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Research article

# Spatial and temporal migratory connectivity of two sympatrically breeding wood-warblers with geographically discordant population trends

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Factors outside the breeding season can affect population trends for migratory species. Yet information on population-specific migration and nonbreeding ecology for most species is lacking, complicating conservation efforts. Louisiana waterthrush *Parkesia motacilla* and worm-eating warblers *Helmitheros vermivorum* are Nearctic–Neotropical migratory songbirds that share breeding habitat associations, and occur in sympatry throughout most of their breeding distributions. Yet these species exhibit variable regional population trends on the breeding grounds, suggesting that processes outside of the breeding period may impact population growth. We used light-level geolocators to track Louisiana waterthrush and worm-eating warblers from four sites spanning their breeding distributions (Arkansas, Tennessee, Ohio, and Pennsylvania, USA). We describe the geographic distribution of populations during the nonbreeding period and quantify interspecific variation in the timing of migration to assess the potential for factors outside the breeding period to impact population dynamics. From 2016 to 2020, we marked 153 individuals (85 Louisiana waterthrush and 68 worm-eating warblers) across the four sites, and estimated migration timing, nonbreeding locations, and migratory connectivity for 24 Louisiana waterthrush and 21 worm-eating warblers. We observed moderately strong migratory connectivity (MC) in both species (Louisiana waterthrush MC = 0.40 [0.25 SE], worm-eating warbler MC = 0.44 [0.13 SE]) between breeding and nonbreeding sites, and a high degree of overlap (i.e. > 50%) among most populations' nonbreeding core-use areas. Moreover, populations experienced largely similar environmental conditions (measured by enhanced vegetation index) during the nonbreeding period. On average, Louisiana waterthrush initiated migration ~ 40 days earlier than worm-eating warblers across the annual cycle, and this trend was strongest in southern breeding populations. These findings emphasize the value of leveraging multiple species into full-annual cycle studies to identify

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when and where factors limiting populations of migratory species may occur. Additionally, we demonstrate that migratory species that co-occur during stationary periods of the annual cycle (i.e. breeding and nonbreeding periods) can experience strong temporal isolation during seasonal migration.

Keywords: light-level geolocator, limiting factors, Louisiana waterthrush, migration ecology, nonbreeding period, worm-eating warbler

## Introduction

Conserving migratory birds is complicated by their reliance on geographically distinct landscapes required to complete their annual cycle. Conservation efforts can be improved by identifying the factors that limit populations and determining when and where throughout the annual cycle they occur (Runge et al. 2014, Torstensen et al. 2024). Populations of migratory species can be limited by lethal and sublethal factors (Nemes et al. 2023) occurring during the breeding period (Hallworth et al. 2021, Ko et al. 2023), during migration (Iwamura et al. 2013, Finch et al. 2014, Hewson et al. 2016), during the nonbreeding period (Robbins et al. 1989, Sherry and Holmes 1995, 1996, Kramer et al. 2018, Morrick et al. 2022), or by a combination of factors occurring across periods of the annual cycle (Lewis et al. 2023, Nemes et al. 2023). Moreover, periods of the annual cycle are connected such that factors or processes operating during one portion of the annual cycle (e.g. habitat quality, severe weather events) can impact individual condition and performance in subsequent periods (i.e. carry-over effects; Rockwell et al. 2012, Latta et al. 2016). Such carry-over effects can ultimately influence downstream fitness and thus population dynamics over time (Harrison et al. 2011). However, information on the movements and connectivity of populations throughout migration and the nonbreeding period is lacking for many migratory birds, complicating targeted conservation efforts (Faaborg et al. 2010a, 2010b, Marra et al. 2015).

To date, most efforts to identify factors limiting populations of migratory species across the annual cycle have focused on linking variation in population trends with temporal and spatial characteristics of migration, or factors occurring within population-specific breeding or nonbreeding areas for a single species (Arlt et al. 2015, McKinnon et al. 2018, Delancey et al. 2020). However, multi-species conservation efforts, wherein conservation actions are implemented with the intention of benefitting more than one species, are common (Brooks et al. 2006, Kramer et al. 2019, Zarri et al. 2024) – including on migratory species' nonbreeding grounds (e.g. shade-grown coffee plantations; Bakermans et al. 2009, Valente et al. 2022) – and determining whether limiting factors are shared among sympatrically breeding species would improve targeted conservation outcomes. Whether co-occurring focal species share limiting factors is rarely known, leading to potentially inefficient or counterproductive conservation outcomes (Kramer et al. 2019). Notably, many species exhibit regional variation in breeding population trends (e.g. *Vermivora* warblers, Kramer et al. 2018; common nighthawks *Chordeiles minor*, Knight et al. 2021; Connecticut warblers *Oporornis agilis*, Hallworth et al. 2021; black-crowned night-herons *Nycticorax nycticorax*, Scarpignato et al. 2021), sometimes contrasting markedly with trends of sympatric, ecologically similar species (e.g. *Vermivora* warblers, Kramer et al. 2018; *Calidris* shorebirds, Lisovski et al. 2021). Differential population trends among co-occurring, ecologically similar species provide opportunity to disentangle the relative effects of limiting factors across different portions of the annual cycle. Namely, interspecific variation in migratory ecology (e.g. migratory routes, stopover sites, migration timing, migratory connectivity) may result in exposure to heterogeneous conditions among individuals (Hill and Renfrew 2019, Lisovski et al. 2021, Buchan et al. 2023, Kramer et al. 2023) and consequently may contribute to observed variation in breeding population trends (Kramer et al. 2018; but see Scarpignato et al. 2021). Specifically, the population trends of co-occurring, ecologically similar species may be potentially limited by similar factors if those species share patterns of space use throughout the annual cycle. If multiple species exhibit similar patterns of strong spatial and temporal migratory connectivity (i.e. wherein individuals that occurred close together during the breeding period also migrated at the same time, used similar migration routes, and co-occurred during the nonbreeding period), limiting factors may be similar for both species. Conversely, different factors could act to limit populations of ecologically similar species that co-occur during the breeding period but occur in temporal or spatial isolation during migration (e.g. factors related to stopover sites; Studds et al. 2017) or the nonbreeding period (e.g. land-use change on nonbreeding grounds; Kramer et al. 2018).

Louisiana waterthrush *Parkesia motacilla* and worm-eating warblers *Helmitheros vermivorum* are two ecologically similar, co-occurring species that present a unique opportunity to assess whether nonbreeding factors could be associated with geographic variation in breeding-population trends. These Nearctic–Neotropical migratory wood-warblers (Parulidae) overlap extensively throughout their breeding and nonbreeding distributions (Fig. 1) and share similar breeding habitat associations (Mattsson et al. 2020, Vitz et al. 2020). Both species breed in primarily deciduous mid- to late-successional forests in eastern North America within landscapes often characterized by steep, hilly terrain and small- to medium-sized streams (commonly first- and second-order tributaries; Mattsson et al. 2020, Vitz et al. 2020). Both species nest on the ground. Louisiana waterthrush nest almost exclusively among detritus and vegetation on streambanks (Bryant et al. 2020, Mattsson et al. 2020) whereas worm-eating warblers

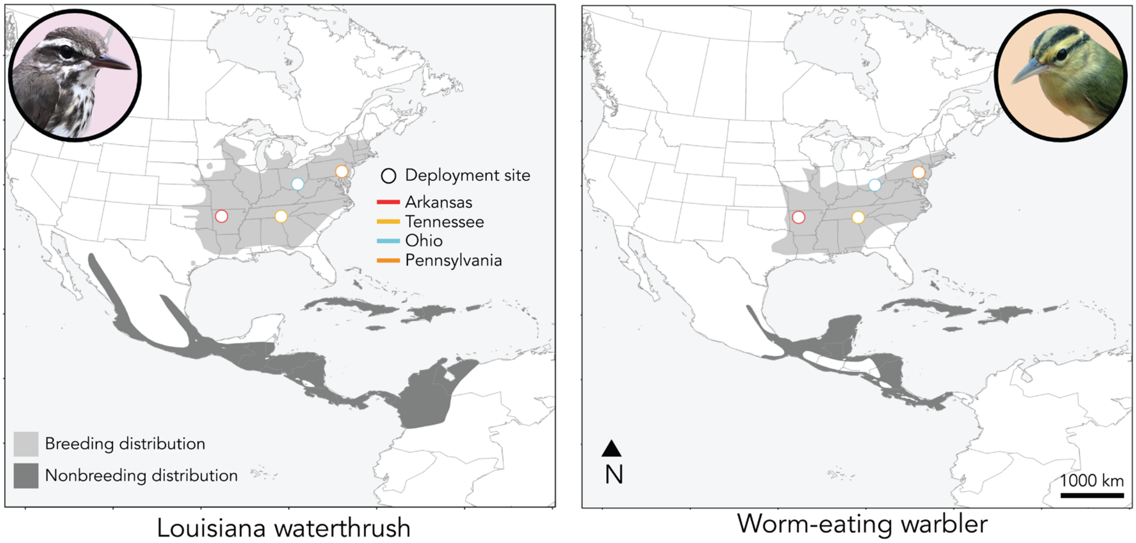


Figure 1. Breeding (light gray) and nonbreeding (dark gray) distributions of Louisiana waterthrush and worm-eating warblers. Circles with colored outlines indicate study areas where we geolocator-marked sympatrically breeding individuals of both species. Distribution map data are from BirdLife International (2016).

