ARTICLE

ECOLOGICAL
APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Integrating data types to estimate spatial patterns of avian migration across the Western Hemisphere

Timothy D. Meehan[1] | Sarah P. Saunders[1] | William V. DeLuca[1] |
Nicole L. Michel[1] | Joanna Grand[1] | Jill L. Deppe[2] | Miguel F. Jimenez[1] |
Erika J. Knight[1] | Nathaniel E. Seavy[1] | Melanie A. Smith[1] |
Lotem Taylor[1] | Chad Witko[1] | Michael E. Akresh[3] | David R. Barber[4] |
Erin M. Bayne[5] | James C. Beasley[6,7] | Jerrold L. Belant[8] |
Richard O. Bierregaard[9] | Keith L. Bildstein[4] | Than J. Boves[10] |
John N. Brzorad[11,12] | Steven P. Campbell[13] | Antonio Celis-Murillo[14] |
Hilary A. Cooke[15] | Robert Domenech[16] | Laurie Goodrich[4] |
Elizabeth A. Gow[17,18] | Aaron Haines[19] | Michael T. Hallworth[20,21] |
Jason M. Hill[21] | Amanda E. Holland[6,7] | Scott Jennings[22] |
Roland Kays[23,24] | D. Tommy King[25] | Stuart A. Mackenzie[17] |
Peter P. Marra[26] | Rebecca A. McCabe[4] | Kent P. McFarland[21] |
Michael J. McGrady[27] | Ron Melcer Jr[28,29] | D. Ryan Norris[18] |
Russell E. Norvell[30] | Olin E. Rhodes Jr[6] | Christopher C. Rimmer[20] |
Amy L. Scarpignato[31] | Adam Shreading[16] | Jesse L. Watson[5,32] |
Chad B. Wilsey[1]

[1]National Audubon Society, New York, New York, USA

[2]National Audubon Society, Washington, District of Columbia, USA

[3]Department of Environmental Studies, Antioch University New England, Keene, New Hampshire, USA

[4]Acopian Center for Conservation Learning, Hawk Mountain Sanctuary Association, Orwigsburg, Pennsylvania, USA

[5]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

[6]Savannah River Ecology Laboratory, Aiken, South Carolina, USA

[7]Warnell College of Forestry & Natural Resources, University of Georgia, Athens, Georgia, USA

[8]Global Wildlife Conservation Center, State University of New York College of Environmental Science and Forestry, Syracuse, New York, USA

[9]Department of Ornithology, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA

[10]Department of Biological Sciences, Arkansas State University, Jonesboro, Arkansas, USA

[11]1000 Herons, Charlotte, North Carolina, USA

[12]Lenoir-Rhyne University, Hickory, North Carolina, USA

[13]Albany Pine Bush Preserve Commission, Albany, New York, USA

[14]U.S. Geological Survey, Eastern Ecological Center, Patuxent Research Refuge, Laurel, Maryland, USA

[15]Wildlife Conservation Society Canada, Whitehorse, Yukon Territories, Canada

[16]Raptor View Research Institute, Missoula, Montana, USA

[17]Birds Canada, Port Rowan, Ontario, Canada

[18]Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada

[19]Biology Department, Millersville University, Millersville, Pennsylvania, USA

[20]Cary Institute of Ecosystem Studies, Millbrook, New York, USA

[21]Vermont Center for Ecostudies, Norwich, Vermont, USA

[22]Cypress Grove Research Center, Audubon Canyon Ranch, Marshall, California, USA

[23]North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA

[24]Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, North Carolina, USA

[25]U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center, Mississippi Field Station, Mississippi State University, Mississippi State, Mississippi, USA

[26]Department of Biology and McCourt School of Public Policy, Georgetown University, Washington, District of Columbia, USA

[27]International Avian Research, Krems, Austria

[28]California State Parks, Sacramento, California, USA

[29]Geography Graduate Group, University of California, Davis, Davis, California, USA

[30]Utah Division of Wildlife Resources, Salt Lake City, Utah, USA

[31]Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, District of Columbia, USA

[32]HawkWatch International, Salt Lake City, Utah, USA

Correspondence
Sarah P. Saunders
Email: sarah.saunders@audubon.org

Present address
Miguel F. Jimenez, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA

Handling Editor: Juan Manuel Morales

Abstract

For many avian species, spatial migration patterns remain largely undescribed, especially across hemispheric extents. Recent advancements in tracking technologies and high-resolution species distribution models (i.e., eBird Status and Trends products) provide new insights into migratory bird movements and offer a promising opportunity for integrating independent data sources to describe avian migration. Here, we present a three-stage modeling framework for estimating spatial patterns of avian migration. First, we integrate tracking and band re-encounter data to quantify migratory connectivity, defined as the relative proportions of individuals migrating between breeding and non-breeding regions. Next, we use estimated connectivity proportions along with eBird occurrence probabilities to produce probabilistic least-cost path (LCP) indices. In a final step, we use generalized additive mixed models (GAMMs) both to evaluate the ability of LCP indices to accurately predict (i.e., as a covariate) observed locations derived from tracking and band re-encounter data sets versus pseudo-absence locations during migratory periods and to create a fully integrated (i.e., eBird occurrence, LCP, and tracking/band re-encounter data) spatial prediction index for mapping species-specific seasonal migrations. To illustrate this approach, we apply this framework to describe seasonal migrations of 12 bird species across the Western Hemisphere during pre- and post-breeding migratory periods (i.e., spring and fall, respectively). We found that including LCP indices with eBird occurrence in GAMMs generally improved the ability to accurately predict observed migratory locations compared to models with eBird occurrence alone. Using three performance metrics, the eBird + LCP model demonstrated equivalent or superior fit relative to the

eBird-only model for 22 of 24 species–season GAMMs. In particular, the integrated index filled in spatial gaps for species with over-water movements and those that migrated over land where there were few eBird sightings and, thus, low predictive ability of eBird occurrence probabilities (e.g., Amazonian rainforest in South America). This methodology of combining individual-based seasonal movement data with temporally dynamic species distribution models provides a comprehensive approach to integrating multiple data types to describe broad-scale spatial patterns of animal movement. Further development and customization of this approach will continue to advance knowledge about the full annual cycle and conservation of migratory birds.

INTRODUCTION

Billions of birds migrate across the globe each year, and their seasonal movements span a broad range of spatial and temporal scales. Approximately 73% of bird species breeding in North America are migratory, and 54% of them are considered Nearctic-Neotropical migrants (Albert et al., 2020). Evidence suggests that migration costs can have significant impacts on individual survival and, ultimately, the viability of a population (Newton, 2006). While consideration of animal movements is often necessary when designing management efforts for the conservation of migratory birds (McGowan et al., 2017; Robertson et al., 2018), their extensive ranges and highly variable occurrence at fine spatial scales present considerable challenges (Kays et al., 2015; Nandintsetseg et al., 2019).

A comprehensive understanding of migratory connectivity, or the extent to which populations are linked throughout the annual cycle (Marra & Studds, 2010), requires quantification of spatial variation in the distribution and abundance of individuals across stationary and migratory stages (Knight et al., 2021; Webster et al., 2002). For many species, spatial patterns during migration remain largely undescribed, especially across hemispheric extents (Nilsson et al., 2019). This knowledge gap contributes to uncertainty about the ecological factors limiting populations (e.g., climate vs. land cover; Howard et al., 2020); the timing, location, and potential delayed impact of those limiting factors (e.g., carryover effects; Akresh et al., 2019); the spatial distribution of threats to habitats (Wilson et al., 2019); and the optimal allocation of conservation efforts that will match species' full-annual-cycle requirements (Runge et al., 2016). Deeper insights into species' spatial migration patterns will not only shed light on these uncertainties but will further advance our understanding of migratory connectivity.

Advancements in tracking technologies, such as the Global Positioning System (GPS), light-level geolocators (LLG), and satellite telemetry (e.g., platform transmitting terminal [PTT]), have improved our understanding of spatial migration patterns by allowing for increasingly accurate estimates of location and quantification of error in animal movements (McKinnon & Love, 2018; Rakhimberdiev et al., 2016). For example, tracking information has been used to reveal individuals' migration routes (e.g., DeLuca et al., 2019), migratory bottlenecks (e.g., Buechley et al., 2018), and conservation priorities for migratory birds (e.g., Knight et al., 2021). Individually banded and re-encountered birds have also contributed invaluable information to our understanding of migratory patterns (e.g., Deppe et al., 2015; Kreakie & Keitt, 2012). However, individual-based data types are often limited by restricted spatial coverage, as well as relatively small sample sizes and low re-encounter rates. Moreover, nonrandom deployment of tracking units and banding efforts could misrepresent species-level patterns of movement and habitat requirements (Buechley et al., 2018; Li et al., 2017).

Recently developed high-resolution species distribution models based on widespread, volunteer-collected eBird data have proved to be an important advancement for capturing landscape-scale, intra-annual distributional dynamics for many avian species (e.g., Johnston et al., 2020; Schuster et al., 2019). The eBird project consists of a global network of volunteers (though with the majority located in North America) who submit bird sightings, which are then verified by regional reviewers (Sullivan et al., 2014). eBird Status and Trends products (ebird.org/science/status-and-trends) use observations submitted since 2005 in machine learning models to characterize species abundance and distribution at a 2.96-km resolution for each week of the year while accounting for the local environment and multiple

sources of sampling bias (see Appendix S1; Fink, Auer, Johnston, Ruiz-Gutierrez, et al., 2020 for more details), effectively capturing localized spatial patterns across broad species ranges. Yet the predictive ability of these models is limited in geographic areas where eBird sightings are absent due to a lack of observers or because cryptic behaviors make direct observation of bird movements challenging during transitory migration periods.

The development of statistically robust methods to integrate individual-based seasonal movement information (i.e., tracking and band re-encounter data) with these temporally dynamic species distribution models (i.e., eBird Status and Trends products) will enable researchers to leverage the unique strengths of these independent sources and advance our understanding of bird migration at relevant spatial and temporal extents for full-annual-cycle conservation planning. Data integration, or the merging of multiple data types within a unified analytical framework, provides a powerful method for sharing information among available data sources while also minimizing their inherent biases (Miller et al., 2019; Zipkin et al., 2021). Here, we present a novel, three-stage approach (Figure 1) for integrating multiple, distinct data types to describe the spatial patterns of bird migration across the Western Hemisphere during species-specific pre- and postbreeding migratory periods, as defined by eBird Status and Trends products (hereafter eBird; see Appendix S1 for species' migration timings). In the first two stages, we quantified migratory connectivity and then used probabilistic least-cost paths (LCPs; Adriaensen et al., 2003; Storfer et al., 2007) to combine connectivity estimates with weekly estimates of relative occurrence probabilities derived from eBird (Fink, Auer, Johnston, Strimas-Mackey, et al., 2020). Traditionally, LCPs have been used to model gene flow across landscapes (Storfer et al., 2007), with resistance surfaces or costs representing geographic or physiological barriers to animal movement (e.g., topographic, elevational, thermal stress; Pullinger & Johnson, 2010). More recently, LCPs have been adapted for estimating species-specific migration routes (e.g., Nourani et al., 2018), and they offer a promising—yet uninvestigated—avenue for broader migration applications, such as filling spatial gaps where volunteer-collected data are sparse or unavailable.

