nor was the overall effect of rain ($\chi^2_{18, 21} = 3.45$, $p = 0.32$). The overall effect of noise was
243 significant ($\chi^2_{19, 21} = 10.3$, $p = 0.005$). The interaction between survey type and day of year was not
244 significant (Table 1), providing no evidence of a difference in the effect of survey method on the
245 observed number of species over the course of the survey season.

246 **3.2 | Relative abundance models**

247 BRT models of relative abundance over time differed in how well they showed the initial period
248 of absence, and the increase in abundance corresponding with the arrival of migrant birds in our study
249 area, depending on the survey method used (Fig. 3). The general pattern of initial absence followed by
250 arrival of migrants can be seen in both the raw data and the model predictions of relative abundance for
251 A_p , A_{30R} and A_{66R} for Winter Wrens (Fig. 3 a, c and d), and for A_p and A_{66R} for Golden-crowned Kinglets
252 (Fig. 3 e, and h).

253 For both Winter Wrens and Golden-crowned Kinglets, the observed abundance indices from
254 ARU surveys were positively correlated with the observed abundance index from point counts (Fig. 4,
255 Fig. 5), indicating that the relative abundance proxies we calculated using ARUs are comparable to
256 relative abundance estimates from in-person observations. Winter Wren showed moderate to strong
257 correlation between the observed abundance index values from point counts and from ARU surveys
258 (Fig. 4, Table 2). Abundance indices for Golden-crowned Kinglets were less correlated than for Winter
259 Wrens, with weak correlation between A_{30C} and A_{30R} in particular (Fig. 5, Table 2). Correlations for
260 predicted values of our abundance indices were moderate to strong for both species (Figs. S1-S2), and
261 were higher than correlation coefficients for observed values of the same index pairs (Table 2). The

262 strong correlation between predicted values of the abundance indices indicates that our models found
263 the same underlying signal regardless of whether training data were from ARUs or point counts.

264 For Winter Wrens, observed abundance indices using randomly selected minutes from ARUs
265 (A_{30R} , A_{66R}) were more closely correlated with the observed abundance index from point counts (A_P) than
266 was the abundance index from 10 consecutive minute ARU surveys (A_{30C}). For both species, A_P was
267 most strongly correlated with A_{66R} .

268 **4 | DISCUSSION**

269 Importantly, abundance models trained with ARU data showed the increase in relative
270 abundance indicating the arrival of migrants at the study site, suggesting that ARUs can be used to
271 track migration phenology in stopover habitat for vocal species. ARUs also provided similar estimates
272 of the number of species detected as point counts when analyzing randomly sampled minutes. Our
273 results suggest that ARUs recording for an extended duration in migration stopover habitat can be just
274 as effective as in-person point counts for monitoring migrating land birds.

275 Data from randomly selected minutes of ARU recordings detected more species and produced
276 modeled abundance estimates that better showed the expected seasonal pattern of migration timing than
277 data from consecutive minutes of ARU recordings. There are two likely explanations for this. First,
278 randomly selected minutes are less temporally auto-correlated than consecutive minutes. For example,
279 during a 10-minute in-person point count, little new information is gained during the seventh minute of
280 the survey compared to what was collected during the sixth minute of the survey; a Winter Wren
281 singing near the end of the sixth minute of a point count survey will likely still be singing in the
282 beginning of the seventh minute. By selecting minutes randomly from across the five-hour survey
283 window, the temporal correlation between each successive minute that is analyzed is minimized.

284 Second, during migration stopover, birds may move more and farther distances within the study area
285 than they would during the breeding season, when they have established a territory. The community of
286 birds within the immediate detection radius of an observer (either a person or a recording ARU) may
287 therefore change over the course of five hours. Using randomly selected minutes provides a more
288 complete sample of the birds using a spatial location over the entire course of the survey window.