nest in leaf litter on steep hillsides often upslope from streams (Ruhl et al. 2018b). During the post-fledging period, and prior to migration, worm-eating warblers are less dependent on large contiguous tracts of mature forest, often using early-successional forest and canopy gaps in mature forest patches (Ruhl et al. 2018a, 2018b; but see Youngman 2017), whereas the presence of a perennial water source seems to be a more meaningful driver of Louisiana waterthrush habitat occupancy during the post-nesting period (McClure and Hill 2012). Despite relatively stable distribution-wide population growth (~ 3–4% $yr^{-1}$) over the past 50 years (Pardieck et al. 2020; Fig. 2), both species are the foci of broad conservation initiatives because of their association with large tracts of mature deciduous forest (Youngman 2017) and water quality in the case of Louisiana waterthrush (O'Connell et al. 2003, Mulvihill et al. 2008). Because of their similar breeding habitat requirements, forest management prioritizing the conservation of large tracts of mature forest within topographically diverse landscapes is presumed to benefit both species (Robinson and Wilcove 1994). However, across their breeding distributions, these species often exhibit locally divergent population trends (Fig. 2 and Supporting information), suggesting the mechanisms driving population dynamics may not be associated within shared breeding landscapes and may involve factors occurring outside the breeding period. For example, in northwestern Arkansas and southern Ohio, Louisiana waterthrush populations have remained numerically stable whereas worm-eating warblers have increased in abundance by > 1.5% annually since 1970 (Fig. 2 and Supporting information). In contrast, population trends are positively correlated for both species in southeastern Pennsylvania (both species increased > 1.8% annually since 1970) and negatively correlated in southeastern Tennessee where Louisiana waterthrush increased by 2.4% annually since 1970 whereas worm-eating warblers have declined by −0.4% annually over the past 50 years (Pardieck et al. 2020; Fig. 2 and Supporting information).

We used light-level geolocators (hereafter geolocators) to track sympatrically breeding Louisiana waterthrush and worm-eating warblers from sites spanning their breeding distributions and to determine whether factors outside the breeding period (i.e. during migration or the nonbreeding period) could be associated with locally discordant population trends (Fig. 1). We hypothesized that populations of Louisiana waterthrush and worm-eating warblers that co-occurred during the breeding period would use geographically isolated regions during the nonbreeding period where regional environmental conditions (e.g. enhanced vegetation index, EVI; Huete et al. 2002, Didan 2021) could correspond with limiting factors that could help explain variation in population trends. Alternatively, we hypothesized that discordance among species' regional breeding population trends may be associated with differences in migration timing which could expose populations to different potentially limiting factors during migratory periods. These data fill critical knowledge gaps in the natural history of these species by describing migratory connectivity, migration timing, and space use of individuals from known breeding populations outside of the breeding period. Moreover, these results demonstrate the value in tracking multiple co-occurring species to determine spatial and temporal overlap throughout the annual cycle and aid in identifying when and where limiting factors may occur to improve conservation outcomes.

## Material and methods

### Study area

We selected four study areas in Arkansas (AR), Tennessee (TN), Ohio (OH), and Pennsylvania (PA), USA, where both

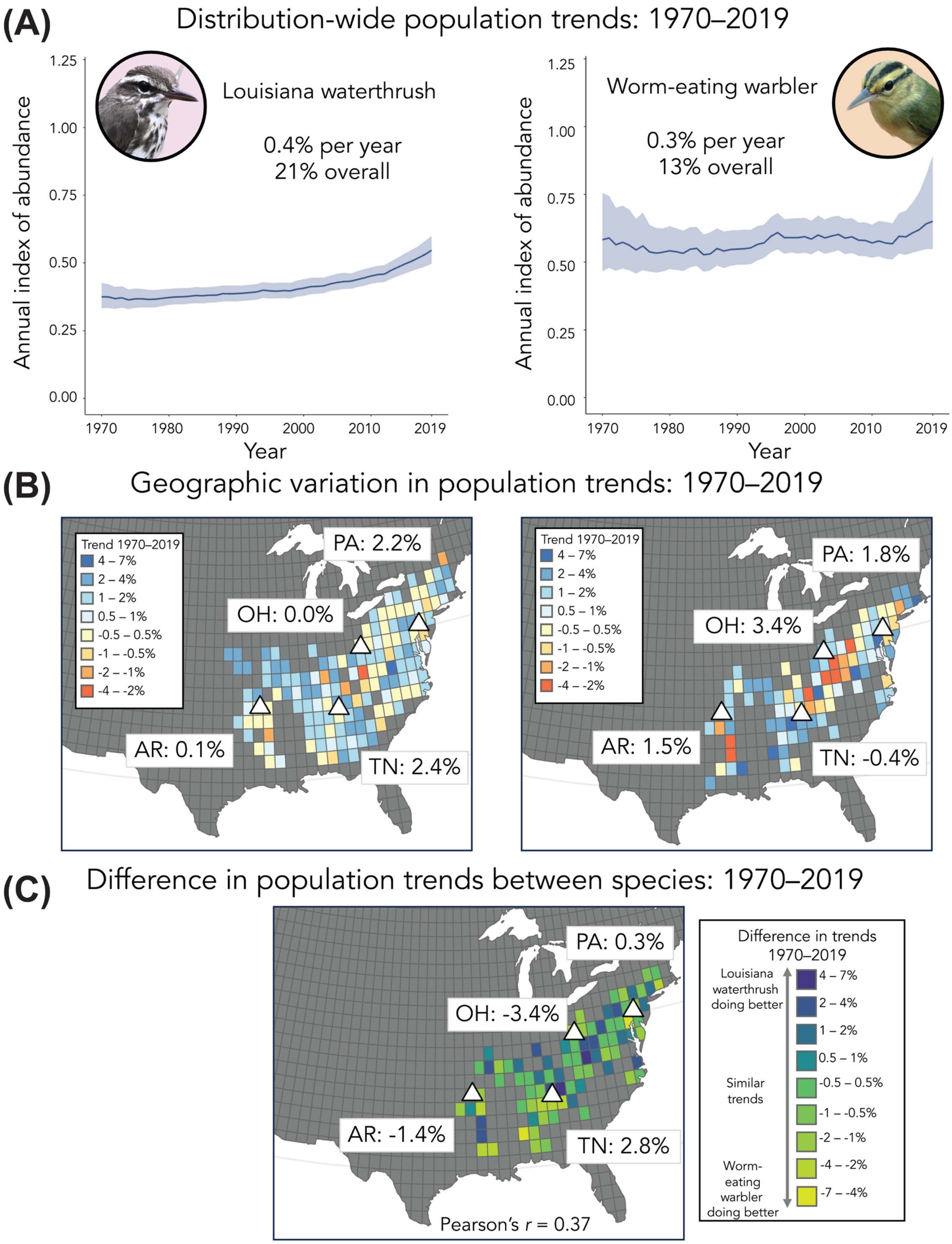


Figure 2. Distribution-wide population trends (A) of Louisiana waterthrush (left) and worm-eating warblers (right) from 1970 to 2019 derived from US Geological Survey Breeding Bird Survey data. Geographic variation in population trends (B) indicate areas where Louisiana waterthrush (left) and worm-eating warblers (right) have increased (cooler colors), decreased (warmer colors), or maintained historical levels of population abundance (light blue, light yellow). The difference between population trends for both species (C) identifies areas where species' population trends are concordant (green cells) or areas where Louisiana waterthrush (purple cells) or worm-eating warblers have exhibited a relatively higher rate of change in abundance. The difference between species' population trends at our study sites are indicated. Cell size is ~ 1.5 × 1.5°. Maps were derived using BBS data (Pardieck et al. 2020) and the 'bbsBayes' package (Edwards and Smith 2021).

species co-occurred during the breeding period but exhibited varying degrees of concordance in decadal population trends, based on estimates derived from the US Geological Survey (USGS) North American Breeding Bird Survey (BBS, Pardieck et al. 2020; Fig. 2 and Supporting information). Specifically, we used the 'bbsBayes' package (Edwards and Smith 2021) in R (ver. 4.3.1; 2023, www.r-project.org) to estimate decadal population trends of Louisiana waterthrush and worm-eating warblers within 1 × 1° blocks from 1970 to 2019. We quantified the concordance of both species' population trends by estimating the Pearson's correlation coefficient (*r*) of decadal breeding population trend estimates for each site. We attached geolocators to breeding adult male Louisiana waterthrush and worm-eating warblers along Little Piney Creek and Big Piney Creek within the Ozark National Forest in Pope County, AR (35.54°N, 93.21°W; Louisiana waterthrush stable [0.1% $\text{yr}^{-1}$], worm-eating warbler increasing [1.5% $\text{yr}^{-1}$], decadal correlation $r=-0.64$), along the Tennessee River within the Tennessee River Gorge in Marion and Hamilton Counties, TN (35.10°N, 85.41°W; Louisiana waterthrush increasing [2.4% $\text{yr}^{-1}$], worm-eating warbler stable [−0.4% $\text{yr}^{-1}$], decadal correlation $r=-0.79$), along Raccoon Creek in Zaleski State Forest and Lake Hope State Park in Vinton County, OH (39.33°N, 82.35°W; Louisiana waterthrush stable [0.0% $\text{yr}^{-1}$], worm-eating warbler increasing [3.4% $\text{yr}^{-1}$], decadal correlation $r=0.98$), and along the Schuylkill River (Birdsboro Waters and Preserve and French Creek State Park) in Berks County, PA (40.23°N, 75.80°W; Louisiana waterthrush increasing [2.2% $\text{yr}^{-1}$], worm-eating warbler increasing [1.8% $\text{yr}^{-1}$], decadal correlation $r=-0.25$; Fig. 2 and Supporting information). Sampling locations within study areas sometimes spanned jurisdictions (e.g. state parks and state forests), but were geographically proximate (i.e. < 10 km apart). We assumed that individuals sampled within each study area comprised a single population. Study areas were characterized by relatively steep, forested slopes surrounding low-volume tributaries ~ 1–15 m wide, with gradients ranging from ~ 8–217 m $\text{km}^{-1}$ (Berz 2021, for detailed site descriptions).

