

RESEARCH ARTICLE

Migratory connectivity and barrier-crossing flights of *Vermivora* warblers are associated with synoptic weather conditions

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Abstract

1. Migratory birds often navigate inhospitable barriers (e.g. oceans, deserts) during migration. Barrier crossings are frequently associated with increased rates of mortality and likely impose selective pressures on migratory species that shape their behaviour and distribution. Therefore, understanding how weather conditions influence the behaviour of migratory birds at a major barrier can provide insight into the adaptive evolution of long-distance migrations involving barrier crossings and how changing climatic conditions might affect migratory species in the future.
2. We used light-level geolocator data from 89 individual *Vermivora* warblers to identify the weather conditions associated with individuals initiating barrier-crossing flights across the Gulf of Mexico (i.e. 'trans-Gulf flights') during both autumn and spring migrations from 2013 to 2017.
3. Weather conditions associated with the initiation trans-Gulf flights differed between autumn and spring. In autumn, the initiation of trans-Gulf flights was positively associated with favourable wind conditions and temperature but negatively associated with relative humidity and 24-h change in barometric pressure. During spring migration, the initiation of trans-Gulf flights was negatively associated with surface-level relative humidity and barometric pressure but not associated with wind conditions. We found that the frequency of days with weather conditions associated with a high-predicted probability of *Vermivora* warblers initiating trans-Gulf flights varied geographically (range 0%–58% of days).

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4. Distinct breeding populations of golden-winged warblers (*V. chrysoptera*) with strong migratory connectivity between breeding and non-breeding regions exhibited weak migratory connectivity and overlapped extensively during migration immediately prior to initiating trans-Gulf flights. Breeding populations of blue-winged warblers (*V. cyanoptera*) exhibited weak migratory connectivity and co-occurred during both autumn and spring migrations and during the non-breeding period.
5. The weak migratory connectivity that we observed in *Vermivora* warblers prior to crossing the Gulf of Mexico may be shaped by shared evolutionary responses to consistent synoptic weather conditions in the region. Predicted future climate conditions including increased humidity and more frequent and/or severe storms may decrease the favourability of conditions associated with initiating trans-Gulf flights during spring migration for *Vermivora* warblers, which could negatively affect populations.

KEYWORDS

climate change, geolocator, Gulf of Mexico, meteorology, migration, migratory behaviour, Parulidae

1 | INTRODUCTION

Migration is a highly variable behaviour that has evolved many times across taxa (Alerstam et al., 2003; Dingle, 2014; Winger et al., 2014). Frequently, migratory species navigate inhospitable landscapes or barriers (e.g. oceans, deserts) during migration (Dingle, 2014). Navigating barriers is often associated with an increased probability of mortality (e.g. Dodd et al., 2004; Fensome & Mathews, 2016; Hu et al., 2021; Kramer-Schadt et al., 2004; Loonstra et al., 2019; Strandberg et al., 2010). Thus, these events likely impose selective pressures on individuals and shape migratory strategies (Hewson et al., 2016; Ward et al., 2018). Therefore, understanding how weather conditions affect species' navigation of barriers can provide insight into the evolutionary origins and maintenance of migration and how changing climatic conditions might affect migratory species (Both et al., 2006; Gill et al., 2009).

One barrier to many Nearctic-Neotropical avian migrants is the Gulf of Mexico (Cooke, 1904; Williams, 1945; Figure 1), a large oceanic basin encircled by southern North America. Every year, billions of individual birds either cross or circumvent the Gulf of Mexico during post-breeding (hereafter, 'autumn') and pre-breeding (hereafter, 'spring') migration (Albert & Siegel, 2024; Dokter et al., 2018; Rappole & Ramos, 1994). Crossing the Gulf can consist of a ~10–24 h non-stop, >800 km, over-water flight or two or more shorter over-water flights (~300–500 km each) with individuals stopping over in Cuba or other islands in the western Caribbean Sea (Lincoln, 1935). Crossing the Gulf of Mexico is often the most direct route (Cooke, 1904; Williams, 1945). However, direct routes may be the most dangerous because terrestrial birds are unable to land and rest on water and therefore must complete the crossing in a single, non-stop flight (Deppe

et al., 2015; Smolinsky et al., 2013). Both endogenous factors (e.g. fuel stores and muscle condition) and exogenous weather factors (e.g. wind speed and direction, precipitation, humidity) can work independently or in concert to impede or facilitate the ability of migrants to complete a barrier crossing, thus affecting their probability of survival (Deppe et al., 2015; Smolinsky et al., 2013). Despite these risks, the fact that diverse species cross the Gulf of Mexico up to twice a year suggests context-dependent adaptive benefits to this behaviour. However, little information exists on how weather conditions influence the initiation of barrier-crossing flights across the Gulf of Mexico (hereafter, 'trans-Gulf flights') and whether conditions associated with the initiation of trans-Gulf flights in small songbirds vary seasonally, temporally or spatially.

Moreover, how patterns in the variation in synoptic weather conditions may shape the migratory connectivity of small songbirds during migration and near a barrier like the Gulf of Mexico is poorly understood. Species exhibiting strong migratory connectivity consist of populations that tend to occur together and in isolation from other populations throughout the annual cycle whereas species with weak connectivity consist of populations that mix during different periods of the annual cycle (Webster et al., 2002). Frequently, assessments of migratory connectivity consider the linkages of populations between the breeding and non-breeding periods, during which individuals tend to be sedentary and populations may be especially vulnerable to limiting factors (e.g. Kramer et al., 2018b). However, limiting factors and bottlenecks also can affect populations that are isolated in time or space during migration periods, especially near barriers (Hewson et al., 2016; Knight et al., 2021). If the directionality of migration is a heritable trait (e.g. Berthold & Helbig, 1992) and synoptic weather conditions facilitating trans-Gulf flights vary regionally,

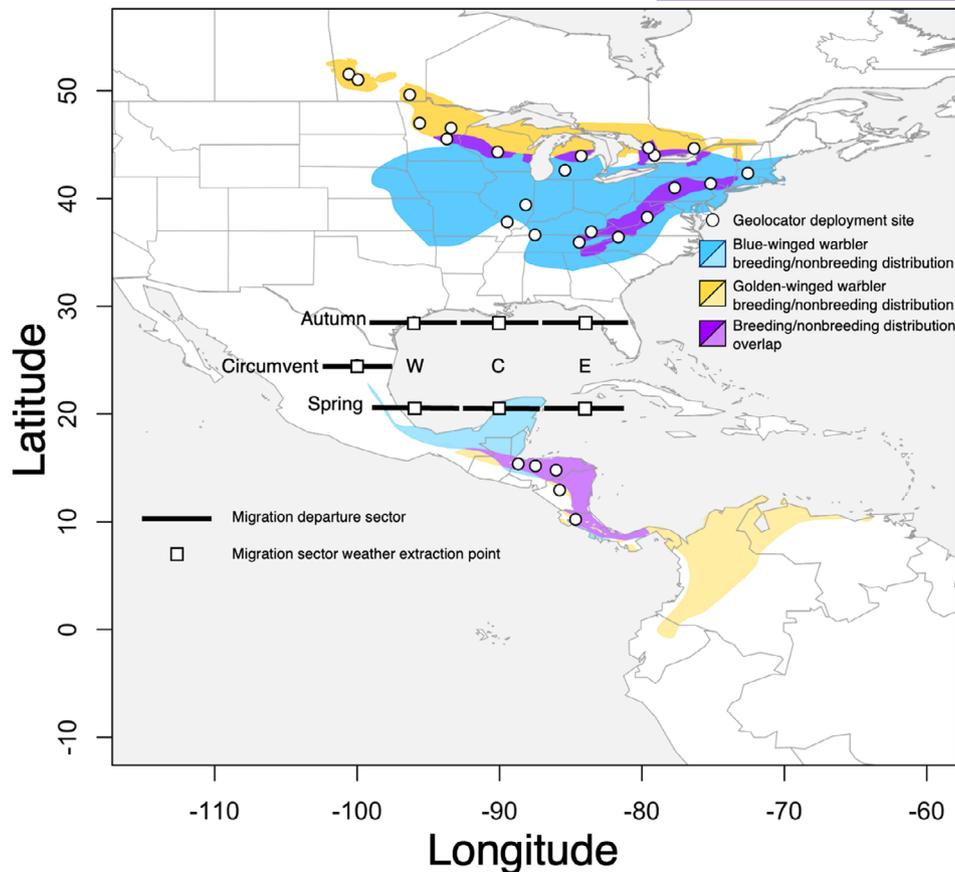


FIGURE 1 Map of breeding and non-breeding distributions of blue-winged warblers (*Vermivora cyanoptera*) and golden-winged warblers (*Vermivora chrysoptera*; WGS 84 [EPSG:4326], no projection). Sites where geolocators were recovered are indicated by white circles. Migration departure sectors (W=west, C=central and E=east) and the points (white squares) from which weather data were extracted are depicted.

natural selection could play a role in shaping the patterns of distribution and migratory connectivity of birds at the Gulf of Mexico during migration. Thus, quantifying the temporal and spatial migratory connectivity of populations near barriers may provide insights into the evolution of barrier-crossing strategies and provide context to improve the conservation of migratory species.

