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Social associations across species during nocturnal bird migration

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Abstract:	An emerging frontier in ecology explores how organisms integrate social information into movement be- havior and the extent to which information exchange occurs across species boundaries1–3. Most migratory landbirds are thought to undertake nocturnal migratory flights alone, guided by information from endogenous genetic programs and past individual experience4,5. However, social information may be an underappreciated contributor to migration behavior and decision-making1,2. 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 landbirds6–8. We used these vocalizations to test whether actively migrating birds distribute non-randomly relative to other species in flight while accounting for similarities in migration phenology, geography, and other non-social factors. We found that nocturnal migrants commonly show non-random social associations with other species; each species engaged in significant associations with an average of 2.7 other species. So- cial associations were stronger among species with similar wing morphologies and similar vocalizations, but associations were surprisingly not explained by evolutionary relatedness. These results suggest that conver- gent vocal signals broadcast during flight maintain in-flight interactions that are structured by flight speed and behavior7,9,10. For small-bodied and short-lived bird species, transient social associations could play an important role in migratory decision-making by supplementing information gained from endogenous or experiential sources11–13. Substantial recent and continuing declines in bird populations14,15 may diminish the frequency and strength of social associations during migration, with currently unknown consequences for populations.
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To the editors of Current Biology,

We respectfully submit a manuscript for your consideration, titled "**Social associations across species during nocturnal bird migration.**" We believe that this work will be of great interest to a broad audience of scientists and non-scientists alike, and that it has the potential to change how we think about bird migration—one of the most widely recognized natural phenomena on Earth.

Animal migrations are essential elements of earth's ecosystems and their biodiversity, but enduring mysteries remain about fundamental processes underlying these behaviors. Current scientific understanding of songbird migration holds that birds migrate alone, guided by inherited migratory programs. An emerging literature of social information use during migration has begun to challenge this view, but this research has been almost entirely focused on single-species perspectives, and we believe broader perspectives are needed. Our case in point: The migratory journeys of diverse taxa overlap in space and time in widely recognized "co-migrations," but a recent review of 817 animal migration studies found only *one* study that explicitly examined interspecific social information use. **Social information exchanged during migration may be an underrecognized factor shaping the movement ecology, individual decision-making, and even fitness of songbird migrants.**

Our research takes an important step towards filling this large knowledge gap by investigating whether nocturnally migrating bird species form consistent social associations during migratory flights. **Drawing on recent advances in artificial intelligence for bioacoustics, we find that, indeed, interspecific social associations are not only present, but *common* during migratory flights.** We identify wing morphology and vocalization structure as two important factors that may drive in-flight associations and reject phylogenetic relatedness as a contributor, lending important insight into how these relationships are structured. **Most importantly, we offer evidence that key elements of our understanding of songbird migration may be incomplete.** The implications of these findings are many, especially for populations experiencing substantial recent and continuing declines, and they raise important questions: What are the consequences of a decline in social information on the success of a migratory journey, and ultimately an individual's survival?

We believe that our combination of big data, cutting edge machine learning methods, and findings that challenge current understanding make this research ideal for the audience of Current Biology.

We thank you for your consideration and look forward to your reply.

Sincerely,
Benjamin Van Doren and co-authors

Social associations across species during nocturnal bird migration

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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 alone, guided by information from endogenous genetic programs and past individual experience[4,5]. However, social information may be an underappreciated contributor to migration behavior and decision-making[1,2]. 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[6–8]. We used these vocalizations to test whether actively migrating birds distribute non-randomly relative to other species in flight while accounting for similarities in migration phenology, geography, and other non-social factors. We found that nocturnal migrants commonly show non-random social associations with other species; each species engaged in significant associations with an average of 2.7 other species. Social associations were stronger among species with similar wing morphologies and similar vocalizations, but associations were surprisingly not explained by evolutionary relatedness. These results suggest that convergent vocal signals broadcast during flight maintain in-flight interactions that are structured by flight speed and behavior[7,9,10]. For small-bodied and short-lived bird species, transient social associations could play an important role in migratory decision-making by supplementing information gained from endogenous or experiential sources[11–13]. Substantial recent and continuing declines in bird populations[14,15] may diminish the frequency and strength of social associations during migration, with currently unknown consequences for populations.

Results

Animal movements and migrations are essential elements of earth's ecosystems and their biodiversity[16], but seasonal migrations are declining due to a range of threats from human activities[17,18]. Enduring mysteries remain about fundamental processes underlying these behaviors and their patterns, including how information about migration routes, timing, and behavior is transmitted across generations[5], among individuals, and potentially even across species[2,13]. Songbirds (Order Passeriformes) compose the bulk of avian migratory species and, among other orders, are thought to rely largely on innate migratory programs[4], particularly during their naïve first migrations[5].

Evidence is emerging that the social environment plays a larger role in shaping an individual's migratory phenotype than previously understood[2,19–21]. Social information that aids navigation, orientation, or survival could be extremely valuable during this dangerous part of the annual cycle[2]. The current understanding of social learning of migration behavior has arisen primarily from single-species studies of long-lived, diurnally-migrating birds such as storks, cranes, and raptors[22–24], as well as other species that move with kin[20]. Some of these species may maintain stable social connections among flockmates[20,25], whereas others engage in more transient interactions[24].