### Geolocator deployment

We captured adult male Louisiana waterthrush and worm-eating warblers in mist-nets using broadcasts of conspecific songs and other vocalizations. Following capture, we marked individuals with an aluminum USGS band and one plastic color band to identify treatment group (i.e. geolocator versus control) and facilitate recovery efforts. We attached geolocators to a subset of individuals using a modified figure-eight leg-loop harness (Rappole and Tipton 1991, Streby et al. 2015b; Table 1). The combined mass of the geolocator and harness (0.40 or 0.50 g depending on model, see below) was < 3% and < 4% of Louisiana waterthrush and worm-eating warbler average body masses, respectively. We followed identical protocols to capture and mark a group of control individuals at each site to test for potential marker effects (Peterson et al. 2015, Taff et al. 2018, Brlík et al. 2020; Table 1). Individuals in the control group were handled identically to geolocator-marked individuals but did not receive a geolocator. In 2017, 2019, and 2021 we systematically and opportunistically searched for returned geolocator-marked and control Louisiana waterthrush and worm-eating warblers. At minimum, we searched for returning individuals within a ~ 500 m radius of the original capture site (Kramer et al. 2017). However, due to the linear nature of the streams around which we focused our sampling, we often extended our search area to include all stream-adjacent land cover within our general study areas.

We deployed 153 geolocators during March–June in 2016 (n = 16), 2018 (n = 121), and 2020 (n = 16; Table 1). We used two geolocator models (Lotek geolocators, ML6140, 2-min light sampling regime, Lotek UK Ltd [2016]; Migrate Technology, Intigeo-W55Z9-DIPv10, 5-min light sampling regime [2018, 2020]), and we note that both tag types produced similar quality data and are regularly used in migration studies (DeLuca et al. 2015, Fischer 2020, Lisovski et al. 2020). We marked a total of 85 Louisiana waterthrush: 15 individuals in AR (2018: n = 15), 39 individuals in TN (2016: n = 16; 2018: n = 15, 2020: n = 8), 15 individuals in OH (2018: n = 15), and 16 individuals in PA (2018: n = 16).

Table 1. Sample size and apparent return rates of Louisiana waterthrush *Parkesia motacilla* and worm-eating warblers *Helmitheros vermivorum* marked with geolocators and as controls (i.e. no geolocator; color bands only) across four breeding sites in Arkansas (AR), Tennessee (TN), Ohio (OH), and Pennsylvania (PA), USA, from 2016 to 2020. *Number resighted includes all birds recaptured plus one geolocator-marked bird that was resighted but not recaptured (one Louisiana waterthrush, AR) and four control birds that were resighted but not recaptured (two Louisiana waterthrush, AR; two worm-eating warblers, OH).

| Species | Site | Year marked | Geo-marked return percentage (resighted*/total marked) | Control return percentage (resighted*/total marked) |
|---|---|---|---|---|
| Louisiana waterthrush | AR | 2018 | 40% (6/15) | 23% (3/13) |
| | TN | 2016 | 31% (5/16) | 33% (5/15) |
| | TN | 2018 | 40% (6/15) | 40% (6/15) |
| | TN | 2020 | 50% (4/8) | 50% (4/8) |
| | OH | 2018 | 27% (4/15) | 0% (0/1) |
| | PA | 2018 | 13% (2/16) | 17% (2/12) |
| Worm-eating warbler | AR | 2018 | 33% (5/15) | 33% (5/15) |
| | TN | 2018 | 40% (6/15) | 40% (6/15) |
| | TN | 2020 | 50% (4/8) | 63% (5/8) |
| | OH | 2018 | 33% (5/15) | 32% (5/16) |
| | PA | 2018 | 40% (6/15) | 25% (1/4) |

We marked a total of 68 worm-eating warblers: 15 individuals in AR (2018: n = 15), 23 individuals in TN (2018: n = 15, 2020: n = 8), 15 individuals in OH (2018: n = 15), and 15 individuals in PA (2018: n = 15). We marked 122 individuals as controls (n = 64 Louisiana waterthrush; n = 58 worm-eating warblers; Table 1). We marked adult males, which may bias our understanding of the migratory ecology of these species if females (Bennett et al. 2019, Fischer 2020, Neate-Clegg and Tingley 2023) and/or juveniles (McKinnon et al. 2014, Neate-Clegg and Tingley 2023) exhibit differences in migration or nonbreeding ecology.

## Geolocator analysis

We downloaded light data from geolocators using the manufacturers' software. We analyzed geolocator data in R (ver. 4.3.1; www.r-project.org) following standardized workflows and using the template-fit method ('FLightR', ver. 4.9: Rakhimberdiev et al. 2015, Kramer et al. 2018, Rakhimberdiev and Saveliev 2019, Lisovski et al. 2020). Briefly, we processed raw light data using the 'TwGeos' package (Lisovski et al. 2016) to define sunrise and sunset transition periods (hereafter, 'twilights') using a threshold < 2. We reformatted drift-adjusted files from both tag types into 'TAGS' format using the 'BAStag' package (Wotherspoon et al. 2016). We calibrated raw light data using periods during which individuals were known or assumed to be present at their breeding sites (e.g. from deployment to ~ 1 July). We used the movement model in 'FLightR' (optimized with 1 million particles) to estimate movements and timing of migration and identify stationary nonbreeding locations (Rakhimberdiev et al. 2016, 2017, Kramer 2018, Delancey 2020). We used a behavioral mask in our movement models which allowed estimated tracks of migrating individuals to cross large bodies of water (e.g. the Gulf of Mexico) but prevented individuals from using stationary sites > 25 km from land (Kramer et al. 2018, Delancey et al. 2020). We constrained the maximum distance between two subsequent twilight-derived estimates to 1200 km to limit the effects of outliers. Additionally, we identified and removed outliers on-the-fly using 'FLightR''s built-in outlier exclusion function. We used the function *stationary.migration.summary()* in 'FLightR' to estimate the location and duration of stopovers (median cutoff probability = 0.2, range = 0.1–0.4 depending on tag; minimum stopover duration = 2 d). We used the function *find.times.distribution()* in 'FLightR' to estimate the onset and commencement of post-breeding migration (i.e. migration from breeding to nonbreeding sites; sometimes called 'autumn' migration) and pre-breeding migration (i.e. migration from nonbreeding to breeding sites; sometimes called 'spring' migration; Albert and Siegel 2024). We created nonbreeding probability density functions spanning transitions when individuals were inferred to be at stationary nonbreeding sites (potential range = 1 August–30 April, mean = 94 transitions [10 SE], median = 76 transitions, range = 4–282 transitions; Supporting information). Louisiana waterthrush and worm-eating warblers are known to defend singular nonbreeding territories (Eaton 1953, Rappole and Warner 1980, Master et al. 2005, Latta et al. 2016). Therefore, we characterized a single stationary nonbreeding site per individual by extracting the coordinates of the cell (0.5 × 0.5° resolution) with the highest probability from individual nonbreeding probability density functions (Kramer et al. 2017, 2018, Delancey et al. 2020, Fischer 2020). We averaged nonbreeding probability density functions of individuals from distinct breeding populations to visualize population-level patterns of space-use during the nonbreeding period (hereafter, 'core-use areas'). Core-use areas were defined using the top 50th percentile of each of the four populations' averaged nonbreeding probability density functions (Kramer et al. 2023). We used the 'geosphere' package (Hijmans 2019) to calculate the Haversine distance (i.e. the great-circle distance or the shortest distance between two points) between individuals' breeding sites and estimated nonbreeding sites as a proxy for migration distance.