Here, we used geolocator data from 89 individual *Vermivora* warblers (golden-winged warblers [*Vermivora chrysoptera*], blue-winged warblers [*V. cyanoptera*] and phenotypic hybrids between these two closely related species; Toews et al., 2016) to quantify associations between weather conditions and the initiation of trans-Gulf flights and assess whether relationships between weather conditions and the initiation of trans-Gulf flights differed between autumn and spring migration periods. We also quantified variation in geographic distribution within and among populations and estimated the migratory connectivity of *Vermivora* warbler breeding populations during autumn and spring migrations to quantify spatial and temporal segregation of breeding populations prior to navigating the Gulf of Mexico. We predicted that the weather conditions associated with the initiation of trans-Gulf flights by golden-winged and blue-winged warblers would be similar between species and associated with conditions previously described to influence barrier crossings in other,

larger passerines (Deppe et al., 2015). We considered weather variables that we predicted might directly affect the ability of migrating songbirds to complete trans-Gulf flights (e.g. wind profit, a combination of the wind direction and speed that could affect the amount of energy required to cross the Gulf of Mexico) and other variables that might be associated with broader weather systems that could influence the future suitability of wind conditions or indicate inclement weather (e.g. humidity; Deppe et al., 2015; Richardson, 1990; Supporting Information). Based on previous evidence from golden-winged warblers (Bennett et al., 2019; Kramer et al., 2017), we expected *Vermivora* warbler populations to exhibit stronger migratory connectivity during autumn migration than during spring migration because individuals returning to breeding sites during spring migration may be under tighter time constraints than individuals during autumn migration and therefore more likely to exhibit flexibility in route use if poor conditions in a region preclude northbound migration (Debeffe et al., 2019; Nilsson et al., 2013; but see Briedis et al., 2018, Gow et al., 2019, van Wijk et al., 2017). Characterizing the associations between abiotic conditions and the barrier-crossing behaviour of small (<10g) birds provides context for understanding the role of barriers in shaping migratory strategies across taxa (Alerstam et al., 2003; Winger et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Geolocator data collection and population assignment

We used published light-level geolocator data from 89 individual *Vermivora* warblers ($n=95$ geolocator tracks; 6 individuals were tracked for 2 years) collected from across their breeding distribution and a portion of their non-breeding distribution from 2013 to 2017 (Bennett, 2019; Kramer et al., 2018a; Supporting Information; Table S1) to assess migration behaviour. Analysing these previously published data did not require ethical approval.

We defined populations of *Vermivora* warblers based on the Bird Conservation Region (BCR) of an individual's breeding site. However, several study areas occurred on the periphery of species' breeding distributions and we assigned individuals at those sites to the nearest BCR containing other study sites and a greater proportion of the species' distribution (Figure 1; Supporting Information; Table S1; Figure S1). Detailed descriptions of study sites and field methods are presented in Kramer et al. (2018b) and Bennett et al. (2019). Both studies used the same model of geolocator (archival data logger; ML6240, 2-min light-sampling regime; Biotrak, Wareham, UK) and modified leg-loop harness to attach geolocators to *Vermivora* warblers (Rappole & Tipton, 1991; Streby et al., 2015). Peterson et al. (2015) found no evidence of any effects of geolocators on the migratory ecology or apparent survival rate of golden-winged warblers using this harness method.

2.2 | Geolocator data processing and delineation of migration routes

We analysed all geolocator data in R (v. 4.0.4; R Core Team, 2021) using the *FLightR* package (v. 4.9; Rakhimberdiev et al., 2015; Rakhimberdiev & Saveliev, 2019). *FLightR* derives location estimates from raw light data using the timing and slope of transition events (i.e. dawns and dusks; Ekstrom, 2004; Rakhimberdiev et al., 2015). To prepare raw light-level data for analysis, we used the package *BAStag* (Wotherspoon et al., 2016) to identify transition events using a threshold of 1.5 (Kramer et al., 2017, 2018b). We calibrated geolocator data using the period that individuals were known (or assumed) to be resident at breeding (Kramer et al., 2018b) or non-breeding (Bennett et al., 2019) deployment sites. We derived daily location estimates from each geolocator using the movement model in *FLightR* (optimized with 1 million particles). We used a behavioural mask that allowed individuals to travel over water but prevented them from being stationary >25 km from land (Delancey et al., 2020). We also constrained the maximum distance between subsequent twilights to 1200 km (maximum distance we assumed an individual could travel in 1 day, Supporting Information), which limited the effects of erroneous location estimates and used the automatic outlier exclusion function to identify and eliminate extreme location estimates (Rakhimberdiev & Saveliev, 2019). We used the function *find.times*.

distribution() in *FLightR* to estimate commencement and termination of seasonal migrations (median date) between known (Kramer et al., 2018b) or estimated (Bennett et al., 2019) breeding sites and known (Bennett et al., 2019) or estimated (Kramer et al., 2018b) non-breeding sites.

2.3 | Identification of full light pattern (FLP) anomalies

We used methods adapted from Adamik et al. (2016) to define the initiation of trans-Gulf flights by the presence and nature of full light pattern (FLP) anomalies in geolocator data from *Vermivora* warblers during autumn and spring migrations. If *Vermivora* warblers initiate migratory flights that begin after sunset and continue throughout the daytime (e.g. during trans-Gulf flights), those events would be readily identifiable as anomalies in the geolocator data because of their unique light profiles containing little or no shade compared to other days (Figure 2; Adamik et al., 2016). We considered FLP anomalies to be evidence of prolonged migratory flight into daytime if (1) dawn was unshaded (i.e. exhibited increasing light levels from first light to full light) and occurred not too rapidly (i.e. <6 min) or too slowly (i.e. >12 min; Supporting Information), (2) recorded light levels remained at maximum intensity (i.e. 64, indicating unshaded conditions for >5 h after dawn) and (3) the timing of dawn and dusk on the day of the FLP anomaly differed from the previous day in a manner consistent with a large magnitude (i.e. >500 km) shift in location in the expected direction (autumn=southward, spring=northward). We tested whether the amount of shading, timing and duration of FLP anomalies differed from light profiles of randomly selected non-FLP days ($n=50$ per season) by fitting a quadratic regression to the light data and calculating the summed absolute residuals (Adamik et al., 2016; Supporting Information).

If individual *Vermivora* warblers had multiple FLP anomalies in the same seasonal migration period, we used the function *find.times.distribution()* in *FLightR* to determine and select the FLP associated with the individual crossing 24.5° (i.e. the approximate latitudinal midpoint of the Gulf of Mexico). Multiple FLP anomalies from a single geolocator-marked *Vermivora* warbler may indicate variation in individual behaviour, different migratory strategies and/or multiple flights involving prolonged flight into daytime (Adamik et al., 2016; Table S3).

2.4 | Determining departure sector

We estimated the longitude of *Vermivora* warblers by summing twilights prior to FLP anomalies ($n=2-12$ twilights; Figure S2). Geolocator-derived estimates of latitude have lower precision (~150–250 km) than estimates of longitude (~25–50 km; Fudickar et al., 2012) and evidence suggests Nearctic–Neotropical migratory birds navigate the Gulf of Mexico in response to synoptic weather patterns (Clipp et al., 2020; Cohen et al., 2021; Shamoun-Baranes et al., 2017). Therefore, we generally classified

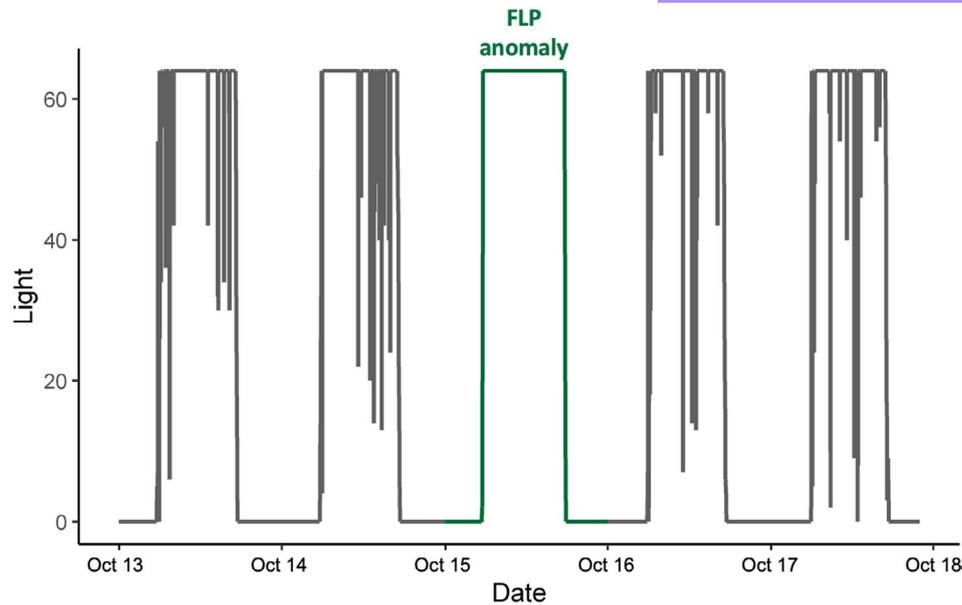


FIGURE 2 Example of full light pattern (FLP) anomaly (green) in geolocator-derived light data indicating a trans-Gulf flight by an individual *Vermivora* warbler. Light curves show the maximum level of ambient light recorded by the geolocator every 2 min. Light levels were recorded on an arbitrary scale from 0 to 64 units. This light curve is from a male golden-winged warbler (*Vermivora chrysoptera*; SLG18; Tables S2 and S3) during autumn migration in 2015. Shading in the geolocator-derived light data indicate this individual initiated a trans-Gulf of Mexico flight on the evening of 14 October 2015 and experienced virtually no shading during 15 October 2015 (FLP anomaly).