Although most research has focused on conspecific social interactions, the migratory journeys of diverse taxa frequently overlap in space and time in "co-migrations" that are widely recognized but rarely studied[13]. Songbird migration is a remarkable example of co-migration, with hundreds of millions of individuals of dozens of species in the air on a given night[26], providing opportunity for valuable and abundant social information exchange. Though existing research on navigation and decision-making during songbird migration has often emphasized endogenous programs, these species also socially associate and interact with each other during stopover[11,27–29] and potentially in flight[9,10,12]. Many taxa actively vocalize during migratory flights[6,7,30], and these vocalizations may be important for communicating social information en route[7,9,10,31–33]. However, it is unknown whether meaningful interactions occur during migratory flights or what information might be exchanged.

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

Songbirds associate with other species during migratory flights

We collected acoustic recordings of 18308.08 hours 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"[7,34]) from audio data using a deep learning model that we designed for this purpose[8], 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 S3). 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, Figure S4; 60-s: 35/210 pairs significant, Figure S4). 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 inter-family associations were less frequent, those that did occur were of similar strength to interspecific 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 non-parametric Mantel tests and again evaluated statistical significance using custom network permutations that accounted for non-social factors. The distance between species' wing lengths and the acoustic distance of their vocalizations were statistically significant predictors of social association (Figure 3; Table 1). These relationships were robust to choice of window size (15-s: Table S2; 60-s: Table S3) and present using parametric and nonparametric matrix correlations (Table S4). These relationships were also present when excluding two large-bodied heron species and including only species in the order Passeriformes (Table S5; Figure S5). Species relationships at stopover, phylogenetic relatedness, spatiotemporal overlap in species' migration routes, non-breeding range overlap, and migration-period habitat relationships were not consistently associated with social association (Figure S6; Table 1), although stopover affiliation index, migration overlap, and non-breeding range overlap showed some support at other window sizes (Table S2; Table S3).

Discussion

Little is presently known about how organisms integrate interspecific information into behavioral decision-making, a topic at the cutting edge of ecology[1,2,13,35]. Our results demonstrate that songbirds, typically thought to be independent migrants, engage in interspecific social associations during 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 common for various species to participate in these associations. Social associations were most frequent among species of the same family, particularly wood-warblers in the family Parulidae, but significant inter-family associations were also frequent and no less strong when present. In contrast, we did not find 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 or flight altitude may be important in structuring in-flight associations[36]. 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. In contrast, we found no consistent evidence that in-flight associations were linked to habitat preferences, geographic ranges, or species affiliations during diurnal stopovers. These results suggest that migrants' interspecific relationships re-shuffle as they alternate between airspace and stopover habitats throughout migration, with variables related to flight behavior shaping in-flight relationships and variables related to foraging behavior shaping stopover relationships[29].

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[37]. This result agrees with[10], which found support for a similar relationship among wood-warblers in the family Parulidae. These findings suggest the possibility that shared migratory behavior may be driving convergent evolution in acoustic signals across species[9].

Growing evidence for the importance of social information during migration

Our study contributes to a growing body of evidence that the social information available to an individual may be an important and underappreciated contributor to migratory behavior and decision-making[2,3]. The use of social information during migration is well documented in some bird species, such as large-bodied birds like cranes and storks that primarily migrate diurnally in groups. For example, cranes (Gruidae) exhibit long-term social learning[22,23], and storks (Ciconiidae) use social information to aid navigation and locate areas of uplift[24]. In addition, other species that commonly form groups or flocks, such as terns (Laridae) and shorebirds (Charadriiformes), are increasingly understood to make use of social information during migration[19,20]. In these species, social information is thought to be of particular importance for younger birds undertaking their first migrations. We suggest that social information transmitted through transient interspecific associations during migration may also be important among small-bodied and short-lived bird species that are generally thought to undertake migration alone, guided by endogenous genetic programs[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. Our study focused only on autumn migration, which is the first migratory journey for first-year birds. Future work should investigate whether association dynamics differ during the return journey in spring, when all individuals have prior migration experience. In addition, not all migratory species vocalize during migration[6,7]; it is currently unknown whether generally silent species, like vireos (Vireonidae) and New World flycatchers (Tyrannidae), also participate in in-flight associations.

Acoustics as a movement ecology tool

Acoustic monitoring is an increasingly important tool for studying movement ecology, especially of flying vertebrates. A study of this scope was made possible only through recent advances in machine learning, which automated an otherwise prohibitively laborious process of manual detection and identification of hundreds of thousands of vocalizations. The use of model fine-tuning was key to this study, as it allowed us to adapt an existing generalist machine learning model to our specific dataset and achieve higher precision than would otherwise have been possible. Despite these advances, we emphasize that the acoustic model does not achieve 100% accuracy, and the manual review steps we employed were key to ensuring high data quality. As scientific studies are increasingly powered by data generated using machine learning models, we emphasize that data review by expert humans is often still a necessity.

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. 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[31,32], 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' source locations to be triangulated, but this technique requires significant logistical challenges to implement on a large scale[38]. Given our results, we would hypothesize that intraspecific social associations also occur, and are potentially common, during nocturnal migratory flights[10].

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[7], and even understanding why some species are more susceptible to anthropogenic hazards like light pollution[33]. Here, we demonstrate that research on these flight calls can also provide a window onto a hidden network of species associations aloft. This study highlights the need for further investigation into the social context of animal migration, including how an individual's social experience might contribute to learning and decision-making during migratory flights. Recent work supports the important role of transient interspecific social relationships during migratory stopover periods[29], and we propose that social associations are also important during migratory flights. Our research emphasizes that species interactions are important to consider when investigating migratory behavior, including in population and conservation contexts. Given substantial recent and continuing declines in migratory bird populations[14], it is likely that the frequency and strength of social associations during migration are diminishing. What are the consequences of this decline in social information on the success of a migratory journey, and ultimately an individual's survival? 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[2,13]. An understanding of these dynamics is essential to assessing and mitigating potential negative impacts.

