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Automated acoustic monitoring captures timing and intensity of bird migration

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1 Abstract

2 1: Monitoring small, mobile organisms is crucial for science and conservation, but is technically challenging.
3 Migratory birds are prime examples, often undertaking nocturnal movements of thousands of kilometres
4 over inaccessible and inhospitable geography. Acoustic technology could facilitate widespread monitoring of
5 nocturnal bird migration with minimal human effort. Acoustics complements existing monitoring methods
6 by providing information about individual behaviour and species identities, something generally not possible
7 with tools such as radar. However, the need for expert humans to review audio and identify vocalizations
8 are challenges to application and development of acoustic technologies.

9 2: Here, we describe an automated acoustic monitoring pipeline that combines acoustic sensors with machine
10 listening software (*BirdVoxDetect*). We monitor four months of autumn migration in the northeastern United
11 States with five acoustic sensors, extracting nightly estimates of nocturnal calling activity of 14 migratory
12 species with distinctive flight calls. We examine the ability of acoustics to inform two important facets of
13 bird migration: (1) the quantity of migrating birds aloft and (2) the migration timing of individual species.
14 We validate these data with contemporaneous observations from Doppler radars and a large community of
15 citizen scientists, from which we derive independent measures of migration passage and timing.

16 3: Together, acoustic and weather data produced accurate estimates of the number of actively migrating
17 birds detected with radar. A model combining acoustic data, weather, and seasonal timing explained 75% of
18 variation in radar-derived migration intensity. This model outperformed models that lacked acoustic data.
19 Including acoustics in the model decreased prediction error by 33%. A model with only acoustic information
20 outperformed a model comprising weather and date (57% vs. 48% variation explained, respectively).

21 4: Acoustics also successfully measured migration phenology: species-specific timing estimated by acoustic
22 sensors explained 71% of variation in timing derived from citizen science observations.

23 5: *Synthesis and applications.* Our results demonstrate that cost-effective acoustic sensors can monitor bird
24 migration at species resolution at the landscape scale and should be an integral part of management toolkits.
25 Acoustic monitoring presents distinct advantages over radar and human observation, especially in inaccessible
26 and inhospitable locations, and requires significantly less expense. Managers should consider using acoustic
27 tools for monitoring avian movements and identifying and understanding dangerous situations for birds.
28 These recommendations apply to a variety of conservation and policy applications, including mitigating the
29 impacts of light pollution, siting energy infrastructure (e.g. wind turbines), and reducing collisions with
30 structures and aircraft.

31 Keywords: acoustic monitoring, machine learning, bird migration, remote sensing, ecology

32 Introduction

33 Accurate, efficient, and non-invasive methods for monitoring animals are essential for biology and conser-
34 vation. Small, highly mobile organisms present distinct challenges in these regards, especially migratory
35 songbirds (order Passeriformes) (Runge et al. 2014). Many species travel thousands of kilometres each
36 year at night (Newton 2008), and these movements can stymie traditional and modern monitoring methods:
37 miniaturized tracking devices (i.e. on-bird sensors) require recapture and are frequently too large or expensive
38 for small birds (Kays et al. 2015); Doppler weather surveillance radars are expensive and cannot separate
39 individuals or identify species (Jacobsen and Lakshmanan 2017, Van Doren and Horton 2018); and visual
40 observation is only possible with bright lights or by moonwatching (Lowery and Newman 1966, Gauthreaux
41 1971, Van Doren et al. 2017). These methods provide significant detail about aspects of birds' behaviours,
42 but none is a universal solution. Given recent population declines among migratory birds and accelerating
43 environmental change (Rosenberg et al. 2019), there is an urgent need for non-invasive tools and robust
44 applied methods to monitor nocturnal avian migrations at individual resolution, under varied conditions,
45 and in areas that are presently inaccessible (e.g. boreal wilderness) or inhospitable (e.g. deserts or ocean).

46 Acoustic monitoring can address these gaps. Migratory birds utter species-specific vocalizations, or “flight
47 calls,” during nocturnal migratory flights (Farnsworth 2005). By recording and identifying flight calls, sci-
48 entists can monitor bird movements across large areas using widely available audio recorders. Acoustic
49 monitoring of flight calls can provide insight into long-distance migrations and reveal poorly known and
50 overlooked local movements that are difficult to detect by traditional means. However, the need for ex-
51 pert human knowledge to detect and identify calls is a major hurdle methods development and a barrier to
52 widespread use (Salamon et al. 2016). Automating detection and identification of flight calls would greatly
53 increase data throughput and allow for continent-wide networks to monitor nocturnal bird migration.

54 Improved acoustic tools for monitoring bird migration would provide an important resource for applied
55 conservation and policy initiatives. Airspace is increasingly recognized as important habitat for volant
56 organisms (Diehl 2013)—a habitat increasingly impinged upon by human structures, vehicles, and lights.
57 Birds’ use of the aerosphere is of great interest to wind energy and aviation industries, particularly for
58 threatened species. Light pollution and light-induced collisions are particular concerns for migratory birds
59 (Loss et al. 2015, Van Doren et al. 2017). Lights-out initiatives are a focus of current policy actions,
60 and increasing evidence suggests that acoustic communication during nocturnal migration is an important
61 factor in birds’ susceptibility to artificial light pollution (Watson et al. 2016, Winger et al. 2019, Gillings
62 and Scott 2021). In addition, understanding the impacts of climate change on organisms is of conservation
63 and policy concern, and additional tools that can monitor their behavioural responses and population are
64 important resources for decision-making. In an era of rapid change, long-term monitoring efforts that can
65 inform science, conservation, and policy are essential.

66 BirdVox is a project funded by the National Science Foundation to develop machine learning software for
67 acoustic monitoring of flight calls (Salamon et al. 2016, Salamon et al. 2017, Lostanlen et al. 2018, 2019b,
68 2019c, Lostanlen et al. 2019a, Cramer et al. 2020b). The project’s *BirdVoxDetect* software processes audio
69 recordings and outputs counts and timings at three taxonomic levels: order, family, and species (Lostanlen
70 et al. 2019c, Cramer et al. 2020b). Despite this progress, it has not yet been demonstrated that any
71 automated acoustic monitoring system can produce reliable estimates of the numbers of migrating birds
72 aloft or accurately measure migration phenology at the species level. Studies using non-automated methods
73 have demonstrated a link between acoustics and migration intensity, but these have been limited in scope
74 due to the demands of manual processing (Larkin et al. 2002, Farnsworth et al. 2004, Sanders and Mennill
75 2014, Horton et al. 2015). If automated acoustic approaches can increase data throughput while achieving
76 reliable estimates of migration intensity and phenology, it may expand the application of this technology
77 and enhance our understanding of animal migration.