geolocator-marked *Vermivora* warblers into four groups based on whether they circumvented the Gulf of Mexico (circumvent) or based on their longitude prior to the initiation of a trans-Gulf flight (i.e. western, central or eastern). We classified individuals as 'circumventing' if they did not exhibit an FLP anomaly during the migration period of interest and occurred too far from major islands in the Caribbean that we deemed it unlikely that they could initiate a trans-Gulf flight and arrive at the island prior to sunrise (i.e. no recorded FLP; threshold $<-84^\circ$ or ~ 600 km from land to the nearest major island). We also classified individuals as 'circumventing' if they exhibited an FLP anomaly, but a straight line connecting their location estimate immediately before and after the FLP anomaly was over land (i.e. $<-97.5^\circ$). We classified individuals that exhibited an FLP anomaly and occurred in locations that required crossing the Gulf of Mexico into three departure sectors depending on their estimated longitude prior to departing to cross the Gulf of Mexico: the western sector included individuals occurring between $<-93^\circ$, the central sector included individuals occurring between -93° and -87° , and the eastern sector included individuals occurring $>-87^\circ$ (Figure 1). We assigned all individuals to a point in the centre of each departure sector (departure point, separated by 6° longitude; Tables S4 and S5), which was also the location for which we extracted weather data (see below).

2.5 | Selecting weather variables and collecting weather data

To understand whether the initiation of trans-Gulf flights by *Vermivora* warblers was associated with weather conditions,

we considered a set of synoptic (i.e. regional) weather variables thought to be associated with the migratory behaviour of Nearctic-Neotropical bird species near the Gulf of Mexico (Table 1; Supporting Information; Bolus et al., 2017; Deppe et al., 2015; Smolinsky et al., 2013). We chose to extract data from single locations to characterize synoptic weather patterns versus extracting weather data from individual point estimates derived from geolocator data because migratory songbirds respond to synoptic conditions when navigating the Gulf of Mexico, the accuracy of geolocator data precluded the use of more specific departure sites (especially during migration), and weather conditions were positively and frequently strongly correlated within departure sectors (Supporting Information, Figure S3). We considered surface-level weather conditions and conditions at 850 hPa (~ 1500 m above ground level) to assess whether the initiation of trans-Gulf flights was associated with conditions at or near potential maximum flight altitudes observed in other species crossing the Gulf of Mexico (~ 400 – 3000 m above ground level; Gauthreaux Jr. et al., 2006).

We obtained weather data from <https://earth.nullschool.net> (Beccario, 2021) for each day in both autumn and spring migration periods. These weather data were derived from Global Forecasting System (GFS) models available from the US National Center for Environmental Prediction and had a spatial resolution of 25 km and a temporal resolution of 3 hrs. It was impossible to determine the exact time of day individuals initiated migratory flights across the Gulf of Mexico from geolocator data. However, data from radar and telemetry research indicate many birds initiate trans-Gulf flights shortly after dusk (Deppe et al., 2015; Van Doren & Horton, 2018). We extracted weather data at 20:00 local time (within 1.5 h of sunset, Table S4) for each departure point. We tested for correlation

TABLE 1 Weather variables used to model the initiation of trans-Gulf flights by *Vermivora* warblers.

Weather variable	Units
Surface (at ground level)	
Wind profit ^a	Unitless
Temperature	°C
Relative humidity	Percent humidity
Barometric pressure	hPa
24-h change in wind profit	Unitless
24-h change in temperature	°C
24-h change in relative humidity	Percent humidity
24-h change in barometric pressure	hPa
850hPa (~1500 m above ground level)	
Wind profit	Unitless
Temperature	°C
Relative humidity	Percent humidity

Note: Weather data were derived from Global Forecasting System (GFS) models available from the US National Center for Environmental Prediction and had a spatial resolution of 25 km and temporal resolution of 3 h (Beccario, 2021). We extracted weather data at the interval nearest local sunset (i.e. 20:00 local time).

^aA function of wind speed multiplied by the directionality of the wind relative to north [0°, autumn] or south [180°, spring]; [Supporting Information](#).

among selected weather variables and excluded variables that were strongly correlated (i.e. Pearson's correlation coefficient; $|r| \geq 0.6$; [Supporting Information](#); [Tables S6](#) and [S7](#)). Following the exclusion of strongly correlated weather variables, we modelled the trans-Gulf flight initiation of *Vermivora* warblers using 10 weather variables in autumn and 7 weather variables in spring ([Supporting Information](#), [Tables S6](#) and [S7](#)). We also tested for differences in weather conditions between days that *Vermivora* warblers initiated trans-Gulf flights versus days without evidence of trans-Gulf flights using simple linear regression ([Figure S4](#)).

2.6 | Modelling and statistical analyses

We built logistic regression models in R to test for associations between weather variables and the initiation of trans-Gulf flights of *Vermivora* warblers during autumn and spring migrations. The dependent variable in our logistic regression models was whether an individual initiated a trans-Gulf flight ('1'; following day classified as an FLP anomaly) or did not initiate a trans-Gulf flight, but was assumed to be near the Gulf of Mexico ('0'; following day was not classified as an FLP anomaly). Determining the period that individual *Vermivora* warblers were near the Gulf of Mexico and did not initiate trans-Gulf flights was difficult given the timing of migration, often near the equinoxes and the coarseness of geolocator data (Fudickar et al., 2012). Therefore, we used a 2-day period to build our logistic

regression models which included the departure day (coded as '1') and the previous day (coded as '0'). We also considered 7-day and a 4-day period models that incorporated longer pre-departure periods ([Supporting Information](#)). Here, we report on the results of the 2-day period models because these results are likely more biologically relevant (less likely to include days when individuals were not present near the Gulf of Mexico) and the relationships and effect sizes of modelling efforts using longer periods were similar ([Supporting Information](#)). In all models, we assumed individual *Vermivora* warblers were present at or near the Gulf of Mexico for the duration of the pre-departure period but did not initiate trans-Gulf flights until the dusk prior to the observed FLP anomaly.

Preliminary models indicated no differences among years, populations or species in the timing or probability of individuals initiating trans-Gulf flights ($\Delta AIC_c > 2$ compared to intercept-only model; [Table S8](#)). Therefore, we grouped data from all years, populations and species for analyses. We used a drop-one modelling approach to determine whether the most parsimonious models describing the initiation of trans-Gulf flights differed between seasons (Tredennick et al., 2021). We constructed a full model containing a suite of all biologically relevant predictor variables associated with synoptic weather conditions (see above) for each season (i.e. autumn and spring) that could affect the initiation of trans-Gulf flights in small migratory songbirds (Ward et al., 2018). We used the *drop1()* function in R to identify and remove weather variables that did not contribute to model performance (based on AIC_c). Final models included variables that did not significantly improve the model performance if dropped (likelihood ratio test, $p > 0.05$; Tredennick et al., 2021). We assessed final model performance using receiver operating characteristic (ROC) curves and transformed logit-scale model coefficients to log-odds ratios for interpretation. We predicted the number of days during autumn and spring migration periods with favourable weather conditions for trans-Gulf flights (i.e. predicted probability of initiating trans-Gulf flight > 0.5) using the final seasonal 2-day model (i.e. based on departure day and the previous day). We used two-sample proportional tests to compare the proportion of individuals using different migration sectors during autumn and spring migration. Although exploratory, this analysis considered a limited suite of variables previously shown to influence the migratory behaviour of songbirds. Therefore, observed associations may warrant future testing using different approaches (e.g. passive telemetry, global positioning system [GPS] tracking; Deppe et al., 2015). Weather variables identified as important in final models derived within the drop-one framework were similar to those with statistically significant effects (i.e. 95% CIs around estimates of effect size did not overlap zero) in full models containing all potential weather variables in each season ([Figures S5](#) and [S6](#)). Predictive accuracy also was similar between full models and final models using a drop-one approach ([Figure S7](#); [Table S9](#)). We assessed whether the predicted favourability of weather conditions experienced during autumn and spring migration (separately and combined) differed among breeding populations of *Vermivora* warblers using one-way ANOVAs and Tukey's HSD tests.

