

RESEARCH ARTICLE

Quantifying nocturnal bird migration using acoustics: opportunities and challenges

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Abstract

Acoustic recordings have emerged as a promising tool to monitor nocturnal bird migration, as it can uniquely provide species-level detection of migratory movements under the darkness of the night sky. This study explores the use of acoustics to quantify nocturnal bird migration across Europe, a region where research on the topic remains relatively sparse. We examine three migration intensity measures derived from acoustic recordings, that is, nocturnal flight call rates, nocturnal flight passage rates and species diversity, in the French Pyrenees in 2021 and 2022. To assess the effectiveness of these acoustic measurements, we compare them with migratory traffic rates estimated by a dedicated bird radar at three taxonomic levels: all birds, passerines and thrushes. We also test if weather conditions influence these relationships and whether combining acoustic data from multiple simultaneous sites improve the predictive performance. Nocturnal flight passage rates, that is, the number of estimated passing birds independent of call abundance, outperformed predictions using species diversity or nocturnal flight call rates. The predictive accuracy of the acoustics data increased with taxonomic detail: predicting thrush migration using acoustics was far more accurate ($R^2 = 63\%$) than for passerines ($R^2 = 29\%$) or birds in general ($R^2 = 27\%$). Prediction using simultaneous acoustics measurements from several sites strongly reduced the uncertainty of the quantification. We did not find any evidence that weather conditions affected the predictive performance of the acoustics data. Accurate, automated monitoring of migratory flows is crucial as many bird species face steep population declines. Acoustic monitoring offers valuable species-specific insights, making it a powerful tool for nocturnal bird migration studies. This study advances the integration of acoustic methods into bird monitoring by testing their benefits and limitations and provides recommendations and guidelines to enhance the effectiveness of future studies using acoustic data.

Introduction

With migratory bird populations declining, climate change accelerating and human–wildlife conflicts increasing, accurate quantification and forecasting of bird migration patterns is critical. About 2.1 billion passerine and near-passerine birds migrate from Europe to Africa each autumn (Hahn et al., 2009). As most of these birds

migrate at night (McLaren et al., 2018), their movements mostly go unnoticed. Nocturnal bird migration has remained relatively understudied compared to diurnal movements (Mukhin et al., 2009). With impactful changes to critical migratory stopover sites (Studds et al., 2017), urban expansion and increasing evidence of migratory bird disorientation due to light pollution (Adams et al., 2021; Burt et al., 2023; Gaston et al., 2013;

Winger et al., 2019), quantifying nocturnal bird migration is now ever more urgent.

Several methods are specifically designed to study the movements of migratory birds in the night sky. Moon-watching and thermal-imaging camera have provided valuable insights into nocturnal bird movements (Bridge et al., 2024; Gauthreaux Jr & Livingston, 2006). Radar in particular, however, has emerged as an important tool for quantifying nocturnal bird migration over the past few decades, with applications ranging from local (Hirschhofer et al., 2024) to (cross-)national (Kranstauber et al., 2023) and continental scales (Dokter et al., 2018; Nilsson et al., 2019). So far, radar methods are notoriously limited in providing taxonomic information (Hüppop et al., 2019).

In contrast, acoustic monitoring does provide species-specific information on nocturnally migrating birds through recording of their flight calls (Evans, 2005; Evans & Mellinger, 1999; Farnsworth, 2005; Graber et al., 1960; Osterhaus et al., 2025; Ross et al., 2023), but the capabilities and boundaries of using acoustics to quantify nocturnal bird migration have yet to be thoroughly assessed. So far, studies in the Nearctic region (Farnsworth et al., 2004; Gagnon et al., 2010; Horton, Shriver, & Buler, 2015; Larkin et al., 2002; Osterhaus et al., 2024; Van Doren et al., 2024) and the Palearctic region (Giuntini et al., 2024; Weisshaupt et al., 2024) have shown mixed results regarding the strength of the relationship between acoustic and radar-based estimates of bird migration, with correlations ranging from 0% to approximately 70%. A recent paper by Van Doren et al. (2023) suggested that up to 57% of the overall variation in post-breeding nocturnal bird migration fluxes at a site in Northeast USA (estimated using Doppler weather radar) could be explained with the acoustic recordings from five devices located at about 45 km away from the weather radar location. Nearctic warblers (e.g. *Parulidae*) are well known for emitting nocturnal flight calls (Farnsworth, 2007; Lanzone et al., 2009), while Palearctic warblers (e.g. *Sylviidae*, *Acrocephalidae*, *Phylloscopidae*) are thought to be mostly silent during migration (Robb, 2018; Weisshaupt et al., 2024). These hemispheric disparities could influence the effectiveness of acoustic methods to quantify bird migration (Farnsworth, 2005). Consequently, acoustic monitoring might be less useful to quantify overall bird migration in such regions. This, however, does not necessarily need be: if overall bird movements are consistently proportional across time to those of species that do vocalize, the acoustic recordings of the latter could still be a viable predictor of overall bird migration.