78 Here, we describe an automated acoustic pipeline that combines a network of sensors with *BirdVoxDetect*
79 software. We use these tools to monitor an autumn migration season and extract nightly estimates of noc-
80 turnal calling activity from migrating birds during migratory flights. We examine the ability of automated
81 acoustic monitoring to provide information about (1) the number of migrating birds aloft and (2) the mi-
82 gration timing of individual species. We use Doppler weather surveillance radar and community science
83 (also known as citizen science) observations to derive independent measures of migration passage and timing,
84 asking whether acoustics can accurately capture these measures—with only a fraction of the expense and
85 effort of those methods. We also ask how information content of acoustic data varies across geographic space
86 by examining the predictive importance of calling activity for radar stations at increasing distances from
87 the acoustic sensor network. Our results demonstrate that cost-effective acoustic sensors could successfully
88 monitor bird migration at wide spatial scales and species resolution, and extract valuable but presently
89 underutilized behavioural information about bird migration aloft.

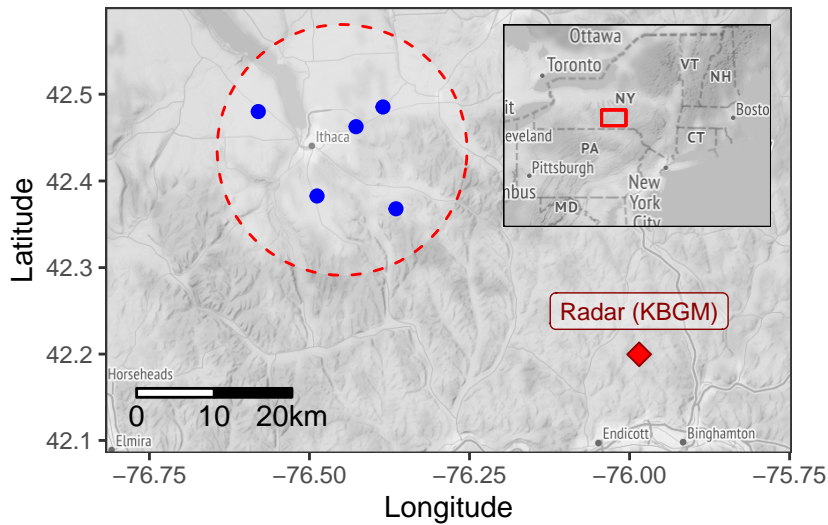


Figure 1: **Study area.** Acoustic sensor locations indicated by blue filled circles. KBGM radar indicated by red diamond. Radar data were extracted above a circular region with radius 16 km, indicated by dashed red circle. The radar is located 46 km from the centroid of the acoustic sensor network. Inset shows location of study area within the northeast US, with the focal area shown by red box.

90 **Materials and Methods**

91 **Acoustic monitoring**

92 **Field sites and acoustic data collection**

93 We collected audio data with nine Recording and Observing Bird Identification Node (ROBIN) bioacoustic
94 sensors developed by the Cornell Lab of Ornithology, deployed in residential areas surrounding the town
95 of Ithaca in Tompkins County, New York State, USA. Each sensor was equipped with an omnidirectional
96 microphone of moderate cost and a Raspberry Pi processing unit. See Salamon et al. (2016) and LOSTANLEN
97 et al. (2022) for further details about the sensor hardware, design, and deployment. No animal ethics
98 approval was required for this passive field study. We received permission from landowners for recording on
99 site. Recording units collected data every night between civil twilight dusk and dawn (when the sun was 6°
100 below horizon); nocturnal bird migration generally begins 30-45 minutes after local sunset (Hebrard 1971).
101 Recording units recorded between 3 August and 8 December 2015, yielding 6651 hours of acoustic recordings.
102 We excluded data from four units that experienced frequent malfunctions or had noise contamination that
103 interfered with monitoring. Overall, we retained data from 5 units (Figure 1), totaling 4879 hours.

104 **Call detection and classification**

105 *BirdVoxDetect* (<https://github.com/BirdVox/birdvoxdetect>) (LOSTANLEN and SALAMON 2022) is a software
106 package for processing continuous audio recordings of nocturnal bird migration. *BirdVoxDetect* can be
107 applied to audio data collected with any hardware and is not specific to devices used in this study. Previous
108 work has presented the method and its performance using a subset of the data processed for the present
109 study (SALAMON et al. 2016, SALAMON et al. 2017, LOSTANLEN et al. 2018, 2019b, 2019c, LOSTANLEN et al.
110 2019a, 2022, CRAMER et al. 2020b). *BirdVoxDetect* applies per-channel energy normalization to reduce the
111 influence of background noise, detects and excludes periods of sensor malfunction, and passes audio to a
112 convolutional neural network to detect flight call vocalizations (LOSTANLEN et al. 2022). Detections are then
113 processed through a second neural network, which classifies calls at three taxonomic levels: order, family,
114 and species. This network was trained on recordings from the BirdVox-ANAFCC-v2 dataset (CRAMER et al.
115 2020a, LOSTANLEN et al. 2022). We enforce taxonomic consistency of predictions by ensuring that predicted
116 family is a member of predicted order and that predicted species is a member of predicted family. See
117 LOSTANLEN et al. (2022) for further details about the classifier and processing pipeline.

118 **Acoustic data processing**

119 The development and validation of *BirdVoxDetect* was previously performed on a subset of the present 4879-
120 hour dataset. Detailed methods and results can be found in Cramer et al. (2020b), LOSTANLEN et al. (2018),
121 LOSTANLEN et al. (2019c), LOSTANLEN et al. (2019a), LOSTANLEN et al. (2019b), SALAMON et al. (2016), and
122 SALAMON et al. (2017), and are summarized in LOSTANLEN et al. (2022).

123 For the present study, we ran *BirdVoxDetect* on the full 4879-hour autumn 2015 dataset. The software
124 classified detections to order, family, and species (Table S1 in Supporting Information). *BirdVoxDetect*
125 makes classifications of 14 species that are common nocturnal migrants and make distinctive calls. Although
126 these species represent only a fraction of all migratory species in North America, they provide a useful sample
127 of nightly migration activity. We retained detections with confidence scores of at least 50%; this threshold
128 represents the optimal tradeoff between true and false positives in this dataset (LOSTANLEN et al. 2022). We
129 further filtered detections to those where order, family, and species were all classified with a confidence of at
130 least 50%. We retained detections belonging to the order Passeriformes, excluding other detections, which
131 included both non-Passerines and non-avian sounds.

132 We summarized call counts by night for each recording unit, calculating the nightly calling rate by divid-
133 ing the number of detections by the nightly recording duration. This procedure accounted for units that
134 malfunctioned and did not record a full night. We calculated total nightly calling rate for all Passerine
135 species together, plus individual call rates for each family and species. We summarized total nightly call rate
136 (for all Passerines) across recording units using principal component analysis, retaining the first principal
137 component, which explained 63.5% of the variance in nightly call rate. This principal component was our
138 nightly measure of overall flight calling activity (hereafter: nightly calling activity). This metric quantifies
139 nightly Passerine calling activity across all species.

