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High spatiotemporal overlap in the non-breeding season despite geographically dispersed breeding locations in the eastern whip-poor-will (*Antrostomus vociferus*)

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Abstract

Aim: A full annual cycle approach to conservation and understanding of regional population trends requires an understanding of migratory connectivity. We present tracking data on the eastern whip-poor-will (*Antrostomus vociferus*), a Neotropical migrant that has declined by 70% in recent decades. When and where populations of this species are limited throughout the annual cycle is poorly understood.

Location: Breeding area: midwestern United States; passage area and winter area: midwestern/southern United States, Mexico, Central America.

Methods: We utilized data from 52 archival GPS tags from five breeding areas covering a 9.5-degree latitudinal span (~1000 km) of the whip-poor-will breeding range in the summers of 2017 and 2019. We identified migratory routes and spatiotemporal bottlenecks, stopover and wintering locations, calculated migratory connectivity throughout migration and on the wintering grounds and tested predictions for three latitudinal connectivity patterns.

Results: Whip-poor-wills circumvented the Gulf of Mexico, and populations across a large latitudinal gradient came together in eastern Texas in early October, resulting in decreased connectivity throughout migration. Breeding-winter migratory connectivity was low ($MC = 0.22 \pm 0.12$), with extensive overlap of core wintering areas in southern Mexico and Guatemala. The overlap of wintering areas by individuals from dispersed breeding latitudes suggests that whip-poor-wills most closely resemble telescopic migrants.

Main conclusions: Circumventing the Gulf of Mexico influenced connectivity in the whip-poor-will, funneling individuals into a small region in eastern Texas in migration and likely influencing breeding-winter connectivity. Thus, geographically dispersed breeding populations overlap in space and time during migration and winter, and non-breeding season conditions affecting populations (both positively and negatively) impact individuals from across the core breeding range. For example, extensive

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deforestation occurring in the whip-poor-will's core wintering area likely impacts individuals from all five deployment locations. We demonstrate that combining multiple indices of spatiotemporal cohesion is critical to fully understand how migratory animals are distributed in the non-breeding season.

KEYWORDS

Caprimulgiform, conservation, eastern whip-poor-will, midwestern United States, migration, migratory connectivity, nightjar, spatiotemporal overlap, telescopic migration

1 | INTRODUCTION

Quantifying connectivity throughout the annual cycle is a critical step towards understanding spatial variation in population trends measured on the breeding grounds. Migratory connectivity can be quantified between the breeding and winter period (i.e. breeding-winter migratory connectivity (BWMC); Webster & Marra, 2005) and throughout migration (i.e. en route migratory connectivity (ERMC); Cohen et al., 2018, 2019; Knight et al., 2021). Both types of connectivity are critical for a full annual cycle approach to conservation planning (Cohen et al., 2018; Faaborg et al., 2010; Webster et al., 2002). Documenting patterns of migratory connectivity helps conservation practitioners understand a species' potential to adapt to threats experienced in migration and on the wintering grounds and to respond to global change (Betini et al., 2015; Taylor & Norris, 2010; Webster & Marra, 2005). ERMC can be particularly important, as migration is thought to be the period with the highest mortality rates in many species (e.g. Klaassen et al., 2014; Rockwell et al., 2017; Sillett & Holmes, 2002). Furthermore, spatiotemporal variation in migration has been directly linked with variation in mortality (Hewson et al., 2016), differences in reproductive success (Visser et al., 2004) and differences in population trends both within (Hewson et al., 2016; Kramer et al., 2018) and among species (Møller et al., 2008). This knowledge facilitates targeted allocation of scarce conservation resources, both regarding key locations for habitat preservation or restoration (e.g. at important wintering areas; Tonra, Hallworth, et al., 2019) and to coordinate actions during critical phases in the annual cycle (e.g. lights-out efforts during migration; Horton et al., 2019).

As quantitative estimates of BWMC only reflect the strength of population cohesion (e.g. MC metric; Cohen et al., 2018), assessing spread metrics and latitudinal distribution patterns (hereafter: connectivity pattern) provides a more detailed understanding of the spatial arrangement of breeding populations on the wintering grounds. Spread metrics are measured as the average distance between individuals on the wintering grounds, and comparing population spread (distance between individuals from a given breeding population) to non-breeding range spread (distance between all individuals irrespective of breeding population) can help quantify how much overlap there is among breeding populations (Finch et al., 2017). Additionally, Newton (2008) reviewed three connectivity patterns based on overlap of breeding populations from different latitudes

on the wintering grounds, two that would be examples of strong connectivity (chain and leapfrog migration; Salomonsen, 1955) and one that would constitute weak connectivity (telescopic migration; Salomonsen, 1955). Briefly, chain migration is when breeding and wintering populations exist in the same latitudinal sequence on the breeding and wintering grounds (migration distance is similar between different breeding populations, but wintering latitude is different; e.g. Chabot et al., 2018). Leapfrog migration is when the latitudinal sequence of populations is reversed during the breeding and winter periods (migration distance increases with breeding latitude, and wintering latitude is different; e.g. Bell, 1997; Kelly et al., 2002). Finally, telescopic migration is when populations breeding at different latitudes winter at a similar latitude (migration distance increases with breeding latitude, and wintering latitude does not differ; e.g. Fraser et al., 2012; Renfrew et al., 2013; Tonra, Hallworth, et al., 2019). These connectivity patterns relate to spread metrics as well. In both chain and leapfrog migration, population spread should be smaller than non-breeding range spread, but in telescopic migration, the two metrics should be similar. Intraspecific competition (Bell, 2000), habitat quality (McKinnon et al., 2015) and trade-offs between migration costs and wintering habitat quality (Alves et al., 2013) can drive these patterns. Therefore, describing connectivity patterns can have important implications for understanding species ecology.

The migratory route taken by individuals can be important in determining both BWMC and ERMC (Cohen et al., 2019; Trierweiler et al., 2014). Individuals from distinct breeding populations converging on a single migratory route could result in high spatial overlap (i.e. bottlenecks), as is often seen when species avoid an ecological barrier (e.g. deserts, oceans, mountains; Bayly et al., 2018; Bildstein, 2006; Newton, 2008), or seek resources that are concentrated in space (e.g. thermals in raptors; Bildstein, 2006; grassland productivity in Bobolinks, *Dolichonyx oryzivorus*; Renfrew et al., 2013). However, there must also be temporal overlap in addition to spatial overlap to observe low ERMC (e.g. Cardenas-Ortiz et al., 2020). On the contrary, species migrating with no spatial overlap (e.g. on opposing sides of a migratory divide; Delmore & Irwin, 2014) will have high ERMC regardless of phenology (see figure 1 in Knight et al., 2021 for a visualization of the spatiotemporal aspects of ERMC). Furthermore, migratory route can influence population mixing during winter (Finch et al., 2017). For example, longitudinal separation observed between distinct breeding populations can be maintained

on the wintering grounds when populations follow distinct flyways on a north-south axis (e.g. Hobson et al., 2015; Knight et al., 2018; Stanley et al., 2015; but see Tonra, Hallworth, et al., 2019).