Next to geographical considerations, methodological choices in the acquisition and processing of acoustic data may also affect the potential of acoustics to quantify bird

migration. Many studies, for example, derive call activity from the acoustic data, that is, the mean number of calls per hour (Farnsworth et al., 2004; Larkin et al., 2002; Van Doren et al., 2023). The equipment and environmental variables associated with an acoustic monitoring station, along with the method used to interpret calling data, affect the number of individuals detected (Evans & Rosenberg, 2000). Yet, other variables may provide similarly useful or additional information, such as species diversity and nocturnal flight passage rates, that is, the frequency of distinct acoustic timing detected, where each timing corresponds to identifiable calls from one or more individuals of the same species. A new flight passage is defined when the interval between two species-specific nocturnal flight calls is sufficiently long to indicate distinct individual(s). This interval, which varies by species, typically ranges from one to five minutes. Passive acoustic monitoring systems can detect most bird sounds at distances of up to 250 or even 500 meters (Evans & Mellinger, 1999; Larkin et al., 2002; Winiarska et al., 2024). Given the limited detection range of acoustic recorders compared to dedicated vertical radars, deploying multiple acoustic devices simultaneously over a given range could provide complementary information, thus enabling more precise bird migration flux estimates.

The magnitude and timing of nocturnal bird migration is partly determined by weather conditions (Haest et al., 2020; Van Doren & Horton, 2018). Birds generally prefer migrating on warm days with favorable weather conditions, which typically include light to moderate tailwinds and little to no precipitation (Åkesson & Hedenström, 2000; Bozó et al., 2018). More importantly for bird migration monitoring using acoustics, the altitudinal flight behavior of birds also changes in response to weather conditions. In the presence of adverse surface winds, birds fly higher up to locate more favorable wind conditions (Aurbach et al., 2018; Liechti, 2006). Migratory birds typically also steer clear of colder layers (Kemp et al., 2013). Moreover, weather conditions also affect migratory call rates (Horton et al., 2015), although the exact relationships remain poorly understood. Next to the effects on migratory bird behavior, atmospheric conditions also influence the technical detection capability of acoustics (Guibard et al., 2022; Horton, Stepanian, et al., 2015). Clearly, there are many possible pathways of how weather might impact the predictive performance of acoustic recordings, and an in-depth understanding is required to adjust for the effect under certain conditions. To enhance the effectiveness of passive acoustic monitoring, it is crucial to further develop its framework by integrating detection areas (Winiarska et al., 2024) and accounting for environmental factors such as weather conditions, topography and sound source characteristics (e.g. frequency, amplitude).

Here, we explore the capabilities and limits of using acoustics for the quantification of nocturnal bird migration by experimenting along several of the current gradients of uncertainty. We (1) investigated the capabilities of 3 acoustics-derived variables, that is, nocturnal flight call, nocturnal flight passage and species diversity, to quantify nocturnal bird migration in Europe as derived by a dedicated vertical radar, that is, over a ground area of 1 km² and at altitudes ranging from 50 to 1000 m above ground level (agl). We filtered acoustic data to focus on three taxonomic levels identified by radar, that is, birds, passerines and thrushes, the latter being one of the primary nocturnal flight passerine families detected by acoustics along the East Atlantic flyway. We did this to investigate the potential of acoustics to quantify migratory movements at different taxonomic levels. We also (2) tested to which extent local weather conditions influence the performance of acoustic parameters to predict nocturnal migration. And (3), we checked how combining the data of multiple simultaneous acoustic surveys affects the overall performance of acoustics to predict nocturnal bird migration. Due to their comparatively low cost and relative ease of deployment in remote areas, acoustic devices are widely regarded as a promising tool to monitor nocturnal bird migration. With this study, we aim to clarify under which conditions and with which methods, acoustic recordings can indeed be successfully used to analyze the scale of nighttime avian migration.

Materials and Methods

Acoustic data

We recorded nocturnal flight calls during post-breeding migration in 2021 and 2022 in southwest France (Fig. 1) using passive acoustic recorders (SM4 Wildlife Acoustics)

equipped with two microphones. From 1 August to 31 October, 2021, the recorders were deployed to Luxe-Sumberraute (43.344° N, −1.068° W, 116 m asl), Port-Larrau (42.973° N, −0.988° W, 1562 m asl), Organ-bidexka (43.036° N, −1.019° W, 1247 m asl), Roncevaux (43.021° N, −1.324° W, 1035 m asl), the Soulor pass (42.960° N, −0.265° W, 1443 m asl), Trona (43.028° N, −1.354° W, 1180 m asl) and La Quillane (42.549° N, 2.110° W, 408 m asl). From 29 July to 4 November 2022, recordings were made in Luxe-Sumberraute only. Post-breeding migration of migratory birds typically occurs from August to November in this region (Lawrence et al., 2022), so our time of recording (and radar measurements), hence, measured activity during at least 72% of the overall post-breeding migratory period. The recordings were made continuously each night from sunset to sunrise (16-bit WAV file recording; sample rate: 32 kHz; gain: 126 dB SPL). In total, we surveyed around 6656 hours.

The microphones of SM4 Wildlife Acoustics recorders have a hyper-cardioid sensitivity and are designed to have acute directional sensitivity in the range of 2,000–10,000 Hz. This range corresponds to the acoustic frequency of most nocturnal migratory bird calls in Europe (Pelikan & Robb, 2021). The acoustic recordings were analyzed manually in Audacity (3.1.3) by looking at spectrogram windows. (Fast Fourier transformation; Blackman type of window; window size 21.5 Hz; 25 seconds interval; frequency range: 500–10,000 Hz). Every single or series of species calls within a short interval of time (from a few seconds to five minutes depending on the species) was identified as a flight passage. For each passage, we identified the species, scored the certainty of the identification as ‘certain’, ‘probable’ or ‘possible’ and counted the number of calls. We retained only the