In a final stage, we used generalized additive mixed models (GAMMs) both to evaluate the ability of estimated LCPs to accurately predict (i.e., as a covariate) observed animal locations derived from tracking and band re-encounter data sets compared to pseudo-absence locations during migratory periods and to create fully integrated (i.e., eBird occurrence, LCP, and tracking/band re-encounter data) prediction surfaces describing spatial patterns of seasonal bird migrations. We apply this modeling framework to a suite of 12 bird species with a variety of migratory strategies and geographic ranges. Accounting for spatiotemporal dynamics strongly influences the success of conservation planning for wide-ranging migratory species (Johnston et al., 2020; Runge et al., 2016), and this methodology of integrating disparate migration data types provides a comprehensive approach for estimating broad-scale spatial patterns of animal movement to advance full-annual-cycle research and conservation efficacy.

MATERIALS AND METHODS

Overview of modeling framework

To identify and evaluate spatial migration patterns using multiple data types, we developed a novel three-stage modeling framework (Figure 1), which we used to describe seasonal migrations of 12 bird species across the Western Hemisphere. In the first stage, we integrated tracking and band re-encounter data sets to estimate migratory connectivity, defined as the relative proportions of individuals migrating between stationary breeding and nonbreeding regions for each species (also referred to as transition probabilities; Marra et al., 2006). In the second stage, we used migratory connectivity proportions developed in the first stage along with eBird occurrence probabilities (i.e., occurrence rate estimates from eBird Status and Trends products; Fink, Auer, Johnston, Strimas-Mackey, et al., 2020) as the conductance surface to produce probabilistic LCP passage indices (hereafter LCP indices) during pre- and postbreeding migratory periods (i.e., spring and fall, respectively). In the final stage, we used GAMMs to evaluate the strength of associations between presence/pseudo-absence data (derived from tracking and band re-encounter data sets) and both LCP indices and eBird occurrence probabilities. We used the resulting GAMM prediction surfaces, which represent a statistical integration of eBird occurrence probabilities and LCP indices (i.e., as predictor variables), as well as tracking and band re-encounter data (i.e., as part of the response variable), to produce the final maps of integrated migration patterns for each species during each migratory period. In what follows, we briefly describe each step of the three-stage modeling framework (Figure 1); see Appendix S1 for additional methodological details.

Focal species

We applied our modeling framework to band re-encounter and tracking data from 12 focal species to estimate migration patterns during pre- and postbreeding
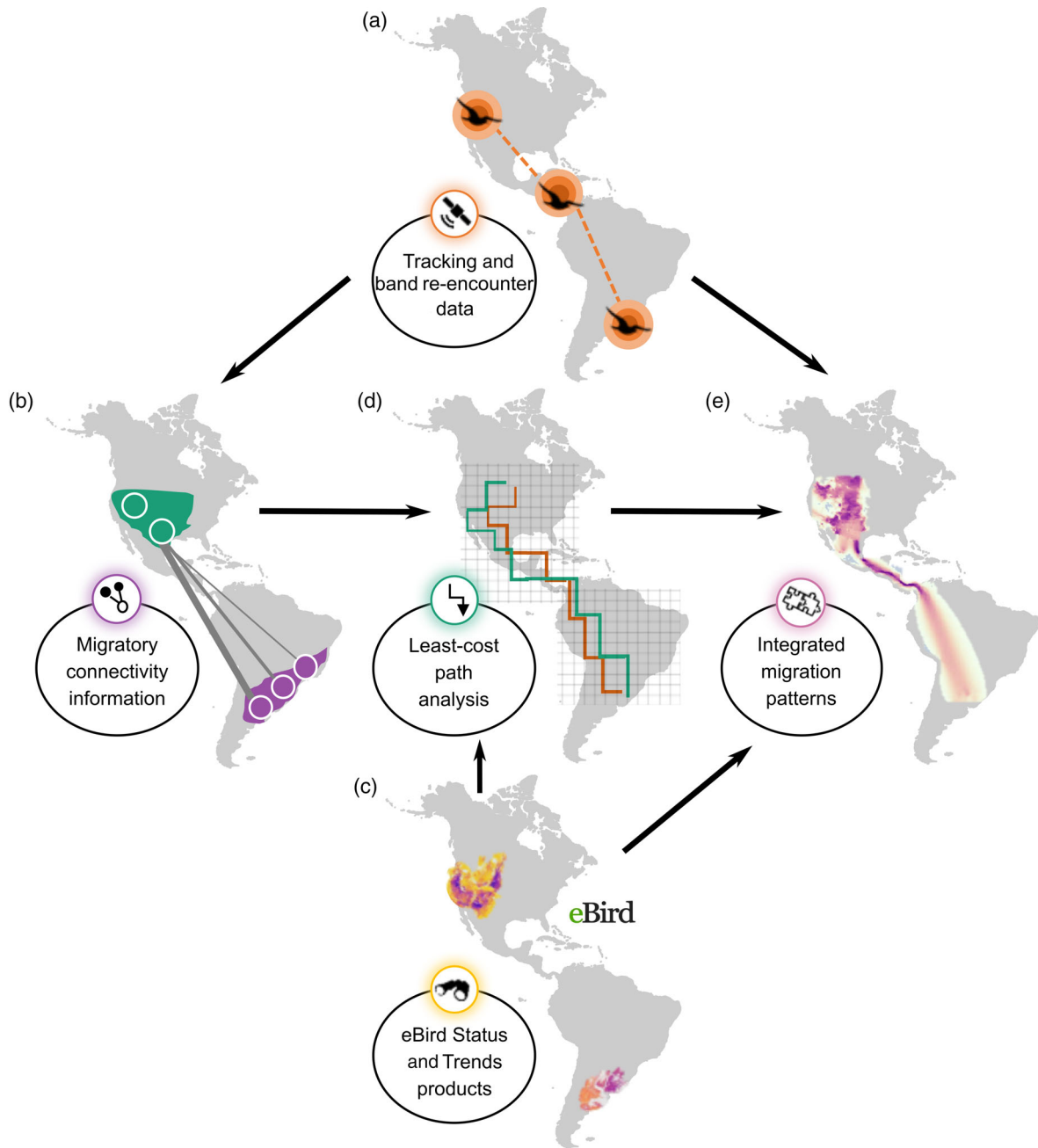
FIGURE 1 Conceptual schematic of the modeling framework, which integrates multiple data types to describe spatial patterns of avian migration across the Western Hemisphere. For each species and migratory season, we (a) statistically integrated tracking and band re-encounter data to (b) estimate migratory connectivity proportions. Migratory connectivity proportions were then used along with (c) eBird Status and Trends products (i.e., occurrence probabilities) to produce (d) least-cost paths (LCPs). We used the LCP indices, as well as eBird occurrence probabilities, as covariates in generalized additive mixed models (GAMMs) to evaluate the strength of association between each predictor and presence/pseudo-absence data (i.e., response variable) obtained from tracking and band re-encounter data sets. The resulting (e) GAMM prediction surface represents the statistical integration (i.e., integrated index) of all available migration information shown.

migratory periods (see Appendix S1 for species-specific migration timings): American white pelican (*Pelecanus erythrorhynchos*), blackpoll warbler (*Setophaga striata*; DeLuca et al., 2015, 2019), broad-winged hawk (*Buteo platypterus*; Haines et al., 2003; McCabe et al., 2020), grasshopper sparrow (*Ammodramus savannarum*; Hill &

Renfrew, 2019), great egret (*Ardea alba*), osprey (*Pandion haliaetus*; Horton et al., 2014; Martell et al., 2014), ovenbird (*Seiurus aurocapilla*; Hallworth & Marra, 2015, Haché et al., 2017), prairie warbler (*Setophaga discolor*), prothonotary warbler (*Protonotaria citrea*; Tonra et al., 2019), Swainson's hawk (*Buteo swainsoni*; Fuller et al.,

1998; Kochert et al., 2011), tree swallow (*Tachycineta bicolor*; Knight et al., 2018), and turkey vulture (*Cathartes aura*; Dodge et al., 2014; Holland et al., 2017, 2019). We selected species to represent a diversity of migratory strategies (e.g., overwater vs. overland, short vs. long distance), geographic range boundaries, avian guilds, tracking technologies, and available data quantities (see *Estimating migratory connectivity*). For the latter, we ensured that all selected species had tracking locations for ≥10 individuals (the approximate number to minimize spatial biases; Knight et al., 2021; O'Toole et al., 2021) because our evaluation procedure required using this data type as part of the response variable (in addition to band re-encounters; see *Integrating data sources and evaluating relative model performance*).

Estimating migratory connectivity

To develop a generalizable approach to describing migratory connectivity between the stationary breeding and nonbreeding seasons across species, we divided the Western Hemisphere into distinct spatial units, referred to as migratory connectivity regions (MCRs) (Figure 2a), that largely corresponded with either predefined Bird Conservation Regions (North America; Bird Canada and North American Bird Conservation Initiative, 2014) or Level II ecoregions (Central and South America; Griffith et al., 1998, see Appendix S1 for more details). To ensure that we did not estimate migratory connectivity between marginal breeding and nonbreeding populations of each species, we only considered MCRs where summed seasonal eBird relative abundance estimates within a given MCR were ≥1% of the summed total seasonal relative abundance across a species' range (see Appendix S1 for details on calculating seasonal abundances from eBird Status and Trends products). We estimated migratory connectivity as the relative proportions of individuals migrating between these selected breeding and nonbreeding MCRs for each species (e.g., Figure 2b). To do this, we statistically integrated (via joint likelihood) band re-encounter and tracking data during the stationary breeding and nonbreeding periods following the method developed by Korner-Nievergelt et al. (2017), which controls for spatial heterogeneity in re-encounter probabilities of marked birds. To maximize sample sizes for inference, we used band re-encounter data obtained from the U.S. Geological Survey (USGS) Bird Banding Laboratory (BBL) since 1930 (e.g., Macdonald et al., 2012; Ryder et al., 2011) and tracking data (LLG, GPS, PTT) obtained by Audubon's Migratory Bird Initiative in partnership with individual researchers (see Appendix S1 for details on data cleaning and filtering procedures). We fit species-specific migratory connectivity models within a Bayesian framework via JAGS (Plummer, 2003) called from R version 4.0.1 (R Core Team, 2019) using the jagsUI package (Kellner, 2016). See Appendix S1 for further details on model implementation and Appendix S2 for details on species-specific migratory connectivity results.