289 For in-person point counts, the time taken to travel to a survey site takes up a major portion of
290 the total time invested, so site visits are typically limited to once per day. With ARUs, no such
291 constraints exist; it is possible to do multiple short-duration surveys from many locations over the
292 course of one day without additional travel and field work logistics. We recommend that studies using
293 ARUs on migration should randomly sample recordings of short periods of time (e.g. one-minute
294 recordings) from a defined survey window relevant to the study question (e.g. the five hours following
295 sunrise for passerines in temperate forest, or twilight to dawn for crepuscular and nocturnal species). In
296 many studies using ARUs during the breeding season, researchers listened to consecutive minutes of
297 recordings (e.g. 10 minutes or 2 minutes in Klingbeil & Willig (2015)). Given the improvement we saw
298 when listening to random rather than consecutive minutes from an extended duration recording, we
299 recommend that future studies using ARUs to monitor birds during wintering or breeding seasons test
300 whether randomly selected minutes provide a more effective sample than consecutive minutes.

301 We did not detect an effect of either wind or rain in our model of the number of species detected.
302 However, because we controlled for adverse weather conditions during our field surveys by not
303 surveying on rainy or windy days, the number of high wind values in our data was low, as was the
304 number of rainy survey days. We also noted anecdotally that occasionally the wind values recorded in
305 person for a survey day did not correlate with the amount of wind heard while conducting our desk-
306 based audio surveys; we speculate that wind direction in relation to the microphone may make a

307 difference in how much wind is actually picked up by the ARU. Given that wind and rain have an
308 effect on the detectability of birds in the study system (Ralph, Droege & Sauer, 1995), they remain
309 important predictors to include, whether or not they appear significant in our model. Likewise, we
310 suspect that the insignificance of the polynomial day of year term is due to sample size limitations.

311 Interpreting the significance of the noise variable is challenging, because we used the variable to
312 describe all non-avian noise in the environment, which could include waves, airplanes, and frogs. We
313 suspect that the overall significance of the noise variable may be due to frogs. Future studies may want
314 to carefully consider whether they wish to distinguish between other vocalizing taxa and surrounding
315 environmental noise. ARUs can be used to simultaneously sample multiple taxa (e.g. crickets and bats;
316 Newson, Bas, Murray & Gillings, 2017) so researchers may want to incorporate analyses of non-bird
317 biotic noise into study designs.

318 Estimates of abundance are more useful than estimates of occupancy for prioritizing
319 conservation resources at dynamic temporal scales, such as during migration (Johnston et al., 2015).
320 ARUs do not solve the problem of how to estimate true abundance in stopover habitat during
321 migration. Imperfect detection means that the number of individuals detected is not necessarily a good
322 estimate of the number of individuals present (MacKenzie & Kendall, 2002). Hierarchical models that
323 account for imperfect detection (MacKenzie et al., 2002; Kéry & Royle, 2016) rely on assumptions
324 about population closure that may be badly violated during migration, when birds do not adhere to
325 territories and are present in stopover habitat for short periods of time. The period in which we can
326 reasonably assume population closure for our study area during migration may be as short as several
327 hours or as long as several days, depending on weather conditions. Therefore disentangling true
328 occupancy or abundance from detectability is difficult, whether using traditional in-person survey
329 methods or ARUs. Using a relative abundance index that does not account for detection probability

330 could result in misleading estimates of abundance if detection probability is not constant (MacKenzie
331 & Kendall, 2002). It is possible that individual birds' vocalizations may increase over the spring
332 migration period, as birds prepare for the breeding season. Using our abundance indices, increases in
333 vocalizations would look like an increase in relative abundance, but the apparent increase would
334 merely be an artifact of changing detectability. However, given the moderate (for Golden-crowned
335 Kinglets) and strong (for Winter Wrens) correlation between A_p (observed abundance from point
336 counts) and our ARU abundance indices, we believe increases in relative abundance seen in our model
337 results (Fig. 3) are not mere artifacts of changes in detectability, but rather show real increases in
338 abundance associated with the arrival of our focal species in the study area. ARUs can therefore
339 provide valuable data about migration phenology and stopover habitat use, even if they cannot be used
340 to estimate true abundance.