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Author contributions

BMVD conceived of the study, collected data, performed analysis, and wrote the initial manuscript draft. JAF, FH, and JD shaped the data analysis. All authors contributed to the final written draft of the manuscript.

Declaration of interests

The authors declare no competing interests.

Supplemental information

Document S1. Tables S1-S7 and Figures S1-S7.

Figures

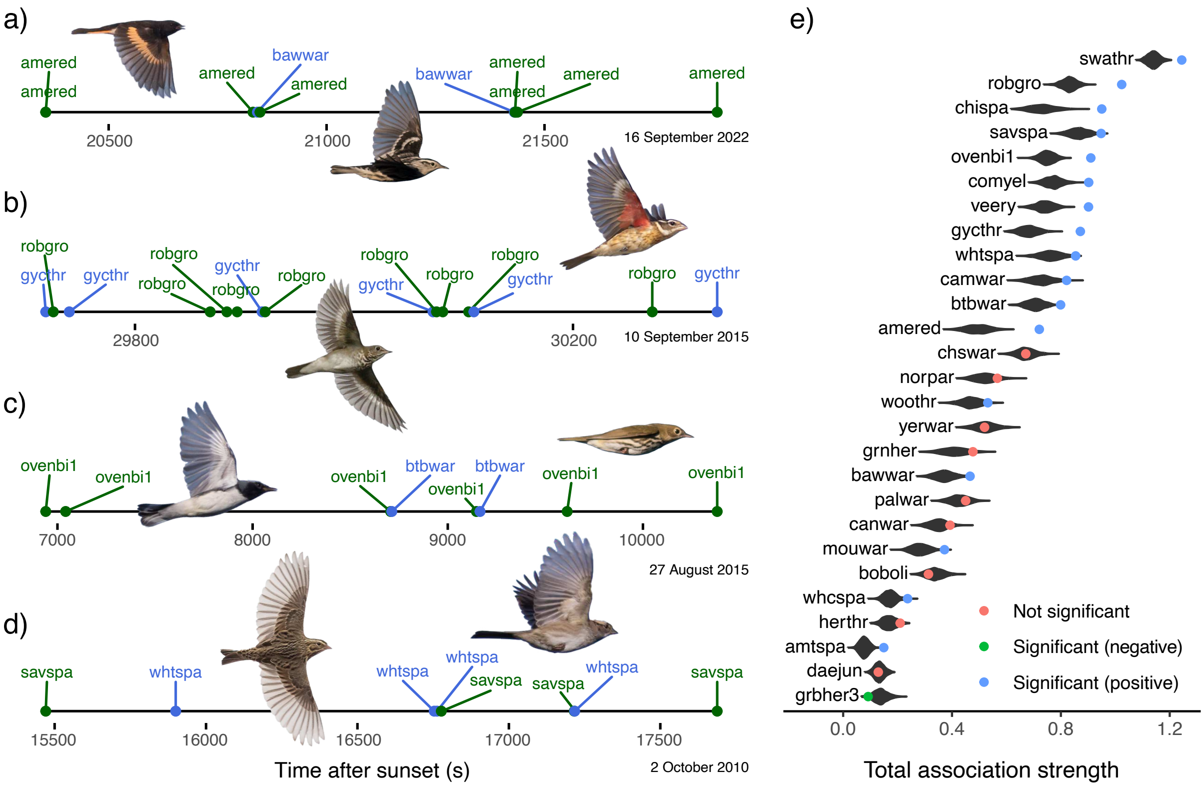

Figure 1: Example time series of detections during nocturnal migration for select species pairs and tests of total association strength for social association network. Photos from the Macaulay Library at the Cornell Lab of Ornithology. (a) American Redstart (amered; ML112702211) and Black-and white Warbler (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 derived from custom permutations that account for similarities in migration phenology, geography, and other non-social factors. Points show the observed degree strength, and statistical significance indicates that a species has a stronger observed degree strength than expected under the null hypothesis.