Producing least-cost paths

Within selected MCRs for each species, we ranked each 2.96-km cell (i.e., native resolution of eBird Status and Trends products) by seasonal relative abundance and selected as the breeding and nonbreeding cores (i.e., high-abundance clusters) the minimum number of cells that represented 30% of the total sum of cells (sensu Schuster et al., 2019; Lin et al., 2020) within each MCR (Figure 2a). Relative abundance models for the breeding and nonbreeding seasons for each of the focal species were expert-reviewed and met performance standards of eBird Status and Trends products (Fink, Auer, Johnston, Ruiz-Gutierrez, et al., 2020). We used these breeding and nonbreeding cores for initiation of LCPs (i.e., source of origin points) for postbreeding and prebreeding migration, respectively, because we were primarily interested in identifying major migratory pathways among population clusters. We designed this approach to incorporate two important attributes of identifying natural population structures in the absence of genetic data: abundance and spatial proximity (Rushing et al., 2016).

We randomly selected 50 grid cells within each breeding MCR core to serve as postbreeding migration origin points for species-specific LCPs. Next, we randomly paired each origin point with a destination point in a randomly selected grid cell ($n = 50$) within nonbreeding MCR cores using the relative proportions estimated from the migratory connectivity analysis described earlier (Figure 2b). We then computed a probabilistic (i.e., randomized) LCP (Adriaensen et al., 2003; Storfer et al., 2007; Wang et al., 2009) between each breeding–nonbreeding core pixel pair that minimized the total cumulative cost, where the cost of moving between paired pixels was determined by the intervening distance weighted by a conductance surface representing average (i.e., arithmetic mean across weeks; see Appendix S1: Table S2) postbreeding occurrence probabilities obtained from eBird (Figure 2c). Thus, higher occurrence values during migration coincided with higher conductance. We chose to use occurrence probabilities as the conductance surface, rather than relative abundances, because abundance values for several focal species were highly right-skewed (e.g., high-abundance aggregations of migrating tree swallows), which resulted in LCPs directed toward regions of unusually high abundance, masking the known movements of smaller, regional populations.
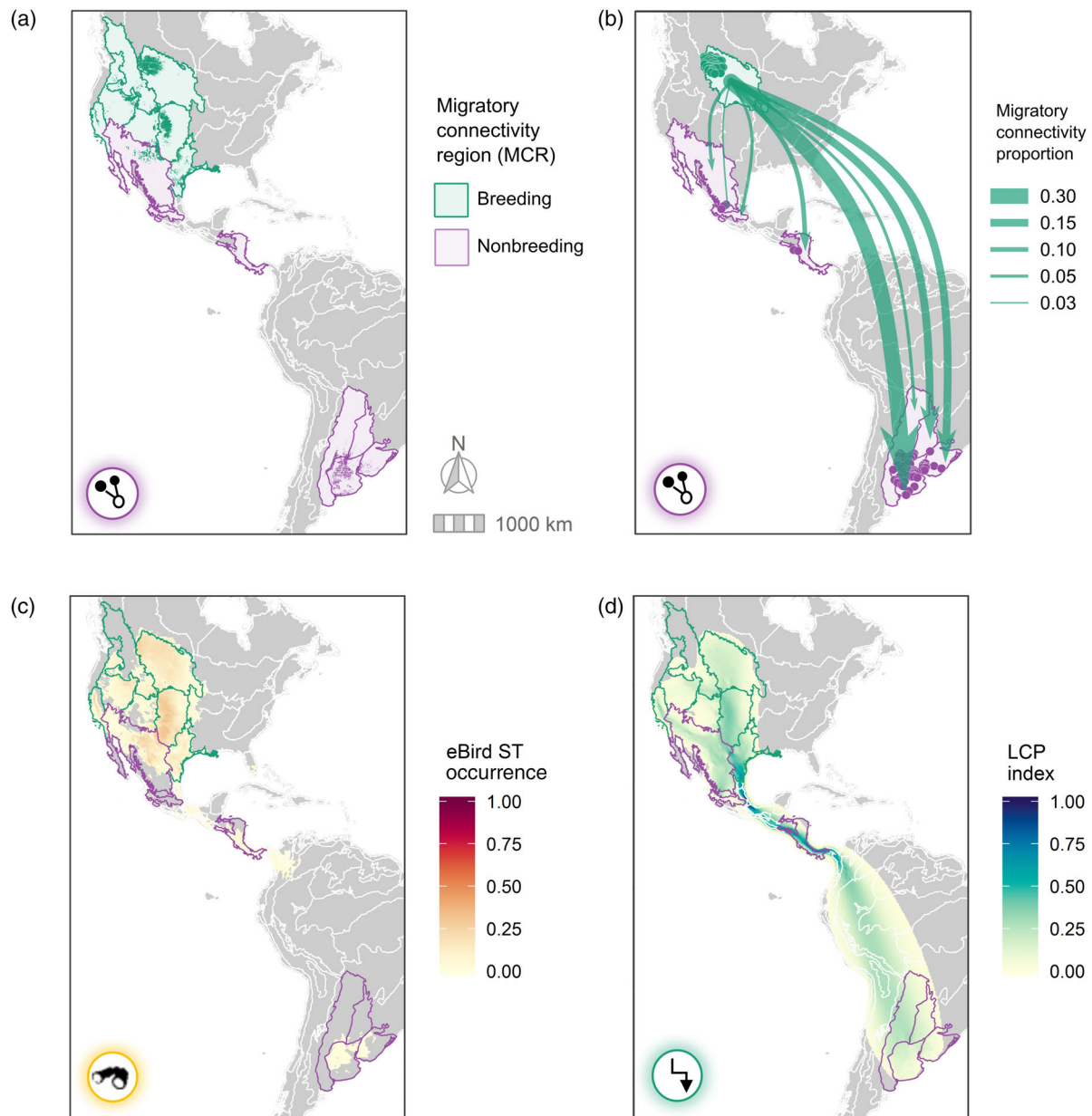
FIGURE 2 (a) Migratory connectivity regions (MCRs) in North, Central, and South America, which we used as the spatial units of the modeling framework. We used Swainson's hawk as an example species to illustrate the breeding (green) and nonbreeding (purple) MCRs selected (i.e., contain ≥1% of total seasonal eBird relative abundance) for inclusion in analyses. Green and purple points represent high-abundance clusters (i.e., sum to 30% of abundance) within each MCR in stationary breeding and nonbreeding seasons, respectively. (b) Estimated proportions from the migratory connectivity analysis for Swainson's hawk integrating tracking and band re-encounter data from stationary breeding and nonbreeding periods; for ease of illustration, the proportions shown refer to a single breeding MCR and, thus, sum to one. (c) Average postbreeding eBird Status and Trends (eBird ST) relative occurrence probabilities of Swainson's hawk (i.e., arithmetic mean of weekly estimates during postbreeding migration period; see Appendix S1: Table S2 for species-specific migration timings). (d) Least-cost path index for Swainson's hawk illustrating probable pathways during postbreeding migration. Icons in bottom left corner of each panel refer to a specific stage of the modeling framework and correspond to those shown in Figure 1.

To create biologically reasonable LCPs, we modified conductance surfaces by adding minimum conductance values where eBird occurrence probabilities were zero or had missing values. These conductance values varied across species to reflect relevant migratory behaviors (e.g., likelihood of long-distance overwater movements).

See Appendix S1 for more details on assigning values to each of the 12 focal species and the potential for customization in future analyses. Partial randomization of the deterministic LCPs was incorporated via a constrained random walk using the passage() function from the gdistance package in R (Van Etten, 2017). The passage

function simulates movements from a starting location to an ending location, with movements between intervening cells governed by a random process superimposed on a cost surface. Random movements are derived from a probability distribution constrained by a parameter that controls the degree of randomization (Saerens et al., 2009). During model development, we evaluated a wide variety of values and algorithms for choosing the degree of randomization and ultimately opted to use half the minimum conductance value, which resulted in individual probabilistic LCPs that had a longitudinal range of ~100 km (see Appendix S1 for more details on the partial randomization process).

Each set of paired grid cells yielded one raster layer (rescaled to a 26.6-km resolution due to computational demands; see Appendix S1) with values between zero and one that described the probability of passage (i.e., LCP index) through a given grid cell during postbreeding migration. We repeated this process for the 50 sets of paired grid cells for each breeding MCR and then repeated the entire procedure in reverse (i.e., nonbreeding season origin points paired with breeding season destination points) using average prebreeding eBird occurrence probabilities as the conductance surface to produce LCP indices during prebreeding migration. Finally, we averaged (i) across the 50 probabilistic LCP surfaces for each season-specific MCR and (ii) across all nonbreeding or breeding MCRs to illustrate probable pathways during pre- and post-breeding migrations, respectively, for each species (Figure 2d). For example, for a species with 10 breeding MCRs, $10 \times 50 = 500$ total LCPs were averaged to produce a postbreeding migration surface.

Integrating data sources and evaluating relative model performance

To integrate additional data sources with LCPs, we first assembled available band re-encounter and tracking data during the pre- and postbreeding migratory periods (i.e., seasonal observations that were not used in previous stages) and followed cleaning procedures similar to those used in migratory connectivity analyses (see Appendix S1 for more details). We also filtered redundant tracking observations by randomly selecting one observation per individual bird per 26.6-km grid cell for each migratory season. Observations were filtered in this way to reduce spatial and temporal autocorrelation (sensu Northrup et al., 2013). For LLG data, we also removed locations over a 20-day period centered on each equinox. At each of these remaining "known presence" locations (e.g., Figure 3a) during each migratory season, we extracted two underlying raster values using geographic coordinates: (i) eBird occurrence probability (Figure 2c) and (ii) LCP index (Figure 2d). We then extracted occurrence probabilities and LCP indices at 10,000 background (pseudo-absence) points drawn from a convex hull across each species' full-annual-cycle range (i.e., the spatial extent of possible migration locations), which we defined by overlaying eBird Status and Trends seasonal ranges with BirdLife International seasonal ranges to encompass peripheral, unmodeled areas (BirdLife International, 2017).