2.7 | Quantifying migratory connectivity throughout migration periods

We used the *estStrength()* and *estMantel()* functions in the *MigConnectivity* package in R (Hostetler et al., 2025; Hostetler & Hallworth, 2020) to estimate overall migratory connectivity of distinct breeding populations at three biologically relevant stages of the annual cycle: (1) during autumn migration prior to navigating the Gulf of Mexico, (2) during the non-breeding period and (3) during spring migration prior to navigating the Gulf of Mexico (Figure 1). We estimated the strength of migratory connectivity by calculating two commonly used metrics: the Mantel correlation coefficient (r_M ; Ambrosini et al., 2009) and the migratory connectivity metric (MC; Cohen et al., 2018). When sampling sites are broadly distributed (Vickers et al., 2021), both metrics are useful for quantifying the strength of migratory connectivity among populations by comparing the distances between individuals during different periods (Cohen et al., 2018). However, MC provides an estimate of migratory connectivity while accounting for incomplete sampling and inherent error in geolocator-derived location estimates (Cohen et al., 2018). We estimated r_M and MC among breeding populations ($n=2$ golden-winged warbler breeding populations, $n=3$ blue-winged warbler populations; Supporting Information) at four autumn and spring departure sectors signifying general route type at the Gulf of Mexico (i.e. circumvent, western, central and eastern) and two potential non-breeding regions (i.e. Central America, South America). We excluded *Vermivora* warblers with hybrid plumage phenotypes ($n=5$) from estimates of migratory connectivity of both parent species. For estimates of MC, we accounted for inherent uncertainty in geolocator-derived location estimates using variance-covariance matrices derived from the error in location estimates during periods when individuals were known to be at geolocator deployment sites (Hostetler & Hallworth, 2020). We also incorporated BCR-level estimates of *Vermivora* warbler abundance (Partners in Flight, 2020) to account for unbalanced sampling effort relative to population abundance (Cohen et al., 2018). Mean r_M and MC estimates for each period were based on 1000 resamples.

Estimates of r_M and MC near zero indicate that there is no relationship between breeding proximity and proximity during other portions of the annual cycle (i.e. weak migratory connectivity and extensive mixing of populations). Positive values of r_M and MC indicate that individuals from proximate breeding locations also occur near one another in subsequent periods of the annual cycle (i.e. strong migratory connectivity) and negative values indicate that individuals that occur closely together in one portion of the annual cycle occur farther apart from one another during subsequent periods (Ambrosini et al., 2009; Cohen et al., 2018). We visualized the general movements of populations throughout the annual cycle using the *ggforce* package in R (Pedersen, 2024) to create line plots. We used a Pearson's χ^2 -test to assess whether the frequency of *Vermivora* warblers that migrated through different sectors near the Gulf of Mexico differed between autumn and spring periods. We then used a two-sample proportion test to identify, which sectors

differed seasonally in their frequency of use by *Vermivora* warblers and estimate the magnitude and direction of changes. We tested whether the observed use of departure sectors by *Vermivora* warblers differed from expectations under a distance-minimization model using a Fisher's exact test. We classified 'expected' departure sectors as those nearest to the seasonally relevant stationary period location (breeding site or non-breeding site; measured by Great Circle distance). We also quantified the seasonal deviation rate as the proportion of individuals that migrated through a sector that differed from the expected sector based on minimizing migration distance.

We created cumulative sum plots to visualize temporal variation in Gulf-crossing behaviour among populations and calculated the ordinal date at which 50% of the population had crossed the Gulf of Mexico (50% passage date). We created simple linear models to test for associations between populations' 50% passage date and average breeding latitude, and non-breeding latitude and longitude to test for temporal connectivity.

3 | RESULTS

We identified 144 FLP anomalies associated with prolonged migratory flight into daylight hours and potential trans-Gulf flights during autumn migration ($n=94$ geolocators, $n=89$ individual *Vermivora* warblers) and 154 during spring migration ($n=87$ geolocators, $n=85$ individuals; Table S3). One individual (1%) did not exhibit FLP anomalies during autumn migration, three individuals (3%) did not exhibit FLP anomalies during spring migration, and one individual (1%) did not exhibit FLP anomalies in either autumn or spring migration periods (Table S3). Most individuals ($n_{\text{autumn}}=57$ [61%]; $n_{\text{spring}}=52$ [60%]) exhibited one FLP anomaly per migration season (Supporting Information). Of individuals that exhibited multiple FLP anomalies in either autumn ($n=32$ [34%]) or spring ($n=33$ [38%]) migration periods, the average was 2.7 (0.3 SE) and 2.4 (0.4 SE) FLP anomalies for autumn and spring, respectively. Furthermore, 17 of those individuals exhibited consecutive FLP anomalies (i.e. two successive days of virtually no shading recorded) with the vast majority occurring during autumn ($n=15$ [88%]) versus spring ($n=2$ [12%]; Supporting Information). Compared to randomly selected days during both autumn ($n=50$) and spring ($n=50$) periods, FLP anomalies had lower absolute residual scores indicating less shading (log-scale; two-way ANOVA, $F_{2,1153}=163.9$, $p<0.0001$; Figure S8) during dawn ($p=0.008$, Tukey HSD) and daytime periods ($p<0.0001$, Tukey HSD) but not during dusk ($p=0.34$, Tukey HSD). Similarly, the duration of dawn and dusk periods was shorter during FLP anomalies compared to randomly selected days (log-scale; two-way ANOVA, $F_{2,1153}=28.7$, $p<0.0001$; $p<0.0001$ for both comparisons, Tukey HSD).

The FLP anomalies indicated that the majority of *Vermivora* warblers directly crossed the Gulf of Mexico using over-water flights during autumn (80%; 75/94) and spring (74%; 63/88) migration periods (Table S3). However, 20% of individuals (19/94; $n=8$ blue-winged warblers; $n=9$ golden-winged warblers; $n=2$ hybrids) circumvented

the Gulf of Mexico during autumn migration and 26% (23/87; $n=3$ blue-winged warblers; $n=18$ golden-winged warblers; $n=2$ hybrids) circumvented the Gulf of Mexico during spring migration based on the lack of an FLP anomaly or on the timing and location of individuals during observed FLP anomalies (Supporting Information). Considering individuals with data for both autumn and spring migration, 12% (10/86; $n=3$ blue-winged warblers, $n=6$ golden-winged warblers, $n=1$ hybrid) circumvented the Gulf of Mexico during both migration periods.

At the Gulf of Mexico, the frequency with which *Vermivora* warblers initiated trans-Gulf flights from various sectors differed between autumn and spring migration periods (Pearson's χ^2 -test, $\chi^2=31.0$, $df=3$, $p<0.001$). A greater frequency of *Vermivora* warblers initiated trans-Gulf flights from the eastern departure sector during autumn (two-sample proportion test, $\chi^2=28.9$, $df=1$, $p<0.001$) compared to spring when more individuals initiated trans-Gulf flights from the central sector (two-sample proportion test, $\chi^2=10.5$, $df=1$, $p=0.001$). The frequency at which individuals initiated trans-Gulf flights from the western sector or circumvented the Gulf of Mexico did not differ between seasons (two-sample proportion test, $p>0.05$ for both comparisons). Most *Vermivora* warblers used departure sectors that differed from those expected if individuals used routes that minimized migration distance (autumn=52% [42%–63% CI]; spring=74% [63%–82% CI]). Moreover, we found no evidence that *Vermivora* warblers used departure sectors as expected under a distance-minimization model (Fisher's exact test, $p>0.10$ for autumn and spring).

3.1 | Effects of weather conditions on the initiation of trans-gulf flights

Weather conditions were associated with the initiation of trans-Gulf flights by *Vermivora* warblers during both autumn and spring migrations. The variables included in final models differed slightly depending on the pre-departure interval considered (i.e. 7-day, 4-day and 2-day intervals; Supporting Information). However, the direction and magnitude of the effect size remained consistent across models with different pre-departure intervals (transformed from logit to log-odds ratio; Figure 3; Figures S5 and S6) and final models adequately characterized the initiation of trans-Gulf flights (all AUC values 0.65–0.80; Figure S7).

Variables included in final models differed between autumn and spring migration periods (Figure 3). Compared to the previous day's weather conditions (i.e. 2-day model), the initiation of trans-Gulf flights during autumn migration was positively associated with wind profit at the surface and surface temperature and negatively associated with relative humidity at the surface and 24-h change in barometric pressure (Figure 3; Figure S6). During spring migration, the initiation of trans-Gulf flights was positively associated with relative humidity at 850hPa and negatively associated with relative humidity at the surface and barometric pressure compared to weather conditions the previous day (2-day model; Figure 3; Figure S6). The

proportion of days during autumn and spring migration periods with a predicted probability of initiating trans-Gulf flight ≥ 0.50 (hereafter, 'favourable days') varied annually (Figure 4), but the average proportion of favourable days was 81% higher during autumn than spring ($\bar{x}_{\text{autumn}}=0.29$, $\bar{x}_{\text{spring}}=0.16$; two-sample t -test, $t_{1,22}=-2.1$, $p=0.05$; Figure 4). Moreover, the average proportion of days with favourable conditions varied among sectors and within seasons with conditions generally being more favourable in the central and eastern sectors during autumn (one-way ANOVA, $F_{2,9}=5.3$, $p=0.03$) whereas the central sector had more favourable conditions during spring (one-way ANOVA, $F_{2,9}=60.9$, $p<0.001$).