341 Differences in how well relative abundance models captured the arrival of migrants seemed to be
342 partly dictated by how well aggregating detections by day reduced the number of "zero" counts in our
343 data. For Golden-crowned Kinglets, the A_p and A_{66R} models seemed to be effective at detecting the
344 increase in abundance associated with initial arrival, though they did not capture a peak of abundance,
345 if one existed during the study period. It is unclear whether days with high counts of Golden-crowned
346 Kinglets represent a real pulse of newly arrived birds, or the same birds already present in the region
347 clustering more densely, or just random variation around a more or less constant number of individuals.
348 A dense network of simultaneously recording ARUs in the region could help answer this question.
349 Future studies might also consider increasing ARU survey effort beyond our maximum of 66 randomly
350 selected minutes per day. The improvement in our models associated with increasing from 30 to 66
351 minutes suggests that increasing the number of minutes surveyed is beneficial.

352 Future studies using ARUs to monitor bird migration may wish to take advantage of ARUs'
353 unique ability to scale research in ways that may be infeasible or prohibitively expensive for in-person
354 field work. For example, ARUs could be deployed in dense, small-scale networks to examine micro-
355 habitat use in stopover regions. Alternatively, they could be deployed on a latitudinal gradient covering
356 hundreds or thousands of kilometers to examine how vocal behavior changes over the spring migration
357 period as birds approach their breeding grounds.

358 Applying the methods described here can facilitate an increase in survey effort in difficult-to-
359 access migratory stopover habitat in high latitude forests. Temporal variation in accessibility in these
360 habitats is dramatic, as unpaved roads typically turn from snow to slush to impassable mud before
361 hardening into reliably dry surfaces in early summer. ARUs can eliminate many of the restrictive
362 logistics and safety concerns for researchers interested in monitoring spring migration. Our method of
363 using desk-based surveys of randomly selected minutes from ARUs can be used by any researcher with
364 the skills to conduct point counts. Researchers can set up ARUs during winter conditions when access
365 to study sites over snow is relatively easy (e.g. using snowmobiles, skis or snowshoes), and revisit to
366 collect the audio data once conditions have stabilized in late spring. Our methods for using ARU data to
367 model relative abundance of focal species and the number of species present during migration can be
368 immediately applied to increase monitoring effort in logistically difficult regions.

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378 **Author Contributions**

379 ER and WG developed the study design and methodology; ER prepared for and performed all field
380 work, and conducted all desk-based audio surveys; ER and WG conducted the data analysis, wrote the
381 manuscript, and gave final approval for publication.

382 **Data Availability Statement**

383 Data and code to reproduce analyses can be found at <https://doi.org/10.5281/zenodo.3964500>
384 (ellieroark, 2020). Audio recording files used to produce this analysis are archived at
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512 **Figure and Table Captions**

513 *Figure 1:* Study area on the Point Abbaye Peninsula in Baraga County, Michigan, USA. Points denote
514 survey locations visited during April and May of 2019. The survey area covers 2.7 km². White lines on
515 the left panel show unploughed four wheel drive roads which are impassible from early April to early
516 May each year.

517
518 *Figure 2:* The number of bird species detected by in-person point counts and automated recording units
519 (ARUs) during the spring migration period on the Point Abbaye peninsula, Michigan, USA in 2019.
520 Points show observed number of species detected, lines show predictions from a generalized linear
521 mixed model, holding weather variables constant. See Box 1 for a description of the species richness
522 index abbreviations. Listening to 10 random minutes of data from an ARU (S_{10R}) allowed for detection
523 of the same number of species as a 10 consecutive minute in-person point count (S_p). Increasing survey
524 effort to 22 random minutes of ARU data (S_{22R}) increased the number of species detected to above the
525 number of species detected by in-person point counts.

