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Automated acoustic monitoring captures timing and intensity of bird migration

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Abstract

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

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

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

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

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

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

Introduction

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

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

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

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

Materials and Methods

Acoustic monitoring

Field sites and acoustic data collection

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

Call detection and classification

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

Acoustic data processing

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

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

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

Weather surveillance radar data

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

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

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

Weather data

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

Community science data (eBird)

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

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

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

Statistical analyses

Quantifying the value of acoustic information for measuring migration densities

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

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

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

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

Geographic range of acoustic information

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

Migration timing at the family and species levels

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

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

Results

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

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

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

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

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

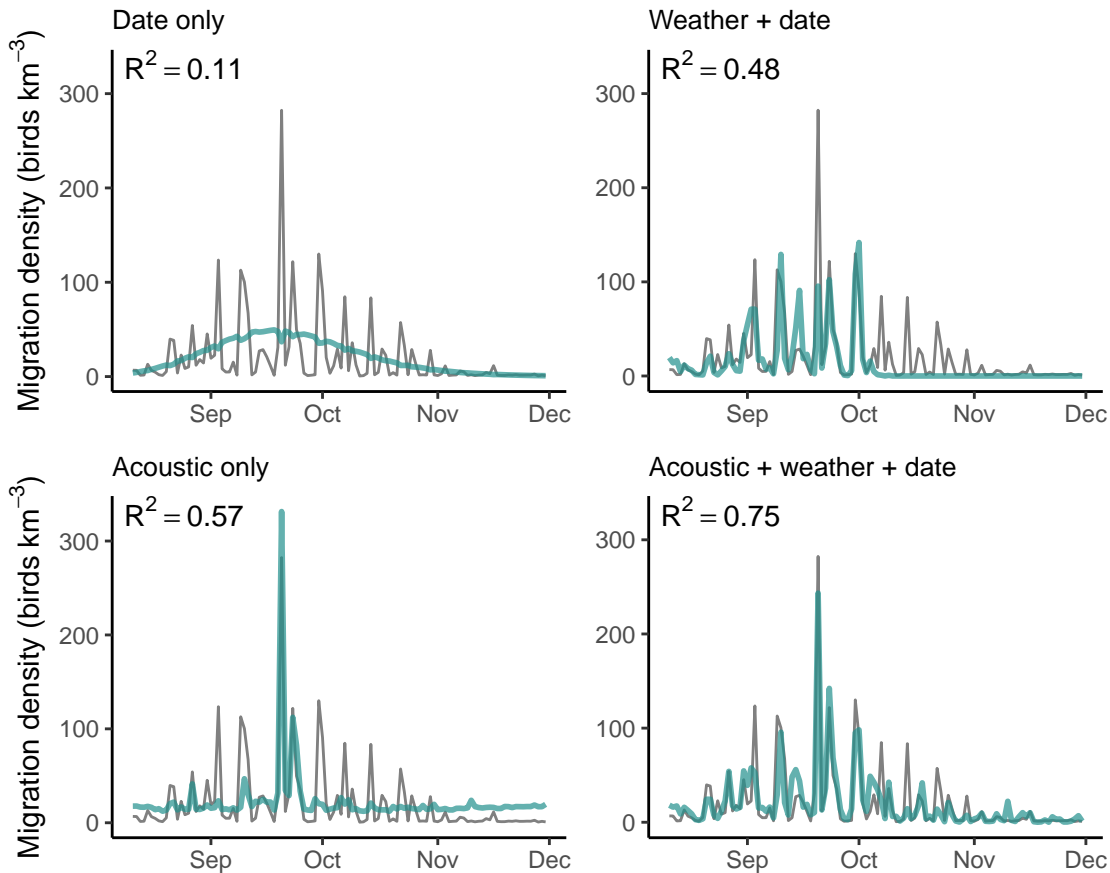


Figure 2: **Migration time series with model predictions.** Gray line shows migration densities observed by radar. Teal lines show cross-validated predictions made with different generalized linear models.