## Quantifying migratory connectivity

We used the 'MigConnectivity' package (Cohen et al. 2018) in R to estimate spatial migratory connectivity of Louisiana waterthrush and worm-eating warblers during the nonbreeding period. We estimated three metrics to quantify the strength of migratory connectivity based on the four breeding populations we monitored (AR, TN, OH, PA): Mantel's correlation coefficient ($r_M$; Ambrosini et al. 2009), the migratory connectivity metric (MC; Cohen et al. 2018), and migratory spread (Cresswell and Patchett 2024). Both $r_M$ and MC are useful for quantifying the strength of migratory connectivity when sampling sites are broadly distributed (Vickers et al. 2021). However, MC estimates strength of migratory connectivity while accounting for incomplete sampling and inherent error in geolocator-derived location estimates (Cohen et al. 2018). Thus, MC estimation required identification of nonbreeding target areas and the transition probabilities between breeding and nonbreeding target areas (ψ; probability of an individual from a distinct breeding population occurring in a specific region during the nonbreeding period). We estimated MC using four nonbreeding target regions (Mexico and western Central America, eastern Central America, South America, and the Caribbean; Fig. 3) that varied in their distance from breeding sites, geopolitical composition, ecological similarity, and history of land-use change (Redo et al. 2012). We accounted for uncertainty in geolocator-derived location estimates by generating species-specific estimates of latitudinal and longitudinal bias using twilights when individuals occupied known breeding locations (Supporting information). We also estimated and compared the migratory spread (i.e. mean distance between the nonbreeding sites used by individuals from distinct breeding sites; Cresswell and Patchett 2024) for each population. Unlike $r_M$ and MC, migratory spread is not affected by distance between breeding and nonbreeding sites (when sample sizes are ≥ 4 per population). Populations with $r_M$ and MC values approaching −1 exhibit patterned dispersion in which individuals that breed closer together occur farther apart during the nonbreeding period. Conversely, strong migratory connectivity occurs in populations with

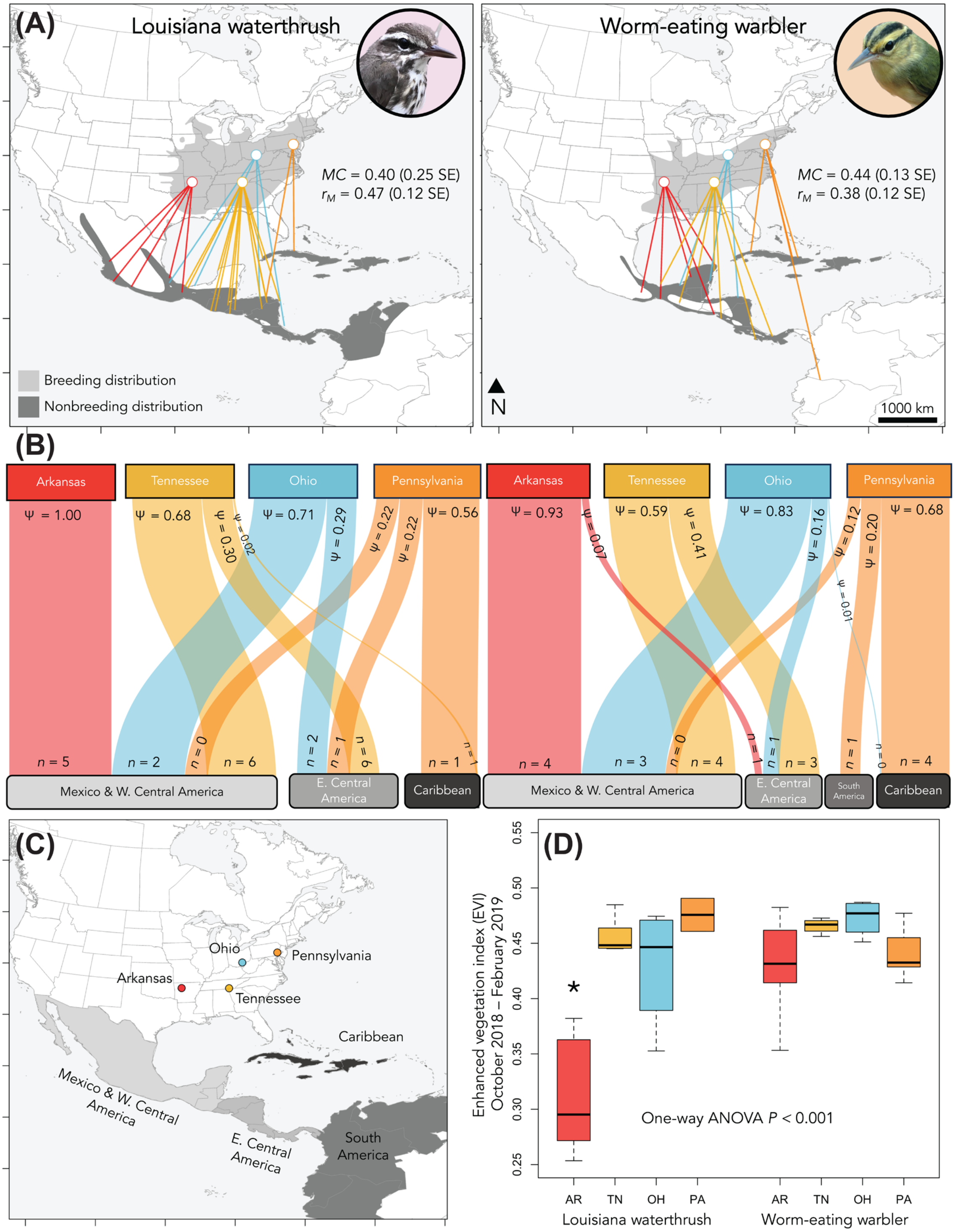


Figure 3. Geolocator-derived nonbreeding locations (A) illustrate connections between breeding sites and the highest probability cell in individuals' nonbreeding probability density function for Louisiana waterthrush and worm-eating warblers in our study. Lines do not represent migration routes. Two estimates of migratory connectivity are presented (migratory connectivity, MC; Mantel's correlation coefficient, $r_M$). Species' breeding and nonbreeding distributions are shaded with light and dark gray, respectively. Alluvial plots with transition probabilities (B) indicate the connections between breeding populations and general nonbreeding regions (defined in C). Boxplot (D) of average monthly enhanced vegetation index values (EVI; MODIS MOD13A3, 1-km resolution) within the top 10th percentile of individuals' nonbreeding probability density functions from October 2018 to February 2019 ($n = 34$) by population and species. Asterisks indicate statistically significant differences among groups ($p < 0.05$). Distribution map data are from BirdLife International (2016).

$r_M$ and MC values approaching 1 wherein individuals from proximate breeding areas occur closer together during the nonbreeding period. Values of $r_M$ and MC near 0 indicate weak migratory connectivity wherein individuals from distinct breeding populations mix and co-occur during the nonbreeding period (Ambrosini et al. 2009, Cohen et al. 2018). We compared the strength of MC estimates between species using the *diffMC()* function in the 'MigConnectivity' package (Cohen et al. 2019).

### Characterizing environmental factors

We used enhanced vegetation index (EVI) data as a proxy for environmental conditions during the nonbreeding period (Didon 2021). We chose to use EVI because it measures vegetation greenness while accounting for atmospheric factors that are known to affect other remotely sensed vegetation indices (e.g. normalized difference vegetation index [NDVI]; Huete et al. 2002). We downloaded average monthly EVI data (1 km resolution) and calculated the average nonbreeding period EVI from October 2018 to February 2019 (NASA EOSDIS, USGS EROS; Didon 2021, AppEEARS Team 2024). We resampled the average monthly EVI data using bilinear interpolation to match the coarser resolution of the geolocator data. We calculated a weighted average nonbreeding period EVI by multiplying the average nonbreeding period EVI within the top 10th percentile of an individual's nonbreeding probability density functions for Louisiana waterthrush and worm-eating warblers tracked during 2018–2019. This allowed us to account for error in nonbreeding location estimates.

### Statistical analysis

We used $\chi^2$ tests of independence to compare apparent return rates between marked and control birds to test for potential effects of geolocators on annual survival for each species. We tested for variation in the timing of migration schedules (i.e. breeding site departure, nonbreeding site arrival, nonbreeding site departure, and breeding site arrival) between species among breeding populations using generalized linear models (GLMs) and assessed model fit using the Akaike information criterion adjusted for sample size ($AIC_c$). We also used GLMs to assess whether the timing of migration was linked across seasons (e.g. whether breeding-area departure was associated with nonbreeding-area arrival). We visualized intraspecific and interspecific variation in the timing of migration using cumulative sum plots and visualized movements of populations between breeding and nonbreeding regions using the 'ggforce' package in R (www.r-project.org, Pedersen 2020). We used Welch's two-sample t-tests and one-way analysis of variance (ANOVA) and post hoc Tukey HSD tests to quantify interspecific and intraspecific differences, respectively, in duration of annual cycle stages (i.e. post-breeding migration, nonbreeding period, pre-breeding migration, and stopover period durations), number of stopovers during post-breeding and pre-breeding migrations, total distance traveled, and rate of migration. We also used an ANOVA to test for differences in average nonbreeding period EVI among populations and species. We used simple linear models to assess relationships between both population average nonbreeding EVI and the variance of population average nonbreeding period EVI with population trends. Prior to running t-tests, we assessed data normality (and thus whether data meet the assumptions for t-tests) using Shapiro–Wilk tests. We considered results of all tests to be statistically significant at $\alpha = 0.05$. All estimates are presented as means ± SD unless otherwise noted.