526

527 *Figure 3:* Predicted (lines) and observed (points) relative abundance of (a) through (d) Winter Wren,
528 and (e) through (h) Golden-crowned Kinglet, in April and May of 2019 on the Point Abbaye peninsula.
529 Points show observed values for each abundance index, while lines show the mean predicted values
530 from 200 five-fold cross validated boosted regression tree models. The vertical axes show the daily
531 abundance index value (see Box 1) calculated from: (a) and (e) three 10-minute in person point counts,
532 (b) and (f) three samples of 10 consecutive minutes of audio recordings from automated recording units
533 (ARUs), (c) and (g) three samples of 10 randomly selected minutes of audio recordings from ARUs, (d)
534 and (h) three samples of 22 randomly selected minutes of audio recordings from ARUs.

535

536 *Figure 4:* Correlation between daily observed values of relative abundance indices (Box 1) for Winter
537 Wren. See Table 2 for Spearman's correlation coefficients for each plot. Abundance indices for ARUs
538 (the proportion of 30-second intervals with a vocalization) are correlated with the abundance index
539 from point counts (mean number of individuals observed per count per day). Note that axis scales vary
540 by abundance index; absolute values are less important here than the relationship between observations.
541 Photo: "Winter Wren" by ilouque, used under license CC BY 2.0. Cropped from original.

542

543 *Figure 5:* Correlation between daily observed values of relative abundance indices (Box 1) for Golden-
544 crowned Kinglet. See Table 2 for Spearman's correlation coefficients for each plot. Abundance indices
545 for ARUs (the proportion of 30-second intervals with a vocalization) are correlated with the abundance
546 index from point counts (mean number of individuals observed per count per day). Note that axis scales
547 vary by abundance index; absolute values are less important here than the relationship between

548 observations. Photo: “Golden-crowned Kinglet” by Laura Gooch, used under license CC BY-NC-SA

549 2.0. Cropped from original.

550

551 *Box 1:* Indices of relative abundance and species richness for both in-person point count observations,
552 and desk-based listening counts using audio data from Automated Recording Units (ARUs).

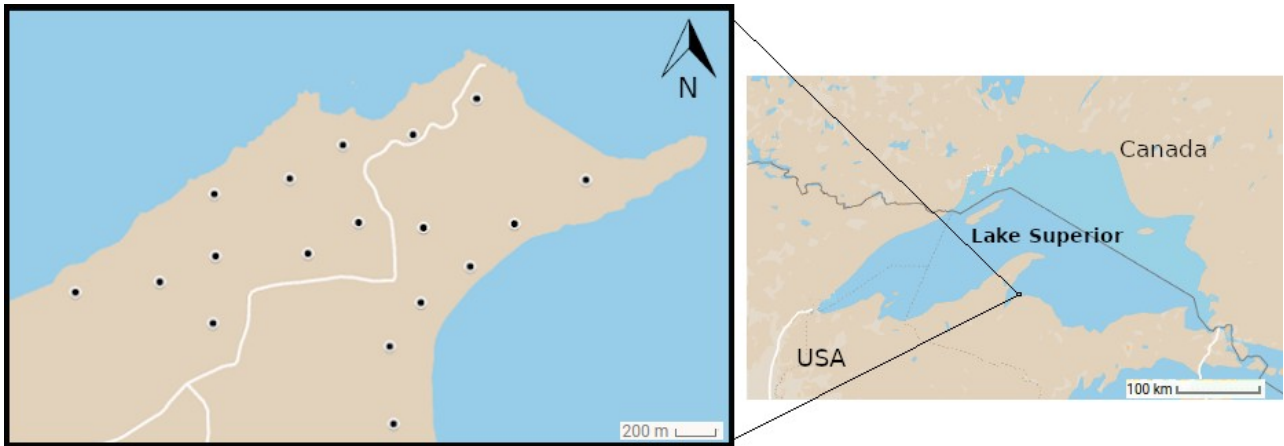
553

554 *Table 1:* Results of a generalized linear mixed model of the number of species detected as a function of
555 day of year, count type and environmental condition covariates. Each variable included in the model is
556 shown, along with the coefficient point estimate, 95% confidence interval, and significance level.