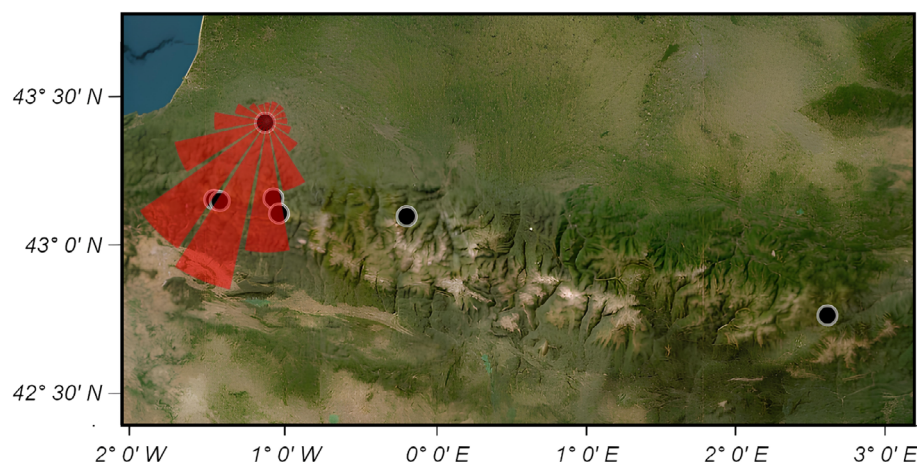


Figure 1. Locations of the acoustic sensors (black dots) and the BirdScan MR1 radar (dark red dot). The red directional rose shows the distribution of bird flight directions.

samples for which the species identification was either ‘certain’ or ‘probable’, accounting for 97% and 2% of the overall detected passages. For passerines, 98% were classified as certain and 1% as probable, while for Turdidae, more than 99% were identified as certain. For each night, we calculated three acoustic variables to describe nocturnal migration: (1) nocturnal flight passage rate, that is, the mean number of flight passages per hour, (2) nocturnal flight call rate, that is, the mean number of calls per hour and (3) nocturnal species diversity, that is, the number of species detected over a 7-day period centered on the target date. For the latter, we used a 7-night period instead of a single night to increase the chances of also capturing rare or infrequently vocalizing species and hence get a better estimate of the likely migratory species diversity during a phenological time window (Shaw et al., 2022). The choice of the rather high number of nights was to ensure acoustic detectability of species phenology, especially for the single-site analyses. During times of strong winds or rain, the extraction of nocturnal flight calls from the spectrograms was not possible. These times were marked as blind times and totaled to 8% of the entire monitoring period. To calculate the nightly acoustic activity during nights with blind times, we scaled the acoustic activity to cover the full night. This process was also replicated for all conceivable combinations of acoustic sites, resulting in average rates of nocturnal flight passage, and nocturnal flight calling, as well as metrics measuring species diversity across three taxonomic tiers: all bird species, passerines and thrushes of the genus *Turdus*. In Western Europe, the *Turdus* genus contains six migratory species. There are about 67 and 169 afro-palearctic migrant passerines and birds (excluding seabirds) migrating between the western Palearctic and Africa South of the Sahara (Newton, 2023). About 320 bird species migrate within France (Dupuy & Sallé, 2022).

Radar data

We set up a vertical-looking radar (BirdScan MR1 radar, software v1.7.0.4) in Luxe-Sumberraute (Fig. 1) to estimate nocturnal bird migration above the radar. The BirdScan MR1 radar is an X-band (9.4 GHz, 3.2 cm wavelength) pulse radar. It is equipped with a vertical-looking horn antenna that rotates with a 2° nutation on its vertical axis. For the purposes of this study, the radar operated in short pulse mode, featuring a pulse length of 65 ns, a pulse rate frequency of 1800 Hz and a range resolution of approximately 7.5 m. As a result, the radar has an estimated detection range from 50 m up to 1000 m for most bird species (Schmid et al., 2019; Weisshaupt et al., 2023).

When a bird (or any flying object) traverses the radar beam, it generates an echo signature characterized by a variation in echo intensity over time (Schmid et al., 2019). From each of these echoes, over 200 variables are extracted that are related to the main flight characteristics (e.g. direction, altitude, speed, wingbeat frequency and size). A dataset of annotated radar echo samples (Haest et al., 2021) is then used to train a Random Forest classifier and automatically classify each object into several categories, including various subgroups of birds (e.g. ‘Swift type’, ‘Passerine type’ and ‘Large bird’) (Schmid et al., 2019; Zaugg et al., 2008). Because of limited data quality when a bird flies close to the edge of the beam, certain features, for example, flight directions, cannot always be estimated. In our dataset, flight directions were estimated for about 64% of the radar echoes.

To eliminate part of the noise caused by movements of local birds, all data of birds flying toward the north ([0–90°] – [270–360°] azimuth) were removed from the dataset (i.e. 15% of the radar echoes). We used the ‘birdscanR’ R package (Haest et al., 2023) to estimate Migration Traffic Rates (MTR; in birds per hour per kilometer). We calculated nightly migration traffic rates for: (1) birds, (2) passerines and (3) thrushes (*Turdus* genus) from 50 up to 1000 m above the radar for each 50 m range increment (i.e. for 19 altitudinal ranges). We excluded nights with radar blind times (e.g. due to rain or technical failures) exceeding 80% of the total nighttime (5% of the recorded nights). To generate the MTR of ‘thrushes’ from the radar data, we selected the ‘Passerine type’ samples with wing flapping frequencies between 8 and 12 Hz (Bruderer et al., 2010; Cochran et al., 2008; Giuntini et al., 2024). The radar operated concurrently with the acoustic recordings in 2021 and 2022 but did not register any data between 24 and 29 September 2022 due to a technical failure.