For each species and migratory season, we built three GAMMs assuming a binomial distribution with a logit-link function to evaluate associations between presence/pseudo-absence data and both eBird occurrence probabilities and LCP indices. The full model had a global intercept, a random intercept that represented either an individual bird (tracking data) or all banded birds (band re-encounter data), and a two-dimensional smooth effect of eBird occurrence probabilities and LCP indices because we expected possible interacting and asymptotic relationships between the predictors and the response variable. The random effect was specified to control for potential correlations in tracking locations within individuals, as well as possible error correlations associated with different data types, while minimizing the number of random-effect levels because of computational challenges (e.g., all band re-encounters were assigned the same level). Random intercept levels for pseudo-absence locations were randomly generated in proportion to the presence data (see Appendix S1 for details). In an eBird-only model, we included both intercept terms as well as a one-dimensional smooth effect of eBird occurrence. In a third model, we included only the two intercepts and considered this the null model. Despite filtering tracking data and specifying random effects for individual birds, there was residual autocorrelation in some species–season models (results not shown). However, we did not expect the autocorrelation of tracking data to impact our inferences regarding the contributions of LCP indices relative to eBird occurrence probabilities because (i) tracking data were included as the response variable in all models (i.e., there were no comparisons of models with and without tracking data) and (ii) spatial or temporal autocorrelation is primarily of concern when hypothesis testing (e.g., resource selection modeling; Gillies et al., 2006; Koper & Manseau, 2012), which we did not do here.

We assessed the added contribution of LCP-derived indices to describing eBird-derived migration patterns by comparing model fits of the full model (i.e., eBird + LCP) versus eBird-only model using three evaluation metrics: Akaike's information criterion (AIC), proportion deviance explained, and area under the receiver operator curve (AUC). The same response data (i.e., tracking and band re-encounters during migration) were used for model comparisons within each species–season combination; see Appendix S1 for more details on GAMM fitting
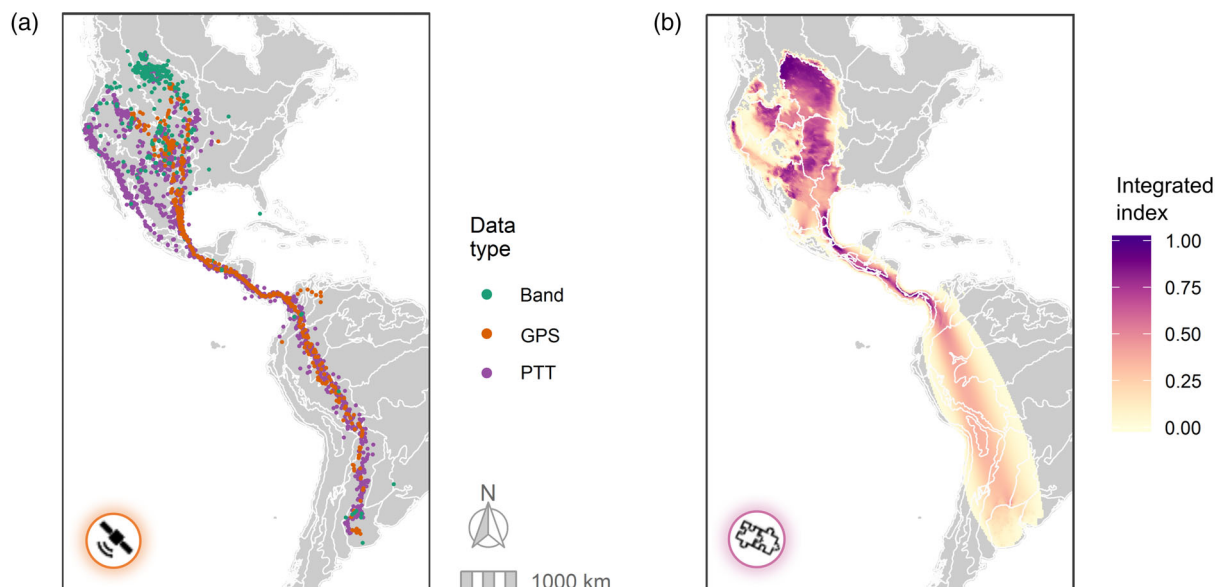
FIGURE 3 (a) Available band re-encounter (green), Global Positioning System (GPS, orange), and platform transmitting terminal (PTT, purple) data for Swainson's hawk during postbreeding migration. These data were considered "known presence" locations and combined with 10,000 background points (i.e., pseudo-absence locations) and used as the response variable in generalized additive mixed models (GAMMs) to create (b) the integrated index illustrating bird migration patterns across the Western Hemisphere (Swainson's hawk shown here). See Appendix S1: Table S3 for sample sizes of the tracking and band re-encounter data sets used in GAMMs for each species–season. Icons in bottom left corner of each panel refer to a specific stage of the modeling framework and correspond to those shown in Figure 1.

and results. We did not evaluate a LCP-only model because we were primarily interested in assessing whether LCP indices provided additional information, beyond that of eBird occurrence probabilities, for describing spatial patterns of avian migration. Although eBird occurrence informed LCP indices, which may have resulted in correlated predictors for some locations, we note that our objective of determining orthogonal added predictive value (rather than hypothesis testing) makes multicollinearity concerns less important.

The resulting GAMM prediction surface (e.g., Figure 3b) for each species in each migratory season represented a statistical integration of eBird occurrence probabilities and LCP indices (i.e., predictor variables in GAMMs), as well as available tracking and band re-encounter data (i.e., as part of the response variable in GAMMs). In what follows, we summarize results across the 12 focal species and illustrate specific results for Swainson's hawk during postbreeding migration as a fully worked case study; see Appendix S3 for all species-specific results and Appendix S4 for data attributions for each of the 12 species analyzed here.

Sensitivity analyses

We conducted post hoc Spearman's correlations using model fit results and quantities and qualities of data types

to evaluate whether our inferences on LCP contributions relative to eBird occurrences were related to data availability or technology type. To further understand the relative effects of data quantity and quality, we ran a multiple linear regression with deviance explained by the full model as a function of the following four predictors that were centered and scaled prior to analysis: number of tracked individuals, number of geolocator-tagged or banded individuals, number of individuals tracked with PTT or GPS tags (i.e., high-quality tracking data), and spatial comprehensiveness of tracking data (i.e., proportion of species-specific breeding and wintering MCRs with ≥1% of the total number of tracking observations). We included the latter metric to determine whether there was a relationship between spatial coverage of tracking data and model fit (see Appendix S1 for more details on sensitivity analyses).

RESULTS

Migratory connectivity

For several focal species (e.g., American white pelican, osprey, ovenbird, prairie warbler), tracking and band re-encounter data suggested relatively high migratory connectivity proportions (i.e., strong connectivity). For example, more than half (0.59) of marked ovenbirds breeding in the

northeastern United States (MCR 14) overwintered in Florida (MCR 31) and the Greater Antilles (MCR 162), while marked ovenbirds breeding in the central/western Canadian boreal region (MCR 6) were generally equally distributed across wintering MCRs in Mexico, Central America, and the Caribbean Islands. For other species, tracking and band re-encounter data supported equivalent (i.e., weak) migratory connectivity among all breeding and nonbreeding MCRs. Given that the migratory connectivity model assumed equal proportions of individuals migrating between breeding and nonbreeding MCR pairs in the absence of available data (i.e., null hypothesis; see Appendix S1), this pattern of uniformly distributed connectivity proportions was a result of data limitations for certain species or for certain breeding–nonbreeding MCR connections within species (see Appendix S2: Table S1 for species-specific sample sizes).

For the Swainson's hawk case study (Figure 2b), the average connectivity proportion between a given breeding MCR and each nonbreeding MCR was 0.13, which was close to the expected (null) proportion of 0.11 (i.e., 1 breeding MCR ÷ 9 nonbreeding MCRs; Figure 2a). Yet our results revealed that proportions were greater than average (i.e., strong connectivity) between the Great Basin (MCR 9) and Northern Prairie (MCR 11) breeding regions of the United States and the Pampas region of Argentina (MCR 232) during the nonbreeding season (0.42 and 0.29, respectively; MCR 11 connections shown in Figure 2b). Further, greater-than-average proportions of individuals breeding in the Central Valley of California (MCR 15) overwintered in the desert regions of the southern United States (Sonoran and Mohave) and northern Mexico (Chihuahuan; MCR 33) and along the Transverse Volcanic Belt (MCR 134) in Mexico (0.23 and 0.22, respectively). Concurrently, Central Valley breeders had lower-than-average proportions of individuals overwintering in the Pampas and Gran Chaco (MCR 134) regions of Argentina (both proportions of 0.06). Though we used these mean connectivity proportions (i.e., posterior means) as a method of incorporating migratory connectivity information into LCPs, we acknowledge that, given limited data, differences in mean connectivity proportions were seldom statistically significant (i.e., 95% credible intervals around mean estimates overlapped; see Appendix S2 for more information). All estimated connectivity proportions for each of the 12 focal species are available on Audubon's GitHub repository: https://github.com/audubongit/migration_data_integration.

Least-cost paths

As designed, LCPs mapped probable migratory pathways and filled in gaps in eBird seasonal occurrence estimates, specifically in areas with a lack of eBird sightings. This pattern was especially apparent for Swainson's hawk during postbreeding migration, where LCP indices provided nonzero estimates over much of South America (e.g., Amazonian rainforest) in areas where eBird occurrence probabilities were zero (Figure 2c,d). Similarly, LCP indices for overwater migrants were nonzero in locations over the Atlantic Ocean and Gulf of Mexico, indicating predicted migratory movements in marine areas where eBird observations were also unavailable (see Appendix S3 for all species-specific results).

In addition to filling in spatial gaps, LCPs mapped migratory bottlenecks or locations where the geographic funneling of migrants could lead to relatively high probabilities of occurrence. For example, for Swainson's hawk during postbreeding migration, the LCP indices over Central America were particularly high relative to the seasonal average occurrence probabilities estimated from eBird (Figure 2c,d). Likewise, several other species demonstrated high-use migratory areas along peninsulas via greater LCP indices (e.g., blackpoll warbler, grasshopper sparrow, prairie warbler, tree swallow in Florida; Appendix S3), as well as stepping stone migratory movements via greater LCP indices in Cuba, where migrants are known to concentrate before or after passage over large expanses of open water (e.g., blackpoll warbler, ovenbird, prairie warbler, prothonotary warbler; Appendix S3).

Relative model performance

When AIC and deviance explained were the evaluation metrics, GAMMs that included LCP indices (i.e., full models) had either equivalent or superior model fit than those that did not (i.e., eBird-only models; Figure 4; Appendix S1: Table S4). However, based on AUC, two species–season models (great egret and prairie warbler during postbreeding migrations) demonstrated poorer fit when LCP indices were included, relative to the eBird-only model. Across the 24 combinations of 12 species and 2 migratory seasons, the inclusion of LCP indices as predictors in GAMMs increased the deviance explained by an average of 57% (range = 0%–163%) and increased AUC by an average of 6% (range = −11%–17%; Appendix S1: Table S4). For Swainson's hawk during postbreeding migration (Figure 3), the addition of LCP indices to the GAMM increased the deviance explained by 67% (Appendix S1: Table S4).