The alarming declines in migratory birds have been consistent across species in several guilds, such as aerial insectivores, for which >70% of species are declining in North America (31.8% overall population decline since 1970; Rosenberg et al., 2019). While some species in this guild have received increasing attention in tracking studies (e.g. Fraser et al., 2012, 2018; Knight et al., 2018), general causes of decline remain poorly understood. The eastern whip-poor-will (*Antrostomus vociferus*; hereafter: whip-poor-will) is one example of an enigmatic, rapidly declining aerial insectivore (~70% in the last 50 years; Rosenberg et al., 2016). As with many nightjars (Family Caprimulgidae), spatial ecology studies are hampered by their nocturnal habits, cryptic plumage and lack of vocalization outside of the breeding season (Cink et al., 2020). Furthermore, whip-poor-wills exhibit high spatial variation in breeding population trends (Appendix S1; Sauer et al., 2017), and variation in migration routes and/or winter habitat have been suggested as potential drivers behind these regional trend differences (English, Mills, et al., 2017; Michel et al., 2016; Spiller & Dettmers, 2019). Thus, tracking technologies are needed to examine migratory connectivity in this species. Past tracking studies have found evidence for an overland migration route, where birds circumvent the Gulf of Mexico (Korpach et al., 2019). If the Gulf acts to funnel individuals from a wide longitudinal gradient into a successively smaller area, we expect spatial overlap to increase as individuals round the Gulf and that breeding and wintering longitude will be unrelated. All prior tracking studies point to primary wintering locations in southern Mexico and northern Central America (English, Mills, et al., 2017; Korpach et al., 2019; Tonra et al., 2019), and there is marginal evidence that Canadian populations exhibit a leapfrog migration pattern (English, Mills, et al., 2017). However, tracking across a greater spatial extent of the range is necessary to better understand migratory connectivity for this species, particularly across a larger latitudinal span of their breeding range to examine connectivity patterns.

We deployed archival GPS tags on whip-poor-wills at 5 breeding areas spanning a 9.5° latitudinal gradient (~1,000 km) in the midwestern United States, which holds roughly half of the species' population (Rosenberg et al., 2016). Deployment of tags occurred in portions of the range that exhibit both increasing and declining population trends (Appendix S1; Rosenberg et al., 2016). Our primary goal was to fill knowledge gaps on migration ecology and migratory connectivity to inform effective conservation of this declining species. Specifically, we addressed 3 objectives. (1) We quantified basic migratory behaviour, identified migration routes, bottlenecks and key stopover areas, and examined patterns in ERM during the migratory period. (2) We identified wintering sites of individuals and quantified the strength of BWMC. (3) We determined the latitudinal connectivity pattern and population/non-breeding range spread to further understand the nature of the observed BWMC score. Specifically, we tested the predictions of each connectivity pattern (chain, leapfrog and telescopic), based on (1) migration distance and

wintering latitude in comparison with breeding latitude and (2) population spread relative to non-breeding range spread.

2 | METHODS

2.1 | Study sites

We captured and tagged whip-poor-wills in five breeding areas across four states in the midwestern United States, spanning a latitudinal gradient of 9.49° (36.88°N to 46.37°N) and a longitudinal gradient of 8.81° (Figure 1). In Ohio, we captured at two distinct areas on opposite sides of the state, hereafter: southern Ohio and northern Ohio. These two breeding areas were maintained separately in analysis, as northern Ohio was previously glaciated and is oak-savannah habitat, whereas southern Ohio was never glaciated and is predominantly oak-hickory forest in the foothills of Appalachia. Furthermore, the two sites are situated 300 km apart. Outside of Ohio, all sites within a state were analysed together and considered single breeding areas (Figure 1). For example, we deployed at three sites in Illinois, two sites in the Ozark Highlands in Missouri and two sites in northern Wisconsin (thus, 9 breeding

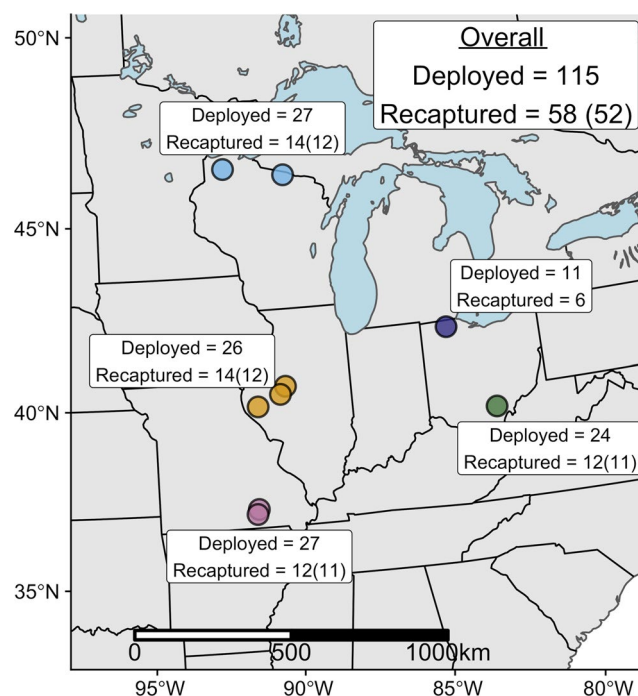


FIGURE 1 Deployment locations for 115 archival GPS tags on whip-poor-wills throughout the midwestern United States. Numbers in parentheses represent the number of functioning tags (all tags worked if no number is listed). Each circle represents a breeding site (9), and all circles of the same colour (colour scheme maintained across all figures) represent a breeding area (5). Locations of breeding sites are as follows: Northern Ohio (41.47°N, -83.84°W), Southern Ohio (39.11°N, -82.40°W), Illinois (38.65°N, -88.77°W; 39.87°N, -90.93°W; 39.87°N, -90.93°W), Missouri (37.03°N, -91.15°W; 36.89°N, -91.21°W) and Wisconsin (46.10°N, -89.31°W; 46.37°N, -91.58°W)

TABLE 1 Mean $\pm$ standard deviation of key migratory variables during fall migration of tagged whip-poor-wills, irrespective of year. Sample sizes are listed in parentheses. Migratory distances include the added inflection points around the Gulf of Mexico if the original track went over the Gulf. For 13 individuals, where no fix was taken between the last migration point and first winter point, no arrival date or migration time was assigned

Population	Migratory distance (km)	Migratory time (days)	Departure date	Arrival date	Duration of first stopover (days)
All populations	3337.3 $\pm$ 663.9 (50)	20.8 $\pm$ 9.5 (37)	28 Sep $\pm$ 6.5 (50)	22 Oct $\pm$ 10.8 (37)	6.7 $\pm$ 3.5 (20)
Illinois	3029.2 $\pm$ 262 (12)	16.1 $\pm$ 4.7 (9)	01 Oct $\pm$ 4.8 (12)	18 Oct $\pm$ 5.7 (9)	5.0 $\pm$ 0.0 (4)
Missouri	2787.6 $\pm$ 370.7 (11)	20.0 $\pm$ 8.2 (7)	28 Sep $\pm$ 6.5 (11)	20 Oct $\pm$ 3.5 (7)	7.5 $\pm$ 5.0 (4)
N Ohio ^a	3656.6 $\pm$ 370.4 (5)	18.0 $\pm$ 2.8 (2)	22 Sep $\pm$ 9.6 (5)	17 Oct $\pm$ 2.8 (2)	5.8 $\pm$ 2.9 (4)
S Ohio ^a	3291.6 $\pm$ 668.6 (10)	19.0 $\pm$ 11.1 (9)	28 Sep $\pm$ 6.5 (10)	17 Oct $\pm$ 8.8 (9)	6.0 $\pm$ 2.8 (5)
Wisconsin	4054.4 $\pm$ 582.4 (12)	27.9 $\pm$ 9.8 (10)	30 Sep $\pm$ 5.4 (12)	28 Oct $\pm$ 10.8 (10)	10.0 $\pm$ 5.0 (3)

^aThe sampling frequency was once every 4 days for the majority of tags deployed at these locations (2017–2018 deployment), which may affect the reported data (e.g. increasing likelihood that a stopover is detected).

sites and 5 breeding areas; Figure 1). Oak trees and shrubs dominate all sites (e.g. oak-hickory forest, black oak savanna and pine-oak woodland), except for Wisconsin, which was predominantly Pine Barren habitat. Breeding areas varied in population trends based on partners in flight estimates (Appendix S1; Rosenberg et al., 2016).