Weather data

We gathered meteorological data from the Luxe-Sumberraute site using the ECMWF ERA5 reanalysis dataset (Hersbach et al., 2020) via the cdsapi 0.6.1 Python package (ECMWF, n.d.). We extracted hourly averages of the North-South and East-West wind components (m/s) and air temperature (°C) at five pressure levels (900, 925, 950, 975 and 1000 hPa) during the nights. Additionally, we also retrieved hourly total cloud cover (%) and cloud base height (m). The study focuses on meteorological conditions within an altitude range of 50 to 1000 meters agl. In the absence of clouds, or if the height of the clouds was greater than 1000 meters agl, the cloud base

height was set to the maximum height of the study window, that is, 1000 meters agl. All variables were averaged by night to match the temporal resolution of the acoustic and radar data. North-South (m/s) and East-West wind components (m/s) were converted into the proportion of tailwind using the ‘*NCEP.Tailwind*’ function of the RNCEP package (Chapman et al., 2011; Kemp et al., 2012). We did this using the median value of all radar-estimated bird flight directions (i.e., 206.02°) as the estimated direction of bird migration. Due to limitations in acoustic detection and radar blinding during rain, which cumulatively affects about 9% of the observed period, we did not analyze the effect of precipitation.

Assessing the performance of single-site acoustic recordings to quantify nocturnal migration of birds, passerines and thrushes

To determine to which extent acoustic data can accurately quantify nocturnal migration of birds, passerines and thrushes, we modeled the radar-estimated migration traffic rates using five different combinations of the acoustic parameters, that is, using: (1) nocturnal flight call rates; (2) nocturnal flight passage rates; (3) nocturnal species diversity; (4) nocturnal species diversity, flight call rates and their interaction; and (5) nocturnal species diversity, flight passage rates and their interaction. We used negative binomial models (because of the presence of overdispersion) with a Poisson distribution (link = log) from the ‘MASS’ R package (Ripley et al., 2024). Prior to modeling, nocturnal flight passage and flight call rates were log-transformed (i.e. we used log–log regression) because they were highly skewed and heteroscedastic, and we expect the relationship between the two count variables (radar and acoustic migration traffic) to be multiplicative, that is, changes in the nocturnal flight passage rates and nocturnal flight call rates should result in proportional changes in radar-estimated migration traffic rates (Wooldrige, 2016). The two models with interaction between nocturnal flight call or passage rates and species diversity were included to test whether calling behavior changes in response to the presence of other species (Coppinger et al., 2020). Prior to modeling, migration traffic rates were rounded to the nearest integer to align with the integer count data required by the negative binomial distribution.

The radar migration traffic rates across nights showed a high autocorrelation at lag 1 (Fig. S1). To avoid inflation of R^2 values due to this autocorrelation, we assessed the predictive power of the acoustics using temporally blocked cross-validation with a test block size of 2, with no overlap and a buffer of 1 day on each side of the test block (Roberts et al., 2017). For each test block, the model is trained on the rest of the data, but excluding the 2 days around

the test block, and predictions are made for the test block. We repeated this until predictions were made for each of the data points that were not on the edges of a continuous time block. Model performance was then assessed using the adjusted R^2 (Miles, 2005). We did this for all three taxonomic scales, that is, birds, passerines, thrushes. To investigate the potential range of acoustic detection, we built nocturnal flight call rate models for the migration traffic rates of all altitudinal ranges between 50 and 1,000 m agl, with 50 m increments.

Assessing the effect of weather on the predictive power of acoustics for nocturnal migration

To test the effect of weather conditions on the relationship between radar migration traffic rates and the acoustic parameters, that is, nocturnal flight passage rates and nocturnal flight call rate, and species diversity, we added the weather variables as interaction terms to the models with the acoustics variables as predictors. We did this for the three weather variables separately: total cloud cover, wind assistance and temperature. We again did this for each of the taxonomic scales, that is, birds, passerines, thrushes. We present both original and Holm–Bonferroni corrected p -values for this analysis to avoid false conclusions due to multiple hypothesis testing.

Assessing whether multiple simultaneous acoustic measurements can improve the quantification of nocturnal migration

To determine whether increasing the number of simultaneous acoustic measurements increases the predictive power of acoustics, we compared the adjusted R^2 values and coefficients of the models predicting the radar migration traffic rates at Luxe-Sumberraute using all possible combinations of the seven acoustic datasets. We did this again for all three taxonomic scales, that is, birds, passerines and thrushes. Because except for the Luxe-Sumberraute site, we only had acoustic data from the post-breeding migration of 2021, this analysis was limited to this period. We used the same block cross-validation procedure and model specifications as for the performance assessment in the single-site analysis.