## Results

Of the 153 individuals we marked with geolocators, only one individual returned without its geolocator and was right-censored from all analyses (worm-eating warbler from PA). Of the remaining 152 geolocator-marked individuals, 53 (35%) returned and were observed the following year (Louisiana waterthrush, 26/85 [31%], worm-eating warblers, 27/67 [40%]). Of the 122 control individuals, 42 (34%) returned and were observed the following year (Louisiana waterthrush, 20/64 [31%]; worm-eating warbler, 22/58 [38%]; Table 1). We found no evidence for a difference in annual return rates between geolocator-marked and control groups (Louisiana waterthrush, $\chi^2 = 0.01$, df = 1, p = 0.93; worm-eating warbler, $\chi^2 = 0.07$, df = 1, p = 0.79). Of the returning individuals, we were unable to recapture 5 (5%); one geolocator-marked Louisiana waterthrush in AR; two control Louisiana waterthrush in AR, and two control worm-eating warblers in OH. Of the 52 geolocators we recovered, seven (13%) contained no data or unusable data, four (8%) contained less than a full year of data, and the remaining 39 (79%) contained a full year of data.

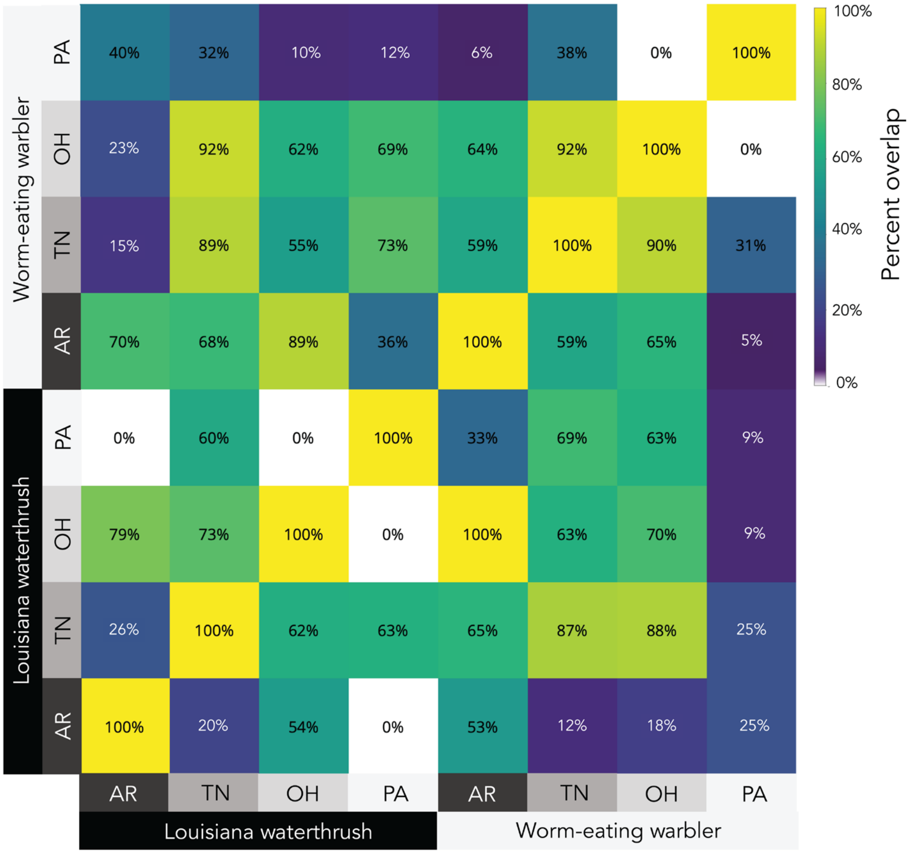
### Nonbreeding locations and migratory connectivity

We derived nonbreeding location estimates for 24 Louisiana waterthrush and 21 worm-eating warblers that returned and were recaptured with geolocators containing sufficient data (Supporting information). In general, Louisiana waterthrush and worm-eating warblers exhibited moderately strong migratory connectivity with individuals from western breeding populations occurring farther west during the nonbreeding period than individuals from eastern breeding populations (difference in MC = 0.04; Fig. 3). Louisiana waterthrush (MC = 0.40 [0.25 SE], $r_M = 0.47$ [0.12 SE], migratory spread range = 649–1032 km) from breeding sites in AR (n = 5; mean migratory spread = 649 km [126 km SE) occurred exclusively in western and central Mexico ($\psi = 1.00$, n = 5; Fig. 3) whereas individuals from breeding sites in PA (n = 2; mean migratory spread = 938 km [no estimate of SE]) occurred farther east in Central America ($\psi = 0.22$) and Cuba ($\psi = 0.56$; Fig. 3). Louisiana waterthrush from sites near the center of their breeding distribution (i.e. TN [n = 17], mean migratory spread = 679 km [90 km SE]; and OH [n = 4], mean migratory spread = 1032 km [258 km SE]) occurred from southern Mexico to Costa Rica but occurred most frequently in eastern Central America ($\psi = 0.30$ TN, $\psi = 0.29$ OH; Fig. 3). One Louisiana waterthrush from a breeding site in TN occurred in Cuba during the nonbreeding period ($\psi = 0.02$; Fig. 3).

Worm-eating warblers ($MC = 0.44$ [0.13 SE], $r_M = 0.38$ [0.12 SE], migratory spread range = 617–1301 km) from breeding sites in AR (n = 5; mean migratory spread = 797 km [128 km SE]) occurred primarily in Mexico ($\psi = 0.93$) and to a lesser extent in eastern Central America ($\psi = 0.07$; Fig. 3) whereas worm-eating warblers from breeding sites in PA (n = 4; mean migratory spread = 1301 km [789 km SE]) occurred in primarily in Cuba ($\psi = 0.68$; Fig. 3). One worm-eating warbler that bred in PA occurred in northern South America on the border of Colombia and Ecuador ($\psi = 0.20$; Fig. 3). Worm-eating warblers from sites near the center of their breeding distribution (i.e. Tennessee [n = 7], mean migratory spread = 1081 km [184 km SE]; and OH [n = 3], mean migratory spread = 617 km [128 km SE]) occurred from central Mexico to Panama but primarily in Mexico and western Central America ($\psi = 0.59$ TN, $\psi = 0.83$ OH; Fig. 3).

Intraspecific overlap of populations' average nonbreeding core-use areas varied between Louisiana waterthrush (mean = 36% [6% SE], range = 0–79%; Fig. 4 and Supporting information) and worm-eating warblers (mean = 42% [10% SE], range = 0–92%; Fig. 4 and Supporting information). Populations of Louisiana waterthrush from breeding sites in TN exhibited the greatest average percent overlap in nonbreeding core-use area compared to other populations (mean = 51% [9% SE], range = 20–73%) compared to populations from breeding sites in OH (mean = 45% [15% SE], range = 0–79%), AR (mean = 30% [13% SE], range = 0–79%), and PA (mean = 21% [13% SE], range = 0–63%; Fig. 4). The average nonbreeding core-use areas of Louisiana waterthrush from AR and PA did not overlap (Fig. 3 and 4). Similarly, populations of worm-eating warblers from breeding populations in TN exhibited the greatest amount of nonbreeding core-use area overlap with other populations of worm-eating warblers (mean = 62% [10% SE], range = 31–92%) compared to populations from breeding sites in OH (mean = 52% [17% SE], range = 0–92%), AR (mean = 43% [12% SE], range = 5–65%), and PA (mean = 13% [7% SE], range = 0–38%).

Interspecific overlap of Louisiana waterthrush and worm-eating warbler populations' nonbreeding core-use areas was variable (range = 9–100%; Fig. 4). On average, Louisiana waterthrush from breeding sites in TN (mean = 66% [15% SE], range = 25–88%) and OH (mean = 61% [19% SE], range = 9–100%) had the greatest amount of



|  |  | Louisiana waterthrush |  |  |  | Worm-eating warbler |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  | AR | TN | OH | PA | AR | TN | OH | PA |
| Worm-eating warbler | PA | 40% | 32% | 10% | 12% | 6% | 38% | 0% | 100% |
|  | OH | 23% | 92% | 62% | 69% | 64% | 92% | 100% | 0% |
|  | TN | 15% | 89% | 55% | 73% | 59% | 100% | 90% | 31% |
|  | AR | 70% | 68% | 89% | 36% | 100% | 59% | 65% | 5% |
| Louisiana waterthrush | PA | 0% | 60% | 0% | 100% | 33% | 69% | 63% | 9% |
|  | OH | 79% | 73% | 100% | 0% | 100% | 63% | 70% | 9% |
|  | TN | 26% | 100% | 62% | 63% | 65% | 87% | 88% | 25% |
|  | AR | 100% | 20% | 54% | 0% | 53% | 12% | 18% | 25% |

Figure 4. Pairwise heatmap of nonbreeding core-use area overlap by species and population. We defined core-use areas as the top 50th percentile of each of the four populations' averaged nonbreeding probability density functions. Cells are colored based on the calculated proportion of overlap between paired nonbreeding core-use areas with the population on the x-axis always serving as the reference (divisor). Higher levels of overlap are indicated by greens and yellows.

nonbreeding core-use area overlap with worm-eating warblers. Populations of Louisiana waterthrush from breeding sites in PA (mean = 44% [14% SE], range = 9–69%) and AR (mean = 37% [12% SE], range = 15–70%) exhibited the lowest levels of nonbreeding core-use area overlap with worm-eating warblers (Fig. 4). On average, populations of worm-eating warblers from breeding sites in AR (mean = 63% [14% SE], range = 33–100%), OH (mean = 60% [15% SE], range = 18–88%), and TN (mean = 58% [16% SE], range = 12–87%) exhibited more nonbreeding core-use area overlap with Louisiana waterthrush populations compared to worm-eating warblers from breeding sites in PA (mean = 17% [5% SE], range = 9–25%; Fig. 4). Focusing on the interspecific overlap between both species breeding at the same site, Louisiana waterthrush and worm-eating warblers from TN exhibited the greatest overlap (89% and 87% considering Louisiana waterthrush and worm-eating warbler as the reference, respectively). Louisiana waterthrush and worm-eating warblers from breeding sites in PA exhibited the least amount of nonbreeding core-area overlap (9% and 12% considering Louisiana waterthrush and worm-eating warbler as the reference, respectively). Louisiana waterthrush and worm-eating warblers breeding in AR and OH exhibited moderate levels of nonbreeding core-use overlap (range = 53–70%; Fig. 4).