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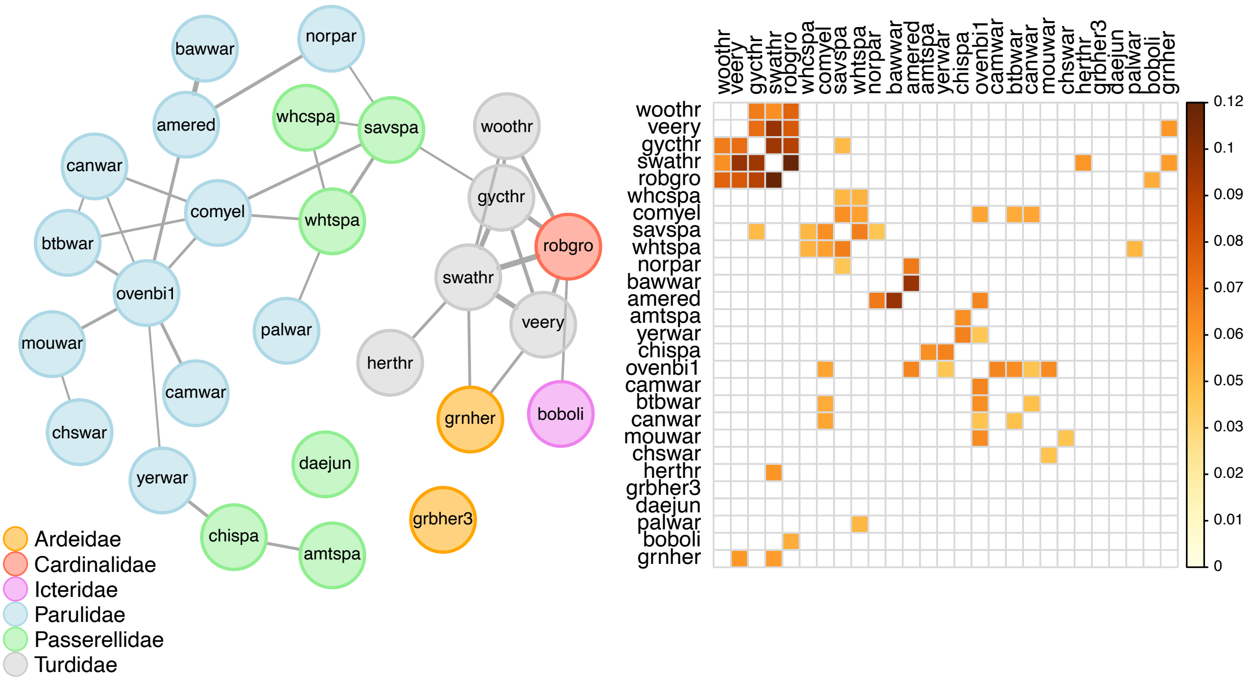

Figure 2: Significant social associations (30-s time windows). Network diagram and heatmap show only statistically significant edges.

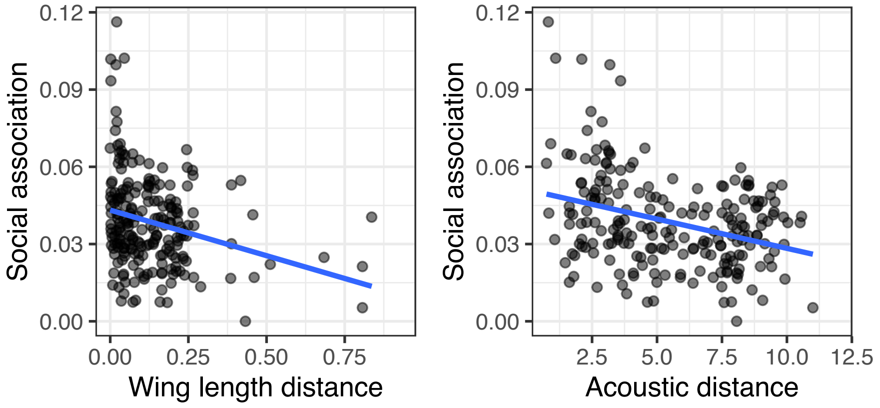

Figure 3: Scatterplots of statistically significant pairwise species relationships. Each point represents a species pair. Best fit line drawn to aid interpretation; refer to matrix correlations for coefficient estimates and statistical significance. Plots shown from data generated with 30-s time windows.

Tables

Table 1: Nonparametric matrix correlations for the response variable of social association, based on 30-s time windows. Each row corresponds to a single-predictor model.

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

Methods

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[39])[40,41]; (Dataset 2) multi-station monitoring in southern New York State during fall 2010-2011[42]; 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 S6. Although the hardware differed by monitoring effort, all units were designed and deployed specifically to record migrating birds' nocturnal flight calls.

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[8]. The Nighthawk core model[8] is freely available[43], and it has been validated on diverse test data, including on the BirdVox-Full-Season dataset (Dataset 1, above)[43]. Performance on target datasets can be improved by conducting additional model training with the dataset in question, termed "fine-tuning"[8]. 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[8]. For Dataset 2, we used existing annotations[42]. 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[8]. That study 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[43]. 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.

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 S7; Figure 1).

Network analysis

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`[44]. 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.

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.

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. 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 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`[45]. We used the `extractTree` function in that package to output a tree and used the `cophenetic.phylo` function in the R package `ape`[46] 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.

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[47] 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)[48]. 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[47]. 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[29].

Following that study[29], 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[49] 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[10]. 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[8] 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[50] to manually draw bounding boxes around each call and used the `spectro_analysis` function in the R package `warbleR`[51] 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`[52]) 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`[53]) 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 S7.

Statistical tests

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. 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 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 first 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.

Testing for social associations among species

We evaluated the statistical significance of each species' 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`[54]): 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[55], using the `mrqap.custom.null` function in the R package `asnipe`[44].

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

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

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

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

Species 1	Species 2	Family 1	Family 2	Social association	P-value
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 S2: Nonparametric matrix correlations for the response variable of social association, based on 15-s time windows. Each row corresponds to a single-predictor model.

Predictor	Correlation	P-value	No. Taxa
Stopover affiliation index	0.127	0.031	22
Phylogenetic similarity	0.056	0.963	27
Migration overlap	0.211	0.091	27
Non-breeding range overlap	0.163	0.082	27
Wing length distance	-0.252	0.000	27
Migration habitat similarity	0.048	0.383	27
Acoustic distance	-0.252	0.000	27

Table S3: Nonparametric matrix correlations for the response variable of social association, based on 60-s time windows. Each row corresponds to a single-predictor model.