Results

Community compositions of the birds, passerines and thrushes in the acoustic and radar data

During the post-breeding migration of 2021 and 2022, the microphone set up at Luxe-Sumberraute detected

nocturnal acoustic activity of 43 migratory species over 161 nights, totaling 38,872 calls and 4,451 passages. Across all 7 sites, 75 migratory species were registered (201,062 calls and 16,906 passages). Passerines accounted for 43% of the species diversity, 34% of the calls and 85% of the passages. We identified five thrush species: Song Thrush (*Turdus philomelos*), Redwing (*Turdus iliacus*), Common Blackbird (*Turdus merula*), Ring Ouzel (*Turdus torquatus*) and Mistle Thrush (*Turdus viscivorus*). While representing only 7% of the overall species diversity, those five taxa accounted for 27% and 72% of the recorded nocturnal calls and passages, respectively. Thrushes were the most abundant family detected by nocturnal flight passages, followed by *Ardeidae* (7%) and *Muscicapidae* (5%). In contrast, Palearctic warblers, including *Sylviidae*, *Phylloscopidae* and *Acrocephalidae* families, showed very low acoustic detection rates, representing less than 1% of the recorded flight passages, with only three species documented. In 2021, the peak of the acoustic detection at Luxe-Sumberraute occurred on 9 October for all birds (11 birds per hour, Fig. S2), but on 7 October when considering either passerines or thrushes (10 passerines per hour; 10 thrushes per hour). In 2022, the peak occurred on 4 October for all birds and passerines (16 birds per hour; 16 passerines per hour, Fig. S3), but on 30 October for thrushes (13 thrushes per hour; Fig. S4).

In the radar data, the migration peaks were detected on 8 October 2021 for all taxonomic categories, (4,128 birds, 2,494 passerines and 1,750 thrushes per hour per kilometer) and on 25 October 2022 (4,444 birds, 2,808 passerines and 1,359 thrushes per hour per kilometer). Passerines and thrushes accounted for 61% and 16% of the overall migratory bird flow detected by the radar, respectively.

Prediction of the nocturnal migration of birds, passerines and thrushes, using single-site acoustic recordings

Nocturnal acoustic call rate predictions performed best for radar migration traffic rates of birds and passerines within the 50–1000 m agl altitudinal range and for thrushes between 50 and 450 m agl (Fig. 2A). Model performance for predictions of radar migration traffic rates stabilized for altitudinal ranges of birds, passerines and thrushes above 400 m agl (i.e. the adjusted R^2 varied with less than 1% above 400 m). Because of this, we only included models with the radar migration traffic rates from 50 to 1000 m agl in further analyses. The predictive ability of the acoustic data increased with increasing taxonomic detail. Nocturnal flight passage rates explained 27% of the variability in bird migration traffic rates, 30% for passerines and 47% for thrush migration traffic

(Fig. 2B and C). Nocturnal flight passage rates emerged as the most effective single predictor for estimating migration traffic, outperforming both nocturnal flight call rates and the nocturnal species diversity variable by 11% and 17%, respectively, in explaining the adjusted variance for thrush MTR estimates (Fig. 2B). For the prediction of thrush migration, the two models that included interaction between passage or call rates and species diversity, outperformed the models with a single acoustic prediction parameter, with an adjusted R^2 of 58% for the nocturnal flight call rates and nocturnal species diversity interaction model and of 63% for the nocturnal flight passage rates and nocturnal species diversity interaction model (Fig. 2B and D). For broader taxonomic scales, that is, passerines and all bird species, interaction models underperformed models based on the single acoustic variable of nocturnal flight passage rates. (Fig. 2B).

Effects of weather on the power to predict nocturnal migration with acoustics

We found little to no support for an effect of weather on the relationship between radar estimates of bird migration (50 to 1000 m agl) and acoustics (Tables 1, S3 and S4). The meteorological interaction with the lowest p -value was mean nighttime temperature $\times$ nocturnal diversity of passerines, with a Holm-corrected p -value equal to 0.08. We found no evidence for an effect of wind assistance or total cloud cover on the relationship between any of the acoustic parameters and radar-estimated bird migration (Holm-corrected p -values were all higher than 0.27). For cloud base height, the p -values for the interaction term with the acoustic variables were all higher than 0.10 (Tables S3 and S4). The coefficient values for all interactions were, furthermore, all lower than 0.10 (Tables 1, S3 and S4), further suggesting a lack of influence on the strength of the relationship between acoustics parameters and radar-based estimates of bird migration traffic rates.

Predictive performance using multiple simultaneous acoustic measurements

The predictive performance varied strongly when we used a single acoustic recorder (Fig. 3A). The median adjusted R^2 value using nocturnal flight passage rates from single acoustic sites ($N = 7$) was 21%, with a gap of 35% between the highest and lowest adjusted R^2 values (Fig. 3A). Using acoustic recordings from multiple sites simultaneously reduced the uncertainty in our model predictions as well as estimate coefficients (Fig. 3B and D). The median adjusted R^2 value for nocturnal bird flight passage rates trained simultaneously on the data from six acoustic sites ($N = 7$) was 28%, with a gap of only 6%