Geographic range of acoustic information

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

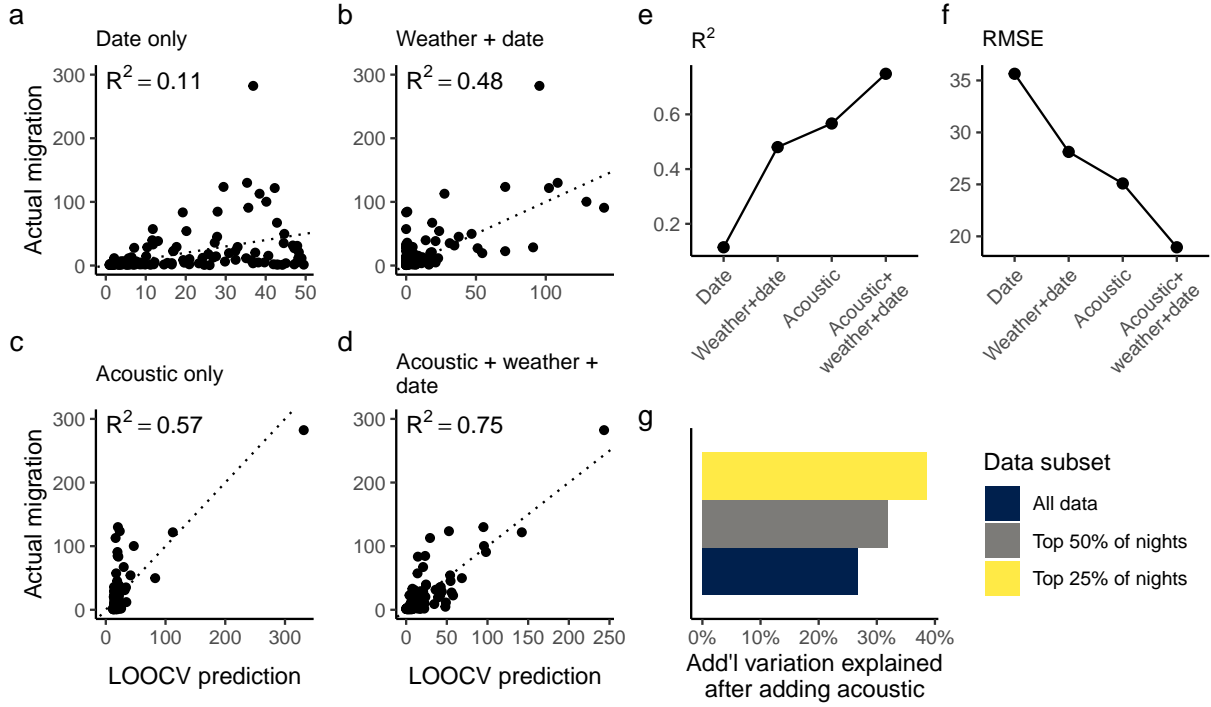


Figure 3: Acoustic information improves estimation of bird migration densities. The response variable is radar-derived migration intensity (labeled “actual migration”). All performance measures were evaluated with leave-one-out cross validation (LOOCV). (a,b,c,d) show predictions for date-only (a), weather-only (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%).

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

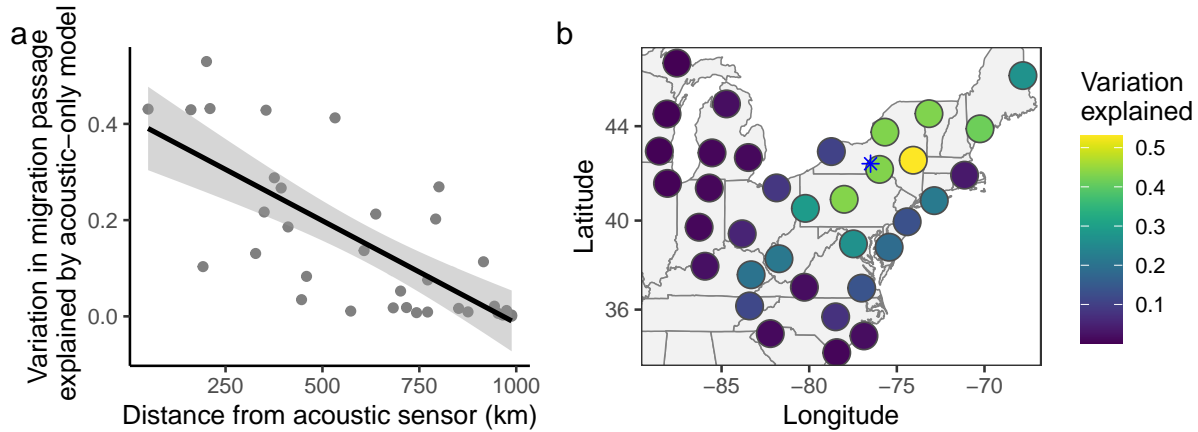


Figure 4: **Acoustic information content degrades with distance.** (a) shows performance of a model containing only acoustic information in predicting migration passage from August to December 2015 at radar stations at varying distances from the acoustic sensor. (b) shows the same information in map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