Integrated prediction surfaces

The degree to which eBird occurrences and LCP indices were represented in each species' GAMM-produced

integrated prediction surface depended on the agreement between each predictor and observed locations obtained from tracking data and band re-encounters. For Swainson's hawk, high values of the integrated index in the northwestern plains of North America were largely due to the spatial agreement between band re-encounter locations (Figure 3a) and high eBird occurrence probabilities (Figure 2c). Conversely, high integrated index values across South America (Figure 3b) were almost entirely due to a congruence between telemetry (GPS and PTT) locations and high LCP index values (Figure 2d). Thus, for this species during the postbreeding migration season, both eBird and LCP prediction surfaces appeared to make important contributions to the integrated surface. Across the remaining species, contributions of the two predictors varied considerably and depended, in part, on the extent to which each species migrated over areas where eBird observations were sparse. See Appendix S3 for detailed results for each of the 12 focal species.

Sensitivity analyses

Correlations between data quality/quantity and model fit (Appendix S1: Table S5) and fit improvement (Appendix S1: Table S6) were all positive. When evaluated together via multiple linear regression, we found weak, positive effects of the number of tracked individuals ($\beta = 0.07$, $p = 0.02$) and number of high-quality tracked individuals ($\beta = 0.04$, $p = 0.06$); a weak, negative effect of number of geolocator-tagged individuals ($\beta = -0.05$, $p = 0.07$); and no detectable effect of spatial comprehensiveness ($\beta = -0.03$, $p = 0.21$).

DISCUSSION

There are many approaches to tracking birds during migration (reviewed in Bridge et al., 2011; McKinnon & Love, 2018; Bernard et al., 2021), yet few attempts have been made to unite these technologies with widespread eBird data within a single integrated modeling framework to share information across data sources and account for associated uncertainties and biases (but see Hallworth et al., 2015; Tonra et al., 2019). Our modeling framework leverages the strengths of multiple data types to describe the spatial patterns of avian migration across the Western Hemisphere during pre- and postbreeding migratory seasons. We applied our approach to a suite of 12 species with varying life histories to illustrate its reproducibility across different migratory strategies, tracking technologies, range boundaries, and data quantities. Overall, we demonstrated that LCPs contributed additional information to eBird occurrence probabilities,

broadening our understanding of migratory patterns at unprecedented spatial extents. Given the rapid declines in migratory species globally (Wilcove & Wikelski, 2008; Wilson et al., 2018), knowledge of both the connectivity among populations and the high-use areas during migration can inform conservation strategies to effectively advance species recovery while avoiding expenditures of limited resources on locations that may have little ability to mitigate declines. Although the variability and complexity of biological systems, along with the nuances of data collection, make it difficult to develop a universal integrated model for describing bird migration, this method represents a powerful starting point for further development and customization based on researcher needs and data availabilities (Appendix S1).

Compared to eBird occurrences alone, we found that inclusion of LCP indices as a covariate in GAMMs generally improved model fit for estimating observed animal locations derived from tracking and band re-encounter data sets. Out of 24 species–season models, all but two (great egret and prairie warbler during postbreeding migrations) demonstrated either equivalent or superior fit of the full model (i.e., eBird + LCP) compared to the eBird-only model across three separate performance metrics (Figure 4). For the two exceptions, fits of the full models were only slightly poorer than the eBird-only models based on AUC (Appendix S1: Table S4). From our post hoc analysis evaluating correlations between data quantity/quality and model fit, we found that all correlations were positive, indicating that increased data availability and quality improved model fit (Appendix S1: Tables S5 and S6). When we evaluated data availability metrics together, we found that the number of tracked individuals was the most significant predictor of model fit. Specifically, the inclusion of high-quality tracking data (PTT and GPS tags) was positively associated with model fit, which likely accounts for the poorer fit of the full model for prairie warbler during postbreeding migration because only LLG data (i.e., tracking technology with the greatest location error) were available for this species (Appendix S3: Figure S16). Although spatial comprehensiveness of the tracking data was not a significant predictor of model fit across species, we found that species with <50% of seasonal MCRs containing tracking observations had more variable model performance, which may partly explain the poorer fit of the full model for great egret during postbreeding migration (32% of MCRs with tracking observations; Appendix S1: Table S3 and Appendix S3: Figure S10). Taken together, these results suggest that model performance is optimal when high-quality tracking data are well distributed throughout a species' range, thereby reducing spatial biases and uncertainties.
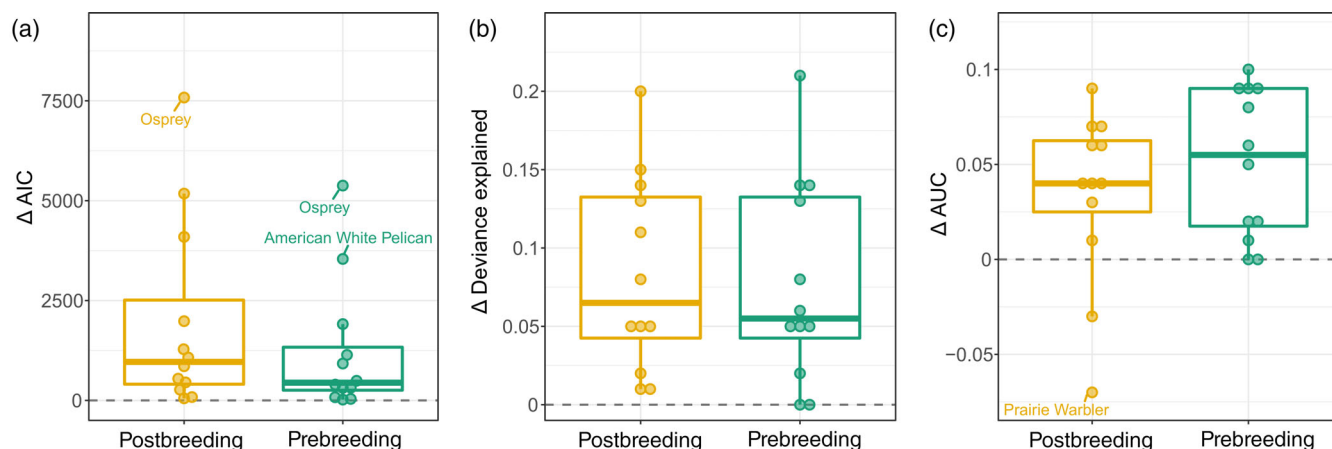
F I G U R E 4 Evaluation metrics—(a) Akaike's information criterion (AIC), (b) deviance explained, and (c) area under receiver operator curve (AUC)—used to assess the difference (Δ) in fits between two generalized additive mixed models (GAMMs): (i) a full model including eBird occurrence probabilities + least-cost path (LCP) passage indices and (ii) a model including only eBird occurrence probabilities as predictors of presence/pseudo-absence data (derived from tracking and band re-encounter data sets during pre- and postbreeding migrations). Positive values (above horizontal dashed line) indicate improvements in model fit with addition of LCP indices (e.g., $AIC_{eBird} - AIC_{full}$ in [a], $DevExp_{full} - DevExp_{eBird}$ in [b], $AUC_{full} - AUC_{eBird}$ in [c]); negative values (below horizontal dashed line) indicate poorer fit of full model relative to eBird-only model; values at zero (on horizontal dashed line) indicate equivalent model fits. Results from 24 species–season model comparisons are shown, with yellow boxplots showing distribution of model fits during postbreeding migration (i.e., fall) and green boxplots showing distribution of model fits during prebreeding migration (i.e., spring). Horizontal lines in boxplots indicate median values, bounds of boxes indicate 25th and 75th percentiles, and labeled points represent outliers. See Appendix S1: Table S4 for additional model fit results.

Species for which LCPs greatly improved model fit via AIC (i.e., positive outliers in Figure 4a), compared to eBird occurrences alone, included osprey and American white pelican, both of which were rich in high-quality tracking data sources (GPS and PTT; Appendix S1: Table S3 and Appendix S3: Figures S1, S2 and S11, S12). LCPs also made a valuable contribution to describing avian migratory patterns for species with overwater movements (e.g., blackpoll warbler in both seasons and prairie warbler during prebreeding migration; Appendix S3: Figures S3, S4 and S15) and those that migrate over land where there are presumably few eBird sightings (e.g., broad-winged hawk and Swainson's hawk in South America; Appendix S3: Figures S5, S6 and S19, S20) and, thus, low predictive ability of eBird Status and Trends models. LCP analysis was designed to model the flow of individuals (or genes) between points on a heterogeneous landscape (Storfer et al., 2007), and our findings demonstrate that this same logic can be applied to birds migrating (i.e., species-specific occurrence estimates) between grid cells at weekly time steps. By supplementing this approach with prior knowledge on migratory connectivity derived from tracking and band re-encounters (i.e., akin to using informed prior distributions in Bayesian frameworks), we are integrating concepts and technologies, enabling LCPs to reflect the migratory behavior of birds at the species level more accurately.

The complexities of avian migration have contributed to a long-standing gap in our knowledge of the full annual cycle and migratory connectivity (Marra et al., 2015; Marra & Studds, 2010). The LCP-derived integrated index of passage probability developed here represents bird space use during migratory seasons and, thus, captures average patterns at the species level. However, we acknowledge that the integrated index is only a proxy for spatially explicit migratory abundances and suggest that it be interpreted within the context of a species' life history to ensure consistency with known migratory patterns. In addition, exploring model modifications, such as spatially varying coefficients for predictor surfaces or a spatial covariance structure, as well as alternative null hypotheses for connectivity analyses (e.g., abundance-weighted or informed by expert opinion or genetic structure), may help overcome potential species-specific challenges.

Although we selected focal species with the goal of developing a robust and widely applicable method, conducting more extensive sensitivity analyses to fully assess model fit across a range of species groups, sample sizes, and tracking technologies is also warranted (see Appendix S1 for further details). For example, we foresee difficulties in applying this modeling framework to species with unusual migrations (e.g., irruptive species like redpolls, grosbeaks, and nuthatches) or with spatially complex distributions of migratory and nonmigratory

populations (e.g., American robin). Species that are primarily aquatic (e.g., terns, loons) or otherwise secretive (e.g., marshbirds), and thus have very low eBird occurrence probabilities terrestrially, will also likely face computational issues during LCP production. While integrating multiple data sources can alleviate some of the limitations of traditional independent analyses, such as filling in spatiotemporal data gaps and increasing the precision of parameter estimates (Zipkin & Saunders, 2018), the caliber of individual data sets ultimately determines the quality of inference, and integrated modeling cannot completely remove biases inherent in each data set. Nevertheless, the resulting integrated index represents a much-needed initial synthesis of several data types that are frequently collected on migratory birds, enabling new insights that may not have been obtained from separate analyses.

