Report

Current Biology

Social associations across species during nocturnal bird migration

Highlights

- Migrating songbirds associate socially with other species during nighttime flights
- Associations are stronger among species with similar calls and flight speeds
- Social information could play an underrecognized role in nocturnal bird migration

Authors

Benjamin M. Van Doren,
Joely G. DeSimone, Josh A. Firth,
Friederike Hillemann, Zach Gayk,
Emily Cohen, Andrew Farnsworth

Correspondence

vandoren@illinois.edu

In brief

Songbirds have long been thought to undertake migration independently. Van Doren et al. find that songbirds associate with other species during migratory flights, connections that may be maintained by vocal signals and flight behavior. Social information could play a larger role in nocturnal bird migration than currently understood.

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Report

Social associations across species during nocturnal bird migration

Benjamin M. Van Doren,[1,2,7,8,*] **Joely G. DeSimone,**[3] **Josh A. Firth,**[4] **Friederike Hillemann,**[5] **Zach Gayk,**[1] **Emily Cohen,**[3] **and Andrew Farnsworth**[2,6]

[1]University of Illinois at Urbana-Champaign, Department of Natural Resources and Environmental Sciences, Urbana, IL 61801, USA
[2]Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA
[3]University of Maryland Center for Environmental Science, Appalachian Laboratory, Frostburg, MD 21532, USA
[4]University of Leeds, Leeds LS2 9JT, UK
[5]Durham University, Department of Psychology, Durham DH1 3LE, UK
[6]Actions@EBMF, New York, NY 10006, USA
[7]Bluesky: migrationbio.bsky.social
[8]Lead contact
*Correspondence: vandoren@illinois.edu

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SUMMARY

An emerging frontier in ecology explores how organisms integrate social information into movement behavior and the extent to which information exchange occurs across species boundaries.[1–3] Most migratory landbirds are thought to undertake nocturnal migratory flights independently, guided by endogenous programs and individual experience.[4,5] Little research has addressed the potential for social information exchange aloft during nocturnal migration, but social influences that aid navigation, orientation, or survival could be valuable during high-risk migration periods.[1,2,6–8] We captured audio of >18,000 h of nocturnal bird migration and used deep learning to extract >175,000 in-flight vocalizations of 27 species of North American landbirds.[9–12] We used vocalizations to test whether migrating birds distribute non-randomly relative to other species in flight, accounting for migration phenology, geography, and other non-social factors. We found that migrants engaged in distinct associations with an average of 2.7 ± 1.9 SD other species. Social associations were stronger among species with similar wing morphologies and vocalizations. These results suggest that vocal signals maintain in-flight associations that are structured by flight speed and behavior.[11,13,14] For small-bodied and short-lived bird species, transient social associations could play an important role in migratory decision-making by supplementing endogenous or experiential information sources.[15–17] This research provides the first quantitative evidence of interspecific social associations during nocturnal bird migration, supporting recent calls to rethink songbird migration with a social lens.[2] Substantial recent declines in bird populations[18,19] may diminish the frequency and strength of social associations during migration, with currently unknown consequences for populations.

RESULTS

The migratory journeys of diverse taxa frequently overlap in space and time.[17] Bird migration is a prime example, with hundreds of millions of individuals of dozens of species often in the air on a given night.[17,20] Though existing research on navigation and decision-making during songbird migration has often emphasized the role of endogenous timing and navigation programs, opportunities for social information exchange occur frequently during stopover[15,21–23] and migratory flight, when many taxa actively vocalize.[10,11,24] In-flight vocalizations may be important for communicating social information en route,[11,13,14,25–27] and social information could aid in navigational decision-making, finding appropriate stopover habitat, or identifying other individuals with which to form mixed-species foraging flocks during stopover. In other contexts, social information use among heterospecifics has been demonstrated empirically (e.g., nest site choice,[28] terrestrial migration stopover,[15] and foraging[29,30]). However, it is unknown what information might be exchanged or used during nocturnal migratory flights.[17]

Here, we investigate whether nocturnally migrating bird species form consistent social associations during migratory flights. We use recordings of in-flight vocalizations to characterize patterns of species' spatial and temporal proximity and test whether species' distributions aloft differ from a null expectation based on non-social factors, including shared phenology and geography. Significant differences from the null hypothesis would suggest an active behavior driving social association among species. We investigate the factors that explain any species associations, hypothesizing that species with similar migration routes, stopover habitats, morphologies, vocalizations, and evolutionary histories will be more likely to socially associate. Finally, we consider how social information exchange could be

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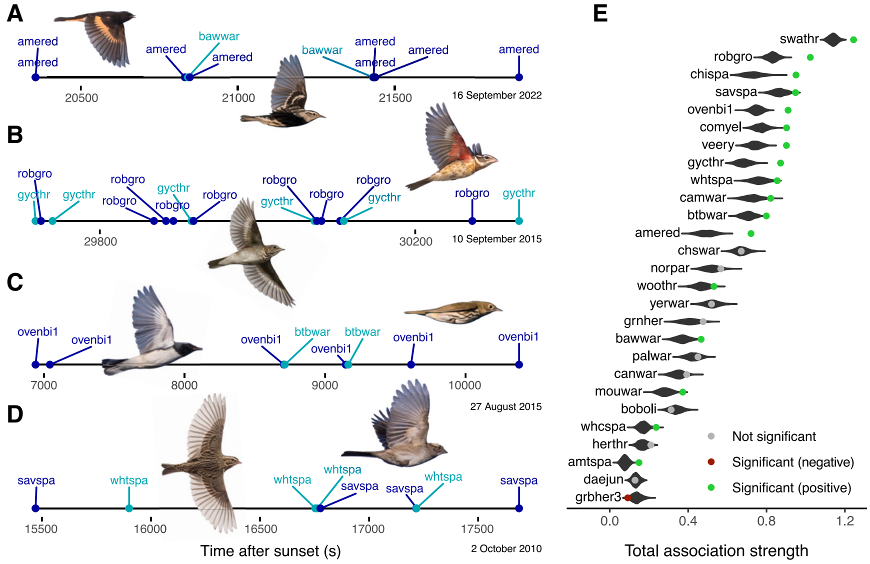

Figure 1. Example time series of detections during nocturnal migration and tests of social association strength

Photos from the Macaulay Library at the Cornell Lab of Ornithology.

(A) American Redstart (amered; ML112702211) and Black-and-white Warbler (bawwar; ML68301071).

(B) Gray-cheeked Thrush (gycthr; ML263074761) and Rose-breasted Grosbeak (robgro; ML356438721).

(C) Black-throated Blue Warbler (btbwar; ML260441631) and Ovenbird (ovenbi1; ML68440361).

(D) Savannah Sparrow (savspa; ML500164831) and White-throated Sparrow (whtspa; ML194675571).

(E) Tests of total association strength (weighted degree centrality) for social association network (30-s windows). Violin plots show null distribution, points show observed node strength, and statistical significance indicates that a species has a stronger or weaker observed node strength than expected under the null hypothesis. Green points indicate that the observed node strength is significantly greater than expected and that heterospecific attraction can be inferred. See Table S4 for explanation of species abbreviations.

an important contributor to the movement ecology of nocturnally migrating birds.