Migration timing at the family and species levels

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

Discussion

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

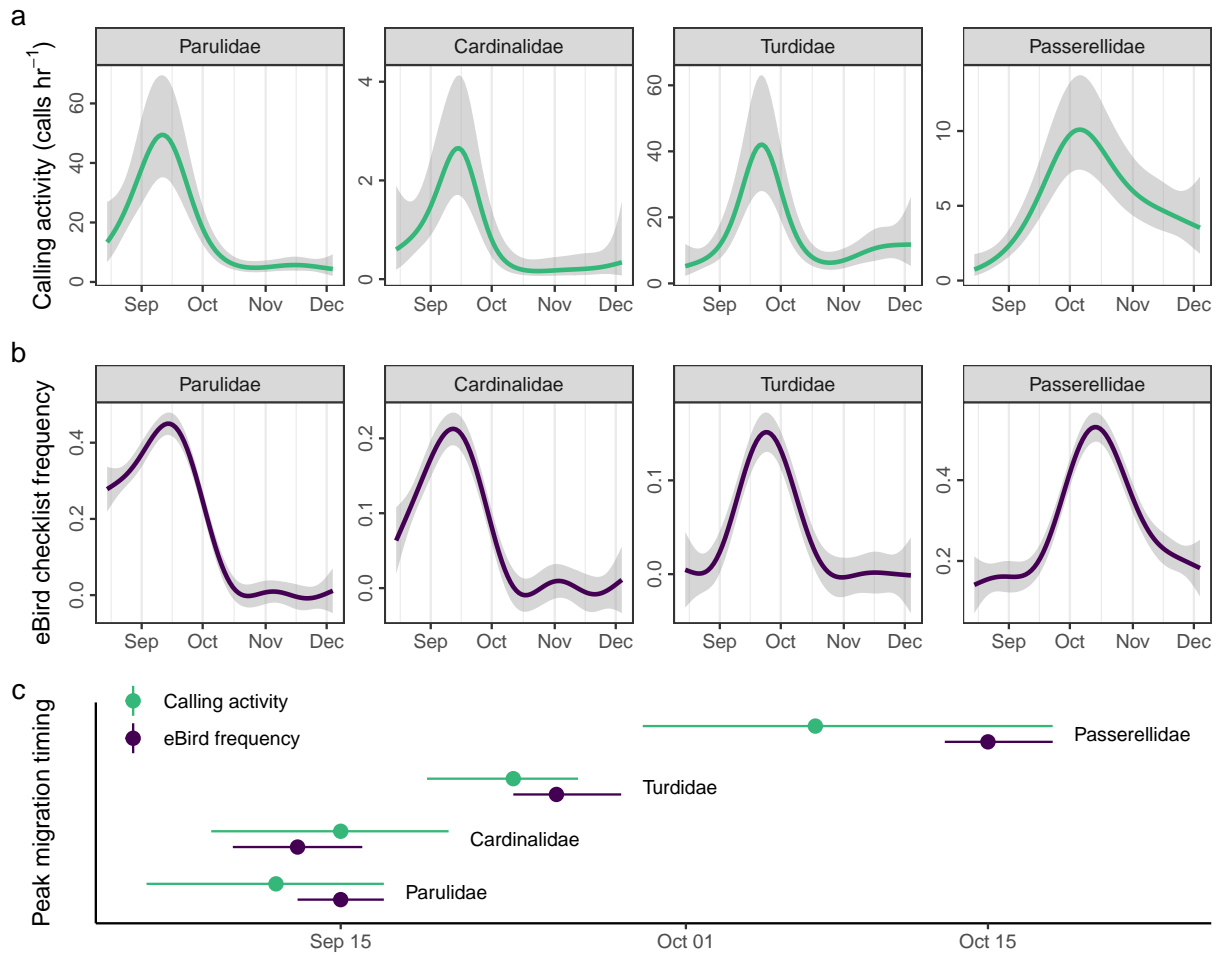


Figure 5: **Comparison of migration timing at the family level, estimated with acoustic and eBird data for fall 2015 in Tompkins County, NY.** (a) shows nightly calling activity with GAM smooths. (b) shows eBird checklist frequency (Tompkins County, NY) with GAM smooths. (c) compares estimates of peak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