There are several potential avenues for further refining this framework (see Appendix S1: Table S7 for more details). Future developments could involve incorporating additional sources of information on migration, including genetic (Ruegg et al., 2020), isotope (Wassenaar, 2019), and Motus (Taylor et al., 2017) data. Although not all of these data types are available for every species, we suggest that researchers could customize the method presented here based on the data available for their species of interest, allowing for a complete, detailed understanding of migratory patterns and connectivity. In the absence of tracking and band-re-encounter data, integrated surfaces could also be produced using the maximum values across eBird occurrence and LCP index surfaces. Indeed, preliminary analyses suggested that using "max" surfaces to generate the integrated index produced results qualitatively similar to those from GAMMs using presence/pseudo-absence locations (see Appendix S1 for more details). For species with long-term tracking data availability that are particularly sensitive to fluctuating environmental conditions (e.g., waterfowl in response to wetland availability), a temporally varying version of this approach (e.g., annual or decadal) could be developed to understand potential shifts in migratory patterns with climate change. While evidence suggests that birds are generally shortening their migration distances as a result of globally rising temperatures (Visser et al., 2009), the rate and magnitude of these changes vary by species' migratory behaviors and winter geographies (Rushing et al., 2020). Estimating and predicting human-induced alterations to animal migrations remains an active area of research (Kubelka et al., 2022).

The acquisition and synthesis of knowledge across technologies is needed to inform the ecology and conservation of migratory birds breeding in North America, which have declined by 2.5 billion since 1970 (Rosenberg et al., 2019). Designing multifunctional landscapes is key to supporting migratory species, and this modeling framework represents a critical step toward predicting where and when (e.g., pre- vs. postbreeding migratory periods) species will be moving through locations, which can help conservationists optimize provisioning of habitat (e.g., stopover) or abatement of threats (e.g., wind turbines, light pollution). Hence, we anticipate several creative uses of this work to advance migration and conservation sciences (Appendix S1: Table S7), including (i) filling knowledge gaps regarding the spatial distribution of species with cryptic life histories that hinder direct observation of movements and (ii) prioritizing localized conservation actions that are responsive to migratory species' spatiotemporal dynamics. Uncovering species' spatial migration patterns during the high-mortality periods of their annual cycles has important implications for migration ecology, migratory bird policies, and conservation actions for populations and species across their ranges. We encourage researchers to explore and advance the methods presented here for other migratory species or systems, which will further expand the scope of inference on spatial patterns of animal movement across hemispheric extents and the full annual cycle.

AUTHOR CONTRIBUTIONS

Timothy D. Meehan conceived the idea for this study in discussion with Nicole L. Michel, Sarah P. Saunders, and William V. DeLuca. Jill L. Deppe, Miguel F. Jimenez, Erika J. Knight, Nathaniel E. Seavy, Melanie A. Smith, Lotem Taylor, and Chad Witko obtained and processed tracking and band re-encounter data as part of Audubon's Migratory Bird Initiative. Timothy D. Meehan and Sarah P. Saunders conducted analyses with help from William V. DeLuca, Nicole L. Michel, and Joanna Grand. Sarah P. Saunders led the writing of the manuscript together with Timothy D. Meehan and William V. DeLuca. All authors contributed to the drafts and gave final approval for submission. Authors listed in Appendix S4 collected and analyzed the tracking data for the 12 focal species.

related to the species-specific tracking projects. We are grateful to M. van Toor and an anonymous reviewer for insightful comments that improved the manuscript.

DATA AVAILABILITY STATEMENT

Tracking data sets for the 12 bird species analyzed here are available on Movebank, band re-encounter data are available through the USGS Bird Banding Laboratory, and Cornell Lab of Ornithology eBird Status and Trends products are available at https://ebird.org/science/status-and-trends. Please see Appendix S4 for data attributions and contact person(s) for each species. Code to run analyses and species-specific migratory connectivity results are provided in Audubon's GitHub repository and permanently archived in Zenodo at https://doi.org/10.5281/zenodo.5996798 (Meehan & Saunders, 2022). Species-specific raster layers of the integrated index shown in Appendix S3 are available in Zenodo at https://doi.org/10.5281/zenodo.6325814 (Meehan et al., 2022).

ORCID

Timothy D. Meehan https://orcid.org/0000-0001-9235-2975

Sarah P. Saunders https://orcid.org/0000-0002-2688-9528

William V. DeLuca https://orcid.org/0000-0002-5099-2293

Nicole L. Michel https://orcid.org/0000-0001-7817-2687
Joanna Grand https://orcid.org/0000-0002-8186-0808
Jill L. Deppe https://orcid.org/0000-0002-6468-7601
Erika J. Knight https://orcid.org/0000-0002-2473-8267
Nathaniel E. Seavy https://orcid.org/0000-0003-0292-3987

Lotem Taylor https://orcid.org/0000-0002-4881-6928
Michael E. Akresh https://orcid.org/0000-0002-8577-2063

David R. Barber https://orcid.org/0000-0002-2919-5011
Erin M. Bayne https://orcid.org/0000-0002-0679-4521
James C. Beasley https://orcid.org/0000-0001-9707-3713
Jerrold L. Belant https://orcid.org/0000-0001-7021-1338
Richard O. Bierregaard https://orcid.org/0000-0001-7445-613X

Than J. Boves https://orcid.org/0000-0002-2382-5684
John N. Brzorad https://orcid.org/0000-0002-6934-8158
Antonio Celis-Murillo https://orcid.org/0000-0002-3371-6529

Hilary A. Cooke https://orcid.org/0000-0002-9435-842X
Laurie Goodrich https://orcid.org/0000-0001-8558-6538
Elizabeth A. Gow https://orcid.org/0000-0001-8890-4503

Aaron Haines https://orcid.org/0000-0001-6893-6102
Michael T. Hallworth https://orcid.org/0000-0002-6385-3815
Scott Jennings https://orcid.org/0000-0002-4922-9661
Roland Kays https://orcid.org/0000-0002-2947-6665
Peter P. Marra https://orcid.org/0000-0002-0508-7577
Rebecca A. McCabe https://orcid.org/0000-0001-7761-6020
Kent P. McFarland https://orcid.org/0000-0001-7809-5503
D. Ryan Norris https://orcid.org/0000-0003-4874-1425
Adam Shreading https://orcid.org/0000-0003-0904-9022
Jesse L. Watson https://orcid.org/0000-0003-4500-6599
Chad B. Wilsey https://orcid.org/0000-0002-1448-1445

REFERENCES

Adriaensen, F., J. P. Chardon, G. De Blust, E. Swinnen, S. Villalba, H. Gulinck, and E. Matthysen. 2003. "The Application of 'Least-Cost' Modelling as a Functional Landscape Model." *Landscape and Urban Planning* 64(4): 233–47. https://doi.org/10.1016/S0169-2046(02)00242-6.

Akresh, M. E., D. I. King, and P. P. Marra. 2019. "Examining Carry-Over Effects of Winter Habitat on Breeding Phenology and Reproductive Success in Prairie Warblers Setophaga Discolor." *Journal of Avian Biology* 50(4). https://doi.org/10.1111/jav.02025.

Albert, S., J. D. Wolfe, J. Kellerman, T. Sherry, B. J. M. Stutchbury, N. J. Bayly, and A. Ruiz-Sánchez. 2020. "Habitat Ecology of Nearctic–Neotropical Migratory Landbirds on the Non-breeding Grounds." *Ornithological Applications* 122(4): duaa055. https://doi.org/10.1093/condor/duaa055.

Bernard, A., A. S. L. Rodrigues, V. Cazalis, and D. Grémillet. 2021. "Toward a Global Strategy for Seabird Tracking." *Conservation Letters* 14(3): e12804. https://doi.org/10.1111/conl.12804.

BirdLife International. 2017. "Bird Species Distribution Maps of the World." Version 2017.2. http://datazone.birdlife.org/species/requestdis.

Bird Studies Canada and North American Bird Conservation Initiative. 2014. "Bird Conservation Regions." Published by Bird Studies Canada on behalf of the North American Bird Conservation Initiative. https://www.birdscanada.org/bird-science/nabci-bird-conservation-regions.

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, et al. 2011. "Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds." *Bioscience* 61(9): 689–98. https://doi.org/10.1525/bio.2011.61.9.7.

Buechley, E. R., S. Oppel, W. S. Beatty, S. C. Nikolov, V. Dobrev, V. Arkumarev, V. Saravia, et al. 2018. "Identifying Critical Migratory Bottlenecks and High-Use Areas for an Endangered Migratory Soaring Bird across Three Continents." *Journal of Avian Biology* 49(7): e01629. https://doi.org/10.1111/jav.01629.

DeLuca, W. V., B. K. Woodworth, S. A. Mackenzie, A. E. M. Newman, H. A. Cooke, L. M. Phillips, N. E. Freeman, et al. 2019. "A Boreal Songbird's 20,000 Km Migration across North America and the Atlantic Ocean." *Ecology* 100(5): 1–4.

DeLuca, W. V., B. K. Woodworth, C. C. Rimmer, P. P. Marra, P. D. Taylor, K. P. McFarland, S. A. Mackenzie, and D. Ryan Norris. 2015. "Transoceanic Migration by a 12 g Songbird." *Biology Letters* 11(4): 20141045. https://doi.org/10.1098/rsbl.2014.1045.

Deppe, J. L., M. P. Ward, R. T. Bolus, R. H. Diehl, A. Celis-Murillo, T. J. Zenzal, F. R. Moore, et al. 2015. "Fat, Weather, and Date Affect Migratory Songbirds' Departure Decisions, Routes, and Time it Takes to Cross the Gulf of Mexico." *Proceedings of the National Academy of Sciences* 112(46): E6331–8. https://doi.org/10.1073/pnas.1503381112.

Dodge, S., G. Bohrer, K. Bildstein, S. C. Davidson, R. Weinzierl, M. J. Bechard, D. Barber, et al. 2014. "Environmental Drivers of Variability in the Movement Ecology of Turkey Vultures (*Cathartes aura*) in North and South America." *Philosophical Transactions of the Royal Society B: Biological Sciences* 369(1643): 20130195. https://doi.org/10.1098/rstb.2013.0195.