Songbirds associate with other species during migratory flights

We collected acoustic recordings of 18,308.08 h of autumn nocturnal bird migration (August to December) from 26 sites in eastern North America (Figure S1). We extracted vocalizations of migrating birds (hereafter "flight calls"[11,31]) from audio data using a deep learning model that we designed for this purpose,[12] and we manually reviewed species detections for accuracy to ensure data quality. We focused on 27 well-sampled species: 25 songbird species (order Passeriformes), plus two heron species (order Pelecaniformes), which we included to examine the potential for associations between songbirds and other orders. We constructed a network that captures the degree to which detections of different species occurred synchronously in the data stream conditional on species co-occurrence (hereafter "social association network"). Using custom network permutation tests, we evaluated whether the observed social association network differed from a null expectation that incorporated shared timing, geography, and other non-social factors that may contribute to network structure (Figure S2). The observed social association network was significantly non-random (network coefficient of variation $P_{30s} = 0$) (Figure S2). We quantified the overall tendency of each species to associate with other species during migratory flights, finding that 17 out of 27 species in the social association network showed significantly elevated total association strengths after accounting for non-social factors (Figure 1). For this study, we considered detections to occur synchronously if they occurred in the same 30-s time window, but we also tested networks constructed using 15-s and 60-s time windows and confirmed that the results were robust to the choice of window size (15-s social association: 17 of 27 significant; 60-s social association: 20 of 27 significant).

We assessed the statistical significance of social association for every species pair in the network using custom permutation tests that accounted for non-social factors that may contribute to network structure. Of 213 species pairs with >100 association opportunities assessed using 30-s time windows, 36 were statistically significant (Figure 2; Table S1). This result was consistent when using other window sizes (15 s: 35/215 pairs significant; 60 s: 35/210 pairs significant). For 30-s windows, species had a mean of 2.7 ± 1.9 SD significant association partners, and 23 of 36 significant associations were between two species of the same family (most commonly within the Parulidae). Although significant interfamilial associations were less frequent, those that did occur were of similar strength to intrafamilial associations (*t* test: $t = 0.4$, $df = 21.5$, $p = 0.69$).

Wing morphology and vocalization similarity explain social associations among species

We tested whether in-flight associations among species could be explained by phylogeny, spatiotemporal distribution, habitat preferences, social relationships during stopover, morphology, or vocalizations. We used nonparametric Mantel tests and again evaluated statistical significance using custom network permutations that accounted for non-social factors. The similarity of species' wing lengths and their vocalizations were statistically significant predictors of social association (Figure 3; Table 1). These relationships were robust to choice of window size and present using parametric and nonparametric matrix correlations (Table S2). These relationships were also present when excluding two large-bodied heron species and including only species in the order Passeriformes (Figures S3A and S3B; Table S2). Species relationships at stopover, phylogenetic relatedness, spatiotemporal overlap in species' migration routes, nonbreeding range overlap, and migration-period habitat relationships were not consistently associated with social association

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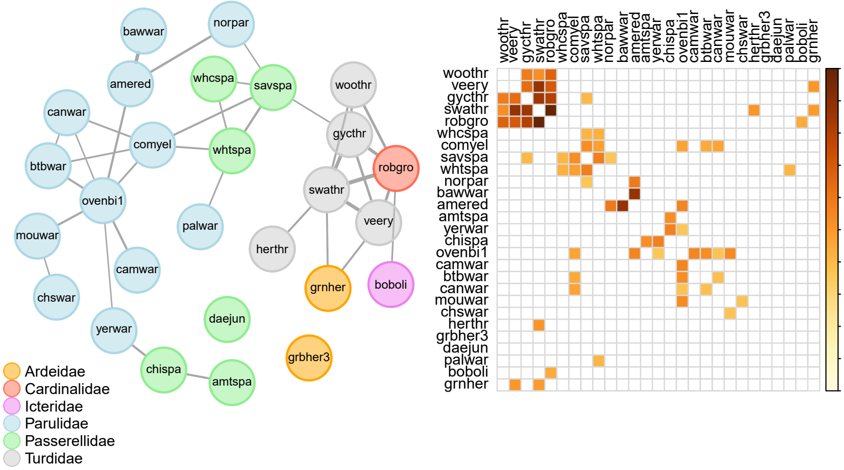

Figure 2. Significant social associations

Network diagram and heatmap show only statistically significant edges (30-s time windows). Heatmap values show association strength for each species pair. See Table S4 for explanation of species abbreviations.

See Figure S2 and Table S1.

(Figures S3C–S3G; Table 1), although stopover affiliation index, migration overlap, and non-breeding range overlap showed some support at other window sizes (Table S2).

DISCUSSION

Little is presently known about how organisms integrate interspecific information into behavioral decision-making, a topic at the cutting edge of ecology.[1,2,17,32] Songbirds migrate primarily at night and are typically thought to do so independently, without information contributions from other birds.[5] However, our results demonstrate that songbirds engage in interspecific social associations during nocturnal migratory flights. The majority of bird species studied showed significantly higher association strengths than expected under null models accounting for species co-occurrence and non-social factors, indicating that it is more likely for these species to occur with heterospecifics than expected by chance. Social associations were most frequent among species of the same family, particularly wood warblers in the family Parulidae, but significant interfamilial associations were also frequent and no less strong when present. In contrast, we did not find strong evidence of social associations across orders (e.g., between Passeriformes and Pelecaniformes).

Stronger social associations tended to occur between bird species with more similar wing lengths, but not closer phylogenetic relatedness, suggesting that flight speed may be important in structuring in-flight associations.[33] Over the course of hours-long migratory flights, individuals with similar flight speeds and altitudes may more easily maintain close proximity and sustain an association, whereas individuals with different flight behaviors are more likely to grow gradually apart, making any such associations ephemeral. Associations were also stronger among species with more similar vocalizations, a finding consistent with the hypothesis that flight calls are used to maintain multi-species associations during migratory flights.[9,14] These findings suggest the possibility that shared migratory behavior may be driving convergent evolution in acoustic signals across species.[13]

In contrast, we found no consistent evidence that fine-scale in-flight associations were linked to habitat preferences, geographic ranges, or species affiliations during diurnal stopovers. This result is surprising given evidence for heterospecific attraction in Palearctic birds, where playback of heterospecific vocalizations can cause migrating birds to land and initiate stopover.[34] Our results suggest that the interspecific relationships among migrants in the Americas reshuffle as they alternate between nocturnal aerial and diurnal terrestrial habitats, with variables related to flight behavior shaping in-flight relationships and variables related to foraging behavior shaping stopover relationships.[23] Previous work has connected vocalization similarity to migration range overlap,[13] but the lack of an association between geographic range and social association in our data suggests that spatial overlap may not be the primary driver of

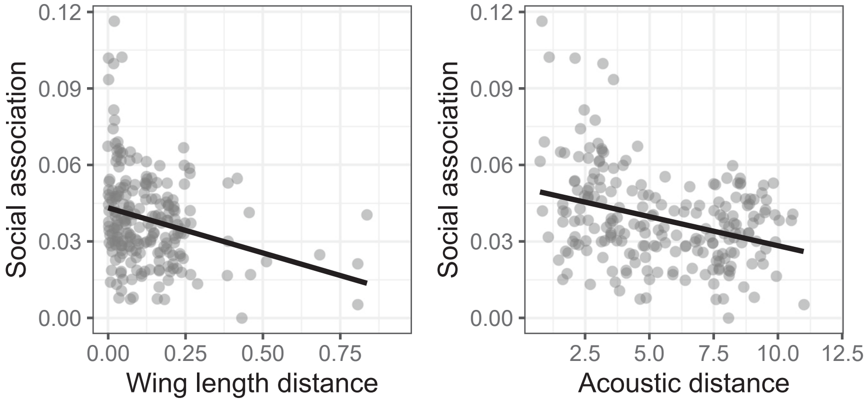

Figure 3. Scatterplots of statistically significant pairwise species relationships

Each point represents a species pair. y axis represents association strength for each species pair, and the x axes show pairwise phenotype distances. Best linear fit drawn to aid interpretation—refer to matrix correlations for coefficient estimates and statistical significance. Plots shown from data generated with 30-s time windows.