140 **Weather surveillance radar data**

141 To estimate densities of actively migrating birds for comparison with acoustic data, we used the United States
142 Next Generation Radar Network (NEXRAD, WSR-88D) (Crum and Alberty 1993, Van Doren and Horton
143 2018). The primary purpose of this network of Doppler weather surveillance radars (hereafter “radars”) is
144 weather detection, but its use as a biological sensor network—particularly for the monitoring of nocturnal
145 bird migration—is well established (Gauthreaux and Belser 2003, Bauer et al. 2017, Van Doren and Horton
146 2018, Dokter et al. 2019). We extracted data from the 35 radar stations within 1000 km of our acoustic
147 sensors using the R package *bioRad* (Dokter et al. 2019), focusing on data between 1 August and 30

148 November 2015. Bird migration through this region has been previously characterized by Farnsworth et al.
149 (2016).

150 We quantified nightly migration passage at each radar station by integrating migration traffic across vertical
151 profiles from 0–3000 m, using the *integrate_profile* function in *bioRad* (Dokter et al. 2019). We then summed
152 nightly migration traffic at each radar. In addition, we used the radar closest to the acoustic sensors (KBGM,
153 Binghamton, NY) to extract bird migration densities directly above the sensors (Figure 1). The KBGM radar
154 is located 46 km from the centroid of the acoustic sensors, and 36–58 km from the closest and farthest sensors,
155 respectively. At these distances, the centre of the radar beam passes 397–705 m above the ground. Following
156 methods from Van Doren et al. (2021), we extracted data from the 0.5-degree elevation angle for a circle
157 with radius 16 km centred on the acoustic sensors. This ensured we sampled airspace above all acoustic
158 sensors.

159 **Weather data**

160 We obtained concurrent weather data from the North American Regional Reanalysis (NARR) (Mesinger et
161 al. 2006). Weather variables used were north-south wind component (m s^{-1}); east-west wind component (m
162 s^{-1}); air temperature (C); total cloud cover (%); and visibility at the surface (m). NARR predictions are
163 made every 3 hours on a 32-km grid. We matched NARR data to radar observations using the closest NARR
164 data in space and time, averaging across the vertical profile (0–3000 m) for all grid cells covered by the radar
165 domain (out to 37.5 km). For variables available at multiple pressure levels, we extracted data from the
166 surface to 300 mb. We calculated altitude above ground level by subtracting surface geopotential height
167 from the geopotential height at each pressure level, and we used linear interpolation to calculate vertical
168 profiles of weather data at 100-m altitude bins from 0–3000 m. We subsequently averaged all observations
169 in a night to produce a nightly summary of weather conditions.

170 **Community science data (eBird)**

171 We used community science (also known as citizen science) data to derive an independent measure of migra-
172 tion timing for comparison with acoustic data. Our data came from eBird, a massive repository of global
173 bird observations (Sullivan et al. 2014). The eBird database is a rich source of information on migration,
174 and species reporting rates are frequently used to study migration phenology (Mayor et al. 2017, Youngflesh
175 et al. 2021). Because eBird data come primarily from diurnal, in-habitat observations rather than nocturnal
176 flights, we do not expect perfect correspondence with acoustic measures. For example, arriving species may

177 be detected during nocturnal migration a few days before they are widely detected by diurnal observers.
178 However, eBird data provide a validated source of phenology information that is independent of our acoustic
179 dataset.

180 We downloaded the eBird Basic Database (February 2021 version) (*eBird Basic Dataset. Version 2021*) and
181 corresponding sampling events file. Using the `auk` R package (Strimas-Mackey et al. 2018), we filtered eBird
182 data to all checklists submitted in Tompkins County, New York, USA. between 1 August and 30 November
183 2015 (n=4710 checklists). We zero-filled data to incorporate effort information and calculated daily reporting
184 frequency of each of 14 focal species (and corresponding families) (Table S1). We only retained data for
185 “complete checklists,” in which observers reported all species. We calculated daily reporting frequency by
186 dividing number of checklists in which the focal taxon was reported by total number of complete checklists
187 submitted on that day.

188 **Statistical analyses**

189 **Quantifying the value of acoustic information for measuring migration densities**

190 Our first analytical objective was to determine whether nightly calling activity is a good measure of migration
191 passage. Because radars directly measure migrating birds aloft, we constructed a statistical model to quantify
192 the association between calling activity and radar-derived migration passage. Weather conditions greatly
193 influence migration (Richardson 1990, Van Doren and Horton 2018) and may influence calling behaviour
194 (Farnsworth 2005), so we also included variables describing weather conditions in our model to account for
195 potential differences in the relationship between calling activity and migratory passage. We compared four
196 models of nightly migration passage: models with (1) acoustic data, plus weather and time of season; (2)
197 weather and time of season only; (3) acoustic data only; and (4) time of season only. By comparing these
198 models, we quantified the value of acoustic data in measuring migration densities aloft.

199 We modelled radar-measured bird densities aloft using a generalized linear model with a Gaussian error
200 distribution and log link function. Our response variable was the average bird density measured directly
201 above Tompkins County (16 km radius, units of birds km⁻³). To construct our base model, containing both
202 weather and acoustic information, we included these predictor variables: nightly calling activity (derived
203 from PCA of acoustic detections); north-south wind component (m s⁻¹); east-west wind component (m
204 s⁻¹); air temperature (C); total cloud cover (%); visibility (m); and ordinal day of year (cubic polynomial
205 term, to account for any additional nonlinear changes in migration activity through the season). We also
206 tested two possible interactions, nightly calling activity × visibility and nightly calling activity × total cloud

207 cover, as previous research indicates calling behaviour may increase with lower visibility and increased cloud
208 cover (Farnsworth 2005). Because our interest was in predictive performance, the final step in constructing
209 our base model was to identify the weather variables of greatest predictive value to carry forward into the
210 evaluation. We used the *dredge* function in the R package *MuMIn* (Barton 2020) to test a set of candidate
211 models that varied only in weather predictors. All models included nightly calling activity and ordinal day
212 of year (cubic polynomial term). The best-performing model measured by the corrected Akaike Information
213 Criterion (AICc) served as our benchmark.

214 We compared the benchmark model, containing weather, acoustic, and date information, to two sub-models:
215 one with *no* acoustic information (only weather and date), and one with *only* acoustic information. Because
216 our interest was primarily in prediction accuracy, we evaluated benchmark and sub-models using leave-one-
217 out-cross-validation (LOOCV). In LOOCV, one observation is removed, the model is re-fit, and the re-fit
218 model is used to predict the withheld observation; this is repeated for every observation. We evaluated
219 performance using a combination of R^2 (percent variance explained) and root mean squared error (RMSE)
220 of the cross-validated predictions. We evaluated performance using both metrics to provide both relative
221 (R^2) and absolute (RMSE) performance measures. We then determined whether the addition of acoustic
222 data improved the ability of the model to estimate the number of migrating birds aloft. We used default
223 model configuration parameters in the R package *caret* (Kuhn et al. 2017) for training.