Fink, D., T. Auer, A. Johnston, V. Ruiz-Gutierrez, W. M. Hochachka, and S. Kelling. 2020. "Modeling Avian Full Annual Cycle Distribution and Population Trends with Citizen Science Data." *Ecological Applications* 30(3): e02056. https://doi.org/10.1002/eap.2056.

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, O. Robinson, S. Ligocki, B. Petersen, et al. 2020. *eBird Status and Trends, Data Version: 2018; Released: 2020*. Ithaca, NY: Cornell Lab of Ornithology. https://doi.org/10.2173/ebirdst.2018.

Fuller, M. R., W. S. Seegar, and L. S. Schueck. 1998. "Routes and Travel Rates of Migrating Peregrine Falcons Falco Peregrinus and Swainson's Hawks Buteo Swainsoni in the Western Hemisphere." *Journal of Avian Biology* 29(4): 433–40. https://doi.org/10.2307/3677162.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. Joanne Saher, C. E. Stevens, and C. L. Jerde. 2006. "Application of Random Effects to the Study of Resource Selection by Animals." *Journal of Animal Ecology* 75(4): 887–98. https://doi.org/10.1111/j.1365-2656.2006.01106.x.

Griffith, G. E., J. M. Omernik, and S. H. Azevedo. 1998. "Ecological classification of the Western Hemisphere." Unpublished report. Corvallis, OR: US Environmental Protection Agency, Western Ecology Division. 49 pp.

Haché, S., E. M. Bayne, M.-A. Villard, H. Proctor, C. S. Davis, D. Stralberg, J. K. Janes, et al. 2017. "Phylogeography of a Migratory Songbird across its Canadian Breeding Range: Implications for Conservation Units." *Ecology and Evolution* 7(16): 6078–88. https://doi.org/10.1002/ece3.3170.

Haines, A. M., M. J. Mcgrady, M. S. Martell, B. James Dayton, M. Blake Henke, and W. S. Seegar. 2003. "Migration Routes And Wintering Locations Of Broad-Winged Hawks Tracked By Satellite Telemetry." *The Wilson Bulletin* 115(2): 166–9. https://doi.org/10.1676/02-106.

Hallworth, M. T., and P. P. Marra. 2015. "Miniaturized GPS Tags Identify Non-Breeding Territories of a Small Breeding Migratory Songbird." *Scientific Reports* 5(1): 11069. https://doi.org/10.1038/srep11069.

Hallworth, M. T., T. Scott Sillett, S. L. Van Wilgenburg, K. A. Hobson, and P. P. Marra. 2015. "Migratory Connectivity of a Neotropical Migratory Songbird Revealed by Archival Light-Level Geolocators." *Ecological Applications* 25(2): 336–47. https://doi.org/10.1890/14-0195.1.

Hill, J. M., and R. B. Renfrew. 2019. "Migratory Patterns and Connectivity of Two North American Grassland Bird Species." *Ecology and Evolution* 9(1): 680–92. https://doi.org/10.1002/ece3.4795.

Holland, A. E., M. E. Byrne, A. Lawrence Bryan, T. L. DeVault, O. E. Rhodes, and J. C. Beasley. 2017. "Fine-Scale Assessment of Home Ranges and Activity Patterns for Resident Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*)." *PLoS One* 12(7): e0179819. https://doi.org/10.1371/journal.pone.0179819.

Holland, A. E., M. E. Byrne, A. Jeffrey Hepinstall-Cymerman, L. Bryan, T. L. DeVault, O. E. Rhodes, and J. C. Beasley. 2019. "Evidence of Niche Differentiation for Two Sympatric Vulture Species in the Southeastern United States." *Movement Ecology* 7(1): 31. https://doi.org/10.1186/s40462-019-0179-z.

Horton, T. W., R. O. Bierregaard, P. Zawar-Reza, R. N. Holdaway, and P. Sagar. 2014. "Juvenile Osprey Navigation during Trans-Oceanic Migration." *PLoS One* 9(12): e114557. https://doi.org/10.1371/journal.pone.0114557.

Howard, C., P. A. Stephens, J. W. Pearce-Higgins, R. D. Gregory, S. H. M. Butchart, and S. G. Willis. 2020. "Disentangling the Relative Roles of Climate and Land Cover Change in Driving the Long-Term Population Trends of European Migratory Birds." *Diversity and Distributions* 26(11): 1442–55. https://doi.org/10.1111/ddi.13144.

Johnston, A., T. Auer, D. Fink, M. Strimas-Mackey, M. Iliff, K. V. Rosenberg, S. Brown, R. Lanctot, A. D. Rodewald, and S. Kelling. 2020. "Comparing Abundance Distributions and Range Maps in Spatial Conservation Planning for Migratory Species." *Ecological Applications* 30(3): e02058. https://doi.org/10.1002/eap.2058.

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski. 2015. "Terrestrial Animal Tracking as an Eye on Life and Planet." *Science* 348(6240): aaa2478. https://doi.org/10.1126/science.aaa2478.

Kellner, K. 2016. "jagsUI: A Wrapper Around rjags to Streamline JAGS Analyses." R package version 1.4.2. https://CRAN.R-project.org/package=jagsUI.

Knight, E. C., A.-L. Harrison, A. L. Scarpignato, S. L. Van Wilgenburg, E. M. Bayne, J. W. Ng, E. Angell, et al. 2021. "Comprehensive Estimation of Spatial and Temporal Migratory Connectivity across the Annual Cycle to Direct Conservation Efforts." *Ecography* 44(5): 665–79. https://doi.org/10.1111/ecog.05111.

Knight, S. M., D. W. Bradley, R. G. Clark, E. A. Gow, M. Bélisle, L. L. Berzins, T. Blake, et al. 2018. "Constructing and Evaluating a Continent-Wide Migratory Songbird Network across the Annual Cycle." *Ecological Monographs* 88(3): 445–60. https://doi.org/10.1002/ecm.1298.

Kochert, M. N., M. R. Fuller, L. S. Schueck, L. Bond, M. J. Bechard, B. Woodbridge, G. Holroyd, M. Martell, and U. Banasch. 2011. "Migration Patterns, Use of Stopover Areas, and Austral Summer Movements of Swainson's Hawks." *The Condor* 113(1): 89–106. https://doi.org/10.1525/cond.2011.090243.

Koper, N., and M. Manseau. 2012. "A Guide to Developing Resource Selection Functions from Telemetry Data Using Generalized Estimating Equations and Generalized Linear Mixed Models." *Rangifer* 32(2): 195–204. https://doi.org/10.7557/2.32.2.2269.

Korner-Nievergelt, F., C. Prévot, S. Hahn, L. Jenni, and F. Liechti. 2017. "The Integration of Mark re-Encounter and Tracking Data

to Quantify Migratory Connectivity." *Ecological Modelling* 344(1): 87–94. https://doi.org/10.1016/j.ecolmodel.2016.11.009.

Kreakie, B. J., and T. H. Keitt. 2012. "Integration of Distance, Direction and Habitat into a Predictive Migratory Movement Model for Blue-Winged Teal (*Anas discors*)." *Ecological Modelling* 224(1): 25–32. https://doi.org/10.1016/j.ecolmodel.2011.10.019.

Kubelka, V., B. K. Sandercock, T. Székely, and R. P. Freckleton. 2022. "Animal Migration to Northern Latitudes: Environmental Changes and Increasing Threats." *Trends in Ecology & Evolution* 37(1): 30–41. https://doi.org/10.1016/j.tree.2021.08.010.

Li, X., Y. Si, L. Ji, and P. Gong. 2017. "Dynamic Response of East Asian Greater White-Fronted Geese to Changes of Environment during Migration: Use of Multi-Temporal Species Distribution Model." *Ecological Modelling* 360(9): 70–9. https://doi.org/10.1016/j.ecolmodel.2017.06.004.

Lin, H.-Y., R. Schuster, S. Wilson, S. J. Cooke, A. D. Rodewald, and J. R. Bennett. 2020. "Integrating Season-Specific Needs of Migratory and Resident Birds in Conservation Planning." *Biological Conservation* 252(12): 108826. https://doi.org/10.1016/j.biocon.2020.108826.

Macdonald, C. A., K. C. Fraser, H. G. Gilchrist, T. K. Kyser, J. W. Fox, and O. P. Love. 2012. "Strong Migratory Connectivity in a Declining Arctic Passerine." *Animal Migration* 1(1): 23–30. https://doi.org/10.2478/ami-2012-0003.

Marra, P. P., D. R. Norris, S. M. Haig, M. Webster, and J. A. Royle. 2006. "Migratory Connectivity." In *Maintaining Connections for Nature*, edited by K. Crooks and S. Muttulingam. New York: Cambridge University Press.

Marra, P. P., and C. E. Studds. 2010. "Migratory Connectivity." In *Encyclopedia of Animal Behavior*, Vol 2, edited by J. Choe, 455–61. Oxford: Oxford Academic Press.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. "A Call for Full Annual Cycle Research in Animal Ecology." *Biology Letters* 11(8): 20150552. https://doi.org/10.1098/rsbl.2015.0552.

Martell, M. S., R. O. Bierregaard Jr, B. E. Washburn, J. E. Elliott, C. J. Henny, R. S. Kennedy, and I. MacLeod. 2014. "The Spring Migration of Adult North American Ospreys." *Journal of Raptor Research* 48(4): 309–24. https://doi.org/10.3356/JRR-14-00035.1.

McCabe, R. A., L. J. Goodrich, D. R. Barber, T. L. Master, J. L. Watson, E. M. Bayne, A.-L. Harrison, P. P. Marra, and K. L. Bildstein. 2020. "Satellite Tracking Reveals Age and Origin Differences in Migration Ecology of Two Populations of Broad-Winged Hawks (*Buteo platypterus*)." *The Wilson Journal of Ornithology* 132(1): 1–14. https://doi.org/10.1676/1559-4491-132.1.1.

McGowan, J., M. Beger, R. L. Lewison, R. Harcourt, H. Campbell, M. Priest, R. G. Dwyer, et al. 2017. "Integrating Research Using Animal-Borne Telemetry with the Needs of Conservation Management." *Journal of Applied Ecology* 54(2): 423–9. https://doi.org/10.1111/1365-2664.12755.

McKinnon, E. A., and O. P. Love. 2018. "Ten Years Tracking the Migrations of Small Landbirds: Lessons Learned in the Golden Age of Bio-Logging." *The Auk* 135(4): 834–56. https://doi.org/10.1642/AUK-17-202.1.

Meehan, T. D., and S. P. Saunders. 2022. "audubongit/migration_data_integration (version 1.0.0)." Zenodo. https://doi.org/10.5281/zenodo.5996798.