2.2 | Tag deployment, schedule and recovery

In 2017 and 2019 (two deployment seasons), birds were lured into mist nets by recorded calls of conspecifics. We aged and sexed individuals, took standard morphological measurements (e.g. mass, wing chord, tail length) and marked all individuals with a U.S. Geological Survey aluminium band. We attached a 1.5-gram archival GPS tag (model PinPoint-10; Lotek Wireless, Newmarket, Ontario, Canada; 2.5–3.0% of body mass) using a backpack-style leg-loop harness (Rappole & Tipton, 1991) constructed from 0.7-mm bead cord (Stretch Magic™) and 1.3-mm metal crimp beads. In 2018 and 2020 (two recapture seasons), we returned to the location where the bird was first caught and repeated the capture procedure. If the bird was not captured at the initial location, we expanded to the neighbouring territories until all nearby vocalizing individuals were identified.

We deployed a total of 115 GPS tags (see Figure 1 for distribution of tags among sites). Twenty-one tags were deployed in Ohio in 2017 (7 in northern Ohio and 14 in southern Ohio) and were programmed to take a GPS fix once every 4th day at 2300 EST; 94 tags were deployed in 2019 across all sites (including Ohio) and were programmed to take a point once every 5th day at 2300 EST. Within Ohio, three tags were deployed on the same individuals in both 2017 and 2019. The winter location data from the Ohio tags deployed in 2017 were reported in Tonra, Hallworth, et al. (2019), but no analyses were conducted regarding migration or migratory connectivity. All tags recorded points from 15 August through 4 May, or until the battery died.

2.3 | Statistical analysis

Across all objectives, we removed 2019 migration data for one individual that was tracked in both deployment years, keeping the 2017 data as it had finer temporal sampling resolution. We also removed the only female bird to avoid confounding sex effects, particularly as evidence suggests whip-poor-wills may exhibit differential migration, where females winter farther south than males (English, Mills, et al., 2017). We report descriptive data for these two individuals separately.

2.4 | Quantifying migratory behaviour and en route migratory connectivity (Objective 1)

We quantified descriptive metrics such as arrival and departure date, migration distance and duration, and stopover length (as in Taylor et al., 2011; Wright et al., 2018) and location for all breeding populations (Table 1; see Appendix S2 for details on how metrics were calculated). We focused on fall migration as information was recorded from all 52 individuals, but we also reported departure ($n = 13$) and arrival ($n = 3$) dates, plus migratory paths for spring migration. We report migratory metrics as mean $\pm$ standard deviation.

We assessed how ERMIC changed throughout the migratory period via two separate methods. First, we estimated a traditional connectivity metric, the Mantel correlation (r_M ; Ambrosini et al., 2009), using the estMantel function (default parameters – 1000 bootstrap samples and 1000 simulations) in the “MigConnectivity” package, which compares distance matrices between the breeding locations (“origin points”) and the locations of birds on successive dates of migration (“target points”). Hereafter, the term “ERMIC” refers only to this analysis. Second, we examined the relationship between interindividual distance (i.e. the average distance between an individual and all other individuals outside of its breeding population on a given date in migration) and date (similar to Ng et al., 2018). We refer to this analysis as “spatiotemporal overlap,” as it

explicitly measures the overlap of distinct breeding populations in time and space, and thus can be used to identify spatiotemporal bottlenecks throughout migration (sensu Cardenas-Ortiz et al., 2020; Knight et al., 2021). To test how spatiotemporal overlap changes throughout migration, we fit a linear mixed-effects model with the response variable interindividual distance, and fixed effects of date, date², date³, breeding latitude, plus the interactions between all polynomials of date and breeding latitude. We included individual as a random effect to account for repeat sampling (Bates et al., 2015). We chose to include polynomials of date through the 3rd order as the hourglass shape of the whip-poor-will's migratory range (wide in the USA, narrowing in Mexico and spreading out again in Central America) could result in a non-linear relationship. To assess statistical significance, we iteratively removed each variable and compared it to a full main-effects model (for testing main effects) or a full interactions model (for testing interactions), using likelihood ratio tests (Zuur et al., 2009). We ultimately removed all non-informative predictors ($p > .1$) and report results on final reduced models.

Although ERM and spatiotemporal overlap are similar conceptually, the two measures should be inversely related. From here on, we use the term "population cohesion" (in the context of migration) to refer to the combination of these two analyses. In population cohesion analyses, we only included the 2019 fall migration data from after-second-year (ASY) males, as phenology could differ by age, sex and year. We analysed only the five dates where all populations had at least one individual migrating (9/20/19–10/10/19). We refer to this period as "peak migration." One individual from Wisconsin exhibited phenology unique from all other individuals (labelled in Figure 2 as "2766") and thus was removed as an outlier.

2.5 | Estimating breeding-winter migratory connectivity (Objective 2)

We used the `estMC` function in the package "MigConnectivity" (Cohen et al., 2018) with default parameters in program R version 4.0.3 (R Development Core Team, 2020). This package is more appropriate than r_M in situations when sampling effort is not proportional to population size, as it weights the migratory connectivity score according to population sizes within predefined deployment ("origin") regions (Appendix S3; Cohen et al., 2018). The `estMC` function also requires delineating potential wintering ("target") regions, to determine the likelihood that populations will winter in specific areas. For deployment region population sizes, we used estimates from Bird Conservation Regions (BCRs) within states (BCR x State) as these provided the most regionally specific population estimates (Rosenberg et al., 2016). There was significant variation in the population estimates by BCR x State, ranging from 15 individuals in BCR 23 within Ohio, to 330,000 in BCR 24 within Missouri. We used these BCR x State polygons as our deployment region, and the countries or U.S. states that fall within the winter distribution as our

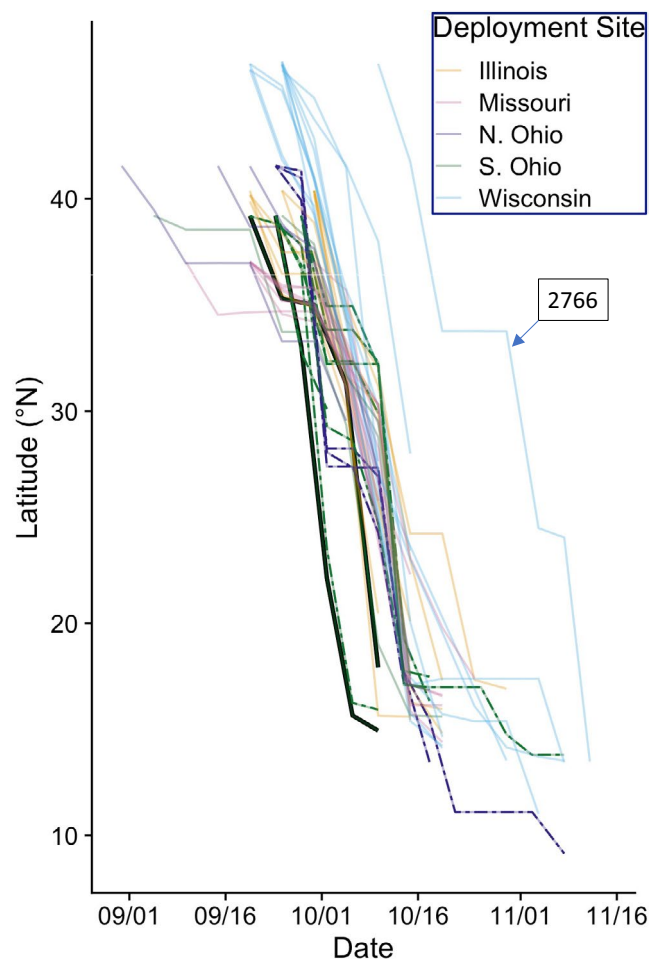


FIGURE 2 Latitudinal progression of fall migration for 51 whip-poor-wills tagged at 5 breeding areas in the midwestern United States. As this plot focuses on phenology, the 13 individuals missing data between migration and the first location on the wintering grounds are plotted only as far as phenology is accurate (i.e. lines do not extend to the wintering location in those 13 birds). Dashed lines represent data from 2017/18 in OH, and solid are from the multi-state 2019/2020 deployment. Opaque black lines represent the same individual tracked in both deployments. Note spatiotemporal overlap of populations ~20–30°N in early- to mid-October. Individual 2766 was identified as an outlier and removed from the model testing spatiotemporal overlap