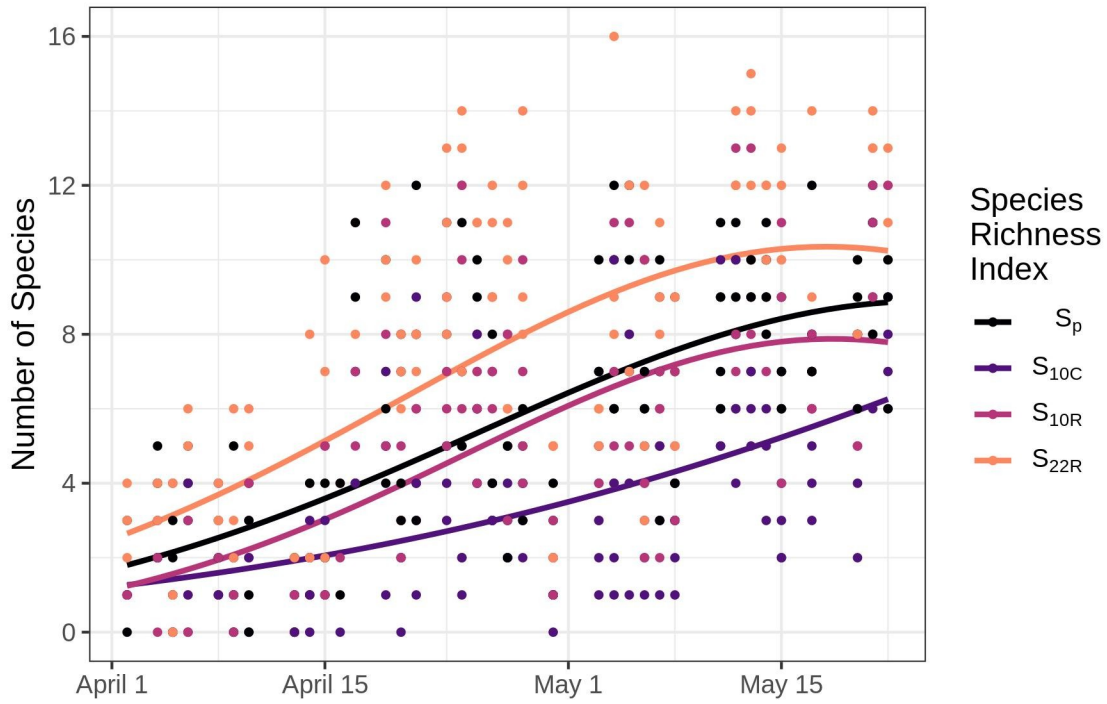
557 *denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.001$