See Figure S3 and Table S2.

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Table 1. Nonparametric matrix correlations for the response variable of social association, based on 30-s time windows

Predictor	Correlation	p value	No. taxa
Stopover affiliation index	0.067	0.308	22
Phylogenetic similarity	0.090	0.899	27
Migration overlap	0.187	0.251	27
Non-breeding range overlap	0.131	0.251	27
Wing length distance	–0.252	0.000	27
Migration habitat similarity	0.081	0.162	27
Acoustic distance	–0.266	0.000	27

Each row corresponds to a single-predictor model. See Table S2.

associations aloft. Although we did not detect a strong spatial signal in our data, we advocate for exploring how social associations may vary across space and how an individual's social behavior is influenced by its spatial-social context.[35]

The importance of social information during migration

Our study provides important context for a growing body of evidence that the social information available to an individual may be an important and underappreciated contributor to migratory behavior.[2,3] The associations and vocalizations we detect during nocturnal bird migration may provide a conduit for information exchange. The use of social information during migration is well documented in some bird species, such as large-bodied cranes (Gruidae) and storks (Ciconiidae),[36–38] as well as other species that commonly form groups or flocks, such as terns (Laridae) and shorebirds (Charadriiformes).[6,7] In these species, conspecific social information is thought to be of particular importance for younger birds undertaking their first migrations.

Our results provide evidence that social information could also be transmitted during migration among small-bodied and short-lived bird species that are generally thought to undertake nocturnal migration independently.[5] Since these species do not learn their migration routes from their parents, social information could play an important role in supplementing information from the innate migratory program, especially for inexperienced birds. Such information could aid navigation, as has been demonstrated in large-bodied diurnal migrants, or be associated with habitat selection, stopover, or other factors. Flight calls may encode information about an individual, such as age and sex, as well as individual identity, which may allow birds to infer the flight direction of other individuals and facilitate the maintenance of group cohesion among both conspecifics and heterospecifics.[9,16,25,26]

Social behavior and information use exchange could take several forms, and our results provide a foundation for testing hypotheses about social influences on migratory behavior. We highlight several questions for future research, adapting those identified by Aikens et al.[2]: (1) What information might flight calls encode, and what can listening individuals learn from these signals? (2) Do individuals respond differently to flight calls over their lifetimes, as the balance shifts between individual experience and social information? (3) How do different migration characteristics, such as distance or complexity, affect how migrants use vocal information? (4) Do species that vocalize during migration show different patterns of migratory evolution? (5) How can vocalization data directly inform conservation and management, for example, to lessen the risk of fatal building collisions?[27]

Acoustics as a movement ecology tool

Bioacoustics is increasingly important for studying movement ecology. A study of this scope was made possible only through recent advances in machine learning that automate an otherwise laborious detection and identification process. Further work with acoustics promises to reveal more about associations among and within species, as well as the decision-making and conservation status of migratory birds. Our inferences drawn from acoustic monitoring will likely be influenced by factors that impact the vocalization rate of species and individuals, such as environmental conditions, social context, and individual traits.[11] Currently, it is not possible to distinguish individuals by call with a standard recording setup, which prevented us from investigating associations among conspecifics. However, recent evidence indicates that flight calls may encode individual identity information in at least some species,[25,26] which suggests that this may be possible as acoustic analysis methods improve. Distinguishing individuals is currently only possible using microphone arrays that allow calling birds' locations to be triangulated, but this technique requires significant logistical challenges to implement at scale.[39] Given our results, we would hypothesize that intraspecific social associations also occur during nocturnal migratory flights.[14] Finally, it is important to recognize that not all migratory species vocalize during migration.[10,11] Future work that integrates acoustic data with thermal imagery or small-scale radar data could provide a more holistic understanding of in-flight behavior during nocturnal migration.

Implications

The vocalizations given by birds during migratory flights provide a valuable resource for monitoring the movements and populations of migratory birds, studying their ecologies,[11] and even understanding anthropogenic hazards like light pollution.[27] Here, we demonstrate that flight calls provide a window onto a hidden network of interspecific associations. This study highlights the need for further investigation into the social context of animal migration. Recent work supports the important role of transient interspecific relationships during stopover,[23] and we propose that social relationships are also important during migratory flights. Given substantial declines in migratory bird populations,[18] it is likely that social associations during migration are diminishing, with unknown consequences. Any such density-dependent effects may be complex; a lack of social information might, for example, impede navigational decision-making, impact the duration and energy expenditure of migration, and increase mortality risk.[2,17] An understanding of these dynamics is essential to assessing and mitigating negative impacts on populations.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Benjamin Van Doren (vandoren@illinois.edu).

Materials availability

This study did not generate new, unique reagents.

Data and code availability

- Data have been deposited at Mendeley Data and are publicly available at (Mendeley Data: https://doi.org/10.17632/dxx5khdzjs.1) as of the date of publication.
- All original code has been deposited at Mendeley Data and is publicly available at (Mendeley Data: https://doi.org/10.17632/dxx5khdzjs.1) as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

B.M.V.D. conceived of the study, collected data, performed analysis, and wrote the initial manuscript draft. J.A.F., F.H., and J.D. shaped the data analysis. All authors contributed to the final written draft of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data and code	This paper	Mendeley Data: https://doi.org/10.17632/dxx5khdzjs.1
Software and algorithms		
R	https://www.r-project.org/	N/A
Nighthawk	https://github.com/bmvandoren/Nighthawk	N/A

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Acoustic data collection

We collected acoustic recordings of autumn nocturnal bird migration (1 August to 7 December) from 26 sites in eastern North America (Figure S1), encompassing 18308.08 hours of monitoring across 379 nights, with an average of 57.3 ± 34.6 SD nights of monitoring per recording station. The recording data come from three monitoring efforts: (Dataset 1) multi-station monitoring in central New York State during fall 2015 (BirdVox-Full-Season[40–42]); (Dataset 2) multi-station monitoring in southern New York State during fall 2010-2011;[43] and (Dataset 3) a 2000-km recording transect across the Appalachian mountain region in eastern North America during fall 2022. Recording locations are shown in Figure S1, and recording data and hardware are summarized in Table S3. Although the hardware differed by monitoring effort, all units were designed and deployed specifically to record migrating birds' nocturnal flight calls. The likely maximum sampling range of the sensors was 300-600 m above ground level, depending on species call characteristics and ambient conditions.[31,44,45]

METHOD DETAILS

Acoustic data processing

To extract nocturnal flight calls from audio data, we used Nighthawk, a machine learning tool designed for detecting and classifying nocturnal flight calls.[12] The Nighthawk core model[12] is freely available,[46] and it has been validated on diverse test data, including on the BirdVox-Full-Season dataset (Dataset 1, above).[46] Performance on target datasets can be improved by conducting additional model training with the dataset in question, termed "fine-tuning"[12]. We therefore fine-tuned models on Datasets 2 and 3 to maximize model accuracy on those datasets. We manually screening a representative sample of audio data for flight calls and using this dataset to fine-tune Nighthawk.[12] For Dataset 2, we used existing annotations.[43] For Dataset 3, which had not been previously analyzed, we randomly sampled 310 segments of audio each 10 minutes in duration (total 51.7 h; 0.8% of Dataset 3) and screened these for nocturnal flight calls. We then set aside one half of screened data for model fine-tuning and the other half for model validation.[12] Van Doren et al.[12] evaluated multiple fine-tuning approaches; we used the custom batch construction strategy described in that paper since it requires only one epoch of additional training while producing a model that performs very well on target data and original test data.