3.2 | Quantifying migratory connectivity throughout migration periods

Migratory connectivity between golden-winged warbler breeding and non-breeding regions was strong (MC=0.85 [0.13 SE]; $r_M=0.73$ [0.07 SE]). However, migratory connectivity was weak prior to navigating the Gulf of Mexico during both autumn (MC=0.05 [0.05 SE]; $r_M=0.03$ [0.05 SE]) and spring (MC=0.06 [0.04 SE]; $r_M=0.06$ [0.05 SE]) migrations (Figure 5). Overall migratory connectivity between blue-winged warbler breeding and non-breeding regions was weak (MC=-0.09 [0.01 SE]; $r_M=0.27$ [0.11 SE]) and remained weak during both autumn (MC=0.16 [0.12 SE]; $r_M=0.14$ [0.12 SE]) and spring migrations (MC=0.12 [0.12 SE]; $r_M=0.15$ [0.11 SE]; Figure 5).

Vermivora warbler populations exhibited temporal variation in the date at which 50% of individuals had crossed the Gulf of Mexico (Figure 6). During autumn, the 50% passage date was associated with average breeding latitude but not with average non-breeding latitude or longitude (Figure S9). Thus, the 50% passage date for golden-winged warblers from Appalachian Mountain BCR breeding sites was 33 days earlier than for golden-winged warblers from breeding sites in the Boreal Hardwood Transition BCR and 7–26 days earlier than blue-winged warbler populations (Figure 6). During spring migration, the difference between the earliest and latest 50% passage date for *Vermivora* warbler populations was smaller (18 days vs. 33 days in autumn) and the timing of the 50% passage date was not associated with any population-specific geographic characteristics (i.e. average breeding latitude, average non-breeding latitude, average non-breeding longitude; Figure 6; Figure S10).

We found no evidence of differences in predicted favourability of conditions among populations of *Vermivora* warblers during autumn migration (one-way ANOVA; $F_{4,70}=0.3$, $p=0.62$) or when considering both autumn and spring migration together (one-way ANOVA; $F_{4,134}=1.2$; $p=0.32$; Figure S10). However, Golden-winged warblers migrating from non-breeding sites in northern South America to breeding sites in the Appalachian Mountains BCR experienced less favourable conditions (i.e. mean difference in daily predicted probability of departure=-0.13; 95% CI=-0.26–0.01; $p=0.05$) than individuals migrating from non-breeding sites in Central America to breeding sites in the Boreal Hardwood Transition BCR during spring migration (one-way ANOVA; $F_{4,59}=2.9$, $p=0.03$).

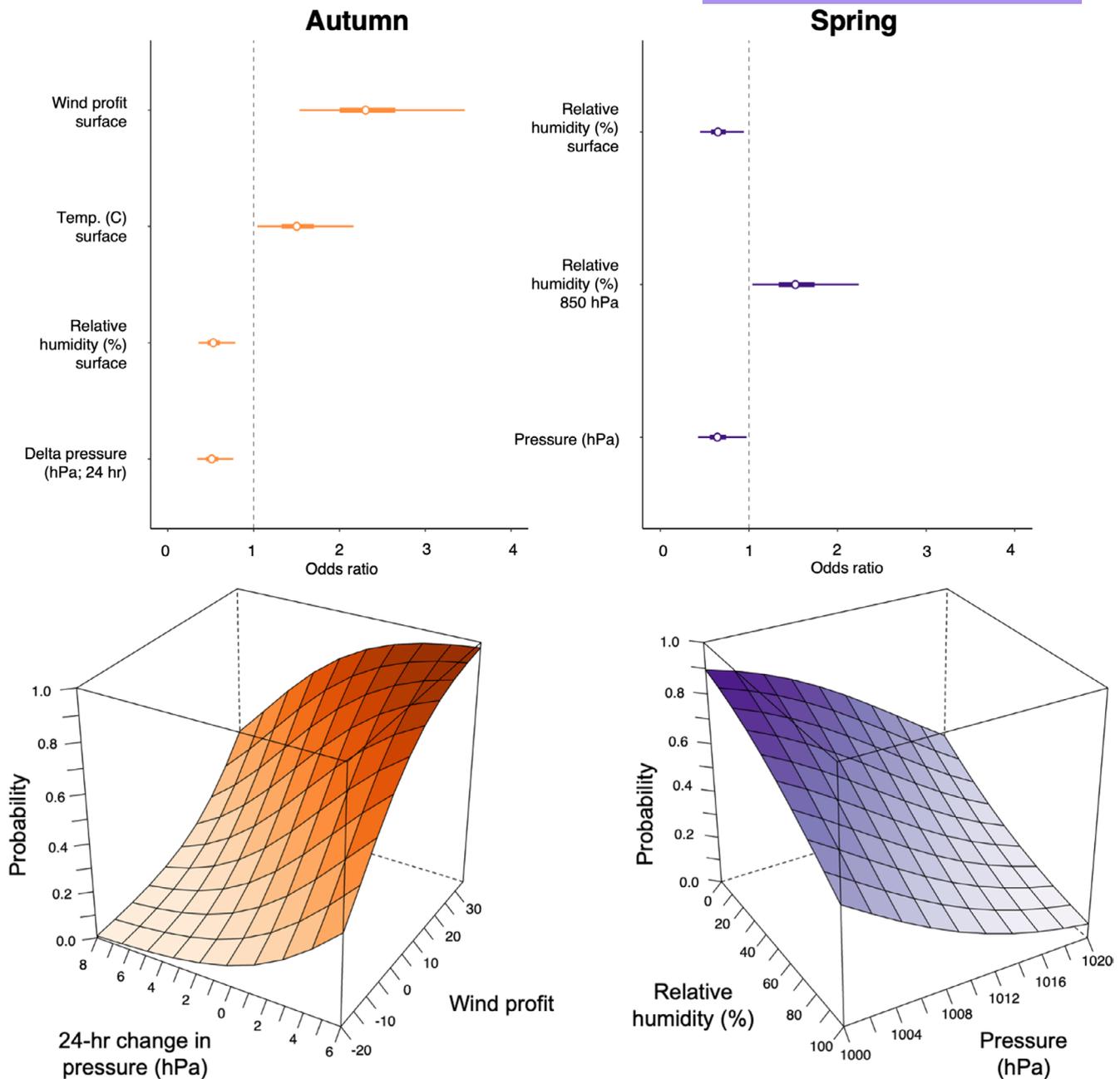


FIGURE 3 Coefficient plot for top multiple logistic regression models exploring the effects of weather conditions on the initiation of trans-Gulf of Mexico flights in *Vermivora* warblers. We considered models exploring the relationship between weather conditions on departure day and during the previous day. In both top panels, an odds ratio of 1 equates to equal odds and odds ratios >1 or <1 equate to increased or decreased odds of initiating trans-Gulf flights, respectively. Bottom panels depict the predicted probability of *Vermivora* warblers initiating trans-Gulf flights as a function of 24-h change in barometric pressure and wind profit during autumn (left, orange) and surface-level relative humidity and barometric pressure during spring migration (right, purple). Predicted probabilities were generated holding all other variables at their estimated average values. Darker hues indicate higher probabilities.

4 | DISCUSSION

We found strong evidence that surface-level weather conditions, but not those aloft, influenced the initiation of trans-Gulf flights by *Vermivora* warblers during both autumn and spring migration periods. During autumn migration, *Vermivora* warblers (10g) exhibited similar relationships with weather conditions (i.e. wind profit, relative humidity and barometric pressure) as three larger passerines

that also cross the Gulf of Mexico: red-eyed vireos (*Vireo olivaceus*; 17g) Swainson's thrush (*Catharus ustulatus*; 33g), and wood thrush (*Hylocichla mustelina*; 46g) tracked with automated telemetry (Deppe et al., 2015). That similar exogenous cues are associated with trans-Gulf departure of three distantly related species with different morphologies and migratory ecologies suggests that the evolutionary pressures shaping barrier-crossing behaviour may be consistent among Nearctic-Neotropical migratory passerines and potentially