Populations of Louisiana waterthrush and worm-eating warblers had similar average nonbreeding period EVI except for Louisiana waterthrush from breeding sites in AR, which occurred in areas with lower EVI (one-way ANOVA, $F_{7,26} = 8.9$, $p < 0.001$; Fig. 3D). However, we found no evidence of a relationship between breeding population trends and average population-level nonbreeding period EVI ($p = 0.22$). We observed a negative relationship between the variance in EVI, and breeding population trends ($p = 0.04$).

### Migration timing, stopovers, and distances

Geolocators recorded post-breeding migration data for 24 Louisiana waterthrush and 21 worm-eating warblers (Supporting information). With these data, we were able to estimate the timing of breeding-area departure (i.e. onset of post-breeding migration) and nonbreeding-area arrival (i.e. culmination of post-breeding migration) for 88% (21/24) of Louisiana waterthrush and 90% (19/21) of worm-eating warblers (Supporting information). On average and across all populations, Louisiana waterthrush and worm-eating warblers departed breeding sites on 9 August ± 15 d and 19 September ± 25 d, respectively, arriving at nonbreeding sites on 20 September ± 34 d and 31 October ± 26 d, respectively. We recovered data from the pre-breeding migration period for 20 Louisiana waterthrush and 20 worm-eating warblers (11% [5/45] of geolocators failed during the nonbreeding period). With those data, we were able to estimate the timing of nonbreeding-area departure (i.e. onset of pre-breeding migration) and breeding-area arrival (i.e. culmination of pre-breeding migration) for 90% (18/20) of Louisiana waterthrush and 95% (19/20) of worm-eating warblers (Supporting information). On average, Louisiana waterthrush departed nonbreeding sites on 1 March ± 22 d and arrived at breeding sites on 31 March ± 21 d. Worm-eating warblers departed nonbreeding sites on 28 March ± 21 d and arrived at breeding sites on 26 April ± 12 d, on average. Thus, Louisiana waterthrush transitioned between stages of the annual cycle (i.e. breeding departure, nonbreeding arrival, nonbreeding departure, and breeding arrival) ~ 40 d earlier than worm-eating warblers (Fig. 5 and Supporting information). This pattern, in which Louisiana waterthrush migrated earlier than worm-eating warblers, generally persisted when we compared the timing of migration of individuals from distinct breeding populations (Fig. 5 and Supporting information). However, the univariate model using species as the only predictor was the top model explaining variation in breeding area departure, nonbreeding area arrival, and breeding area arrival compared to models with site as the only predictor and more complex models accounting for site and species and the interaction between both predictors (Supporting information). The top supported model for nonbreeding area departure included species and site as predictors. Louisiana waterthrush and worm-eating warblers from breeding sites at lower latitudes (i.e. AR and TN) exhibited less overlap in the timing of average breeding area departure and nonbreeding area arrival compared to more northern sites (i.e. OH, PA; Fig. 5).

Despite considerable differences in migration initiation (i.e. ~ 40 d), we found no evidence of differences in nonbreeding period duration (i.e. duration of the period following the culmination of post-breeding migration until the onset of pre-breeding migration) between Louisiana waterthrush (mean = 158 ± 35 d) and worm-eating warblers (mean = 145 ± 19 d; $t = 1.37$, $df = 25.22$, $p = 0.18$). Similarly, duration of post-breeding migration (Louisiana waterthrush mean = 42 ± 29 d; worm-eating warbler mean = 42 ± 24 d), pre-breeding migration (Louisiana waterthrush mean = 30 ± 15 d; worm-eating warbler mean = 29 ± 15 d) were nearly identical between both species ($p \geq 0.9$ for both comparisons). During post-breeding migration, Louisiana waterthrush and worm-eating warblers made, on average, 1.7 ± 1.8 and 1.8 ± 1.5 stopovers with a mean duration of 23 ± 14 and 21 ± 13 d, respectively, with no difference between species ($p > 0.7$ for both comparisons). However, during pre-breeding migration, Louisiana waterthrush made both fewer (mean = 0.5 ± 0.6) and shorter stopovers (mean = 8 ± 3 d) compared to worm-eating warblers (mean = 1.5 ± 1.6 stopovers with mean duration = 20 + 9 d; $p < 0.05$ for both comparisons). Among all four worm-eating warbler populations, there was no difference in the number or duration of post-breeding or pre-breeding migration stopovers (all $p > 0.7$). Among Louisiana waterthrush, individuals breeding in OH made more pre-breeding stopovers (mean = 1.3 stopovers) than those from breeding sites in AR (mean = 0.0 stopovers; $p = 0.009$). There was no difference in number or duration of stopovers when comparing other breeding populations during both post-breeding and pre-breeding migration ($p > 0.05$ for all other comparisons).

On average across all populations, Louisiana waterthrush and worm-eating warblers migrated similar distances between breeding and nonbreeding sites (Louisiana

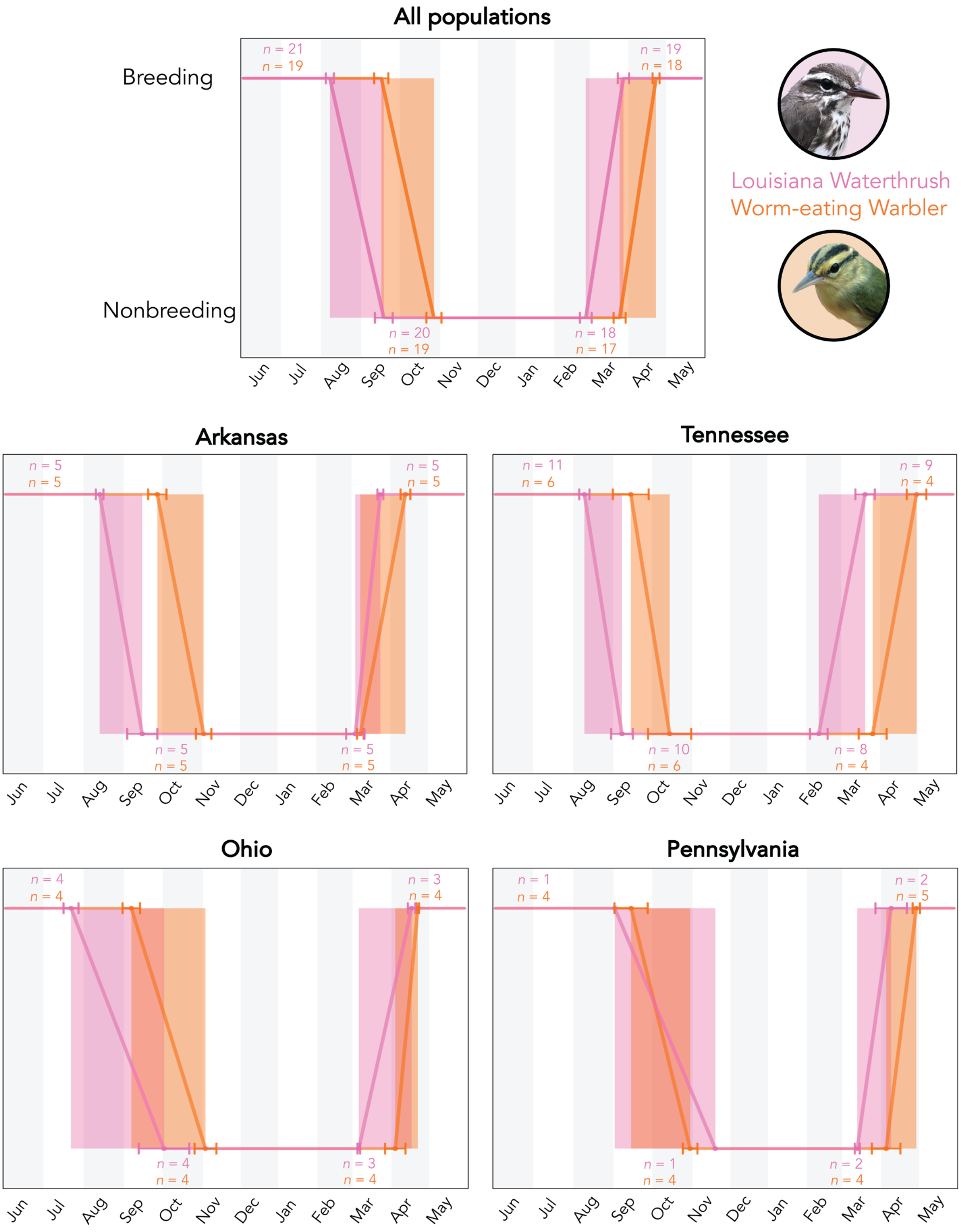


Figure 5. Migration timing plots displaying the average timing of major migration events (+/- SE) for Louisiana waterthrush (pink) and worm-eating warblers (orange). Shaded polygons span the average departure and arrival and effectively constitute the average migration period for each species.