After fine-tuning, we ran Nighthawk on all data using the freely available Python utility.[46] For Dataset 1, we used the core model provided in the public package. For Datasets 2 and 3, we substituted in the corresponding fine-tuned model. We used the following important parameters when running the model:

- **–no-calibration**: do not apply default calibration parameters.
- **–threshold 50**: export all detections with a probability score of 0.50 or greater.
- **–ap-mask 0**: do not filter out taxa based on performance on the core Nighthawk test dataset.
- **–tax-output**: export outputs for each taxonomic level independently.

We performed data processing on Amazon Web Services to parallelize inference across thousands of CPU cores. We mapped each detection to time relative to nautical twilight, when the center of the sun is 12 degrees or more below the horizon. We retained detections occurring during the nocturnal period after nautical dusk or before nautical dawn, when any detected flight calls can confidently be attributed to individuals in active nocturnal migratory flight.

Nighthawk returns classifications at multiple taxonomic levels, including order, family, and species. Because we were focused on testing relationships among well-represented species, we only included detections at the species level for species with >250 detections across the dataset. Although our focus is on Passeriformes, we also included two nocturnal migrant species in the order Pelecaniformes to examine the potential for associations between passerines and other orders.

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Because our analysis relies on high quality detection data, we used a multi-step review process to ensure detection accuracy. First, we randomly sampled up to 200 detections per species per dataset and manually screened these detections for accuracy. We used the results to set confidence thresholds for each species in each dataset to target a precision of approximately 0.95 on all classes. After retaining detections with confidence scores above the corresponding thresholds, authors BMVD and AF manually reviewed all acoustic detections from the subset of 30-s time windows that included multiple taxa. In other words, we manually reviewed all data that contributed to any potential associations among species pairs. In total, we reviewed 64909 detections. We conservatively removed all detections with any ambiguity in species identity, primarily recordings with a low signal-to-noise ratio. In total, we removed 6538 detections (10.1% of those reviewed). After all filtering steps, our acoustic dataset comprised 177962 detections of flight calls from 27 species (Table S4; Figure 1).

Network generation: Fine co-occurrence networks

We used acoustic detections to construct networks of observed species co-occurrence in the acoustic temporal data stream. In these networks, stronger connections among species indicate that those species were recorded together more frequently during migratory flights. To construct networks, we split our acoustic data streams into independent, nonoverlapping 30-s windows and grouped species detected in the same 30-s window into "events." Although this choice was somewhat arbitrary, an interval of 30 s corresponds to a maximum linear distance of 450 m, assuming a bird's groundspeed of 15 ms^{-1}; we reasoned that migrating birds recorded in the same 30-s window would likely be close enough to hear one another and potentially exchange information. We quantified network connections from these 30-s events using the default Simple Ratio Index formula implemented in the get_network function in the R package asnipe.[47] For a given pair of species, the Simple Ratio Index is calculated by dividing the number of events (i.e. 30-s windows) in which both species occur by the number of events in which either one or both species occur. We also constructed networks using 15-s and 60-s windows to assess whether the results were sensitive to the choice of window length. Networks generated from different window sizes were very tightly correlated using Mantel correlations (30-s vs. 60-s: r = 0.99; 30-s vs. 15-s: r = 0.99). We refer to these networks as **fine co-occurrence networks** because they capture the degree to which vocalizations of each species pair occur close together in our data stream.

Network generation: Coarse co-occurrence network

The network connection strength among species in fine co-occurrence networks is partly a function of species' similarity in migration timing, geographic distributions, and other factors unrelated to social associations. We accounted for this by constructing an acoustic network as described above, but with events defined using longer 15-*minute* time windows. Rather than considering fine-scale social associations, this **coarse co-occurrence network** captures broader species co-occurrence in the dataset driven by shared seasonal timing, geography, and consistent behavioral patterns over the nocturnal period. See Figure S2.

Network generation: Social association networks

Because connections among species in fine co-occurrence networks may arise from factors that are unrelated to species' propensity to actively associate, we used the coarse co-occurrence network to control for these factors. The goal was to generate networks that explicitly captured the degree to which species' vocalizations occurred synchronously, independent of shared timing, geography, or other non-social factors. We calculated **social association networks** as follows: for each species pair, we subset the data to only the 15-minute time periods in which both species were detected. Then, we calculated the Simple Ratio Index on this subset using 30-s windows as described above. To ensure that our measures were reliable, we did not calculate social association for species pairs for which there were less than 100 15-minute windows in which the two species occurred (i.e. <100 association opportunities). After performing these calculations for all pairs of species, the resulting social association network captured the degree to which vocalizations of each species pair occur close together, *conditioned* on the time periods during which both species are detected (Figure S2). Because this metric is conditioned on species co-occurrence, these networks do not depend on seasonal migration timing or nocturnal vocalization patterns; they only quantify the degree of acoustic synchronicity among species pairs independent of broader temporal or geographic patterns. As above, we also generated social association networks for 15-s and 60-s window durations to assess whether our results were sensitive to the choice of window length. Networks generated from different window sizes were very tightly correlated using Mantel correlations (30-s vs. 60-s: r = 0.93; 30-s vs. 15-s: r = 0.94).

Generating network covariates

To test hypotheses about the drivers of species associations during migration, we generated seven covariates that summarize the similarity of each species pair in phylogeny, spatiotemporal distribution, habitat preferences, social relationships during stopover, morphology, and vocalization structure.

Phylogenetic relationships

We obtained a phylogenetic tree of the species included in our study using the R package clootl.[48] We used the extractTree function in that package to output a tree and used the cophenetic.phylo function in the R package ape[49] to convert the tree topology to pairwise phylogenetic distances for all species pairs. We used the inverse of these distance values as measures of phylogenetic similarity.

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Species geographic ranges

For each species pair, we calculated pairwise range overlap scores for their non-breeding ranges. We used species ranges modeled by eBird Status & Trends[50] to calculate pairwise overlap for each species pair. We used the eBird Status & Trends models accessible in the R package ebirdst (v. 2.2021.3).[51] We downloaded Status & Trends data for each species and used the load_ranges function to extract the modeled ranges. We then calculated the range overlap for each species pair by dividing the area of the intersection of the two ranges by the area of the union of the two ranges.

Migration overlap

We estimated the overall migration similarity for each species pair using a spatiotemporal measure of overlap in the species' geographic distribution during migration season. We extracted weekly 27x27 km relative abundance rasters for each species using the ebirdst package and subset these to the migration period for that species as defined by eBird in the package. For each species pair, we found the total number of cells where modeled relative abundance was greater than zero for both species, and we divided this by the total number of raster cells where relative abundance was greater than zero for either species. This resulted in a proportion of overlapping cells for each week. Finally, we took the mean weekly overlap proportion across all weeks of the migration periods. This resulted in a single proportion value for each species pair that captured the spatiotemporal overlap in their geographic distributions during the migration period.