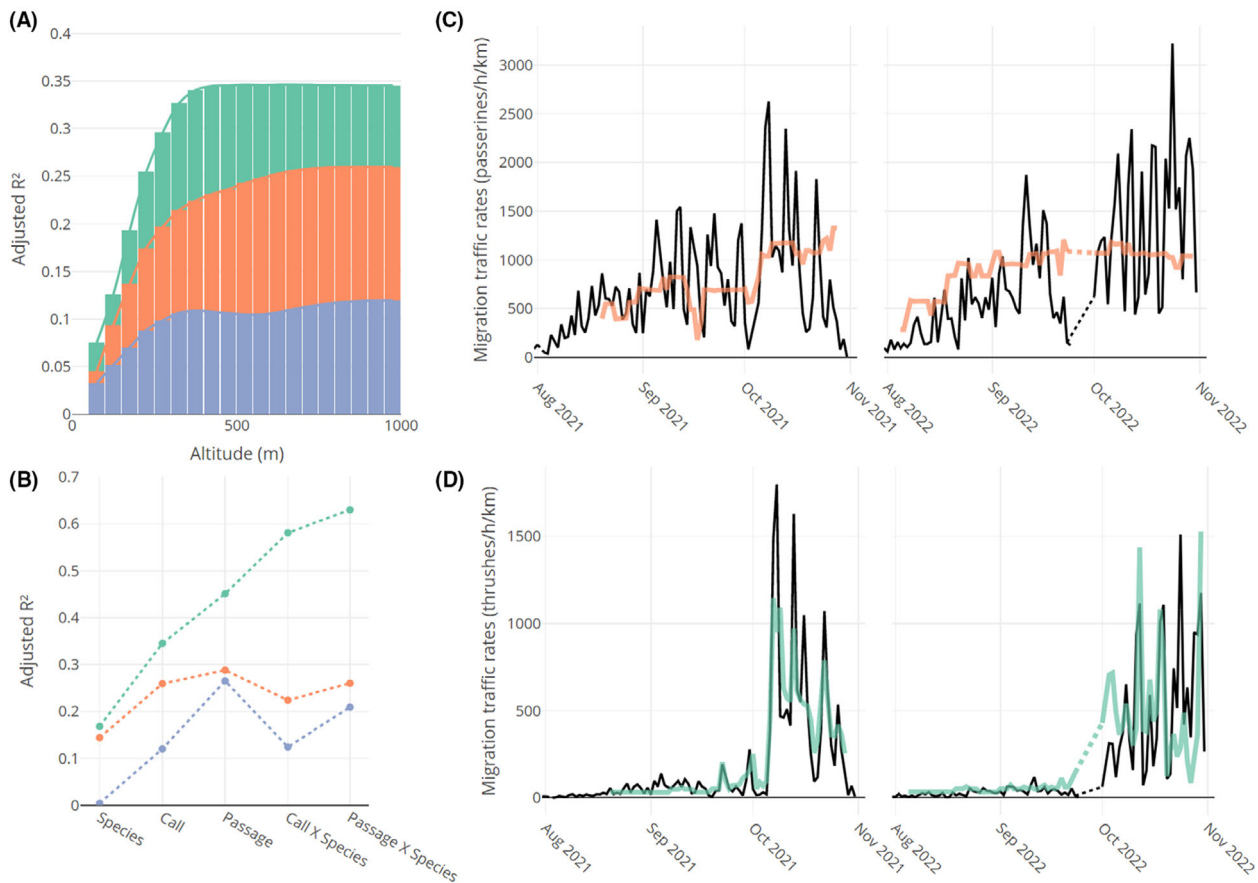


Figure 2. Predictive performance of the models using acoustic parameters to quantify bird (blue), passerine (red) and thrush (green) migration, as measured by radar. (A) Adjusted R^2 values for the prediction of incrementally increasing altitudinal ranges of the radar migration traffic rates using nocturnal flight call rates. (B) Adjusted R^2 values for the five models using different combinations of the acoustic parameters to estimate radar-derived migration traffic rates. (C) Time series of passerine migration traffic rates as measured by radar and model predictions (in red) using acoustic species diversity as the only predictor (adjusted $R^2 = 0.16$). (D) Time series of thrush migration traffic rates as measured by radar and model predictions (in green) using nocturnal flight passage rates, species diversity and their interaction as predictors (adjusted $R^2 = 0.63$).

Table 1. Effect sizes, p -values and Holm-corrected p -values of weather (i.e. temperature, total cloud cover, cloud base height, wind assistance) and nocturnal species diversity interaction terms for the prediction of radar-based migration traffic rates of birds, passerines and thrushes in Luxe-Sumberraute.

	Species × Temperature	Species × Total cloud cover	Species × Cloud base height	Species × Wind assistance
Birds				
Coefficient	−3.15 e-03	−5.26 e-04	1.49 e-05	−7.20 e-02
p -value	0.49	0.45	0.75	0.27
Holm p -value	0.98	0.90	1.00	0.69
Passerines				
Coefficient	1.44 e-02	2.20 e-04	3.73 e-05	−9.29 e-03
p -value	0.03	0.81	0.57	0.33
Holm p -value	0.08	1.00	1.00	0.66
Thrushes				
Coefficient	−1.05 e-02	1.38 e-03	−8.62 e-05	−6.06 e-03
p -value	0.40	0.42	0.50	0.75
Holm p -value	0.72	0.42	0.50	1.00