waterthrush mean = 2263 ± 384 km versus worm-eating warbler mean = 2265 ± 706 km; t = 0.0, p = 0.99). Louisiana waterthrush from breeding sites in OH migrated 738 and 566 km farther than individuals from AR and TN populations, respectively ($F_{3,18} = 4.8$, p = 0.01; Tukey HSD $p < 0.05$). There was no evidence of differences in migration distance among worm-eating warbler populations ($F_{3,15} = 0.3$, $p > 0.05$). During post-breeding migration, Louisiana waterthrush and worm-eating warblers traveled similar minimum average daily distances (128 ± 177 km $d^{-1}$ versus 85 ± 77 km $d^{-1}$; $t = 1.0$, $p = 0.33$). Similarly, Louisiana waterthrush and worm-eating warblers traveled similar minimum average daily distances during pre-breeding migration (123 ± 136 km $d^{-1}$ and 116 ± 127 km $d^{-1}$, respectively; $t = 0.2$, $p = 0.86$).

We found a positive relationship between breeding-area departure (i.e. the onset of post-breeding migration) and nonbreeding-area arrival for both Louisiana waterthrush ($x = 1.05$, $p = 0.03$) and worm-eating warblers ($x = 0.61$, $p = 0.01$) such that individuals that departed breeding areas earlier tended to arrive at nonbreeding areas earlier (Fig. 6). Similarly, nonbreeding-area departure (i.e. onset of pre-breeding migration) was positively associated with breeding-area arrival for both Louisiana waterthrush ($x = 0.74$, $p < 0.001$) and worm-eating warbler ($x = 0.41$, $p = 0.002$; Fig. 6). However, we found no relationship between the timing of breeding-area departure and breeding-area arrival in the following year for Louisiana waterthrush ($x = 0.32$, $p = 0.38$) or worm-eating warblers ($x = -0.03$, $p = 0.85$; Fig. 6).

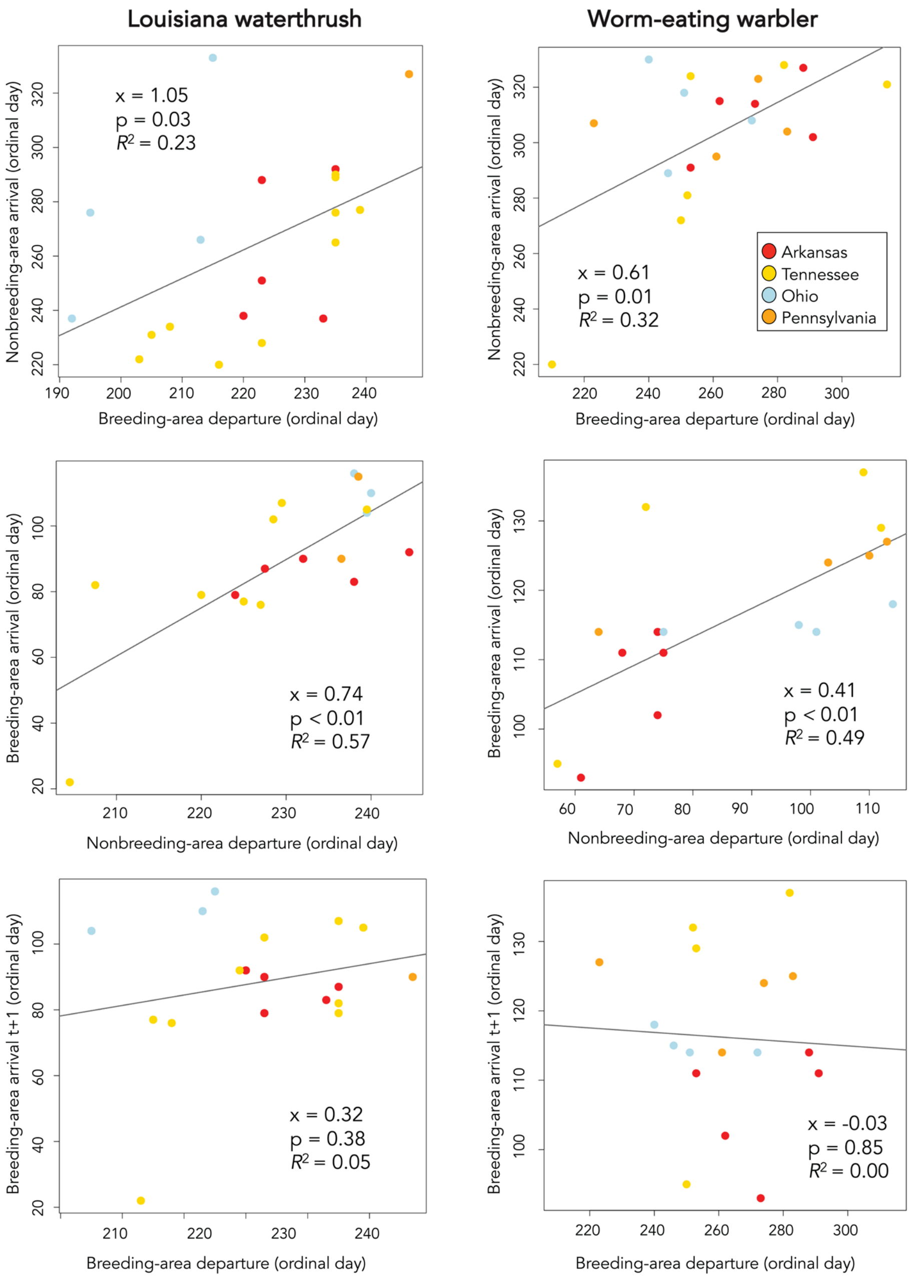


Figure 6. Simple linear regression plots displaying the relationships between major migration events spanning the annual cycle for Louisiana waterthrush (left) and worm-eating warblers (right). Associations between breeding area departure and nonbreeding area arrival (top), nonbreeding area departure and breeding area arrival (middle), and breeding area departure and breeding area arrival in the subsequent year (bottom) are presented. Points representing individual geolocator-marked Louisiana waterthrush and worm-eating warblers are colored by study site.

## Discussion

Louisiana waterthrush and worm-eating warblers exhibited similar patterns of range-wide migratory connectivity and nonbreeding dispersion wherein populations that co-occurred during the breeding period also tended to co-occur regionally during the nonbreeding period (Fig. 3, 4). However, we detected consistent and significant interspecific differences in migration timing such that populations exhibited strong temporal isolation during seasonal migrations (Fig. 5). Namely, Louisiana waterthrush arrived at nonbreeding sites when worm-eating warblers were beginning post-breeding migration and Louisiana waterthrush arrived at breeding sites when worm-eating warblers were beginning pre-breeding migration. Thus, although regional breeding populations of Louisiana waterthrush and worm-eating warblers tended to occur in similar landscapes during the nonbreeding period, they initiated and completed seasonal migration in temporal isolation from one another. Therefore, locally discordant population trends could be associated with unique, limiting factors experienced during migration, such as more frequent exposure to inclement weather (Dionne et al. 2008), temporally variable anthropogenic threats (e.g. wind energy, exposure to artificial light at night; Barrios and Rodríguez 2004, Van Doren et al. 2017), or other factors that result in direct mortality or have sublethal consequences (i.e. carry-over effects; Nemes et al. 2023). Alternatively, it is possible that discordant population trends in these species are driven by demographic stochasticity (Sæther et al. 2016) or mechanisms operating at shared breeding sites (Hallworth et al. 2021, Ko et al. 2023), such as density dependence (Rodenhouse et al. 2003) or finer-scale differences in life-history strategies that are masked by the species' co-occurrence and apparent ecological similarity (Durham et al. 2024). The observed population trends are likely driven by multiple, dynamic factors throughout the annual cycle (Newton 2004), but the inherent complexity of disentangling population limitation among sympatric species requires further research.