Stopover habitat

To calculate the degree of similarity in the habitat preferences of each species pair during the migration season, we extracted weekly habitat associations from eBird Status & Trends data.[50] We filtered habitat association data to the migration period for each species using the migration period dates provided in the ebirdst package. Using all available habitat association characters, we used the dist function in R to calculate a pairwise distance matrix that captured the overall pairwise similarity in habitat associations for all species pairs.

Social affiliations during stopover

To assess migratory species' social networks at stopover sites, we used over half a million records of banded migratory birds collected during spring and fall migration seasons by Braddock Bay Bird Observatory (43.324, -77.717), Long Point Bird Observatory's banding stations at Old Cut (42.584, -80.398) and Breakwater (42.561, -80.284), Powdermill Avian Research Center (40.164, -79.268), and Michigan State Bird Observatory's Burke Lake banding station (42.812, -84.383). More details about these datasets are reported in DeSimone et al.[23]

Following that study,[23] we calculated species associations from the banding data using the Simple Ratio Index. Next, we calculated generalized affiliation indices by regressing the species associations against measures of temporal overlap, spatial overlap, and relative abundance. The standardized residuals of the regression are the generalized affiliation indices for each species pair. The affiliation indices quantify the degree to which two species associate after accounting for structural features of the data, including temporal overlap, spatial overlap, and relative abundance. We calculated fall affiliation indices separately for each site and averaged affiliation values across sites. We included only species with >100 fall captures.

Wing-length measurements

Because body morphology impacts flight behavior and could contribute to in-flight dynamics, we extracted wing-length measurements from the AVONET dataset[52] for each species. Wing length is associated with flight speed and flight style and may influence species' in-flight associations. For each species pair, we calculated the Euclidean distance between the base-10 logarithms of their wing lengths as a measure of the difference in wing length (hereafter "wing length distance").

Acoustic distance

It is possible that bird species with more acoustically similar flight calls may be more likely to interact during migration.[14] To evaluate this hypothesis, we calculated the acoustic distance of the vocalizations given by species in our dataset. We randomly sampled 200 vocalizations for each species from the expert-verified set of recordings used in[12] and selected recordings with sufficiently clean spectrograms for further analysis. We retained a mean of 61.1 ± 16.8 SD (range 13–89) vocalizations per species. We used Raven Pro 1.6[53] to manually draw bounding boxes around each call and used the spectro_analysis function in the R package warbleR[54] to extract a series of 26 spectrographic measurements. See warbleR documentation for a description of measurements. We summarized these measurements using a Principal Component Analysis (PCA function in R package FactoMineR[55]) and extracted the first 5 components, comprising 89.7% of total variance. We used the centroids of each species in multidimensional PCA space to generate a distance matrix (dist function in the base R package stats[56]) that describes acoustic distance among species. Smaller values indicate more similar vocalizations. An ordination plot of these species in PCA space for the first two principal components is show in Figure S4.

QUANTIFICATION AND STATISTICAL ANALYSIS

Generating null network distributions with permutations

To test the statistical significance of network parameters, including the strength of species connections in co-occurrence and social association networks, we generated null distributions of network parameters using custom permutations of the original data stream. See Table S4 for the sample size of detections for each of 27 species in the data stream. The permutation procedure was as follows: first, we divided acoustic detection data into 15-minute periods for each site and date. Then, *for each species* in each 15-minute period, we shifted the timing of all detections by a random time interval between 0–15 minutes. Each species present in the

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15-minute period was shifted by a different random interval, and all calls of that species in that period were shifted by the same amount. If the procedure shifted any detections further than the bounds of the 15-minute period, those detections were "wrapped around'' to the beginning of the period. In this way, each permuted time period maintained the same quantity and the same temporal structure of vocalizations of each species as the original dataset. This procedure randomly changed the degree to which different species' vocalizations occurred relative to other species, allowing us to test a null hypothesis of no association among species in vocalization patterns. After applying this permutation procedure independently to every 15-minute period in the dataset, we calculated co-occurrence and social association networks from the permuted data using the procedures described above. We repeated this procedure 1000 times, yielding 1000 null networks for 15-, 30-, and 60-s window sizes.

Testing for network randomness

We evaluated whether networks of co-occurrence and social association differed significantly from random. We calculated the network coefficient of variation by taking the standard deviation of the adjacency matrix and dividing it by the mean of the adjacency matrix. We performed this calculation for observed networks and for all permuted networks. If the observed coefficient of variation was greater than the 0.95 quantile of the corresponding null (permutation) distribution, we considered the network non-random at the $P<0.05$ level. Networks contained $n = 27$ species.

Testing for social associations among species

We evaluated the statistical significance of each species' ($n = 27$) connections with other species in networks using null distributions derived from the permuted networks. For each species, we quantified its overall tendency to occur with other species during migratory flights by summing the strength of all network connections between the focal species and other species, also known as the weighted degree centrality. Larger degree values indicate that a species shows stronger and/or more numerous connections to other species in the network. We compared total association strength values calculated from observed co-occurrence and social association networks to those calculated from the corresponding permuted networks. We considered a species to show statistically significant associations with other species if the observed total association strength for that species was greater than the 0.95 quantile of the corresponding null distribution derived from the permuted networks.

We assessed statistical significance for every species pair in co-occurrence and social association networks using the same procedure: we compared the connection strength for a given species pair with the null distribution of values derived from the corresponding null networks. We again assessed significance by comparing observed values to the corresponding null distribution. We corrected p-values for multiple testing using a false discovery rate correction with a false discovery rate of 0.05.

Explaining migrant associations

Finally, we tested whether in-flight associations among species could be explained by phylogeny, spatiotemporal distribution, habitat preferences, social relationships during stopover, morphology, or vocalization structure. We constructed single-predictor statistical models in which the response variable was social association. As described above, social association does not depend on seasonal migration timing or nocturnal vocalization patterns; it quantifies the degree of social association among species pairs independent of broader temporal or geographic patterns.

We evaluated statistical significance using a modification of the Mantel test procedure (mantel function in R package vegan[57]): for each predictor, we calculated the Mantel matrix correlation between that predictor and the social association matrix; then, we compared this observed statistic to the null distribution of test statistics obtained from our custom set of permuted social association networks. For each test, the p-value was the proportion of permuted networks that achieved a Mantel correlation equal to or more extreme than the observed statistic. To eliminate any bias from skewed data distributions, where outliers could exert a strong influence on the correlation value, we calculated Mantel statistics using the nonparametric Spearman rank correlation. For comparison, we also obtained results using the standard Pearson correlation. For the single-predictor case, the Pearson-based tests of statistical significance were equivalent to those obtained using Multiple Regression Quadratic Assignment Procedure (MRQAP) to regress predictor matrices on the response matrix, as recommended for networks,[58] using the mrqap.custom.null function in the R package asnipe.[47] The number of taxa in each model ranged between 22–27 and is reported for each model in Table 1; Table S2.

We elected to use a series of single-predictor models instead of multiple matrix regression for the following reasons: first, we did not have stopover affiliation data for all species, and this imbalance would have required removing those species from a multiple regression model and/or running multiple sets of models; second, we wanted to avoid collinearity among predictor variables from biasing coefficient estimates; third, we found matrix correlation statistics, which vary between -1 to 1, to be more easily interpretable than multiple regression coefficients, which are unbounded; and fourth, this allowed us to test our hypotheses using more robust nonparametric rank correlations.