wintering polygons. Thus, we had 5 origin locations and 12 potential target locations. We also calculated r_M using the `estMantel` function in the same package for comparison's sake (Appendix S3). For both functions, we used the capture coordinates as the origin points, and the first wintering location if there were multiple sites (eight individuals had two wintering locations; Skinner, 2021). To aid in the visualization of wintering distributions, we used the "adehabitatHR" package to calculate the core (50%) wintering ranges of our 5 breeding populations (Calenge, 2006), and the "raster" package (Hijmans, 2020) to create a summed probability raster from all 5 populations (Figure 3). See Appendix S4 for additional details regarding the creation of Figure 3.

2.6 | Understanding the observed breeding-winter migratory connectivity metric (Objective 3)

To examine latitudinal migratory connectivity patterns, we estimated two models, using breeding latitude as a predictor of migration distance and wintering latitude. As these are latitudinal distributional patterns (Newton, 2008), we used the straight-line distance between the breeding and the first or only wintering site instead of the actual migration distance, although these two variables are highly correlated ($r = 0.94$, $p < .001$, $t = 18.6$, $df = 48$). We

made three predictions, one for each connectivity pattern (chain, leapfrog or telescopic), based on the combined results of these two models. For chain migration, we predicted breeding latitude would be positively related to wintering latitude, but unrelated to migration distance. For leapfrog migration, we predicted breeding latitude would be negatively related to wintering latitude and positively related to migration distance. For telescopic migration, we predicted breeding latitude would be unrelated to wintering latitude, but positively related to migration distance. We ran an additional univariate model examining breeding longitude's effect on

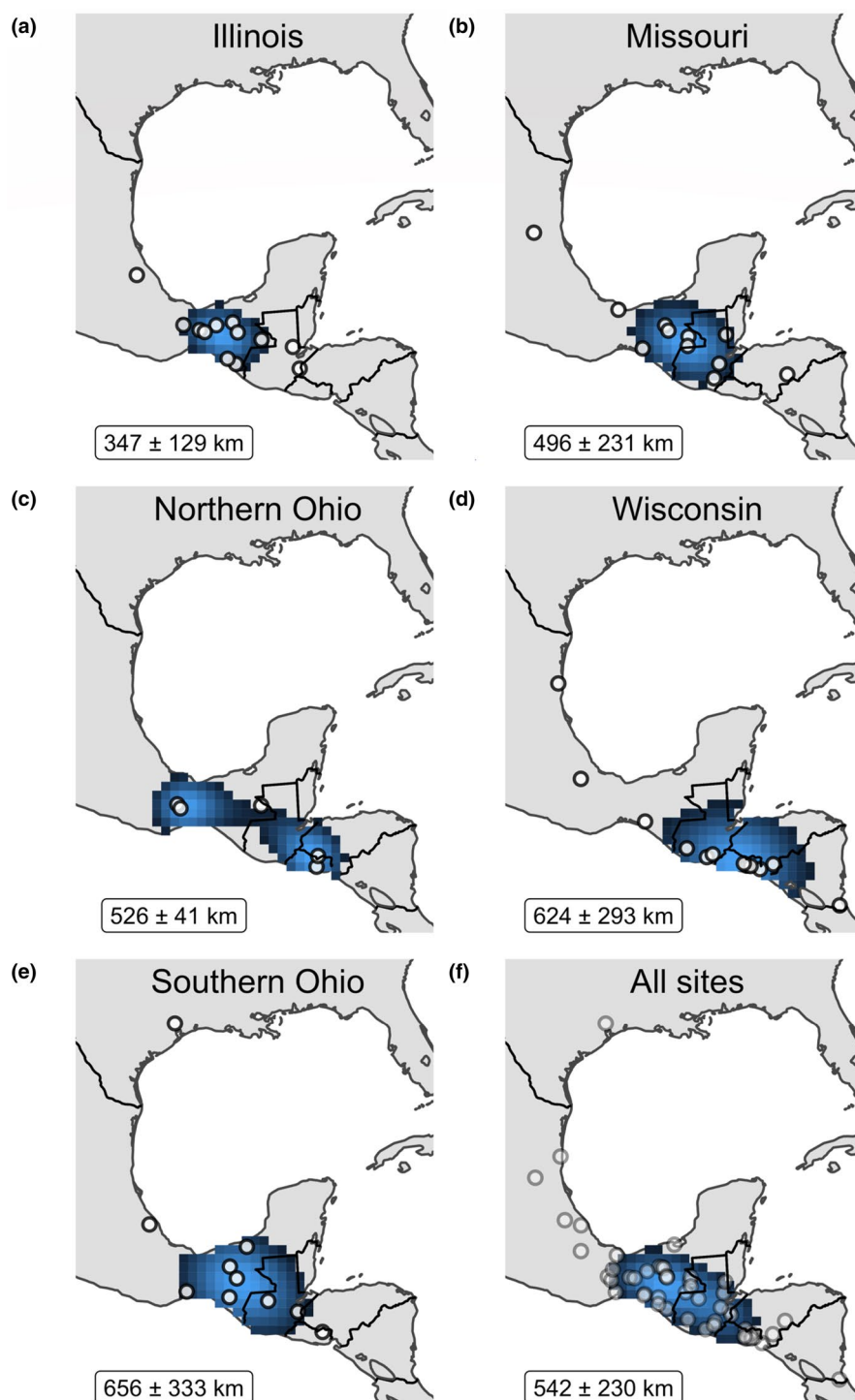


FIGURE 3 Wintering locations (grey circles) of all individual whip-poor-wills tracked from breeding sites across the midwest, listed at the top of each panel (Lambert conformal conic projection). Heatmaps show the 50% (core) utilization distributions of each breeding population in Panels a–e (ordered by increasing spread), and the summed probability raster from all 5 populations in Panel f. Lighter blues indicate greater probability of use. Population spread (i.e. mean distance between wintering sites of individuals from the same population) is listed for the 5 breeding populations (bottom left of Panels a–e), and the non-breeding range spread is listed for all sites combined (Panel f)

wintering longitude to determine whether the observed BWMC score was related to latitudinal or longitudinal spread, or both.

To gain additional insight into the migratory connectivity score, we also calculated non-breeding range spread and mean population spread, following Finch et al. (2017). Population spread represents the degree to which individuals from a single breeding population spread out on the non-breeding grounds, whereas non-breeding range spread represents the degree that individuals, irrespective of breeding population, spread out across the non-breeding range. Both metrics involve calculating the mean great-circle pairwise distances between a bird's non-breeding location and other birds' non-breeding locations, but population spread only includes birds that come from the same breeding population, whereas non-breeding range spread includes all birds in the analysis (see Finch et al., 2017). We ran a paired *t* test comparing non-breeding range spread and population spread.

Across all models under Objectives 2 and 3, we included second-year (SY) birds and 2017 data based on two lines of reasoning. First, landbirds generally do not change wintering location after their first migration (Blackburn & Cresswell, 2016; Cresswell, 2014). Second, we examined models with SY and 2017 birds and compared results with 3 models that excluded these birds (excluding just SYs, just 2017 birds, or both). Exclusion of SY and 2017 birds did not significantly alter coefficients (at $p < .1$) in any models.