558

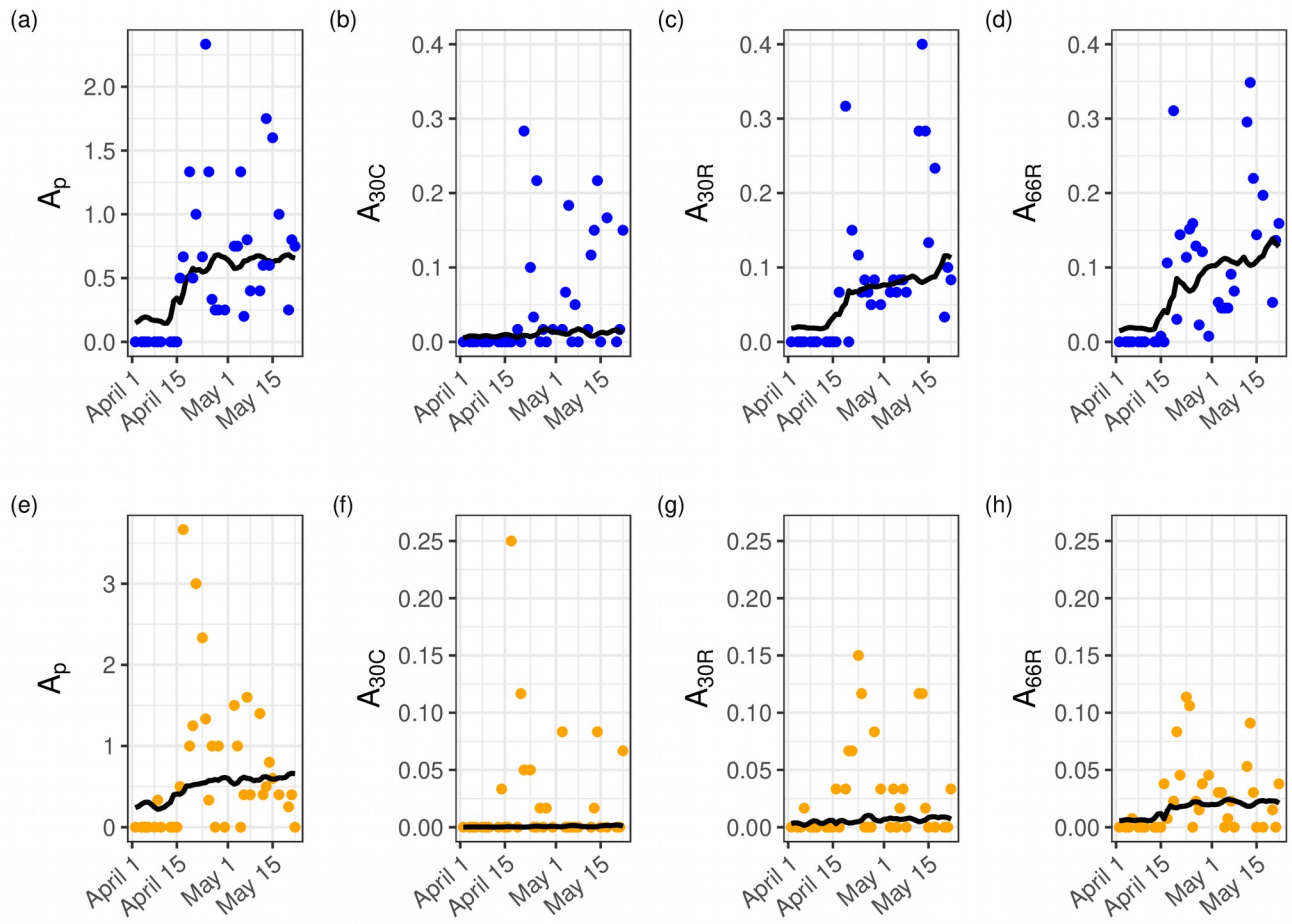
559 *Table 2:* Spearman's rank correlation coefficients for each combination of abundance indices. We did
560 not report a correlation for A_{30R} and A_{66R} because A_{30R} data is a subset of A_{66R} data.