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Supplemental Information

Social associations across species during nocturnal bird migration

Benjamin M. Van Doren, Joely G. DeSimone, Josh A. Firth, Friederike Hillemann, Zach Gayk, Emily Cohen, and Andrew Farnsworth

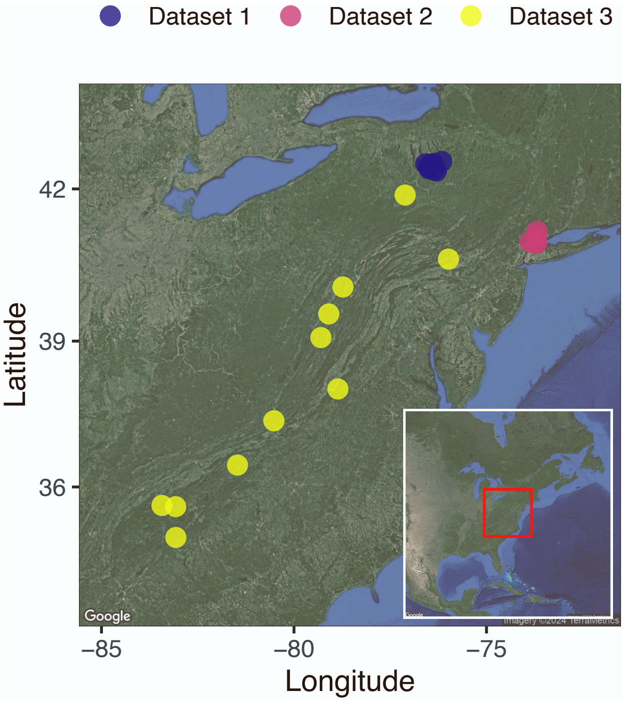

Figure S1: **Recording locations, Related to STAR Methods.** Red box in inset shows bounds of focal region.

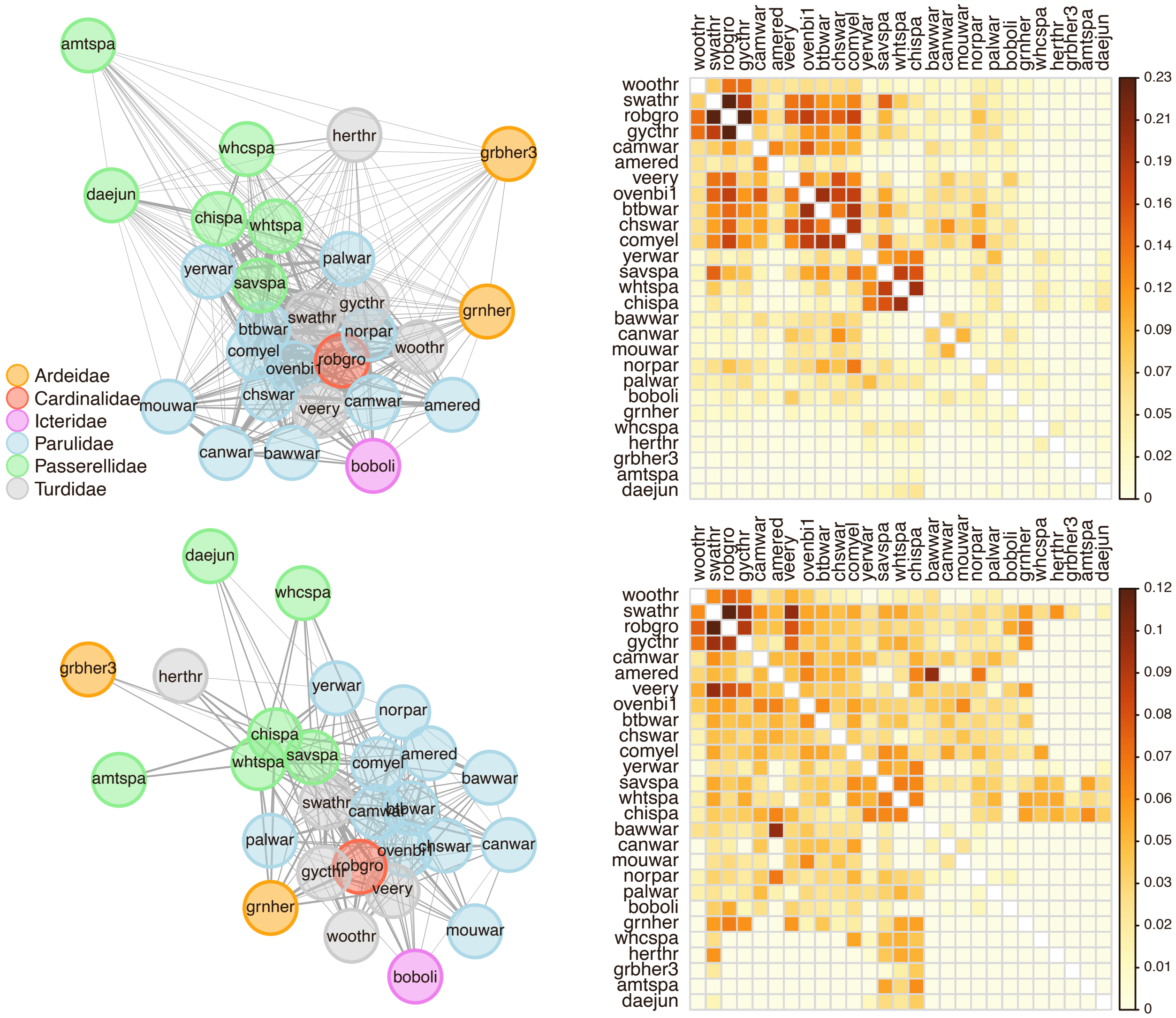

Figure S2: **Observed networks, Related to Figure 2 and STAR Methods.** (Upper) Observed coarse co-occurrence network. Species are ordered by hierarchical clustering on co-occurrence data. (Lower) Observed social association network based on 30-s time windows. Vertices are colored by family, and labels are species codes assigned by the eBird database. Edge weights and heatmaps show connection strength.