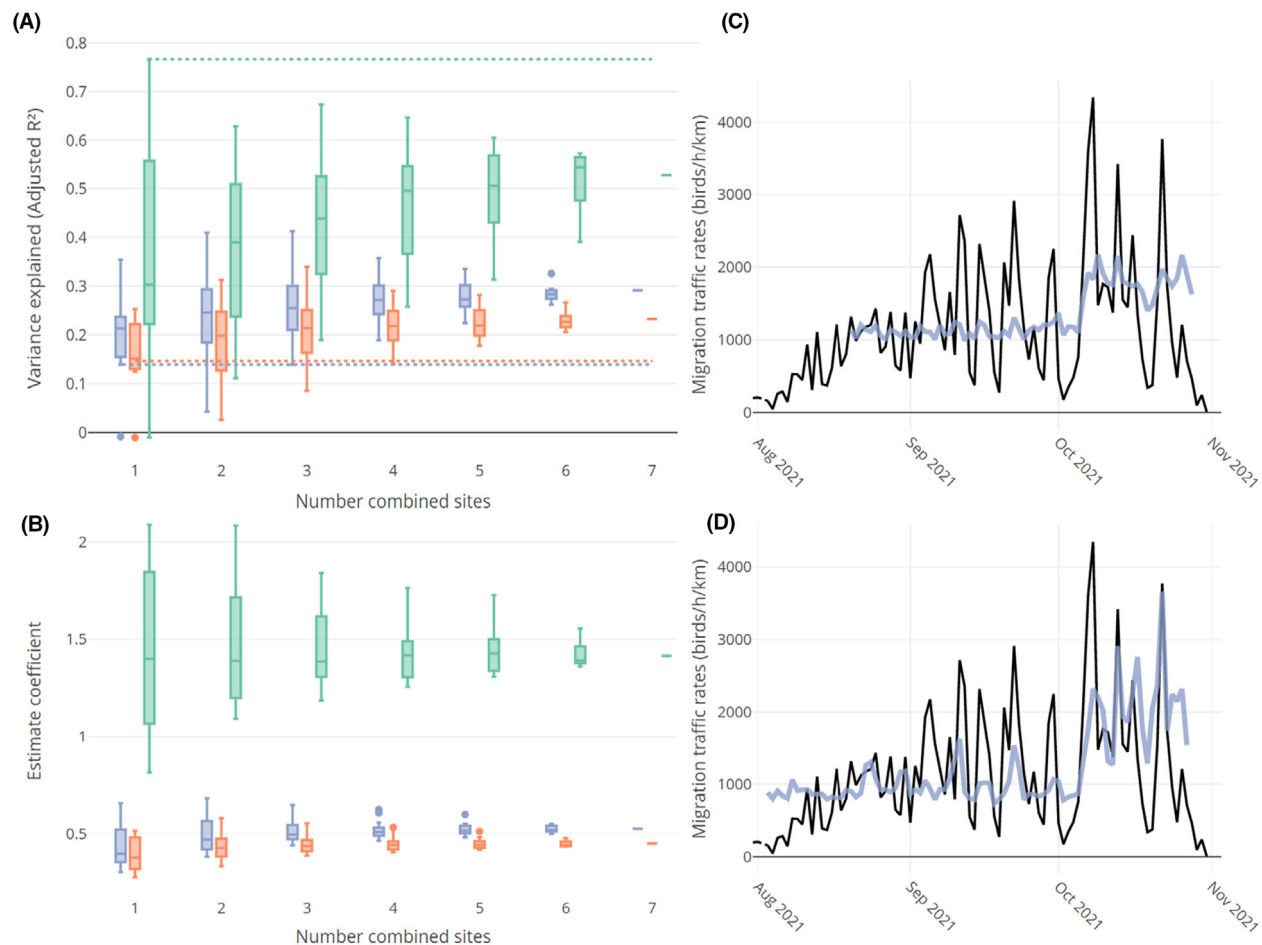


Figure 3. (A) Predictive performance and variation thereof to quantify post-breeding bird migration traffic rates (as measured by radar) using nocturnal flight passage rates from an increasing number of distinct geographical locations and (B) coefficients of the bird flight passage rates variable. Values for birds are in blue, in red for passerines and in green for thrushes. The dotted lines represent the performance of bird flight passage rate models trained with the Luxe-Sumberraute (i.e. the location of the radar) acoustic data only. (C) Migration traffic rates as measured by radar (black) and predictions (blue) for a model trained on the Luxe-Sumberraute acoustic data only ($\text{Adjusted } R^2 = 0.14$) and (D) on the acoustic information from seven simultaneous acoustic sites ($\text{Adjusted } R^2 = 0.29$).

between the highest and lowest adjusted R^2 values (Fig. 3A). For all models, the use of several simultaneous sites improved the median value of the adjusted R^2 and reduced the uncertainty (Fig. S5).

Discussion

In this study, we explored the strengths and weaknesses of using acoustic methods to quantify nocturnal bird migration. From the three different acoustic variables, we tested, nocturnal flight passage rates, which measure bird acoustic activity regardless of numbers of individuals or call abundance, was the single most effective factor for the quantification of nocturnal bird migration, questioning the appropriateness of the more commonly used bird

call rates. The predictive accuracy of the acoustics data increased with taxonomic detail. Predictions were far more accurate (R^2 up to 63%) for thrushes, a family known for vocalizing strongly during nocturnal migration, than it was for passerines (R^2 up to 29%) or birds in general (R^2 up to 27%). We also showed that using simultaneous acoustics measurements from several sites lowers the uncertainty of the quantification. We also tested whether weather conditions affected the predictive performance of the acoustics data because of changes in migratory behavior or in the range detection of the acoustics recordings but did not find any support for this. Perhaps surprisingly, the performance of the acoustics did also not decrease when quantifying incrementally higher (altitudinal) migration.