562 *Figure 1*
563
564
565



566
567 *Figure 2*

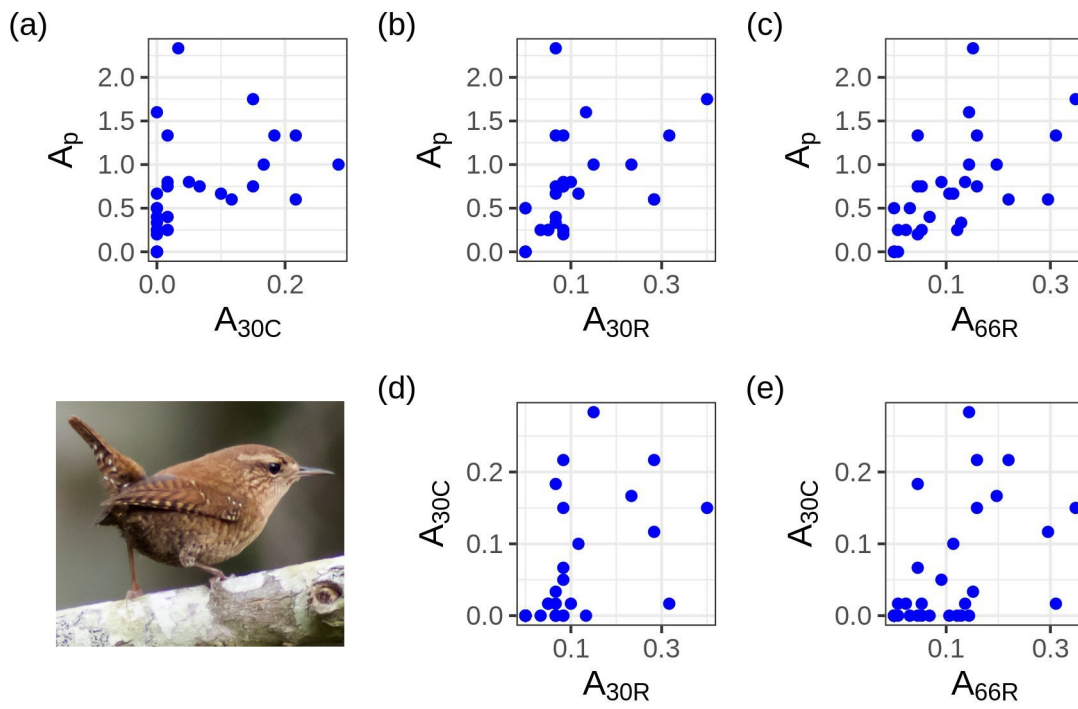


568 *Figure 3*

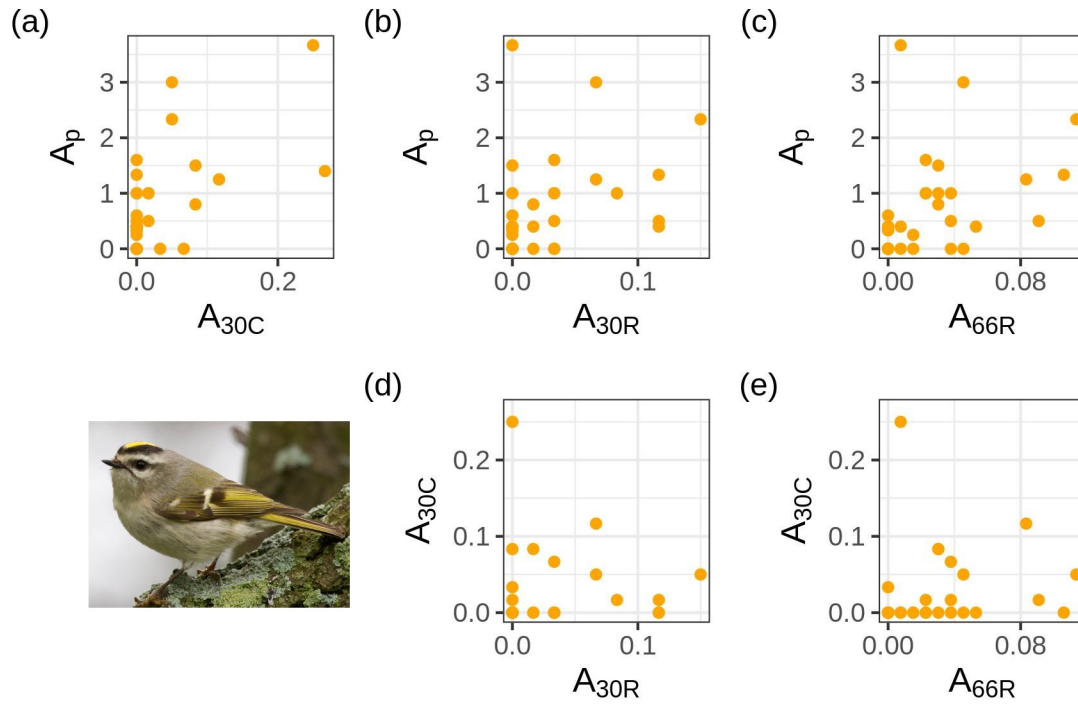
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570