224 **Geographic range of acoustic information**

225 After estimating the value of acoustic data for quantifying migration densities above the acoustic sensor,
226 we sought to determine the geographic extent across which acoustic data provide meaningful information
227 about migration. We fit a model with the same predictor variables as the benchmark model above (weather,
228 acoustics, and time of season); the response variable was nightly migration traffic at the radar closest to the
229 acoustic sensors (KBGM). We then made predictions using this model at all radar stations within 1000 km of
230 Tompkins County, NY, and measured R^2 , the proportion of variation explained by the model. Predictions at
231 external radar stations used weather data drawn from those locations, but the model formula was unchanged;
232 this test therefore simulated a scenario in which an acoustic model is trained at one location (here, from
233 Tompkins County, NY) and applied elsewhere without re-training. We performed the same evaluation with
234 a model that contained only acoustic data (no weather or date information). Finally, we quantified how
235 acoustic information content degrades with distance from the acoustic sensor using a simple linear model.

236 Migration timing at the family and species levels

237 We used identifications made by *BirdVoxDetect* to measure migration timing at family and species taxonomic
238 levels, and we compared these with independent timing measures derived from the eBird database. To ensure
239 reliable estimates, we only used species with average daily eBird reporting frequencies of at least 1% of
240 checklists and average nightly call rates of at least 0.25 calls per hour. Ten out of 14 focal species satisfied
241 these criteria.

242 Our timing measure was date of *peak* migration passage through Tompkins County. For eBird reporting
243 frequency and nightly calling activity, we quantified migration timing with a generalized additive model (R
244 package `mgcv`) (Wood 2017) with these parameters: `bs="ds"` (Duchon splines), `k=7`. We used a negative
245 binomial family (log link) for nightly calling activity and a Gaussian family (identity link) for eBird reporting
246 frequency. The date corresponding to the maximum value of the curve was our peak timing measure for both
247 modalities. We quantified uncertainty in timing estimates by simulating from the model 10,000 times and
248 recording peak date each time, from which we derived 95% confidence intervals. The simulation generated
249 10,000 model coefficient vectors using the `mvnorm` function in the R package `MASS` (Venables and Ripley
250 2002) and used the “`lpmatrix`” option in the `mgcv predict` function to generate model predictions for each
251 simulated coefficient vector. For each prediction vector, we saved the date corresponding to the maximum
252 value of the curve and calculated 95% credible intervals from the simulation. We performed these assessments
253 at family and species levels. We also quantified the correlation between species-level acoustic-derived and
254 eBird-derived timing measures. We evaluated this correlation over model simulations to quantify uncertainty.

255 Results

256 Running *BirdVoxDetect* on the 4879-hour autumn 2015 dataset yielded 233124 detections, of which 90% were
257 classified to family and of which 44% were classified to one of 14 focal species (Table S1). Total computation
258 took approximately 1000 CPU-hours.

259 Quantifying the value of acoustic and weather information for measuring migration densities

260 We used AICc-based model selection to identify the single best generalized linear model containing weather
261 and acoustic information for predicting radar-measured migration densities aloft. This benchmark model
262 included north-south and east-west wind components in addition to nightly calling activity and time of
263 season (Table S2). It performed well, explaining 75% of variation (Figure 2). The AICc-best model did

264 not contain air temperature, cloud cover, visibility, or interaction terms. However, models containing cloud
265 cover and visibility also received support (i.e. within ~ 2 AICc units of the best model).

266 Acoustic information greatly improved model performance, and acoustic data explained radar-observed mi-
267 gration densities better than weather alone (Figures 2 and 3). Acoustic information increased model per-
268 formance by 27 percentage points of variation (Figure 3g); prediction error decreased by 33% (Figure 3f).
269 Notably, accuracy gains were particularly evident for the nights with the largest migration events.

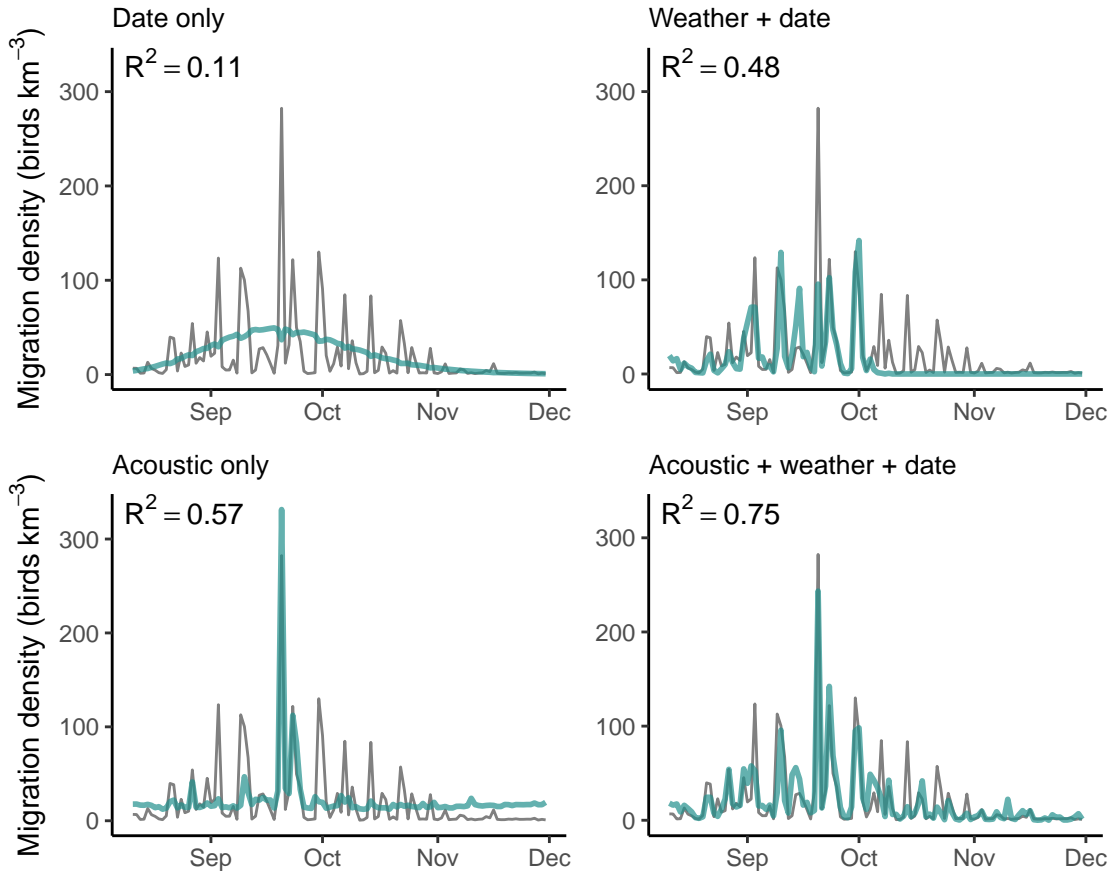


Figure 2: **Migration time series with model predictions.** Gray line shows migration densities observed by radar. Teal lines show cross-validated predictions made with different generalized linear models.