3 | RESULTS

We recovered 58 of 115 deployed tags (50%; Figure 1). In 2018, we recaptured 11 of 21 (52%) tags from Ohio, and in 2020, we recaptured 47/94 tags (50%) from all five breeding areas. We recaptured a single ASY male in southern Ohio in both 2018 and 2020 (hereafter: repeat-track individual). Recapture rates were similar between sites, ranging from 44 to 54% (Figure 1). We caution use of our tag recovery rates as indicative of survival rates of tagged birds, as the global COVID-19 pandemic hampered our overall recapture effort in 2020. Six tags did not collect any usable data from the 2019–2020 field seasons, leaving 41 tags from 2019 to 2020 and 52 tags overall that contained usable data. Of the 52, 6 were from SY birds, 44 were ASY, and 2 were not aged.

3.1 | Migratory routes, stopovers and phenology (Objective 1)

Migration locations were consistent with circumvention of the Gulf of Mexico in fall, as no points were recorded over open water and all paths followed the eastern coast of Texas and Mexico. Birds departing from Wisconsin, Illinois and Missouri took similar routes aimed south-southwest, largely through Arkansas and eastern Texas. The Ohio breeding populations travelled largely southwest through Kentucky, Tennessee and the Mississippi Alluvial Valley before converging with the more western breeding populations,

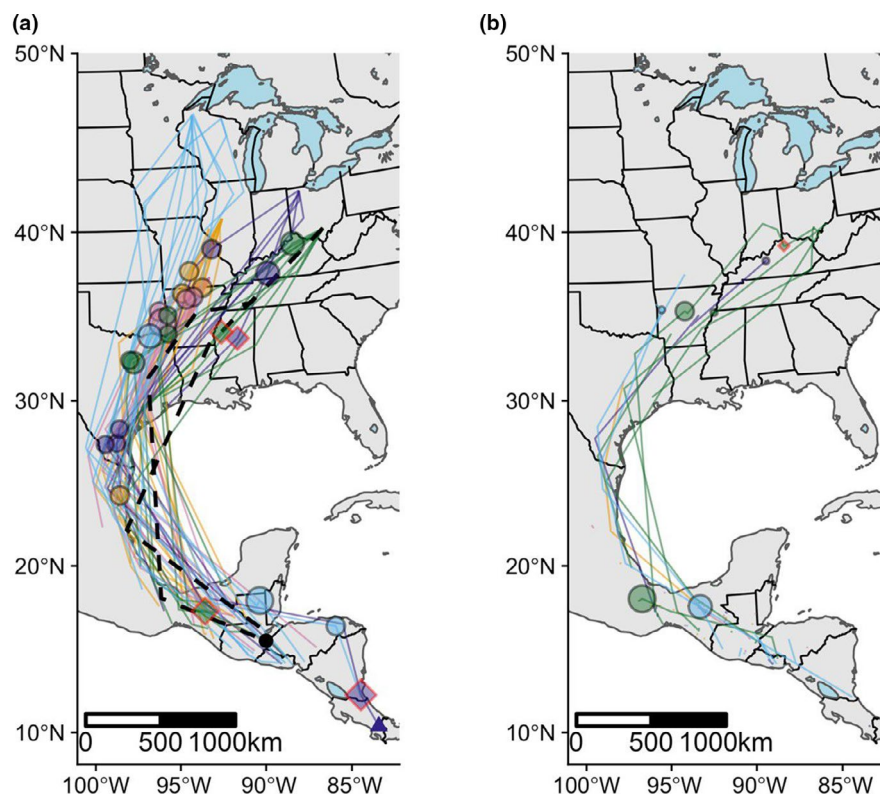
largely in eastern Texas, before continuing south through Mexico (Figure 4a). We confirmed at least one stopover (minimum possible stopover detection was 4 days) for 20 of 50 individuals, occurring between Kentucky and El Salvador. Of confirmed stopovers, 12 individuals stopped in one of the following regions: the Ozark Plateau, the Ouachita Mountains or the prairie/forest ecoregion of eastern Texas (Figure 4a). Three individuals stopped a second time, ranging latitudinally from Mississippi to southern Mexico. Average minimum duration of the first stopover was 6.7 ± 3.5 days (range: 4–15 days) and 6.0 ± 1.7 days (range: 5–8 days) for the second stopover. The repeat-track individual did not have confirmed stopovers in either year. The female stopped twice, once in southern Texas for 4 days and once in southern Nicaragua for 12 days.

Migration distance ranged from roughly 1600 km for the bird wintering in Texas to nearly 5000 km for a Wisconsin breeder wintering in Nicaragua (Table 1). Migration time averaged 20.8 ± 9.5 days and ranged from 4 (bird wintering in Texas) to 45 days (a Wisconsin breeder wintering in southern Honduras and stopping over in Guatemala for 15 days; Table 1). Migration time was positively correlated with migration distance ($r = 0.65$, $p < .001$, $t = 5.04$, $df = 35$). These relationships resulted in different migration times by breeding location. For example, birds departing from Wisconsin spent >10 additional days on migration than birds departing from Illinois, on average (Table 1). The female migrated 5122 km over 40 days. The average date for commencement of spring migration was 20 March ± 7.2 days ($n = 8$ from 2018, $n = 5$ from 2020), and the average arrival date to the breeding grounds was 17 April ± 14.1 days ($n = 3$ from 2018). These data are biased towards the 2017–2018 Ohio deployment, although departure dates were also recorded for three birds from Wisconsin and a single bird from Missouri and Illinois in 2020. Average time for spring migration was 22.7 ± 16.2 days ($n = 3$). There were no GPS fixes over the Gulf of Mexico during spring migration either (Figure 4b).

3.2 | Spatiotemporal overlap and en route migratory connectivity (Objective1)

Visual inspection of latitude by successive dates during migration shows convergence around late September and early October, at latitudes between 30°N and 37°N (Figure 2). Overall, spatiotemporal cohesion increased throughout peak migration, as spatiotemporal overlap (measured via the analysis of interindividual distance with date) increased while ERM (measured via r_M on successive dates) decreased (Figure 5a; $n = 149$). Mantel correlation values decreased as follows: 20 September $r_M = 0.94$; 25 September $r_M = 0.85$; 30 September $r_M = 0.61$; 5 October $r_M = 0.26$; 10 October $r_M = 0.13$ (Figure 5a). We found that date^2 ($\chi^2 = 24.38$, $df = 1$, $p < .001$), date^3 ($\chi^2 = 65.39$, $df = 1$, $p < .001$) and the interaction of date and breeding latitude ($\chi^2 = 16.93$, $df = 1$, $p < .001$) were all important predictors of interindividual distance. Interactions between higher order polynomials (i.e. date^2 and date^3) and breeding latitude did not improve the model (all $p > .55$). The interaction of date and breeding latitude

FIGURE 4 Fall ($n = 52$; panel a) and spring ($n = 13$; panel b) migration paths of whip-poor-wills from 5 breeding areas across the midwestern United States (Lambert conformal conic projection). Transparent circles represent first stopover locations of ≥ 4 days, and diamonds with a red outline represent second stopover locations. Size of points represents the duration of the stay (4–16 days), with larger points representing longer stays. In panel a, the black dashed lines represent the migratory paths of the repeat-track individual, the black circle represents its repeated wintering location, and the purple triangle (southern Costa Rica) represents the single female with tracking data



suggests that as migration progressed, interindividual distance decreases faster for birds coming from higher latitudes ($\beta = -638.39$, 95% CI: $-925.55, -342.58$). Within peak migration, spatiotemporal overlap was the greatest on 5 October, with an individual's average location at 33.1 ± 2.5 degrees' latitude and -95.2 ± 1.1 degrees' longitude (about 150 km east of Dallas) and a mean interindividual distance of 343 ± 186 km (Figure 5b).