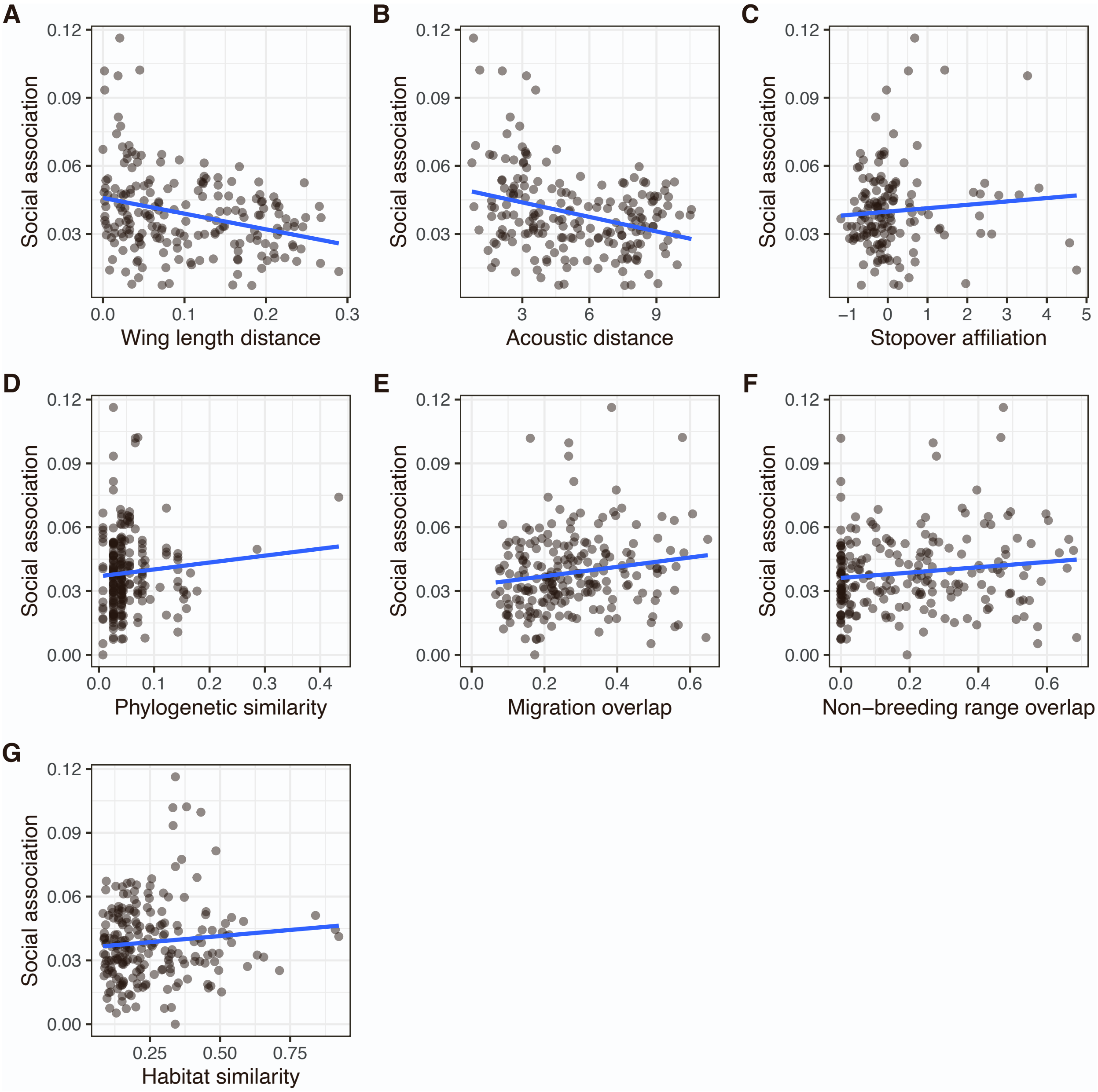

Figure S3: **Scatterplots of pairwise species relationships, Related to Figure 3.** (A,B) Statistically significant relationships for order Passeriformes. (C,D,E,F,G) Non-significant relationships for all species. Each point represents a species pair. Best fit line drawn to aid interpretation; refer to matrix correlations for coefficient estimates and statistical significance. Plots shown from data generated with 30-s time windows.

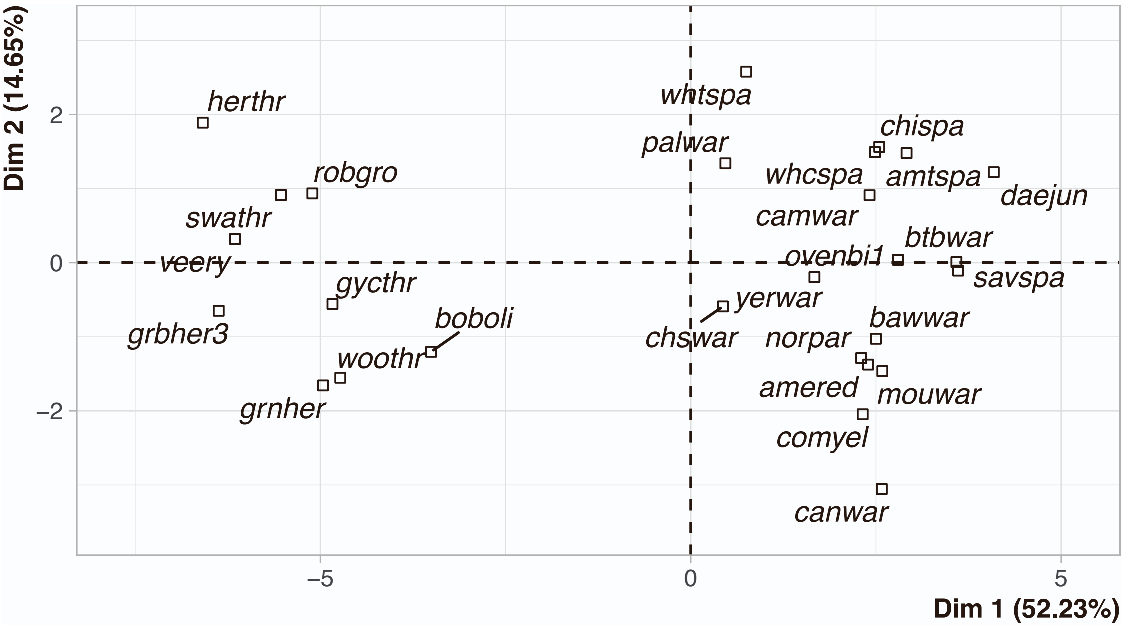

Figure S4: **Ordination from principal component analysis showing acoustic distance among species, Related to STAR Methods.** The scatterplot shows the centroids of each species in PCA space for the first two principal components

Species 1	Species 2	Family 1	Family 2	Social association	P-value
Swainson's Thrush	Rose-breasted Grosbeak	Turdidae	Cardinalidae	0.116	0.000
Black-and-white Warbler	American Redstart	Parulidae	Parulidae	0.102	0.000
Veery	Swainson's Thrush	Turdidae	Turdidae	0.102	0.000
Swainson's Thrush	Gray-cheeked Thrush	Turdidae	Turdidae	0.100	0.000
Rose-breasted Grosbeak	Gray-cheeked Thrush	Cardinalidae	Turdidae	0.093	0.000
Veery	Rose-breasted Grosbeak	Turdidae	Cardinalidae	0.081	0.000
Rose-breasted Grosbeak	Wood Thrush	Cardinalidae	Turdidae	0.077	0.000
Veery	Gray-cheeked Thrush	Turdidae	Turdidae	0.074	0.000
Northern Parula	American Redstart	Parulidae	Parulidae	0.069	0.027
Wood Thrush	Gray-cheeked Thrush	Turdidae	Turdidae	0.068	0.000
Savannah Sparrow	White-throated Sparrow	Passerellidae	Passerellidae	0.067	0.000
Yellow-rumped Warbler	Chipping Sparrow	Parulidae	Passerellidae	0.066	0.000
Ovenbird	American Redstart	Parulidae	Parulidae	0.065	0.000
Ovenbird	Cape May Warbler	Parulidae	Parulidae	0.065	0.000
Ovenbird	Mourning Warbler	Parulidae	Parulidae	0.063	0.000
Ovenbird	Black-throated Blue Warbler	Parulidae	Parulidae	0.062	0.000
Swainson's Thrush	Wood Thrush	Turdidae	Turdidae	0.062	0.000
American Tree Sparrow	Chipping Sparrow	Passerellidae	Passerellidae	0.061	0.000
Savannah Sparrow	Common Yellowthroat	Passerellidae	Parulidae	0.061	0.000
Swainson's Thrush	Hermit Thrush	Turdidae	Turdidae	0.059	0.000
Veery	Green Heron	Turdidae	Ardeidae	0.059	0.048
Swainson's Thrush	Green Heron	Turdidae	Ardeidae	0.057	0.021
Common Yellowthroat	White-throated Sparrow	Parulidae	Passerellidae	0.055	0.008
Ovenbird	Common Yellowthroat	Parulidae	Parulidae	0.054	0.000