270 Geographic range of acoustic information

271 Models comprising only a single acoustic predictor and trained on the radar station closest to the acoustic
272 sensor predicted migration passage most accurately at radar stations close to the sensor (Figure 4). However,
273 nightly calling activity in Tompkins County still explained significant variation in migration traffic at more
274 distant radar sites (Figure 4). Nightly calling activity alone explained $>30\%$ of variation at radar stations

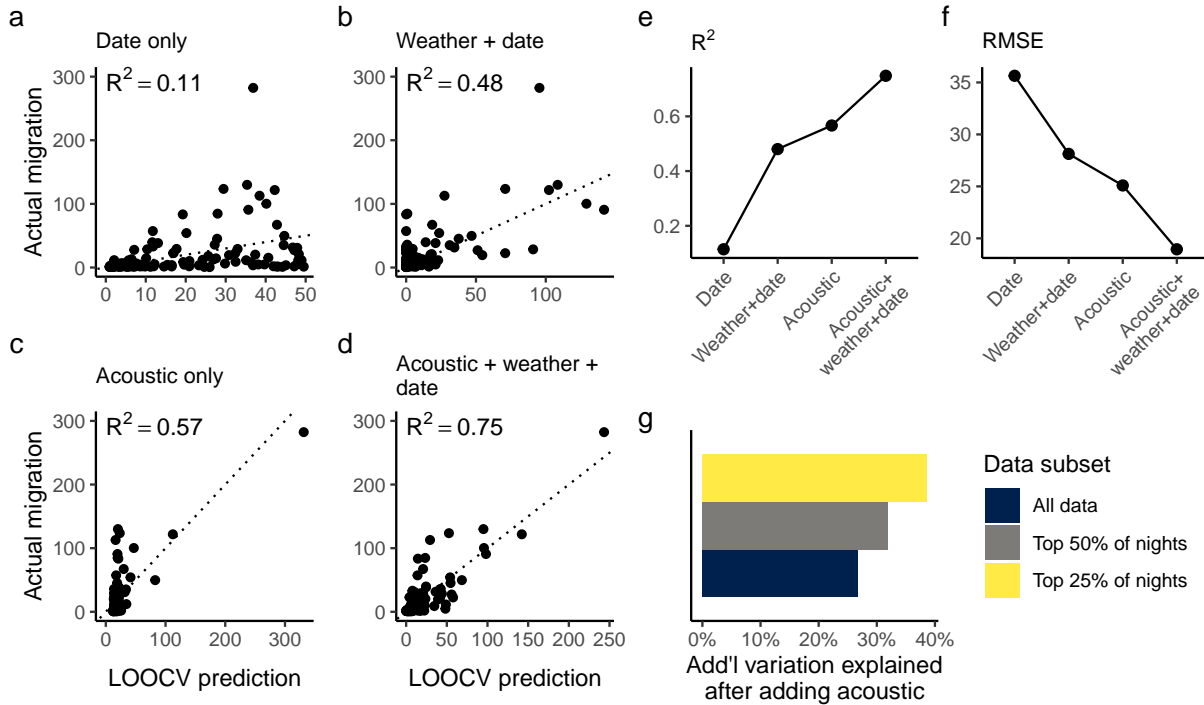


Figure 3: **Acoustic information improves estimation of bird migration densities.** The response variable is radar-derived migration intensity (labeled “actual migration”). All performance measures were evaluated with leave-one-out cross validation (LOOCV). (a,b,c,d) show predictions for date-only (a), weather-only (b), acoustic-only (c), and acoustic + weather (d) generalized linear models. (e) and (f) compare prediction performance for these three GLMs, evaluated with R^2 (higher indicates more variation explained) (e) and root mean square error (lower indicates less error) (f). (g) compares R^2 between weather and acoustic + weather models, showing how performance increases with the addition of acoustic data. Colours show evaluation performance on different subsets of data, focusing on how well the model predicts the largest migration events (specifically, top 50% and top 25%).

275 up to 500 km away (although some sites within 500 km also showed weak relationships). Distance was not
276 the only factor governing performance; acoustic information appeared best linked to radars following an
277 inland corridor from southern Maine to southern central Pennsylvania (Figure 4b). Radar stations along the
278 Atlantic coast, Great Lakes, and Midwest showed lower associations. We observed similar patterns with a
279 model comprising weather, acoustic, and date (Figure S1).

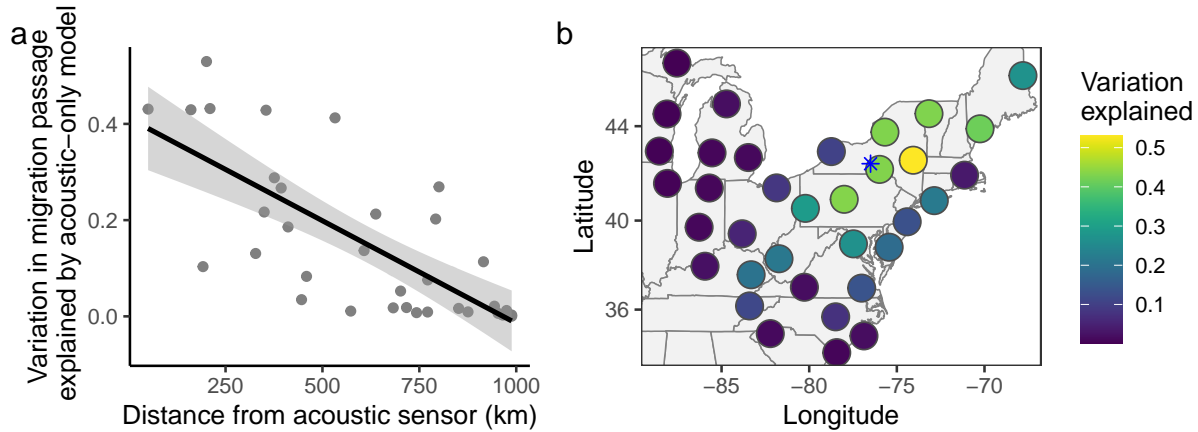


Figure 4: **Acoustic information content degrades with distance.** (a) shows performance of a model containing only acoustic information in predicting migration passage from August to December 2015 at radar stations at varying distances from the acoustic sensor. (b) shows the same information in map form. The blue asterisk is the location of the acoustic sensor.

280 Migration timing at the family and species levels

281 We subdivided nightly calling activity by family and species to compare acoustic information with ground
282 observations of species from eBird data. Seasonal timing measured by acoustic sensors was consistent with
283 that quantified by eBird at both taxonomic levels (Figures 5 and 6). At the species level, peak migration
284 timing estimated from acoustic data explained 71% (95% CI [15% ,86%]) of variation in peak migration
285 timing estimated from eBird (Figure 6).