571



572 *Figure 4*



574 Figure 5

Box 1

Index Abbreviation	Survey type	Temporal continuity	Measured Value
A_p	Point count	Consecutive	Relative abundance measured as the mean number of observed individuals per 10 minute point count per day
A_{nC}	Automated Recording Unit	Consecutive	Relative abundance measured as the proportion of 30 second intervals with a vocalization calculated by surveying n minutes in sections of 10 consecutive minutes
A_{nR}	Automated Recording Unit	Random	Relative abundance measured as the proportion of 30 second intervals with a vocalization calculated by surveying n minutes in sections of 1 minute chosen randomly from the full five hour survey window.
S_p	Point count	Consecutive	Number of species detected during a 10 minute in person point count
S_{nC}	Automated Recording Unit	Consecutive	Number of species detected during n consecutive minutes, in sections of 10 consecutive minutes
S_{nR}	Automated Recording Unit	Random	Number of species detected during n minutes, chosen randomly from the full five hour survey window

576

Table 1

Variable	Coefficient estimate	95% CI lower bound	95% CI upper bound	P-value
Survey type (S _{10C})	-0.6146	-0.7824	-0.4467	<0.0001***
Survey type (S _{10R})	-0.065	-0.213	0.0829	0.3888
Survey type (S _{22R})	0.3056	0.1702	0.441	<0.0001***
Wind (2)	-0.0301	-0.135	0.0748	0.574
Wind (3+)	-0.1007	-0.2644	0.0629	0.2277
Rain (Wet)	-0.1984	-0.4624	0.0657	0.1409
Noise (1)	0.1552	0.0595	0.251	0.0015**
Noise (>2)	0.0544	-0.147	0.2557	0.5967
Day of year	0.4346	0.305	0.5641	<0.0001***
Day of year ²	-0.1159	-0.2496	0.0178	0.0892
Survey type (S _{10C}) x Rain (Wet)	-0.0163	-0.3944	0.3617	0.9325
Survey type (S _{10R}) x Rain (Wet)	0.1861	-0.1374	0.5096	0.2595
Survey type (S _{22R}) x Rain (Wet)	0.2288	-0.0677	0.5252	0.1304
Survey type (S _{10C}) x Day of Year	0.0153	-0.1191	0.1498	0.823
Survey type (S _{10R}) x Day of Year	0.0595	-0.0659	0.1849	0.3525
Survey type (S _{22R}) x Day of Year	-0.0709	-0.1808	0.0389	0.2058
Survey type (S _{10C}) x Day of year ²	0.086	-0.048	0.2199	0.2083
Survey type (S _{10R}) x Day of year ²	-0.0583	-0.1825	0.0659	0.3575
Survey type (S _{22R}) x Day of year ²	-0.0148	-0.125	0.0953	0.7917

577

Table 2

Relative Abundance Index Pairs		Golden-crowned Kinglet		Winter Wren	
		<i>Correlation of Observed Values</i>	<i>Correlation of Predicted Values</i>	<i>Correlation of Observed Values</i>	<i>Correlation of Predicted Values</i>
A_P	A_{30C}	0.532	0.794	0.72	0.822
A_P	A_{30R}	0.499	0.652	0.781	0.882
A_P	A_{66R}	0.588	0.813	0.817	0.854
A_{30C}	A_{30R}	0.286	0.817	0.716	0.757
A_{30C}	A_{66R}	0.485	0.897	0.676	0.736

578