Canada Warbler	Common Yellowthroat	Parulidae	Parulidae	0.054	0.000
Black-throated Blue Warbler	Common Yellowthroat	Parulidae	Parulidae	0.052	0.000
Rose-breasted Grosbeak	Bobolink	Cardinalidae	Icteridae	0.051	0.008
White-throated Sparrow	White-crowned Sparrow	Passerellidae	Passerellidae	0.050	0.008
White-throated Sparrow	Palm Warbler	Passerellidae	Parulidae	0.048	0.000
Savannah Sparrow	White-crowned Sparrow	Passerellidae	Passerellidae	0.048	0.016
Savannah Sparrow	Gray-cheeked Thrush	Passerellidae	Turdidae	0.047	0.021
Black-throated Blue Warbler	Canada Warbler	Parulidae	Parulidae	0.044	0.048
Ovenbird	Canada Warbler	Parulidae	Parulidae	0.044	0.027
Mourning Warbler	Chestnut-sided Warbler	Parulidae	Parulidae	0.043	0.039
Savannah Sparrow	Northern Parula	Passerellidae	Parulidae	0.043	0.021
Ovenbird	Yellow-rumped Warbler	Parulidae	Parulidae	0.042	0.048

Table S1: **Statistically significant pairwise species associations assessed using 30-second time windows, Related to Figure 2.** P-values have been adjusted using a false discovery rate correction.

Win.	Taxa	Type	Predictor	Correlation	P-value
15 s	22	Nonparametric	Stopover affiliation index	0.127	0.031
15 s	27	Nonparametric	Phylogenetic similarity	0.056	0.963
15 s	27	Nonparametric	Migration overlap	0.211	0.091
15 s	27	Nonparametric	Non-breeding range overlap	0.163	0.082
15 s	27	Nonparametric	Wing length distance	-0.252	0.000
15 s	27	Nonparametric	Migration habitat similarity	0.048	0.383
15 s	27	Nonparametric	Acoustic distance	-0.252	0.000
60 s	22	Nonparametric	Stopover affiliation index	0.036	0.652
60 s	27	Nonparametric	Phylogenetic similarity	0.013	1.000
60 s	27	Nonparametric	Migration overlap	0.241	0.045
60 s	27	Nonparametric	Non-breeding range overlap	0.175	0.043
60 s	27	Nonparametric	Wing length distance	-0.208	0.000
60 s	27	Nonparametric	Migration habitat similarity	0.081	0.273
60 s	27	Nonparametric	Acoustic distance	-0.206	0.000
30 s	22	Parametric (Pearson)	Stopover affiliation index	0.085	0.182
30 s	27	Parametric (Pearson)	Phylogenetic similarity	0.084	0.873
30 s	27	Parametric (Pearson)	Migration overlap	0.161	0.343
30 s	27	Parametric (Pearson)	Non-breeding range overlap	0.133	0.472
30 s	27	Parametric (Pearson)	Wing length distance	-0.261	0.000
30 s	27	Parametric (Pearson)	Migration habitat similarity	0.097	0.056
30 s	27	Parametric (Pearson)	Acoustic distance	-0.334	0.000
30 s	22	Nonparametric (Pass. only)	Stopover affiliation index	0.067	0.308
30 s	25	Nonparametric (Pass. only)	Phylogenetic similarity	0.089	0.941
30 s	25	Nonparametric (Pass. only)	Migration overlap	0.251	0.044
30 s	25	Nonparametric (Pass. only)	Non-breeding range overlap	0.188	0.044
30 s	25	Nonparametric (Pass. only)	Wing length distance	-0.273	0.000
30 s	25	Nonparametric (Pass. only)	Migration habitat similarity	0.058	0.375
30 s	25	Nonparametric (Pass. only)	Acoustic distance	-0.245	0.000

Table S2: **Matrix correlations for the response variable of social association for different model specifications, Related to Figure 3.** Each row corresponds to a single-predictor model. 'Win.' column refers to audio window length. 'Pass. only' refers to model with only Order Passeriformes.

Dataset	Description	Hardware	Total Hours	Reference
1	Multi-station monitoring in central New York State during fall 2015.	Cornell ROBIN recording units	6663	[S1]
2	Multi-station monitoring in southern New York State during fall 2010-2011.	Wildlife Acoustics Song Meter 2 with plate microphone	4884	[S2]
3	Transect across Appalachian mountains during fall 2022.	OldBird 21c microphones with custom Cornell SWIFT recorder.	6760	This paper

Table S3: **Summary of model datasets, Related to STAR Methods.**

Common Name	Species Code	Order	Dataset 1	Dataset 2	Dataset 3
American Tree Sparrow	amtspa	Passeriformes	2755	0	9
Black-and-white Warbler	bawwar	Passeriformes	352	22	128
Bobolink	boboli	Passeriformes	290	210	117
Black-throated Blue Warbler	btbwar	Passeriformes	3850	133	355
Cape May Warbler	camwar	Passeriformes	1314	0	2926
Canada Warbler	canwar	Passeriformes	507	115	47
Chipping Sparrow	chispa	Passeriformes	2580	5262	2129
Chestnut-sided Warbler	chswar	Passeriformes	2280	651	793
Common Yellowthroat	comyel	Passeriformes	2779	1221	271
Dark-eyed Junco	daejun	Passeriformes	314	508	291
Great Blue Heron	grbher3	Pelecaniformes	88	192	0
Green Heron	grnher	Pelecaniformes	312	162	37
Gray-cheeked Thrush	gycthr	Passeriformes	2848	132	1712
Hermit Thrush	herthr	Passeriformes	202	0	145
Mourning Warbler	mouwar	Passeriformes	410	12	0
Northern Parula	norpar	Passeriformes	686	577	133
Ovenbird	ovenbi1	Passeriformes	5418	0	1436
Palm Warbler	palwar	Passeriformes	307	292	228
Rose-breasted Grosbeak	robgro	Passeriformes	5663	1040	2633
Savannah Sparrow	savspa	Passeriformes	6980	7486	252
Swainson's Thrush	swathr	Passeriformes	36908	7775	39104
Veery	veery	Passeriformes	4812	1660	988
White-crowned Sparrow	whcspa	Passeriformes	369	16	22
White-throated Sparrow	whtspa	Passeriformes	6502	1824	1841
Wood Thrush	woothr	Passeriformes	419	66	882
Yellow-rumped Warbler	yerwar	Passeriformes	975	752	127
American Redstart	amered	Passeriformes	0	0	1328

Table S4: **Summary of model detections by species and dataset included in the analysis after dataset-specific filtering steps, Related to STAR Methods.** All recordings are from autumn. Dataset 1 is from central New York State (2015); dataset 2 is from southern New York State (2010-2011); and dataset 3 is from a transect across Appalachia (2022).

Supplemental References

S1. Farnsworth, A., Van Doren, B.M., Kelling, S., Lostanlen, V., Salamon, J., Cramer, A., and Bello, J.P. (2022). BirdVox-full-season: 6672 hours of audio from migratory birds. Zenodo. https://doi.org/10.5281/zenodo.5791744.

S2. Van Doren, B.M., Sheldon, D., Geevarghese, J., Hochachka, W.M., and Farnsworth, A. (2015). Autumn morning flights of migrant songbirds in the northeastern United States are linked to nocturnal migration and winds aloft. The Auk 132, 105–118. https://doi.org/10.1642/AUK-13-260.1.