3.3 | Breeding-winter migratory connectivity (Objective 2)

Most individuals from our deployment locations wintered in southern Mexico and northern Central America (particularly Guatemala and El Salvador), although individuals wintered from Texas to Costa Rica (Figure 4). The high amount of overlap on the wintering grounds resulted in weak migratory connectivity ($MC = 0.22 \pm 0.12$), regardless of the method used to calculate migratory connectivity (Appendix S3; $rM = 0.15 \pm 0.06$). The repeat-track individual wintered in the exact same location in eastern Guatemala in both 2017/2018 and 2019/2020.

3.4 | Understanding the breeding-winter migratory connectivity score (Objective 3)

According to the predictions laid out in the methods, our analyses are consistent with leapfrog migration; however, a biologically informed interpretation suggests telescopic migration. We begin with

the evidence supporting leapfrog migration. There was a relatively weak negative relationship between breeding latitude and wintering latitude (Figure 6a; $r^2 = 0.08$, $\beta = -0.25$, $p = .05$, $n = 50$), but a strong positive relationship between the straight-line distance from the breeding to wintering site and breeding site latitude (Figure 6b; $r^2 = 0.74$, $\beta = 133.09$, $p < .001$, $n = 50$), which matches our prediction for leapfrog migration. However, we highlight the low r^2 value in the breeding latitude and wintering latitude model ($r^2 = 0.08$). This indicates that the average distance between any two individuals on the wintering grounds is not explained by their respective breeding population and that there is a high amount of overlap between wintering populations, both of which are more consistent with a telescopic migration pattern. Breeding longitude had no effect on wintering longitude ($r^2 = 0.001$, $\beta = -0.06$, $p = .62$, $n = 50$). Additionally, we found no difference between non-breeding range spread (526.0 ± 261.4 km) and population spread (542.0 ± 230.3 km; $t = 1.00$, $df = 49$, $p = .32$). The average distance between individuals from the same breeding site ranged from 346.6 km for Illinois to 656.1 km for southern Ohio populations (Figure 3).

4 | DISCUSSION

Elucidating breeding-winter connectivity and spatiotemporal cohesion throughout migration is important for a full annual cycle approach to conservation in migratory birds (Marra et al., 2015), yet these data have remained elusive for small birds until the advent of miniaturized tracking technology (McKinnon & Love, 2018). We examined the migratory ecology of a cryptic, nocturnal and rapidly

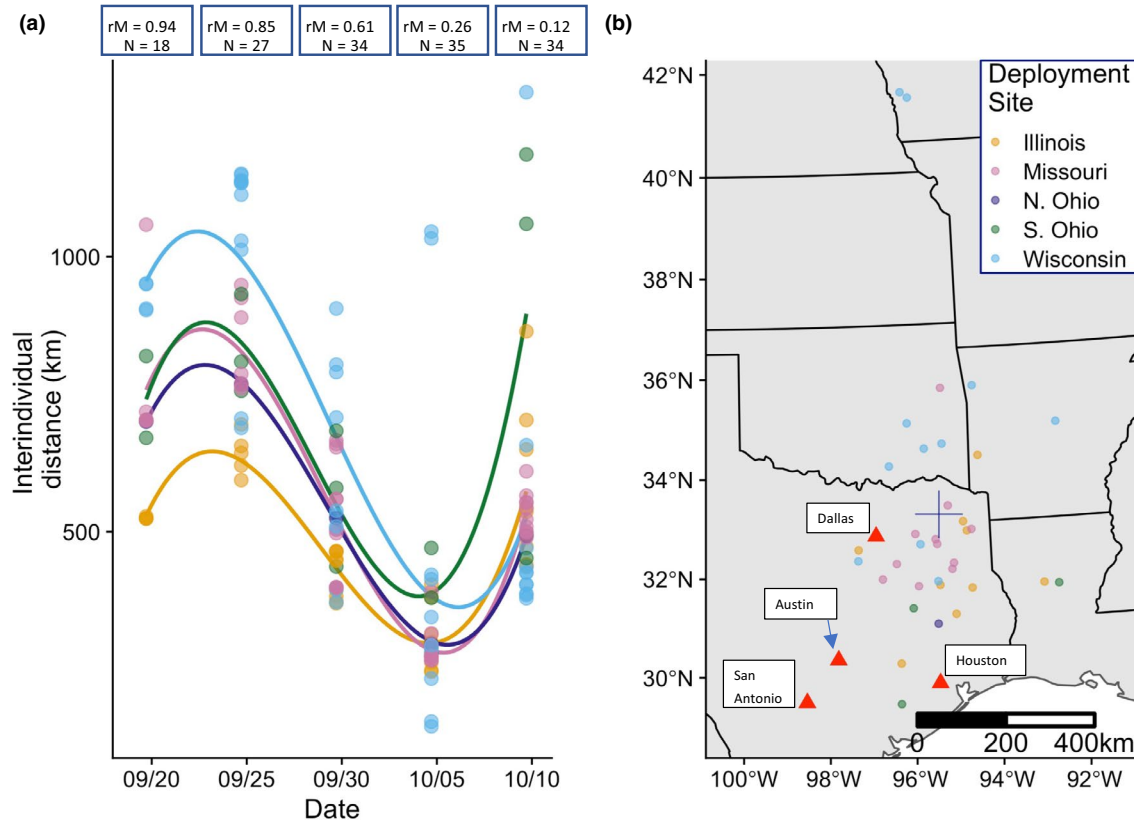


FIGURE 5 Analysis of spatiotemporal overlap through peak migration in whip-poor-wills. Panel a depicts the third-order polynomial of date on the average straight-line distance (km) between an individual whip-poor-will and all individuals from the other four deployment sites in 2019/2020. Only dates when at least one individual was moving from each deployment location are shown ('peak migration', 5 time steps: every 5 days between 20 September 2019 and 10 October 2019). Mantel correlation values (r_M) and sample sizes are shown above each date in the blue boxes. Panel b shows the locations in the central United States of all whip-poor-wills on 5 October 2019 the date when interindividual distance was at a minimum. The blue cross depicts the mean latitude and longitude (33.1°N, -95.2°W) of all individuals. Red triangles show four major urban areas that whip-poor-wills likely traverse during fall migration

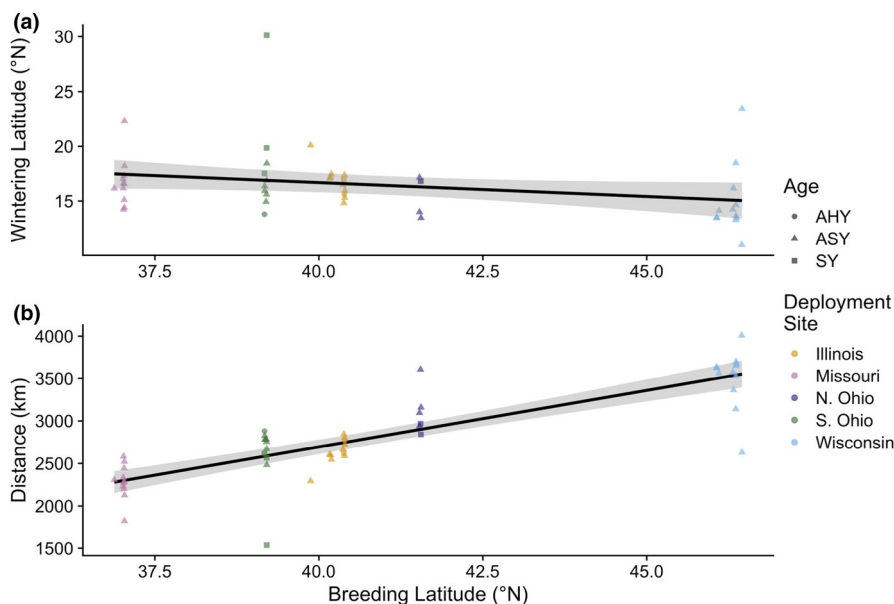


FIGURE 6 The effect of a whip-poor-will's breeding latitude on wintering latitude (panel a) and the straight-line distance between its breeding and wintering sites (panel b). The line of best fit in panel a is $y = 26.83 - 0.25x$, $R^2 = 0.08$, $p = .046$, $n = 50$; and in panel b is $y = -2650.18 + 133.09x$, $R^2 = 0.74$, $p < .001$, $n = 50$. Shape of points represents the age of individuals, where AHY (unknown age) birds are represented as circles, ASY (adult) birds are represented as triangles, and SY (juvenile) birds are represented as squares. Grey shaded area represents the 95% confidence intervals around the line of best fit

declining aerial insectivore using archival GPS tags. We found that whip-poor-wills from across an area containing 50% of the breeding population converged on a shared migratory path while avoiding the Gulf of Mexico, with a spatiotemporal bottleneck in early October.