286 Discussion

287 Methods to monitor and characterize nocturnal bird migration have received much attention from the ap-
288 plied ecology and conservation communities. Acoustic monitoring presents distinct advantages over radar
289 and human observation, especially in inaccessible and inhospitable locations, and requires significantly less

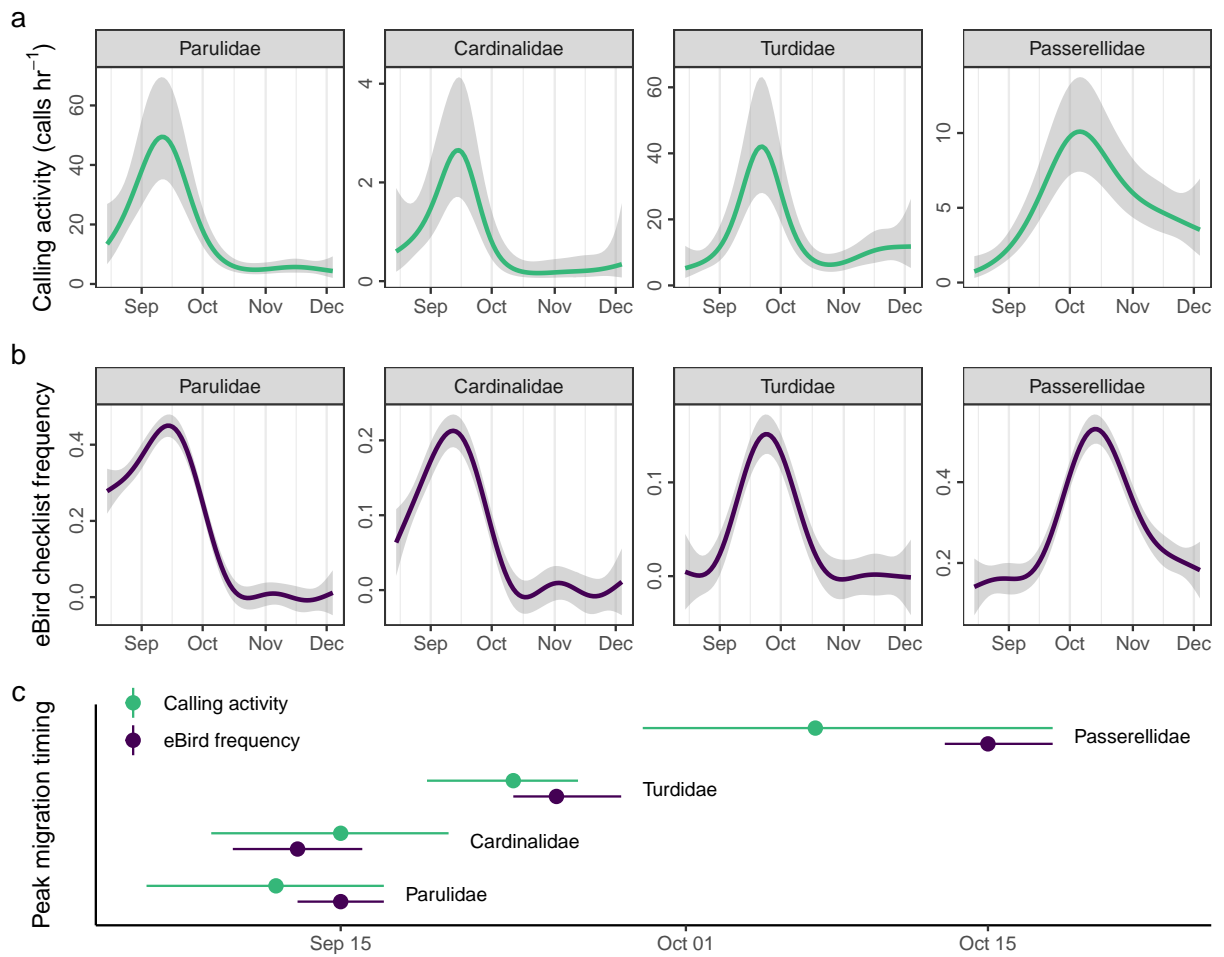


Figure 5: **Comparison of migration timing at the family level, estimated with acoustic and eBird data for fall 2015 in Tompkins County, NY.** (a) shows nightly calling activity with GAM smooths. (b) shows eBird checklist frequency (Tompkins County, NY) with GAM smooths. (c) compares estimates of peak migration timing (95% CI) using acoustic and eBird data, estimated from the above smooths (uncertainty estimated with simulations).

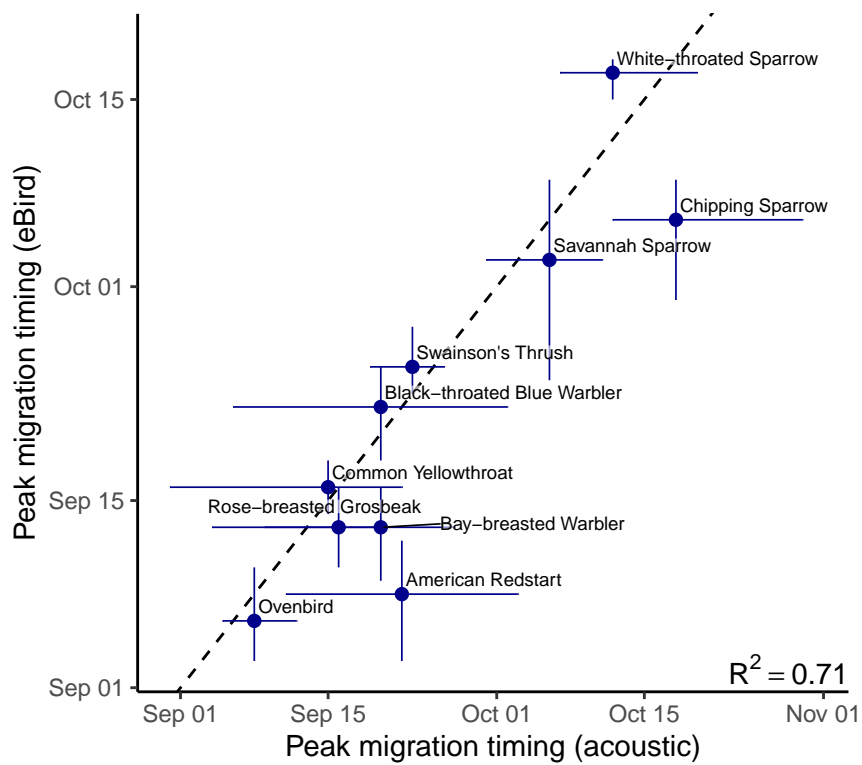


Figure 6: **Comparison of migration timing at the species level, estimated with acoustic and eBird data.** Each point represents one species, with confidence bars showing 95% credible intervals for acoustic and eBird estimates (fall 2015, Tompkins County, NY). The dashed line is the identity line; when the acoustic confidence interval (x-axis) intersects the identity line, the 95% CI in acoustic timing overlaps the eBird estimate.

290 expense. We show that automated acoustic technologies can quantify the magnitude and species composi-
291 tion of bird migration. Our model combining acoustics with weather and seasonal timing explained much
292 of the variation in radar-measured migration passage, despite acoustic sensors being up to 200,000 times
293 less expensive than a WSR-88D weather surveillance radar (compare e.g. \$50 AudioMoth (Hill et al. 2018)
294 vs. \$10 million WSR-88D (Council 2008)). Furthermore, migration timing estimates from acoustics were
295 consistent with those from a massive community science database, despite the fact that no humans needed
296 to be present to collect acoustic data. Overall, automated acoustic methods provide a pathway to local,
297 cost-effective bird migration monitoring at the species level.