Meehan, T. D., S. P. Saunders, W. V. DeLuca, N. L. Michel, J. Grand, J. L. Deppe, M. F. Jimenez, et al. 2022. "Integrating Data Types to Estimate Spatial Patterns of Avian Migration across the Western Hemisphere (Version 1.0.0)." Zenodo. https://doi.org/10.5281/zenodo.6325814.

Miller, D. A. W., K. Pacifici, J. S. Sanderlin, and B. J. Reich. 2019. "The Recent Past and Promising Future for Data Integration Methods to Estimate Species' Distributions." *Methods in Ecology and Evolution* 10(1): 22–37. https://doi.org/10.1111/2041-210X.13110.

Nandintsetseg, D., C. Bracis, K. A. Olson, K. Böhning-Gaese, J. M. Calabrese, B. Chimeddorj, W. F. Fagan, et al. 2019. "Challenges in the Conservation of Wide-Ranging Nomadic Species." *Journal of Applied Ecology* 56(8): 1916–26. https://doi.org/10.1111/1365-2664.13380.

Newton, I. 2006. "Can Conditions Experienced during Migration Limit the Population Levels of Birds?" *Journal of Ornithology* 147(2): 146–66. https://doi.org/10.1007/s10336-006-0058-4.

Nilsson, C., A. M. Dokter, L. Verlinden, J. Shamoun-Baranes, B. Schmid, P. Desmet, S. Bauer, et al. 2019. "Revealing Patterns of Nocturnal Migration Using the European Weather Radar Network." *Ecography* 42(5): 876–86. https://doi.org/10.1111/ecog.04003.

Northrup, J. M., M. B. Hooten, C. R. Anderson, Jr., and G. Wittemyer. 2013. "Practical Guidance on Characterizing Availability in Resource Selection Functions under a Use–Availability Design." *Ecology* 94(7): 1456–63. https://doi.org/10.1890/12-1688.1.

Nourani, E., K. Safi, N. M. Yamaguchi, and H. Higuchi. 2018. "Raptor Migration in an Oceanic Flyway: Wind and Geography Shape the Migratory Route of Grey-Faced Buzzards in East Asia." *Royal Society Open Science* 5(3): 171555. https://doi.org/10.1098/rsos.171555.

O'Toole, M., N. Queiroz, N. E. Humphries, D. W. Sims, and A. M. M. Sequeira. 2021. "Quantifying Effects of Tracking Data Bias on Species Distribution Models." *Methods in Ecology and Evolution* 12(1): 170–81. https://doi.org/10.1111/2041-210X.13507.

Plummer, M. 2003. "JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling." In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing, DSC 2003* 20–2. Vienna, Austria: Vienna University of Technology.

Pullinger, M. G., and C. J. Johnson. 2010. "Maintaining or Restoring Connectivity of Modified Landscapes: Evaluating the Least-Cost Path Model with Multiple Sources of Ecological Information." *Landscape Ecology* 25(10): 1547–60. https://doi.org/10.1007/s10980-010-9526-6.

Rakhimberdiev, E., N. R. Senner, M. A. Verhoeven, D. W. Winkler, W. Bouten, and T. Piersma. 2016. "Comparing Inferences of Solar Geolocation Data against High-Precision GPS Data: Annual Movements of a Double-Tagged Black-Tailed Godwit." *Journal of Avian Biology* 47(4): 589–96. https://doi.org/10.1111/jav.00891.

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing https://www.R-project.org/.

Robertson, E. P., R. J. Fletcher, C. E. Cattau, B. J. Udell, B. E. Reichert, J. D. Austin, and D. Valle. 2018. "Isolating the Roles

of Movement and Reproduction on Effective Connectivity Alters Conservation Priorities for an Endangered Bird." *Proceedings of the National Academy of Sciences* 115(34): 8591–6. https://doi.org/10.1073/pnas.1800183115.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, et al. 2019. "Decline of the North American Avifauna." *Science* 366(6461): 120–4. https://doi.org/10.1126/science.aaw1313.

Ruegg, K. C., R. J. Harrigan, J. F. Saracco, T. B. Smith, and C. M. Taylor. 2020. "A Genoscape-Network Model for Conservation Prioritization in a Migratory Bird." *Conservation Biology* 34(6): 1482–91. https://doi.org/10.1111/cobi.13536.

Runge, C. A., A. I. T. Tulloch, H. P. Possingham, V. J. D. Tulloch, and R. A. Fuller. 2016. "Incorporating Dynamic Distributions into Spatial Prioritization." *Diversity and Distributions* 22(3): 332–43. https://doi.org/10.1111/ddi.12395.

Rushing, C. S., J. Andrew Royle, D. J. Ziolkowski, and K. L. Pardieck. 2020. "Migratory Behavior and Winter Geography Drive Differential Range Shifts of Eastern Birds in Response to Recent Climate Change." *Proceedings of the National Academy of Sciences* 117(23): 12897–903. https://doi.org/10.1073/pnas.2000299117.

Rushing, C. S., T. B. Ryder, A. L. Scarpignato, J. F. Saracco, and P. P. Marra. 2016. "Using Demographic Attributes from Long-Term Monitoring Data to Delineate Natural Population Structure." *Journal of Applied Ecology* 53(2): 491–500. https://doi.org/10.1111/1365-2664.12579.

Ryder, T. B., J. W. Fox, and P. P. Marra. 2011. "Estimating Migratory Connectivity of Gray Catbirds (*Dumetella carolinensis*) Using Geolocator and Mark—Recapture Data." *The Auk* 128(3): 448–53. https://doi.org/10.1525/auk.2011.11091.

Saerens, M., Y. Achbany, F. Fouss, and L. Yen. 2009. "Randomized Shortest-Path Problems: Two Related Models." *Neural Computation* 21(8): 2363–404. https://doi.org/10.1162/neco.2009.11-07-643.

Schuster, R., S. Wilson, A. D. Rodewald, P. Arcese, D. Fink, T. Auer, and J. R. Bennett. 2019. "Optimizing the Conservation of Migratory Species over their Full Annual Cycle." *Nature Communications* 10(1): 1754. https://doi.org/10.1038/s41467-019-09723-8.

Storfer, A., M. A. Murphy, J. S. Evans, C. S. Goldberg, S. Robinson, S. F. Spear, R. Dezzani, E. Delmelle, L. Vierling, and L. P. Waits. 2007. "Putting the 'Landscape' in Landscape Genetics." *Heredity* 98(3): 128–42. https://doi.org/10.1038/sj.hdy.6800917.

Sullivan, B. L., J. L. Aycrigg, J. H. Barry, R. E. Bonney, N. Bruns, C. B. Cooper, T. Damoulas, et al. 2014. "The EBird Enterprise: An Integrated Approach to Development and Application of Citizen Science." *Biological Conservation* 169(January): 31–40. https://doi.org/10.1016/j.biocon.2013.11.003.

Taylor, P., T. Crewe, S. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, et al. 2017. "The Motus Wildlife Tracking System: A Collaborative Research Network to Enhance the Understanding of Wildlife Movement." *Avian Conservation and Ecology* 12(1): 8. https://doi.org/10.5751/ACE-00953-120108.

Tonra, C. M., M. T. Hallworth, T. J. Boves, J. Reese, L. P. Bulluck, M. Johnson, C. Viverette, et al. 2019. "Concentration of a Widespread Breeding Population in a Few Critically Important Nonbreeding Areas: Migratory Connectivity in the Prothonotary Warbler." *The Condor* 121(2): 1–15. https://doi.org/10.1093/condor/duz019.

Van Etten, J. 2017. "R Package Gdistance: Distances and Routes on Geographical Grids." *Journal of Statistical Software* 76: 1–21.

Visser, M. E., A. C. Perdeck, J. H. V. Balen, and C. Both. 2009. "Climate Change Leads to Decreasing Bird Migration Distances." *Global Change Biology* 15(8): 1859–65. https://doi.org/10.1111/j.1365-2486.2009.01865.x.

Wang, I. J., W. K. Savage, and H. Bradley Shaffer. 2009. "Landscape Genetics and Least-Cost Path Analysis Reveal Unexpected Dispersal Routes in the California Tiger Salamander (*Ambystoma californiense*)." *Molecular Ecology* 18(7): 1365–74. https://doi.org/10.1111/j.1365-294X.2009.04122.x.

Wassenaar, L. I. 2019. "Introduction to Conducting Stable Isotope Measurements for Animal Migration Studies." In *Tracking Animal Migrations with Stable Isotopes*, 2nd ed. 25–51. Cambridge, MA: Academic Press.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. "Links between Worlds: Unraveling Migratory Connectivity." *Trends in Ecology & Evolution* 17(2): 76–83. https://doi.org/10.1016/S0169-5347(01)02380-1.

Wilcove, D. S., and M. Wikelski. 2008. "Going, Going, Gone: Is Animal Migration Disappearing." *PLoS Biology* 6(7): e188. https://doi.org/10.1371/journal.pbio.0060188.

Wilson, S., R. Schuster, A. D. Rodewald, J. R. Bennett, A. C. Smith, F. A. La Sorte, P. H. Verburg, and P. Arcese. 2019. "Prioritize Diversity or Declining Species? Trade-Offs and Synergies in Spatial Planning for the Conservation of Migratory Birds in the Face of Land Cover Change." *Biological Conservation* 239(11): 108285. https://doi.org/10.1016/j.biocon.2019.108285.

Wilson, S., J. F. Saracco, D. T. Richard Krikun, T. Flockhart, C. M. Godwin, and K. R. Foster. 2018. "Drivers of Demographic Decline across the Annual Cycle of a Threatened Migratory Bird." *Scientific Reports* 8(1): 7316. https://doi.org/10.1038/s41598-018-25633-z.

Zipkin, E. F., E. R. Zylstra, A. D. Wright, S. P. Saunders, A. O. Finley, M. C. Dietze, M. S. Itter, and M. W. Tingley. 2021. "Addressing Data Integration Challenges to Link Ecological Processes across Scales." *Frontiers in Ecology and the Environment* 19(1): 30–8. https://doi.org/10.1002/fee.2290.

Zipkin, E. F., and S. P. Saunders. 2018. "Synthesizing Multiple Data Types for Biological Conservation Using Integrated Population Models." *Biological Conservation* 217: 240–50. https://doi.org/10.1016/j.biocon.2017.10.017.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Meehan, Timothy D., Sarah P. Saunders, William V. DeLuca, Nicole L. Michel, Joanna Grand, Jill L. Deppe, Miguel F. Jimenez, et al. 2022. "Integrating Data Types to Estimate Spatial Patterns of Avian Migration across the Western Hemisphere." *Ecological Applications* e2679. https://doi.org/10.1002/eap.2679