Thus, spatiotemporal overlap increased through peak migration. Extensive overlap of core wintering areas in southern Mexico and northern Guatemala resulted in weak BWMc, similar non-breeding range and population spread, and evidence of a connectivity pattern

most strongly resembling telescopic migration. The geographic scope of our deployment allowed us to demonstrate that birds across a wide portion of the breeding range overlap during multiple stages of the non-breeding period. This suggests that spatial variation in breeding season population trends cannot readily be explained by events occurring in the non-breeding season.

4.1 | Migration route, spatiotemporal overlap and key stopover areas (Objective 1)

Population cohesion increased throughout the migratory period. As found in previous studies of Canadian populations (English, Mills, et al., 2017; Korpach et al., 2019), migratory paths from individuals we tracked, regardless of breeding longitude, are consistent with circumventing the Gulf of Mexico. Although the temporal resolution of our data does not allow us to rule out water crossings on the western edge of the basin, the Gulf of Mexico appears to act as a barrier, resulting in a spatiotemporal bottleneck in the southern United States and eastern Mexico. Both density-dependent (e.g. competition for food) and independent (e.g. extreme weather events) regulation can play an important role at migratory bottlenecks (Cardenas-Ortiz et al., 2020; Newton, 2006), and conserving high-quality habitat in this region will be particularly important (Bayly et al., 2018; Gómez et al., 2019). Circumvention of the Gulf of Mexico in this species contrasts with other Neotropical migrants that maintain longitudinal separation on southward migration before crossing over the Gulf (e.g. ovenbird *Seiurus aurocapilla* in Hallworth et al., 2015; wood thrush *Hylocichla mustelina* in Stanley et al., 2015). Similarly, other nightjar species also cross ecological barriers on migration, including the common nighthawk (*Chordeiles minor*), which consistently crosses the Gulf (Knight et al., 2021; Ng et al., 2018), and the European nightjar (*Caprimulgus europaeus*) which cross both the Mediterranean Sea and the Sahara desert (Evens et al., 2017; Norevik et al., 2020). Differing winter destinations, flight efficiency, barrier size and daytime light tolerance (Adamik et al., 2016; Agostini et al., 2015; Korpach et al., 2019) may alter the balance of trade-offs regarding barrier crossing in these Caprimulgids (Alerstam, 2001).

More than half of birds with confirmed stopovers used a relatively small region spanning about 600 km from the Ozark Plateau in southern Missouri, to the plains and forest of north-eastern Texas. Four of five of our populations (excluding the northern Ohio population), and at least some Canadian populations (English, Mills, et al., 2017; Korpach et al., 2019), used these regions for stopover. However, many more individuals may have made stopovers of <4 days (~65% of detected stopovers were <4 days in Korpach et al., 2019) in this area, but these details were beyond the temporal resolution of the fix schedules in this study. Making multiple stopovers (as suggested by Korpach et al., 2019) and avoiding barrier crossings are consistent with an energy-minimizing migration strategy (Alerstam, 2001; Alerstam & Lindström, 1990); this strategy has also been suggested in the European nightjar (Norevik et al., 2020), and evidence for energy-conserving life-history strategies (Brigham

et al., 2006; Lane et al., 2004) implies that this migratory strategy may be common in Caprimulgids. Making multiple, relatively short stopovers, combined with the fact that nightjars likely forage throughout migration when environmental conditions are optimal (Norevik et al., 2019), suggests that conservation of a single critical stopover site will be insufficient, and instead, conservation efforts should be focused at broader spatial scales (Newton, 2008). The key stopover corridor utilized by whip-poor-wills is predominantly forested, and forest is selected for by whip-poor-wills during migration (M. Bakermans pers. comm.). Threats to forest in the region include climate change, agricultural and urban expansion, and pests such as the red oak borer (*Enaphalodes rufulus*, Stephen et al., 2001; Wang et al., 2019). Studies of stopover ecology and fine-scale habitat preferences are needed to understand whip-poor-will foraging habits during migration, and ultimately, what constitutes high-quality habitat for this species (Bayly et al., 2016, 2018).

The spatiotemporal bottleneck in eastern Texas, one of the most heavily urbanized regions in North America, represents both an extreme threat to migrating whip-poor-wills and a conservation opportunity. Birds from both the United States and Canada (Korpach et al., 2019) traverse several large cities in eastern Texas (Dallas, Houston, Austin and San Antonio), which include two of the top three threats regarding artificial light for migrating birds (Horton et al., 2019). Whip-poor-wills are at particularly high risk for high-rise building collisions (Loss et al., 2014), and thus, early October (when spatiotemporal overlap peaked) may be a significant source of mortality in migrating whip-poor-wills. On the contrary, coordinated efforts to reduce light pollution in these cities at this time of year may have outsized benefits for migrating whip-poor-wills from across the breeding range. Future research should prioritize how light-sensitive nocturnal species migrate through heavily urbanized regions (Horton et al., 2019; Van Doren et al., 2017).

4.2 | Breeding-winter migratory connectivity (Objective 2)

Although individuals from our study wintered from southern Texas to Costa Rica, southern Mexico and northern Central America were the key wintering regions for all breeding populations in our study. This area also appears to be heavily used by populations from the northern limit of the breeding range in Canada (English, Mills, et al., 2017; Korpach et al., 2019). We determined that whip-poor-wills have weak migratory connectivity, both objectively (between 0 and 0.33 is considered low; Hallworth et al., 2015) and relative to other species breeding in the Nearctic and Palearctic (Knight et al., 2018). As described by Finch et al. (2017), we believe that the avoidance of the Gulf on migration diluted the longitudinal separation between breeding populations and thus played a key role in determining BWMC. Regardless, changes on the wintering grounds likely have an effect on populations throughout the whip-poor-will breeding range (Betini et al., 2015; Finch et al., 2017; Taylor & Norris, 2010). Primary threats to this region include widespread deforestation (Aide et al.,

2013; Hansen et al., 2008), which is particularly concerning given whip-poor-will use of closed-canopy forests during the wintering period (Skinner, 2021; Tonra, Wright, et al., 2019). Furthermore, agricultural pesticide use could be altering prey abundance or composition (Klemens et al., 2000). Destruction of habitat in this area could be responsible for a disproportionate amount of observed and future population declines in the whip-poor-will, along with a diverse suite of forest-dependent Neotropical migrants that winter in this region (La Sorte et al., 2017; Taylor & Stutchbury, 2016; Wilson et al., 2019).