We observed moderate spatial migratory connectivity in both Louisiana waterthrush (MC = 0.40) and worm-eating warblers (MC = 0.44) indicating some degree of spatial overlap among distinct breeding populations during the nonbreeding period (Fig. 3). The strength of migratory connectivity that we observed in Louisiana waterthrush and worm-eating warblers was weaker than has been reported for golden-winged warblers *Vermivora chrysoptera* (MC = 0.84; Kramer 2021) and tree swallows *Tachycineta bicolor* (MC = 0.54; Knight et al. 2018) but stronger than the migratory connectivity observed in Connecticut warblers (MC = −0.20; Hallworth et al. 2021), blue-winged warblers *Vermivora cyanoptera* (MC = −0.10; Kramer 2021), prothonotary warblers *Protonotaria citrea* (MC = 0.07; Tonra et al. 2019), common nighthawks ($r_M$ = 0.29; Knight et al. 2021), and cerulean warblers *Setophaga cerulea* MC = 0.36; Raybuck et al. 2022). The strength of migratory connectivity in Louisiana waterthrush and worm-eating warblers was similar to that observed in black-throated blue warblers *Setophaga caerulescens* (MC = 0.42; Lewis et al. 2023). In other species with strong migratory connectivity (e.g. golden-winged warblers, MC = 0.84), spatial segregation of regional populations during the nonbreeding period can drive variation in population trends on the breeding grounds (Kramer et al. 2018). Conversely, breeding-grounds factors have been implicated in limiting populations of species with weak migratory connectivity wherein populations are highly clustered during the breeding period but individuals mix broadly during the nonbreeding period (e.g. Connecticut warblers, MC = −0.20, Hallworth et al. 2021). Most populations of Louisiana waterthrush and worm-eating warblers experienced similar environmental conditions (as measured by EVI) during the nonbreeding period. However, Louisiana waterthrush from breeding sites in AR occurred in areas with lower EVI during the nonbreeding period compared to other populations. Breeding population trends of Louisiana waterthrush in AR remained numerically stable from 1970 to 2019 despite increasing in other portions of their distribution (e.g. PA, TN; Fig. 2B). Notably, we observed no evidence of a relationship between breeding population trends of either species and the average nonbreeding EVI, suggesting that distribution-wide patterns in average EVI may not be driving patterns of variation in population trends. We observed a negative relationship between the variance of EVI during the nonbreeding period and breeding population trends, which may indicate that areas with high landscape heterogeneity may be associated with lower habitat availability or quality. We investigated the relationship between EVI and population trends at a relatively coarse scale, and future research exploring these relationships at a finer scale is warranted.

We found evidence that most populations of sympatrically breeding Louisiana waterthrush and worm-eating warblers overlapped extensively during the nonbreeding period (53–89% overlap of nonbreeding core-use areas). These findings suggest that, for many populations of sympatrically breeding Louisiana waterthrush and worm-eating warblers, a large proportion of individuals experience similar conditions within shared breeding and nonbreeding areas. Notably, Louisiana waterthrush (n = 2) and worm-eating warblers (n = 5) breeding in PA exhibited the lowest level of nonbreeding core-use area overlap (9–12%), suggesting that interspecific variation in population trends at those sites may be associated with factors occurring within species-specific nonbreeding areas. Our sample size of geolocators recovered from Louisiana waterthrush breeding in PA was modest (n = 2) and additional sampling of this population may provide a more comprehensive understanding of the degree of spatial overlap between this population and others. However, decadal variation in breeding population trends for these species are highly concordant at this site (r = 0.98), indicating that the population trends of both species may be associated with a shared factor on the breeding grounds, or by some other combination of factors that lead to the observed concordant patterns by chance. Thus, our results suggest that the factors driving the populations dynamics of sympatrically breeding Louisiana waterthrush and worm-eating warblers may vary geographically but are not likely to be associated with regional patterns of land-use change that have occurred in the Neotropics over the past 50 years (Hansen et al. 2013). It is possible that habitat-associated factors or climate on the breeding or nonbreeding grounds may be acting on a finer scale than we were able to assess to differentially affect survival or cause carry-over effects (Norris 2005, Both et al. 2006). Louisiana waterthrush are riparian-obligate habitat specialists during both the breeding and nonbreeding periods (Master et al. 2005, McClure and Hill 2012), and are considered bioindicators in forested riparian areas (O'Connell et al. 2003, Mulvihill et al. 2008). Accordingly, Louisiana waterthrush may be more sensitive than worm-eating warblers to specific types of anthropogenic disturbances (e.g. shale gas development, mining, stream acidification, agricultural runoff) that negatively impact water quality and stream invertebrate communities over the full annual cycle (Frantz et al. 2018, 2019). Whether variation in fine-scale, habitat–species relationships can explain locally discordant population trends of Louisiana waterthrush and worm-eating warblers that breed and winter in sympatry will require additional research using different tracking devices or methods (e.g. higher-precision barometric pressure geolocators; Rhyne et al. 2024). We are not aware of any robust methods to compare the characteristics of migratory dispersion and geographic structure of numerous populations of multiple species. It was beyond the scope of our analysis to develop a quantitative assessment to characterize the similarity in migratory connectivity of two species, but we envision multi-species tracking studies to become more common in the future and, as such, the development of a metric that allows for comparing the arrangement of individuals from multiple populations and multiple species would be beneficial.

Despite relatively high levels of spatial overlap of sympatrically breeding populations during breeding and nonbreeding periods, we found evidence of biologically relevant temporal isolation between sympatric populations of Louisiana waterthrush and worm-eating warblers during seasonal migration periods. Consequently, despite occupying similar areas on the breeding and non-breeding grounds, sympatric populations may experience different phenological stages of any shared landscapes throughout their annual cycles, which could contribute to discordance in population trends if limiting factors vary seasonally. Within periods of rapid phenological change, especially the spring and autumn periods of temperate regions, the same habitat can exhibit marked differences in temperature, precipitation, vegetative cover, food availability, and other habitat characteristics. The temporal isolation between our two study species was driven by Louisiana waterthrush migrating ~ 40 d earlier than worm-eating warblers. Migrating earlier may have consequences for individuals and populations if the conditions that facilitate long-distance migration change throughout the post-breeding migration period (Ward et al. 2018, Kramer 2021). Notably, strong weather events such as hurricanes can cause mortality or alter behavior leading to demographic consequences when they coincide with peak migration events (Dionne et al. 2008, Streby et al. 2015a; but see Lisovski et al. 2018, Streby et al. 2018). Historically, hurricane season in the Gulf of Mexico extends from August to October with the peak in activity occurring in September (Biasutti et al. 2011). Our data suggest that Louisiana waterthrush tend to complete their post-breeding migration prior to the peak hurricane season, which may reduce their likelihood of encountering hurricanes as they cross the Gulf of Mexico compared to worm-eating warblers that navigate the Gulf of Mexico during peak hurricane months. Additionally, species that are earlier migrants may be more capable of adjusting to phenological shifts associated with climate change (Both and Visser 2001). However, it is important to note that apparent adjustments to climate change and advancing phenology can be misleading and fail to capture tradeoffs (Shipley et al. 2020).

Given the amount of spatial overlap among populations throughout the annual cycle, we found no evidence that a singular factor is likely to be limiting populations of Louisiana waterthrush and worm-eating warblers. Thus, a one-size-fits-all strategy focused on breeding or nonbreeding habitat conservation may not benefit the intended populations and a more nuanced approach may be warranted in the case of these two species. Like many other migration studies focused on small songbirds, we tracked adult males because they are easier to capture and have higher apparent breeding site fidelity than females. However, sex- and age-based differences in nonbreeding habitat associations and migration ecology can have biologically relevant implications (McKinnon et al. 2014, Bennett et al. 2019, Fischer 2020). Thus, future efforts to characterize the full-annual cycle ecology of Louisiana waterthrush and worm-eating warblers should prioritize describing the migratory ecology and nonbreeding space use of females and/or juveniles. Quantifying the migratory connectivity of more species of migratory birds will elucidate whether the patterns we observed in Louisiana waterthrush and worm-eating warblers are common (Finch et al. 2017, Kramer et al. 2018).

Ideally, comprehensive conservation of migratory species and ecologically distinct populations would ensure the availability of sufficient habitat across the annual cycle (Faaborg et al. 2010b). However, funds to implement conservation actions and conserve critical habitat are often limited, requiring managers to prioritize actions based on the best available information. Identifying opportunities to implement management solutions that provide co-benefits to multiple Nearctic–Neotropical migratory species that co-occur during periods of the annual cycle would allow for the efficient use of limited conservation resources (Torstensen et al. 2024). Filling knowledge gaps related to the migratory connectivity and migration ecology of co-occurring Nearctic–Neotropical migrants is the first step toward identifying and conserving critical areas, mitigating threats and limiting factors, and evaluating species responses to future landscape alteration and climate change.

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*Permits* – We captured, marked, and collected data from birds with permission from the U.S. Geological Survey Bird Banding Laboratory (permit no. 24072, no. 24138 and no. 23340) and following Protocol 108708 approved by the University of Toledo Institutional Animal Care and Use Committee (IACUC) and Protocol no. 19-01 approved by the University of Tennessee at Chattanooga IACUC.

## Author contributions

**Gunnar R. Kramer, Silas E. Fischer** and **Patrick J. Ruhl** contributed equally to this publication. **Gunnar R. Kramer**: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Writing – original draft (equal). **Silas E. Fischer**: Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Funding acquisition (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Patrick J. Ruhl**: Conceptualization (equal); Data curation (equal); Funding acquisition (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Eliot S. Berz**: Data curation (equal); Funding acquisition (equal); Writing – review and editing (equal). **Rick Huffines**: Conceptualization (lead); Data curation (supporting); Funding acquisition (equal); Writing – review and editing (supporting). **David A. Aborn**: Writing – review and editing (supporting). **Henry M. Streby**: Conceptualization (lead); Data curation (supporting); Formal analysis (equal); Funding acquisition (lead); Writing – review and editing (supporting).

### Data availability statement

Raw geolocator data and R code to recreate analyses are available from the Open Data Repository of Iowa State University: https://doi.org/10.25380/iastate.25872271 (Kramer et al. 2025).

### Supporting information

The Supporting information associated with this article is available with the online version.

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