Predictor	Correlation	P-value	No. Taxa
Stopover affiliation index	0.036	0.652	22
Phylogenetic similarity	0.013	1.000	27
Migration overlap	0.241	0.045	27
Non-breeding range overlap	0.175	0.043	27
Wing length distance	-0.208	0.000	27
Migration habitat similarity	0.081	0.273	27
Acoustic distance	-0.206	0.000	27

Table S4: Parametric matrix correlations for the response variable of social association, based on 30-s time windows. Each row corresponds to a single-predictor model.

Predictor	Correlation	P-value	No. Taxa
Stopover affiliation index	0.085	0.182	22
Phylogenetic similarity	0.084	0.873	27
Migration overlap	0.161	0.343	27
Non-breeding range overlap	0.133	0.472	27
Wing length distance	-0.261	0.000	27
Migration habitat similarity	0.097	0.056	27
Acoustic distance	-0.334	0.000	27

Table S5: Nonparametric matrix correlations for order Passeriformes for the response variable of social association, based on 30-s time windows. Each row corresponds to a single-predictor model.

Predictor	Correlation	P-value	No. Taxa
Stopover affiliation index	0.067	0.308	22
Phylogenetic similarity	0.089	0.941	25
Migration overlap	0.251	0.044	25
Non-breeding range overlap	0.188	0.044	25
Wing length distance	-0.273	0.000	25
Migration habitat similarity	0.058	0.375	25
Acoustic distance	-0.245	0.000	25

Table S6: Summary of model datasets

Dataset	Description	Hardware	Total Hours	Reference
1	Multi-station monitoring in central New York State during fall 2015.	Cornell ROBIN recording units	6663	Farnsworth et al. 2022
2	Multi-station monitoring in southern New York State during fall 2010-2011.	Wildlife Acoustics Song Meter 2 with plate microphone	4884	Van Doren et al. 2015
3	Transect across Appalachian mountains during fall 2022.	OldBird 21c microphones with custom Cornell SWIFT recorder.	6760	None

Table S7: Summary of model detections by species and dataset included in the analysis after dataset-specific filtering steps. 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).

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

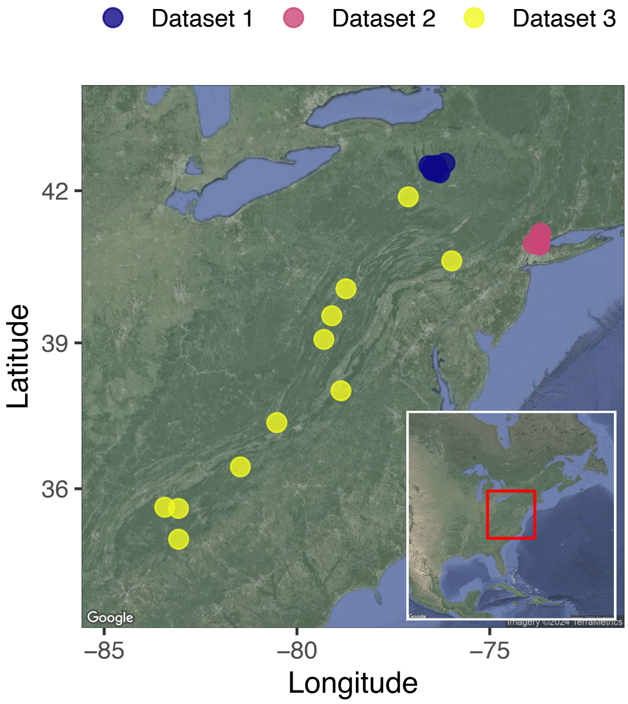

Figure S1: Recording locations. Red box in inset shows bounds of focal region.

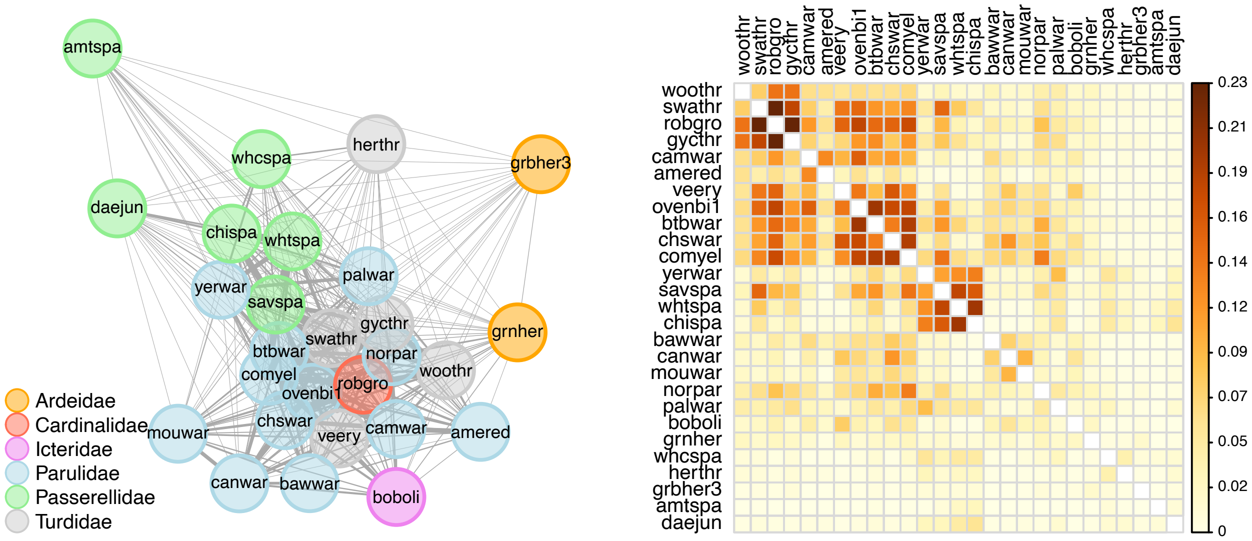

Figure S2: Observed coarse co-occurrence network. Vertices are colored by family, and labels are species codes assigned by the eBird database. Edge weights and heatmaps show connection strength. Species are ordered by hierarchical clustering on co-occurrence data.