4.3 | Understanding the observed breeding-winter migratory connectivity score (Objective 3)

As BWMC calculations result in only a single metric, determining connectivity patterns and comparing spread metrics can help ecologists better understand how distributions change throughout the annual cycle. Our findings suggest a primarily telescopic connectivity pattern. However, when based solely on the relationships of migration distance and wintering latitude with breeding latitude, the prediction that whip-poor-wills exhibit leapfrog migration was marginally supported. Additionally, the small amount of migratory connectivity we observed ($MC = 0.22 \pm 0.12$) was likely due to this latitudinal separation, given that breeding and wintering longitude were unrelated. However, the relationship between breeding and wintering latitude was weak, with northern breeders wintering only slightly farther south (core area in Guatemala vs. southern Mexico), and all populations exhibited extensive overlap. Traditional examples of leapfrog migration generally showcase little population overlap and much greater differences in wintering latitudes (e.g. Bell, 1997; Kelly et al., 2002). Furthermore, the lack of difference between population and non-breeding range spread is consistent with the expectations of a telescopic connectivity pattern. Lastly, whip-poor-wills breeding in Canada also appear to concentrate in southern Mexico and northern Central America (English, Mills, et al., 2017; Korpach et al., 2019), adding further evidence for a telescopic migration pattern, as these populations are farther north than our Wisconsin sites. Like other classifications in ecology (e.g. *r*- vs. *K*-selection, Pianka, 1970; capital vs. income breeding, Stephens et al., 2009), connectivity patterns exist more on a continuum. Additional data from unstudied regions of the breeding range (e.g. the south-eastern and far north-eastern United States) will be critical for a range-wide understanding of migratory connectivity and patterns (McKinnon & Love, 2018).

The primarily telescopic pattern of migratory connectivity is important for understanding the potential threats faced by distinct populations, and the eco-evolutionary pressures shaping differences in life-history strategies between populations (Newton, 2008). Both telescopic and leapfrog connectivity patterns result in vastly different distances travelled for different breeding populations (e.g. Bell, 1997; Fraser et al., 2018; McKinnon et al., 2015). In our study, Wisconsin and northern Ohio populations travel ~1000 kilometres further than the Missouri and Illinois populations, on average. Migration time and distance were positively correlated, suggesting that more northerly

populations are non-stationary for a greater proportion of the annual cycle. Increased migration distances and times generally result in increased energetic costs (Pennycuik, 2008) and mortality risk (Taylor & Norris, 2010). The resolution of population trend data was not fine enough to comment on the relationship between migration distance and trends in our study (Appendix S1), but studies have found that long-distance migrants are declining more than short-distance migrants and residents (Both et al., 2010; Møller et al., 2008). Future research quantifying the life-history trade-offs (e.g. productivity vs. survival) in populations residing across a latitudinal (and migration distance) gradient would be beneficial for both conservation efforts and basic ecological theory (Winger & Pegan, 2021).

4.4 | Metrics for understanding population cohesion throughout the full annual cycle

There are an ever-increasing number of ways to quantify population cohesion throughout the full annual cycle (Ambrosini et al., 2009; Cohen et al., 2018; Finch et al., 2017; Knight et al., 2021; van Toor et al., 2018), and we have implemented many of these approaches here. Specifically, we combined population and non-breeding range spread metrics (Finch et al., 2017), Cohen et al.'s (2018) MC metric and r_M (Ambrosini et al., 2009) to estimate BWMC and assign whip-poor-wills a migratory pattern. In addition, we used r_M and a non-linear inter-individual distance by date model (spatiotemporal overlap) to assess population cohesion throughout migration. While the three methods for BWMC were largely in agreement, there are some key differences in the two methods used to quantify population cohesion throughout migration. r_M is still the most prevalent approach for quantifying connectivity throughout migration (e.g. Knight et al., 2021; Norevik et al., 2020; but also see Cohen et al., 2018, 2019; Knight et al., 2018). The main advantage of r_M is that it is standardized (i.e. the output is always between -1 and 1) and easy to implement. However, r_M on migration is calculated by iteratively correlating two distance matrices (a breeding matrix and the migration date matrix), and thus, the scores are always relative to the distribution of the initial breeding populations. Interindividual distance, on the other hand, has not been widely implemented (but see Ng et al., 2018) and is not standardized, making comparisons between species, studies and geographic regions difficult. However, it exactly measures spatiotemporal overlap between populations, which can be more useful for implementing conservation actions. For example, the minima in Figure 5a marks a spatiotemporal bottleneck, providing a date and specific location where conservation efforts would impact the largest number of individuals from across the breeding range. Its' output is also in kilometres instead of a scaled value between -1 and 1, making interpretation more straightforward. Importantly, the two metrics will not always coincide (as in this study), and correct interpretation of each metric is critical for successful conservation action. Simulation studies should compare differences between r_M , spatiotemporal overlap and Cohen's MC (not measured here) analyses, while varying breeding population distributions, migratory paths, population abundance and sampling effort.

4.5 | Conclusions

We calculated migratory connectivity for the first time in the whip-poor-will, identified key winter and migratory regions for conservation efforts and tested hypotheses regarding connectivity patterns in this species. Documenting distributional and phenological patterns is especially important if we are to understand the challenges species face in adapting to anthropogenic environmental change. Presently, migration tracking data only exist for two nightjar species in North America (see Knight et al., 2021; and Ng et al., 2018 for common nighthawk migration), and thus, there remains a need to expand this research approach to additional species to determine common factors limiting populations in this declining Family (Spiller & Dettmers, 2019). Obtaining data from young birds and females will be important to fully understanding population limitation (e.g. Rushing et al., 2017), given the bias towards adult males in existing studies.

The core wintering region for whip-poor-wills has also been identified as a key migratory (Bayly et al., 2018) and wintering (La Sorte et al., 2017; Wilson et al., 2019) region for many other North American birds. When benefits provided to tropical residents and intra-tropical migrants are considered, conservation efforts on the wintering grounds would likely affect more species for more months of the year relative to investment on the whip-poor-will breeding grounds (Faaborg et al., 2010; Wilson et al., 2021). There is also a high prevalence of marginally protected areas in the region (La Sorte et al., 2017) and high rates of deforestation (Aide et al., 2013; Hansen et al., 2008), suggesting that rapid conservation intervention here is critical. However, given the spatiotemporal overlap we observed in whip-poor-wills during the non-breeding season, breeding grounds' stressors are likely more important for explaining the differential population trends observed on the breeding grounds in the whip-poor-will in particular. One possibility is that non-breeding season threats negatively affecting populations from across the breeding range help explain the precipitous declines in overall trends, yet local conditions on the breeding grounds also greatly influence population trends, resulting in spatial heterogeneity (Cresswell, 2014). In fact, whip-poor-will abundance on the breeding grounds is negatively associated with anthropogenic disturbance and positively linked to food abundance (English et al., 2017; Souza-Cole, 2021), providing support for this hypothesis. More formal analyses involving simulation or decision-theoretic approaches, and integrating across a large number of species, are required to determine the most important locations for investment of conservation dollars (La Sorte et al., 2017; Martin et al., 2007; Schuster et al., 2019).

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CONFLICT OF INTEREST

The authors have no conflicts of interest.

AUTHOR CONTRIBUTIONS

All authors contributed to study design, acquiring funding, field data collection, and manuscript editing. A.A.S. conducted data analysis and wrote the original draft of the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13477>.

DATA AVAILABILITY STATEMENT

Raw GPS location files are deposited on the Movebank Data Repository, <https://doi.org/10.5441/001/1.k6s7916g> (Skinner et al., 2022) and Dryad <https://doi.org/10.5061/dryad.hhmqnkh9>.

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BIOSKETCH

In collaboration with a diverse research team, Aaron A. Skinner conducted this research as part of his Master's thesis under the direction of Dr. Chris Tonra. A.A.S. is an ecologist interested in movement ecology and elucidating threats to migratory birds across the full annual cycle, ultimately leveraging this knowledge towards their conservation. Additionally, he is interested in how working landscapes promote wildlife conservation, particularly by creating more permeable landscapes and connecting protected areas at large spatial scales.

SUPPORTING INFORMATION

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

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