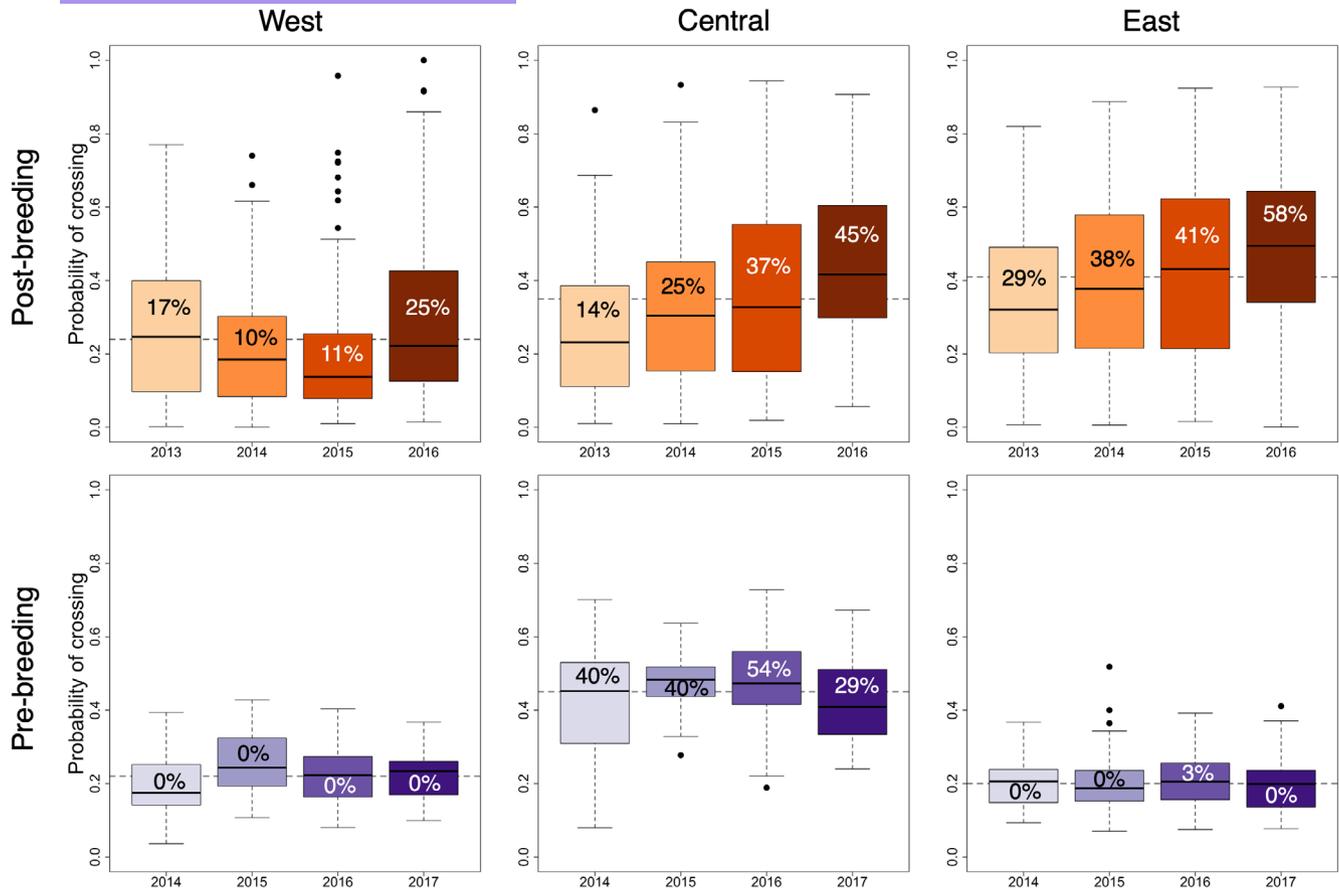


FIGURE 4 Boxplots summarizing the daily-predicted probability of *Vermivora* warblers initiating trans-Gulf flights by year (indicated by different colours), sector (west, central and east) and season (autumn, top row; spring, bottom row). Probabilities estimated using the top-performing 2-day model (i.e. departure day and previous day) and represent the favourability of weather conditions. The horizontal dashed line indicates the mean probability of each sector across all years. Values within boxes specify the percent of days with favourable conditions (i.e. probability of initiating trans-Gulf flight ≥ 0.50). Total duration of autumn and spring migration periods differed ($n_{\text{autumn}} = 92$ days, $n_{\text{spring}} = 30$ days).

other taxa (e.g. insects [Drake & Farrow, 1988], bats [Solick & Newman, 2021]). Historical and contemporary reports documenting the highly episodic nature of migration in Nearctic–Neotropical birds wherein large numbers of diverse migrant species arrive together in distinct waves at migratory stopover sites along the Gulf of Mexico provide additional support for this hypothesis (Paynter Jr., 1953; Van Doren & Horton, 2018). It was not possible to infer the endogenous, physiological conditions (i.e. fat stores and/or pectoral muscle volume) of individual *Vermivora* warblers prior to initiating flight crossing the Gulf of Mexico in our study, although they likely interact with environmental conditions to affect barrier-crossing behaviour (Deppe et al., 2015).

Compared to autumn migration, less is known about how weather conditions influence the initiation of trans-Gulf flights by Nearctic–Neotropical migrants during spring migration. We found that weather variables associated with the initiation of trans-Gulf flights during spring migration differed from those associated with the initiation of trans-Gulf flights during autumn migration. In spring, the initiation of trans-Gulf flights was negatively associated with surface-level relative humidity and barometric pressure and positively associated with

relative humidity aloft (at 850 hPa, ~1500 m) but surprisingly not associated with wind profit. Similarly, purple martins (*Progne subis*) did not exhibit a preference for favourable wind conditions during spring migration (Abdulle & Fraser, 2018; Lavallée et al., 2021). This may be related to timing constraints that *Vermivora* warblers and other Nearctic–Neotropical migrants face during spring migration when individuals must balance arriving at breeding sites early enough to secure mating opportunities and establish territories, but late enough to ensure weather conditions and the availability of resources are suitable for survival and reproduction (Kramer et al., 2017; Pulido & Widmer, 2005; Shipley et al., 2020; but see Briedis et al., 2018; Gow et al., 2019; van Wijk et al., 2017). During autumn migration, individuals may be less likely to initiate trans-Gulf flights under neutral or unfavourable wind conditions because there may be less of a fitness penalty associated with waiting for conditions to become more favourable than in spring. Alternatively, variation in the use of favourable weather conditions between spring and autumn could be associated with where the Gulf of Mexico (or another barrier) fits into the overall migration journey; waiting for favourable weather conditions may be more beneficial when the Gulf crossing occurs

Migratory connectivity of *Vermivora* warblers during the annual cycle

Golden-winged warbler

Blue-winged warbler



MC = Migratory connectivity metric
 r_M = Mantel correlation coefficient

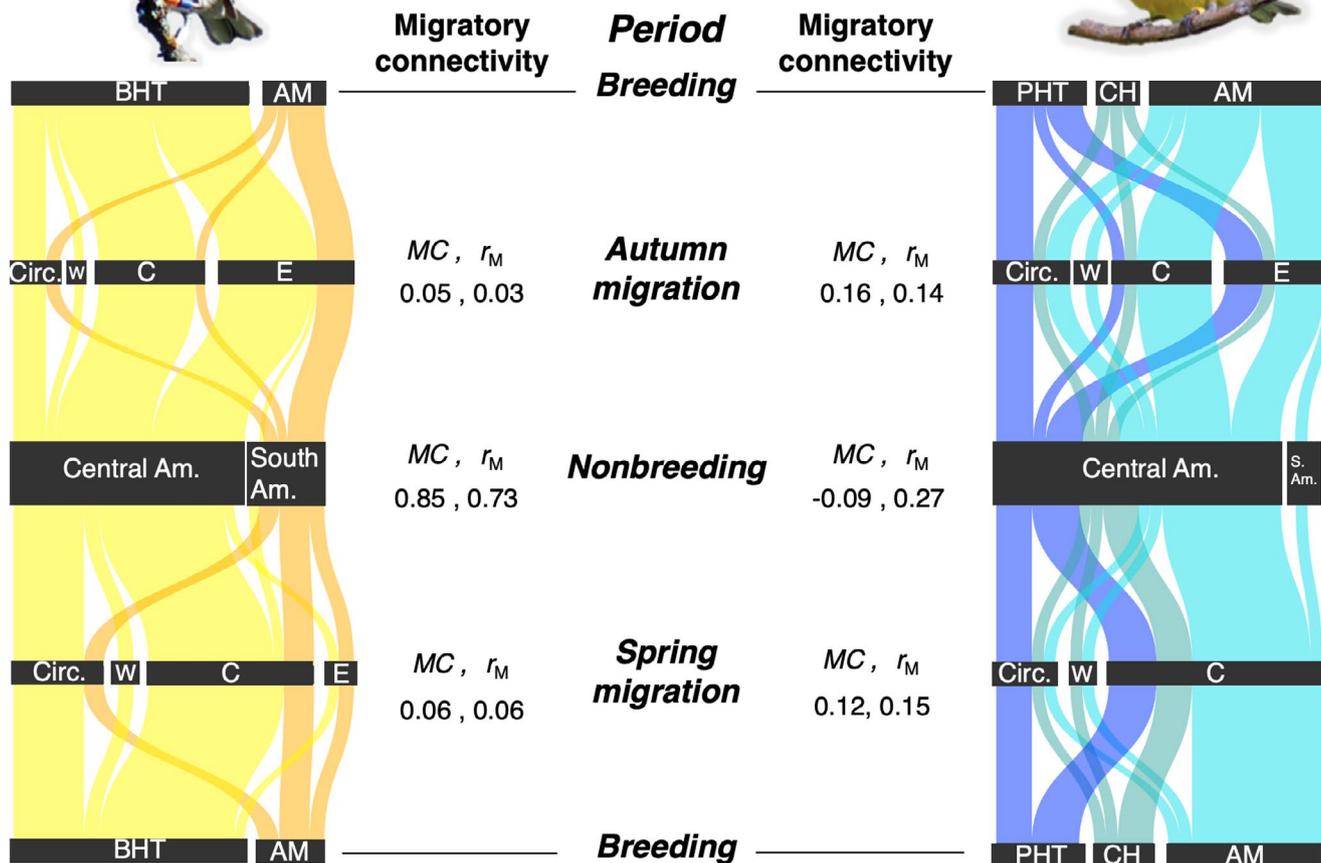


FIGURE 5 Seasonal distribution of blue-winged warblers (*Vermivora cyanoptera*) and golden-winged warblers (*Vermivora chrysoptera*) and sites where individuals were tracked with geolocators. Line plots show the proportion of individuals from distinct breeding populations using different autumn departure sectors, non-breeding regions and spring departure sectors. Migratory connectivity of breeding populations estimated with the MC metric, and Mantel correlation coefficient (r_M) are shown for each portion of the annual cycle. Populations were delimited based on Bird Conservation Region (BCR): Boreal Hardwood Transition BCR (BHT), Appalachian Mountain BCR (AM), Prairie Hardwood Transition BCR (PHT) and Central Hardwood BCR (CH). Migration sectors were classified as based on the departure longitude (circumvent [Circ.], west [W], central [C] or east [E]). Non-breeding regions were classified as either occurring in Central America or South America.