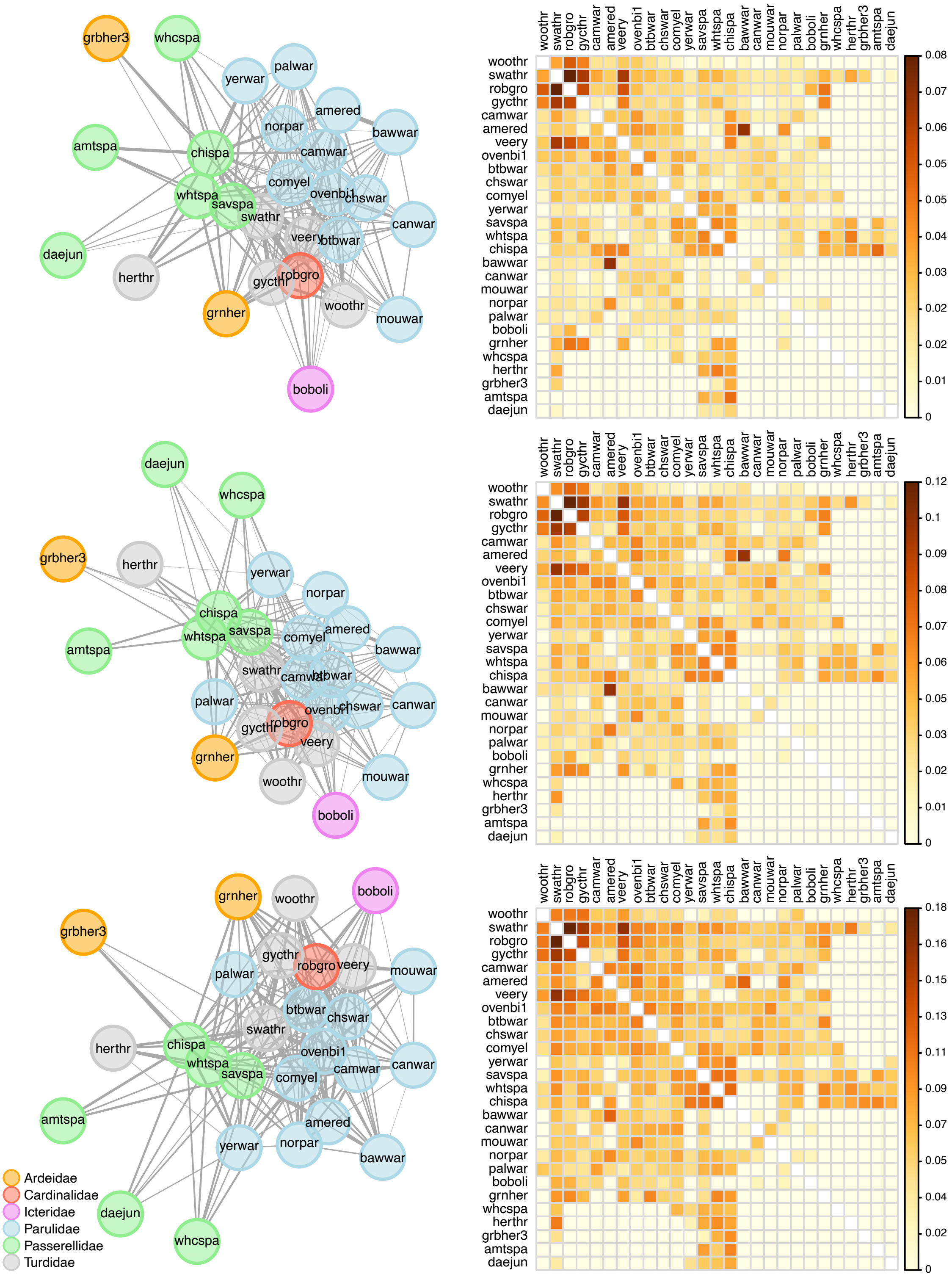

Figure S3: Observed social association networks. (Top) Network based on 15-s time windows. (Center) Network based on 30-s time windows. (Bottom) Network based on 60-s time windows. Vertices are colored by family, and labels are species codes assigned by the eBird database. Edge weights show association strength. All networks were significantly non-random.