298 The link between counts of nocturnal flight calls and migration (e.g. intensity and phenology) has been a topic
299 of much exploration (summarized in Farnsworth 2005). Previous studies have found relationships between
300 acoustic activity and migration intensity measured by radar, thermal cameras, or mist nets, but acoustics
301 typically explain little variation in migration intensity (Larkin et al. 2002, Farnsworth et al. 2004, Sanders
302 and Mennill 2014, Horton et al. 2015). Nevertheless, flight calls have been used to study how migrants
303 interact with topography and respond to weather (Smith et al. 2014, Gesicki et al. 2016) and light pollution
304 (Watson et al. 2016, Winger et al. 2019, Gillings and Scott 2021). To our knowledge, no studies have used
305 flight calls to track species-specific phenology (but see e.g. Smith et al. (2014)). Here, we demonstrate
306 that flight calls *do* encode useful measures of migration intensity after incorporating information on weather
307 conditions and time of season, and likewise that acoustic data accurately capture migration timing.

308 Studies employ radar for characterizing nocturnal migration and providing accurate estimates of migrant
309 densities aloft (Gauthreaux and Belser 2003, Dokter et al. 2011, Bauer et al. 2017, Van Doren and Horton
310 2018). However, radars are not everywhere, and data may not be reliably available from governments and
311 other entities even where they do exist (Shamoun-Baranes et al. 2021). Furthermore, radar has a very
312 limited ability to discriminate species or individuals. This shortcoming precludes its use for important moni-
313 toring tasks, such as: estimating species' passage rates; tracking changing species phenology; understanding
314 species' interactions with local landscape features, light pollution, and weather; and revealing conspecific
315 and heterospecific interactions during migratory flights. Acoustics can address these challenges, many of
316 which are crucial to understanding birds' responses to a changing world. Ultimately, acoustic data may be
317 most valuable when used together with existing tools. Analyses combining taxonomic specificity of acoustic
318 monitoring with the long-range, large-scale reach of weather surveillance radar will lead to a more complete
319 understanding of nocturnal bird migration than either modality alone could provide.

320 Acoustic monitoring can provide valuable information about migration in locations not covered by a radar
321 and/or not frequented by birdwatchers. In our study, acoustic data in central New York State provided

322 meaningful information about migration passage at sites up to 500 km away. At the same time, acoustic
323 sensors provide highly local information, which a large, stationary radar can only accomplish at locations close
324 enough to the radar site. Acoustic monitoring has great potential to understand effects of local landscape
325 features on different species of birds during active migration. Here, acoustic information from inland sensors
326 was most predictive of migration activity along an inland corridor from Maine to Pennsylvania—and poorly
327 predictive of coastal activity—aligning with previous work highlighting connectivity of migration in this
328 region (Farnsworth et al. 2016). That study found that migration activity was correlated among inland
329 radar stations in the northeast US but uncorrelated with migration activity at coastal stations. Our findings
330 provide additional evidence that migration activity in the northeast US is characterized by separate inland
331 and coastal flyways.

332 Repositories of community science data collected by birdwatchers are powerful tools for studying and mon-
333 itoring migratory birds (Sullivan et al. 2014). Our estimates of migration phenology derived from acoustic
334 data were consistent with analogous metrics derived from nearly 3000 observation hours by nearly 400 vol-
335 unteer observers in the birdwatching community. Although timing estimates we obtained with community
336 science data were more precise (compare confidence bands in Figures 5 and 6), this is unsurprising given
337 that Tompkins County, NY is the home of the Cornell Lab of Ornithology and enjoys exceptional commu-
338 nity science coverage. Most areas do not approach this level of community science effort. Understanding
339 migration phenology is of particular utility in biomes experiencing rapid climate change (e.g. tundra), which
340 may have low human population densities and consequently minimal community science coverage. Acoustic
341 monitoring could play an important role in tracking changing phenology in these regions.

342 Despite the many advantages of acoustic monitoring, several important caveats warrant consideration. First,
343 converting call counts to numbers of individuals is difficult, due to variation in calling behaviour by species,
344 time of night, social environment, artificial lighting, and weather conditions. Acoustic arrays that can localize
345 individuals are promising solutions (Gayk and Mennill 2020). Encouragingly, our study finds that acoustic
346 activity (derived from call counts) is a valuable predictor of radar-derived measures of birds aloft, suggesting
347 that the challenge of counting individuals is not a major issue. Second, not all migratory species vocalize
348 regularly during migration. In North America, a large proportion of migratory species give flight calls, and
349 decades of research have been invested in the species identification of calls. However, this is not true for all
350 regions (e.g. Europe), which may limit the utility of acoustic monitoring in certain contexts. Third, ground-
351 based acoustic sensors detect migrants flying in the lower atmosphere, and may be of limited utility for
352 higher-flying migrants; this bias may vary within and among nights, as well as by species. Finally, acoustic
353 sensors cannot easily discern the direction of movement of animals (unless an array is used), making it more

354 challenging to distinguish local movements from long-distance migration. Going forward, combining acoustic
355 information with other data sources (e.g. tracking, radar and community science data) will allow scientists
356 to monitor avian movements more accurately than any one approach alone.

357 Contrary to our expectations, we did not find evidence through statistical interactions that cloud cover and
358 visibility impact the relationship between call counts and migration passage rates. This suggests that call
359 counts can reliably estimate migration passage under varied weather conditions. However, factors including
360 weather and light pollution clearly calling behaviour (Farnsworth 2005, Van Doren et al. 2017). In addition,
361 the 95% confidence set of models included many with cloud cover, visibility, and their interactions (Table
362 S2). This indicates the importance of continuing explorations to understand and to account for relationships
363 between weather conditions and calling behaviour in future studies. Acoustic data were particularly impor-
364 tant for accurately quantifying nights with the largest migration events. These largest nights of migration
365 drive the strong association between acoustics and migration intensity, but these events are also the most
366 important to predict correctly, especially for applied science and targeted conservation action (e.g. light
367 pollution mitigation).

368 Overall, our study demonstrates that automated acoustic methods can accurately characterize bird migration
369 at the species level, despite requiring only a small fraction of the expense and effort of multimillion-dollar
370 radars and large-scale community science programs. This makes acoustic monitoring well-suited for areas
371 outside of radar coverage, or where local-scale monitoring is of particular interest. Local-scale information
372 on migration passage is essential for numerous applications, including infrastructure placement (e.g. wind
373 and solar), aviation collision avoidance, and understanding how birds interact with the built and natural
374 environments (e.g., stopover habitat selection, interactions with urbanized areas, and susceptibility to light
375 pollution). These concerns are particularly salient for species of conservation interest, and acoustics monitor-
376 ing is the only remote sensing method that can detect these species during nocturnal movements. Finally, we
377 emphasize that acoustic monitoring is a viable and cost-effective approach for monitoring active nocturnal
378 bird migration at species resolution across large scales and landscapes that are otherwise difficult to sample.
379 Investing in widespread and acoustic monitoring infrastructure would provide an invaluable window onto
380 global migration biology—an increasingly important task as these species continue to disappear at alarming
381 rates (Rosenberg et al. 2019).