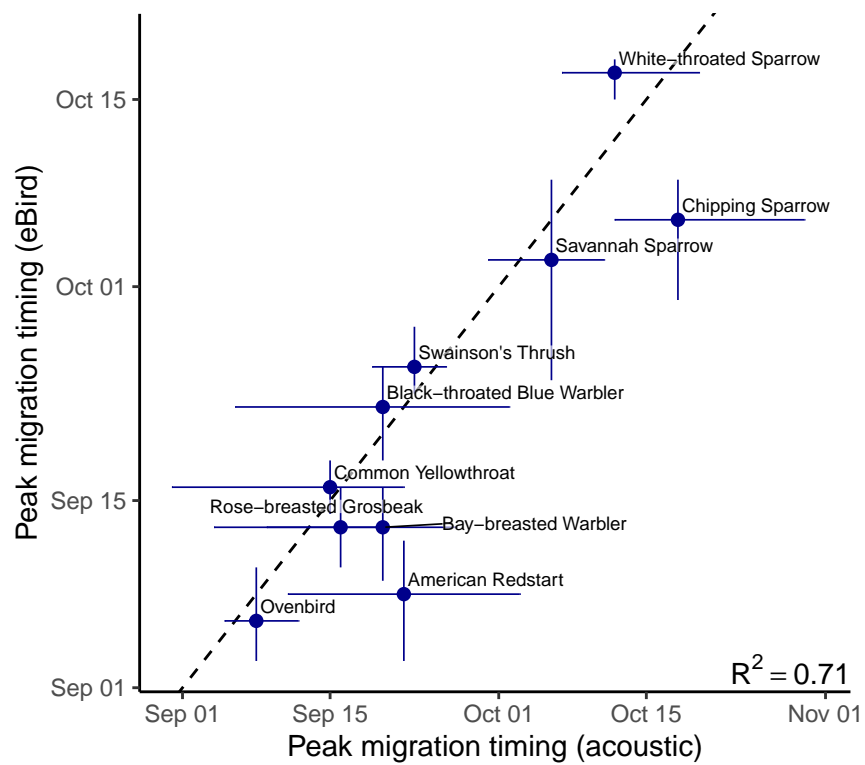


Figure 6: **Comparison of migration timing at the species level, estimated with acoustic and eBird data.** Each point represents one species, with confidence bars showing 95% credible intervals for acoustic and eBird estimates (fall 2015, Tompkins County, NY). The dashed line is the identity line; when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

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

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

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

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

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

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

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

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

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

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

Data Availability Statement

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

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Conflict of Interest Statement

The authors have no conflicts of interest to declare.

Author Contributions

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

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Supporting Information

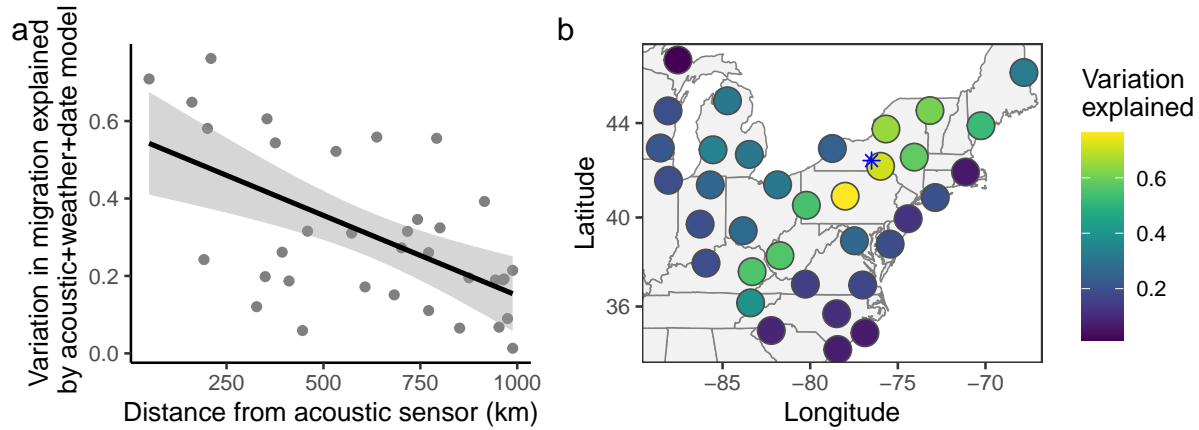


Figure S1: **Acoustic and weather information content degrades with distance.** (a) shows the performance of a model containing acoustic and weather information when predicting migration passage at radar stations at varying distances from the acoustic sensor. Line is a loess smoother. (b) shows the same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