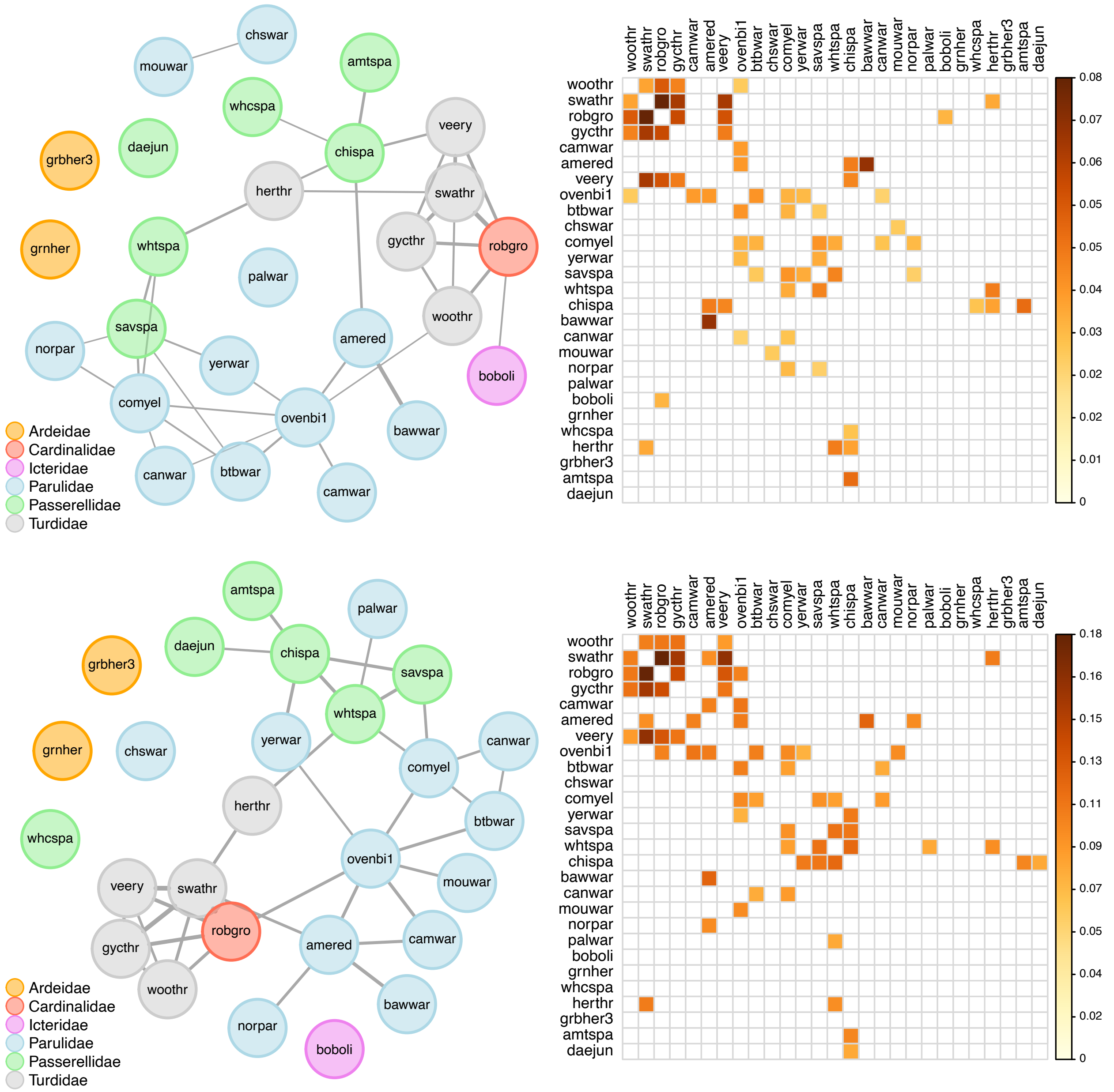

Figure S4: Significant social associations (top: 15-s time windows; bottom: 60-s time windows). Network diagram and heatmap show only statistically significant edges after applying a false discovery rate correction.

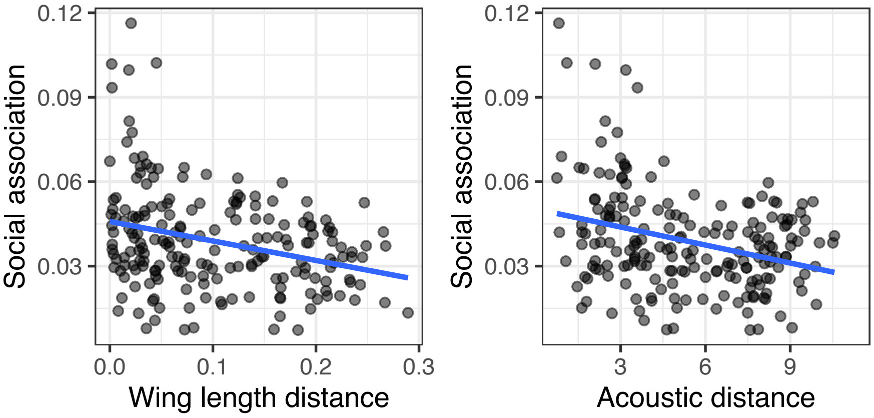

Figure S5: Scatterplots of statistically significant pairwise species relationships for order Passeriformes. Each point represents a species pair. Best fit line drawn to aid interpretation; refer to matrix correlations for coefficient estimates and statistical significance. Plots shown from data generated with 30-s time windows.