The predictive performance of nocturnal flight call rates to estimate migration traffic rates was rather limited when we used recordings from a single site, with median R^2 values of 14% for all birds, 19% for passerines and 39% for thrushes (Fig. S5), but improved to 20%, 28% and 63%, respectively, when we used data from multiple sites. These results seem somewhat in contrast to those of a recent study in the US (Van Doren et al., 2023), in which multi-site acoustically measured call rates from eleven target passerines could predict weather radar-based post-breeding bird migration traffic rates with an R^2 value of 57%. Part of the difference in performance may arise from the fact that we used a more restrictive temporal blocking cross-validation (Roberts et al., 2017) for the calculation of the predictive R^2 values. However, it is also very likely to reflect differences in calling behavior of the migratory bird communities detected at both locations, as exemplified by the large increase in performance when we targeted the very vocal group of thrushes. The migratory bird species community in Europe is indeed thought to contain proportionally much less species that emit (frequent) nocturnal flight calls than is the case in North America (Farnsworth, 2005). The disproportionate high percentage of nocturnal call (27%) and passage rates (72%) by the five thrush species (amounting to only 7% of the overall species diversity) in our acoustic dataset provides further support for this hypothesis. Our results, hence, corroborate those of a recent European study in Finland, which also showed rather limited correlations between acoustic bird passage rates and weather radar estimates of overall bird migration (Weissaupt et al., 2024), highlighting the importance of considering geographical context when using acoustic recordings for the prediction of nocturnal bird migration. In regions in which the proportion of the migratory species community that emit migratory calls is rather low, the accuracy of using acoustics to quantify bird migration beyond the frequently calling species especially warrants explicit testing or integration with additional information sources. These gaps also suggest that substantial variation has not yet been captured, making it difficult to generalize results.

Many studies that have used acoustics to predict nocturnal bird migration have used nocturnal flight call rates as the acoustic measure of bird migration intensity (Farnsworth et al., 2004; Gagnon et al., 2010; Horton, Shriver, & Buler, 2015; Larkin et al., 2002; Strand et al., 2023; Van Doren et al., 2024). Our predictions based on bird passage rates, however, consistently outperformed those based on bird call rates, with the adjusted R^2 for nocturnal flight passage rates being 15%, 3% and 11% higher for birds, passerines and thrushes, respectively (Fig. 1). Given the high variation in nocturnal flight call abundance between species (Farnsworth, 2005), this result

is perhaps not surprising. In our dataset, for instance, we estimated that Common cranes (*Grus grus*) call about 225 times per passage and Song thrushes (*Turdus philomelos*) on average only 5 times. These results strongly suggest that bird passage rates are the most accurate single acoustic variable to quantify bird migration traffic. Thus, when human resources permit in current monitoring systems of migratory birds, it would be advisable to derive bird passage rates instead of bird call rates. If automated acoustic call processing software developers also focus efforts on the accurate derivation of bird passage rates, this would substantially boost the usefulness of acoustics for the quantification of bird migration in regions with lower percentages of vocal species.

We found very little to no support for an effect of weather, that is, temperature, cloud cover, cloud base height and wind assistance on the predictive power of acoustics for bird, passerine or thrush migration. This suggests that, regardless of the weather conditions (but excluding times of rain or heavy winds), acoustic recordings on the ground provide similar estimates of migratory traffic rates between 50 and 1000 m agl, and both changes in migratory bird behavior and recording capabilities due to weather do not affect the predictive ability. Moon phase and moonlight intensity were also considered in our analysis but ultimately removed, as they were not significant in measuring migration timing rates (MTR). We used ERA5 (Hersbach et al., 2020) weather data from a single $0.25 \times 0.25^\circ$ grid cell in this study. ERA5 provides simulated data generated using numerical weather prediction models that provide very useful information for large-scale studies, but are perhaps not the best approach to accurately study the effects of local weather intricacies at a single site. Hence, unraveling the influence of weather on the ability of acoustics to quantify bird migration warrants further studies that use dedicated, locally captured weather data.

We manually extracted the species call data from the acoustic data. For larger-scale applications, automated extraction of individual bird features from acoustics, including species identification, will be key. This, however, lies very much within reach, with current developments for automated extraction of bird migration features from acoustic recordings continuously and rapidly improving the output quality (Van Doren et al., 2024). Our results show that for species that are vocally active during migratory flight, quantification using acoustics could indeed yield highly effective predictors of migration traffic (Fig. 2). Furthermore, using multiple simultaneous acoustic recordings at several sites stabilized the predictive performance by reducing its uncertainty (Figs. 3 and S5). The latter result is similar to the findings of studies using acoustics to estimate local bird densities in a more general

setting (Pérez-Granados & Traba, 2021). Our acoustic sampling locations were not specifically selected to test the limits of predictive performance of multi-site measurements. Some sites were in fact up to 250 km away from the radar location (Fig. 1). To truly verify the potential and limits of using multi-site acoustic recordings for the quantification of nocturnal bird migration, future studies should use an acoustic sampling scheme designed for this purpose, for example, a repeated circular sampling scheme with recorders at increasing distances.

Given the documented decline in the population of many migratory bird species (Bairlein, 2016; Vickery et al., 2023), accurate quantification of their migratory flows is imperative. Acoustic methods present several advantages to do so (e.g. species-level identification, low cost, easy to use in remote locations). In this study, we have explicitly explored many of the possible advantages and constraints of using acoustic methods to quantify nocturnal bird migration, resulting in the following set of specific recommendations and guidelines for future studies. We have shown that targeting the right selection of species given a regional context is paramount to the quality of the prediction, as is the choice of the acoustic variable (i.e. nocturnal flight passage rate). When possible, using several microphones located at different locations within the target region is also likely to produce more stable estimates. With further insights into the effects of meteorological parameters on calling behaviors, such as increasing acoustic vocal activity due to light pollution (Cabrera-Cruz et al., 2018; Gillings & Scott, 2021), and nocturnal flight calls detection ranges, we are confident that an efficient, generalized method for studying bird migration through acoustics should emerge in the near future.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supinfo S1.

Data S1.