after travelling greater distances than when the crossing occurs earlier in the migratory route. Moreover, the proportion of days during the migration period with a predicted probability of initiating trans-Gulf flights >0.50 was greater during autumn than during spring. Therefore, individuals experiencing unfavourable conditions at the Gulf of Mexico during autumn migration likely wait shorter periods before conditions become more favourable compared to spring migration. We considered synoptic conditions to assess the effects of regional weather on the migratory behaviour of *Vermivora* warblers. However, it is possible that individuals responded to weather cues at finer temporal and spatial scales than we captured in our analysis

and future efforts to explore these relationships are warranted (e.g. using tags that record barometric pressure; Rhyne et al., 2024).

The strength of migratory connectivity of *Vermivora* warblers was weak prior to crossing the Gulf of Mexico during both autumn and spring migration periods. Migratory connectivity of blue-winged warblers remained weak throughout the annual cycle, including during both sedentary periods. Conversely, strong breeding–non-breeding migratory connectivity exhibited by golden-winged warblers broke down during migration. The weak migratory connectivity of *Vermivora* warblers during migration was similar to findings in common nighthawks (*Chordeiles minor*; $r_M < 0.30$), especially at latitudes

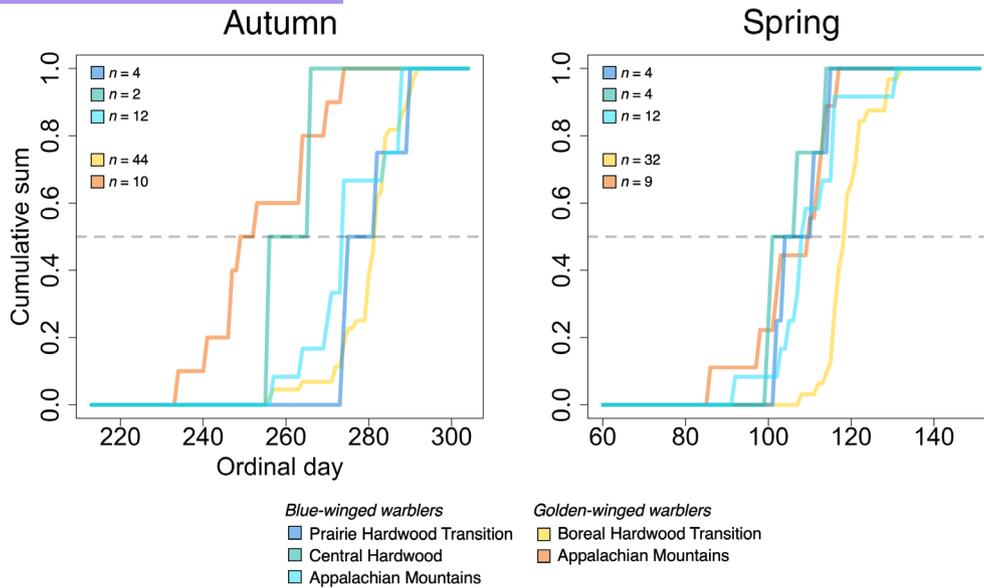


FIGURE 6 Cumulative sum plots illustrating the proportion of individual *Vermivora* warblers that crossed the Gulf of Mexico by ordinal day and population. Colours indicate populations based on Bird Conservation Regions. The threshold at which 50% of individuals crossed the Gulf of Mexico (50% passage rate) is indicated by the dashed grey line.

around the Gulf of Mexico ($r_M \sim 0.10$; Knight et al., 2021). Relatively weak spatial migratory connectivity during migration suggests that variation in population trends of *Vermivora* warblers (and especially golden-winged warblers) is unlikely to be linked to landscape factors experienced during migration near the Gulf of Mexico (Kramer et al., 2017, 2018b, 2023).

Populations of *Vermivora* warblers exhibited evidence of temporal connectivity at the Gulf of Mexico during autumn migration (based on 50% passage dates), which was associated with breeding site latitude. Despite low rates of spatial migratory connectivity during autumn migration, golden-winged warblers from Appalachian Mountain BCR breeding sites tended to initiate trans-Gulf flights much earlier (up to 33 days on average) compared to other populations, which could result in those individuals experiencing different conditions that could affect survival and population dynamics. Notably, golden-winged warblers from Appalachian Mountain BCR breeding sites initiated trans-Gulf flights on days associated with lower predicted favourability of conditions compared to golden-winged warblers from breeding sites in the Boreal Hardwood Transition BCR (Figure S10). If less favourable conditions are associated with greater mortality during migration, conditions experienced during migration could contribute to ongoing population declines in golden-winged warblers breeding in the Appalachian Mountains. Further research is warranted to identify factors influencing survival during trans-Gulf flights compared to survival at stopover sites and whether differences in migratory behaviour (e.g. higher frequency of multi-day flights) or timing are associated with mortality rates.

We found no evidence that *Vermivora* warblers migrated through departure sectors in a manner that minimized migration distances suggesting that other factors could be driving variation in space use prior to navigating the Gulf of Mexico. The observed breakdown

in spatial migratory connectivity in *Vermivora* warblers (especially golden-winged warblers) may be linked to geographic variation in the availability of favourable conditions for crossing the Gulf of Mexico. The favourability of conditions varied spatially during both autumn and spring. Most *Vermivora* warblers initiated trans-Gulf flights from the central sector during spring migration where conditions were relatively favourable compared to the western and eastern sectors. If synoptic weather conditions tend to be more favourable for migration in specific areas, migratory individuals that use those areas may have higher survival and potentially experience greater fitness due to both direct (i.e. increased survival; Hewson et al., 2016) and indirect effects (i.e. carry-over effects; Legagneux et al., 2012). If the directionality of migratory movements is an innate and heritable trait in *Vermivora* warblers as it appears to be in some other species (Berthold & Helbig, 1992) and individuals that use areas with more favourable conditions experience greater relative fitness, then natural selection (via historically consistent weather conditions) may have shaped the observed patterns of space use in *Vermivora* warblers around the Gulf of Mexico during migration. Thus, general weather patterns during migration periods may explain the breakdown of otherwise strong migratory connectivity in golden-winged warblers and the maintenance of weak migratory connectivity in blue-winged warblers during autumn and spring migration. Notably, a single gene is associated with differences in non-breeding locations in *Vermivora* warblers (Toews et al., 2019). Therefore, it is likely that other aspects of migratory behaviour also may be under genetic control in *Vermivora* warblers and may underlie patterns in the spatial and temporal distribution of individuals from this species complex. Which genes or regulatory processes are associated with different migratory behaviours and whether those same genes also are associated with the apparently convergent strategies of other

Nearctic–Neotropical migrants and/or other taxa remains unknown (Harringmeyer et al., 2021).

An alternative explanation for the patterns in connectivity that we observed is that *Vermivora* warblers migrate through all sectors of the Gulf of Mexico region in equal numbers but the survival rate is lower in areas with less favourable conditions and therefore we primarily retrieved data from individuals that used routes that also conferred favourable conditions. Other factors including geographic variation in the availability of resources, the quality and availability of stopover sites and greater rates of interspecific or intraspecific competition could also cause or contribute to the patterns we observed. However, individual golden-winged warblers are known to exhibit plasticity in route use among years, suggesting that individuals may be able to respond to temporally variable conditions experienced during migration (Kramer et al., 2017). The data from *Vermivora* warblers in this study were collected over 4 years and longer-term monitoring could quantify the consistency of associations among weather conditions, resource availability, space use and barrier-crossing behaviour in this species complex. Further efforts to understand the fitness consequences of different migration routes, timing and speed might provide insight into the evolutionary development and maintenance of diverse migratory behaviours near barriers.