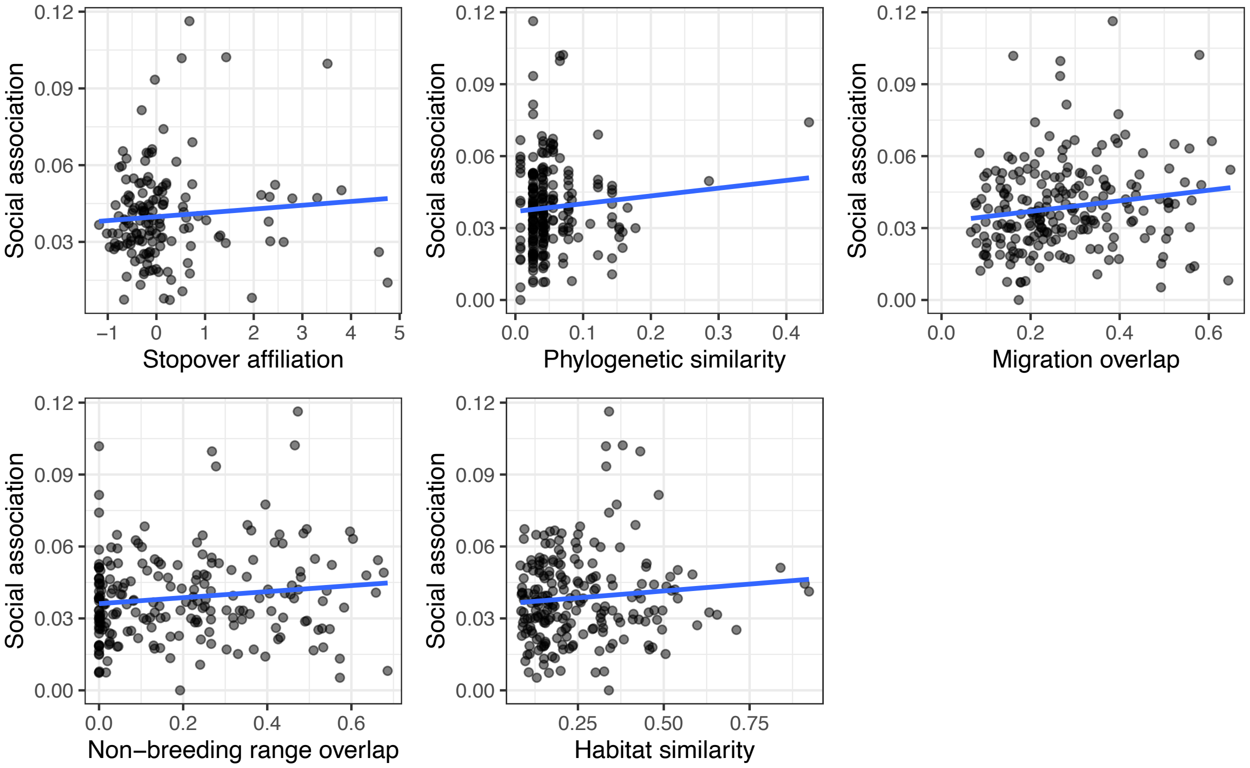

Figure S6: Scatterplots of non-significant pairwise species relationships. Each point represents a species pair. Best fit line drawn to aid interpretation; refer to matrix correlations for coefficient estimates. Plots show from data generated with 30-s time windows.

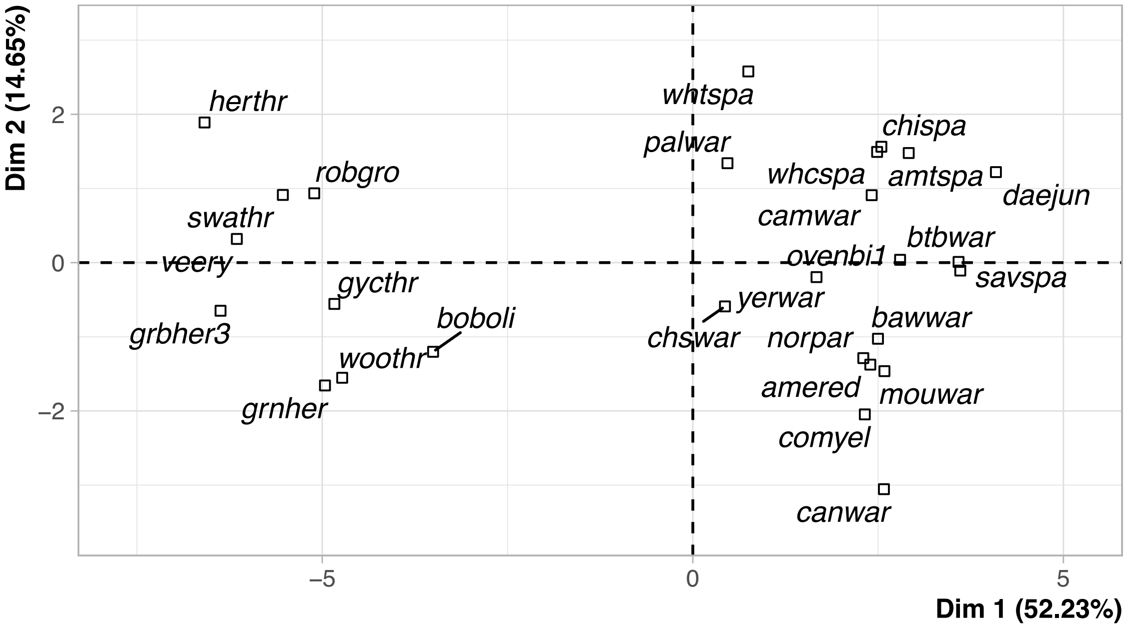

Figure S7: Ordination from principal component analysis showing acoustic distance among species. The scatterplot shows the centroids of each species in PCA space for the first two principal components

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