382 **Data Availability Statement**

383 All BirdVox software is open source. BirdVoxDetect can be found on GitHub at [https://github.com/](https://github.com/BirdVox/birdvoxdetect)
384 [BirdVox/birdvoxdetect](https://github.com/BirdVox/birdvoxdetect) (Lostanlen and Salamon 2022). The BirdVox-full-season audio dataset is archived
385 at <https://doi.org/10.5281/zenodo.5791744> (Farnsworth et al. 2022). Code and data associated with this
386 paper are available via Mendeley Data at <https://doi.org/10.17632/m4sgc32fpv.1> (Van Doren et al. 2022).

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396 **Conflict of Interest Statement**

397 The authors have no conflicts of interest to declare.

398 **Author Contributions**

399 Benjamin M. Van Doren designed the study, analysed data, and led the writing of the manuscript; Vincent
400 Lostanlen, Aurora Cramer, Justin Salamon, Juan Pablo Bello, Steve Kelling, and Andrew Farnsworth de-
401 veloped the acoustic analysis pipeline to process data; Adriaan Dokter processed radar data. All authors
402 contributed critically to the drafts and gave final approval for publication. The authors have no conflicts of
403 interests to declare.

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Supporting Information

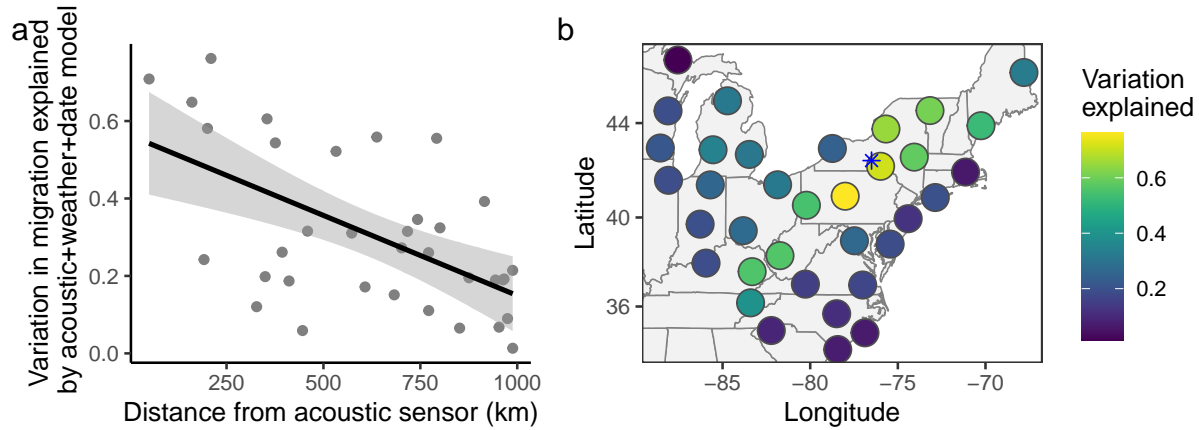


Figure S1: **Acoustic and weather information content degrades with distance.** (a) shows the performance of a model containing acoustic and weather information when predicting migration passage at radar stations at varying distances from the acoustic sensor. Line is a loess smoother. (b) shows the same information in map form. The blue asterisk is the location of the acoustic sensor.

Table S1: **Species included in the *BirdVoxDetect* classifier..**

Family	Common Name	Scientific Name
Passerellidae	American Tree Sparrow	Spizelloides arborea
Passerellidae	Chipping Sparrow	Spizella passerina
Passerellidae	Savannah Sparrow	Passerculus sandwichensis
Passerellidae	White-throated Sparrow	Zonotrichia albicollis
Cardinalidae	Rose-breasted Grosbeak	Pheucticus ludovicianus
Turdidae	Gray-cheeked Thrush	Catharus minimus
Turdidae	Swainson's Thrush	Catharus ustulatus
Parulidae	American Redstart	Setophaga ruticilla
Parulidae	Bay-breasted Warbler	Setophaga castanea
Parulidae	Black-throated Blue Warbler	Setophaga caerulescens
Parulidae	Canada Warbler	Cardellina canadensis
Parulidae	Common Yellowthroat	Geothlypis trichas
Parulidae	Mourning Warbler	Geothlypis philadelphia
Parulidae	Ovenbird	Seiurus aurocapilla

Table S2: **Model selection for prediction of radar-derived bird densities using acoustic and weather data.** Shown is the 95% confidence set of models (cumulative AICc weight sums to 0.95). All models include nightly calling activity and time of season. Note that the “Date (cubic)” variable represents a cubic polynomial term, not a single term with an exponent. Columns are as follows: “Rsqr” is R^2 , the proportion of variance explained by the model; “df” is the number of model parameters; “logLik” is the model log-likelihood; “AICc” is the corrected Akaike Information Criterion; “delta” is the difference in AICc from the best (first-listed) model; “weight” is the AICc weight; “cumulative weight” is the cumulative AICc weight.

terms	Rsqr	df	logLik	AICc	delta	weight	cumulative weight
Date (cubic) + Calling activity + E/W wind + N/S wind	0.802	8	-474.779	966.957	0.000	0.249	0.249
Date (cubic) + Calling activity + E/W wind + Visibility + N/S wind	0.804	9	-474.027	967.818	0.862	0.162	0.411
Date (cubic) + Cloud cover + Calling activity + E/W wind + N/S wind	0.802	9	-474.659	969.082	2.126	0.086	0.497
Date (cubic) + Cloud cover + Calling activity + E/W wind + Visibility + N/S wind	0.806	10	-473.488	969.154	2.197	0.083	0.580
Air temp. + Date (cubic) + Calling activity + E/W wind + N/S wind	0.802	9	-474.747	969.259	2.302	0.079	0.658
Date (cubic) + Calling activity + E/W wind + Visibility + N/S wind + Calling activity \times Visibility	0.806	10	-473.681	969.539	2.583	0.068	0.727
Air temp. + Date (cubic) + Calling activity + E/W wind + Visibility + N/S wind	0.805	10	-473.868	969.915	2.958	0.057	0.783
Date (cubic) + Cloud cover + Calling activity + E/W wind + Visibility + N/S wind + Calling activity \times Visibility	0.808	11	-472.862	970.363	3.406	0.045	0.829
Date (cubic) + Cloud cover + Calling activity + E/W wind + N/S wind + Cloud cover \times Calling activity	0.802	10	-474.644	971.466	4.509	0.026	0.855
Air temp. + Date (cubic) + Cloud cover + Calling activity + E/W wind + N/S wind	0.802	10	-474.654	971.487	4.530	0.026	0.881
Air temp. + Date (cubic) + Calling activity + E/W wind + Visibility + N/S wind + Calling activity \times Visibility	0.806	11	-473.447	971.535	4.578	0.025	0.906
Air temp. + Date (cubic) + Cloud cover + Calling activity + E/W wind + Visibility + N/S wind	0.806	11	-473.486	971.613	4.656	0.024	0.930
Date (cubic) + Cloud cover + Calling activity + E/W wind + Visibility + N/S wind + Cloud cover \times Calling activity	0.806	11	-473.487	971.615	4.658	0.024	0.954