Identifying the exogenous factors that are associated with migration in small songbirds like *Vermivora* warblers may help in predicting how climate change will affect migratory animals (Crick, 2004). In the case of *Vermivora* warblers, predicted increases in the frequency of days with high relative humidity (i.e. predicted ~150-fold increase in frequency by 2080; Coffel et al., 2017), especially near large bodies of water like the Gulf of Mexico, may result in fewer favourable migration days during spring migration. Conversely, warming temperatures and stronger winds predicted to occur in the future may improve the frequency of favourable days for crossing the Gulf of Mexico during autumn migration (Chen, 2020; Zeng et al., 2019). A reduction in the number of favourable days during a migration period may lead to individuals stopping over for longer durations or needing to accumulate more energy reserves prior to barrier-crossing, which could lead to increased mortality during migration and/or carry-over effects in other portions of the annual cycle (Legagneux et al., 2012). Moreover, the frequency and intensity of severe storms (e.g. hurricanes) are predicted to increase in the Gulf of Mexico and eastern Atlantic Ocean regions (Mann & Emanuel, 2006), which could pose a substantial risk to migratory birds. Exactly how changing weather conditions and increasing frequency of severe storms will interact to affect the movements and barrier-crossing behaviour of migrating animals remains unknown (Newton, 2007). Continued efforts to characterize the effects of environmental factors on the migratory behaviour of diverse taxa will provide context for understanding the ecological (Howard et al., 2024; Kubelka et al., 2022; Lamb et al., 2025; Lisovski et al., 2024) and evolutionary (Cooke et al., 2024; Thorup et al., 2021; Weeks et al., 2020) implications of climate change on migration and may aid in developing effective conservation strategies for migratory species (Torstenson et al., 2024).

AUTHOR CONTRIBUTIONS

Gunnar R. Kramer, David E. Andersen, David A. Buehler, Petra B. Wood and Henry M. Streby conceived of the study and designed the methodology; Gunnar R. Kramer analysed data; Gunnar R. Kramer led the writing of the manuscript with support from David E. Andersen, David A. Buehler, Petra B. Wood and Henry M. Streby; Gunnar R. Kramer, David E. Andersen, David A. Buehler, Petra B. Wood, Sean M. Peterson, Justin A. Lehman, Kyle R. Aldinger, Lesley P. Bulluck, Sergio R. Harding, John Anthony Jones, John P. Loegering, Curtis Smalling, Rachel Vallender and Henry M. Streby contributed critically to drafts of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code available from the Open Data Repository of Iowa State University: <https://doi.org/10.25380/iastate.30559685> (Kramer et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Summary table of geolocator data collected from individual *Vermivora* warblers at 26 sites across the North American breeding distribution and 5 sites within the Central American nonbreeding distribution. Breeding sites are stratified by Bird Conservation Region (BCR) based on occurrence of each site within, or its proximity to BCRs containing meaningful populations of *Vermivora* warblers (see Methods for details).

Table S2. Metadata of geolocator-marked *Vermivora* warblers including individual identification code (ID), U.S. Geological Survey band number (Band #), geolocator deployment year (Year), species (Species; GW=golden-winged warbler, BW=blue-winged warbler, H=hybrid), corresponding Bird Conservation Region (BCR) of breeding location, breeding and nonbreeding coordinates (Breeding latitude, Breeding longitude, Nonbreeding latitude, Nonbreeding longitude). Cells for which geolocator data were not collected or for which data were not available are denoted by “n/a”.

Table S3. Metadata of geolocator-marked *Vermivora* warblers including number and timing of full-light period (FLP) anomalies. Individual identification code (ID), geolocator deployment year (Year), species (Species; GW=golden-winged warbler, BW=blue-winged warbler, H=hybrid), corresponding Bird Conservation Region (BCR) of breeding location, number of autumn and spring

FLPs identified (Number aut. FLPs, Number spr. FLPs), date of FLP associated with crossing the Gulf of Mexico (Date aut. trans-Gulf FLP, Date spr. trans-Gulf FLP), and departure sector (Aut. departure sector, Spr. departure sector). Individuals that circumvented the Gulf of Mexico are denoted by "Circ." Cells for which geolocator data were not collected or for which data were not available are denoted by "n/a".

Table S4. Geographic coordinates of departure sectors used to characterize the location of *Vermivora* warblers before initiating trans-Gulf flights and extract weather data.

Table S5. Estimated departure longitude of individual *Vermivora* warblers used in analyses. Individual ID (ID), deployment year (Year), species (Species; "GW"=golden-winged warbler, "BW"=blue-winged warbler, "H"=hybrid), Bird Conservation Region (BCR; "BHT"=Boreal Hardwood Transition, "CH"=Central Hardwoods, "AM"=Appalachian Mountains, "PHT"=Prairie-Hardwood Transition), departure sector (Departure sector; "C"=central, "E"=east, "W"=west, "Circ."=circumvent), and season (Autumn vs. Spring) are presented. Whether departure longitude is derived from an estimate ("Estimated"), or assigned ("Assigned") to the departure sector mid-point is indicated.

Table S5. Correlation matrix among autumn weather variables used in logistic regression modeling of the initiation of trans-Gulf flights by *Vermivora* warblers. Strongly correlated variables (i.e., $r > 0.60$, $p < 0.05$) are bold.

Table S6. Correlation matrix among spring weather variables used in logistic regression modeling of the initiation of trans-Gulf flights by *Vermivora* warblers. Strongly correlated variables (i.e., $r > 0.60$, $p < 0.05$) are bold.

Table S7. Performance of generalized linear models exploring whether the probability of exhibiting full light pattern (FLP) anomalies was associated with year, population, or both variables' interactions with ordinal day. Top-performing models (based on Akaike's Information Criterion adjusted for sample size; AIC_c) are bold. Model name (Model), the number of estimated parameters (k), difference from AIC_c of top-performing model (ΔAIC_c), model deviance ($-2 \times \log$ -likelihood), and migration period (Period) are presented.

Table S8. Performance of generalized linear models exploring the relationship between weather conditions and the initiation of trans-Gulf flights by *Vermivora* warblers. Models were parameterized using a drop-one modeling approach (Drop-one) or contained variables for all weather conditions considered (Full). Null (intercept-only) models also are presented. Top-performing models (based on Akaike's Information Criterion adjusted for sample size; AIC_c) are bold. Model name (Model), the number of estimated parameters (k), difference from AIC_c of top-performing model (ΔAIC_c), model deviance ($-2 \times \log$ -likelihood), and migration period (Period) are presented.

Figure S1. Map of breeding distributions, geolocator deployment sites, and Bird Conservation Regions relevant to blue-winged warblers (left) and golden-winged warblers (right).

Figure S2. Geolocator-derived estimates of departure longitude for individual *Vermivora* warblers (blue-winged warblers, top row; golden-winged warblers, bottom row) initiating flights across

the Gulf of Mexico during autumn (left panels) and spring (right panels). Departure sectors used in analyses are indicated by letter (W=west, C=central, E=east) and breeding population (based on Bird Conservation Region [BCR]) is indicated by different colors.

Figure S3. Correlation among weather conditions at three coastal sites per departure region. Sites were spread across potential coastal departure sites by season (Aut=autumn, Spr=spring) and region (W=west, C=central, E=east). Sites used in the analysis (Base sites) are mapped as triangles whereas replicate sites are mapped as circles. Color indicates region (a). The strength of correlation (Pearson's correlation coefficient; r) among base sites and replicate sites are presented for temperature (b), pressure (c), relative humidity (d), wind direction (e), and wind speed (f). Strength and direction of correlation is indicated by color with red characterizing a strongly positive correlation blue representing a strongly negative correlated between conditions at base and replicate points.

Figure S4. Boxplots comparing weather conditions on days that *Vermivora* warblers initiated trans-Gulf flights ("Departed", green) versus days with no observed initiation of trans-Gulf flights (gray) based on the absence of full light period (FLP) anomalies in light-level geolocator data. We tested for differences in conditions on days that *Vermivora* warblers initiated trans-Gulf flights versus those without evidence of initiation of trans-Gulf flights during both autumn and spring migration periods using linear models and presented the results (mean difference and associated p -value) in each graph. Conditions that differed significantly between seasons (i.e., $p < 0.05$) are bold and noted with an asterisk. See main text for detailed descriptions of weather variables. X-axis labels are presented in top-row only but apply to all plots.

Figure S5. Coefficient plot for fully parameterized logistic regression models exploring the effects of weather conditions on the initiation of trans-Gulf of Mexico flights in *Vermivora* warblers. Models contain all weather terms considered in each migration season. We considered models exploring the relationship between weather conditions on departure day and during the previous day (2-day model), departure day and the previous 3 days (4-day model), and departure day and the previous 6 days (7-day model).

Figure S6. Coefficient plot for top multiple logistic regression models exploring the effects of weather conditions on the initiation of trans-Gulf of Mexico flights in *Vermivora* warblers. We considered models exploring the relationship between weather conditions on departure day and during the previous day (2-day model), departure day and the previous 3 days (4-day model), and departure day and the previous 6 days (7-day model). In both panels, an odds ratio of 1 equates to equal odds and odds ratios > 1 or < 1 equate to increased or decreased odds of initiating trans-Gulf flights, respectively.

Figure S7. Receiver operating characteristic (ROC) curves of logistic regression models containing all weather variables considered (Full) and final models selected using a drop-one modeling approach (Drop-1) that included all terms that, if dropped, would reduce model performance (based on AIC_c). We considered models exploring the relationship between weather conditions on the day that *Vermivora* warblers initiated trans-Gulf flights ("departure day") and on the

previous day (2-day model), departure day and the previous 3 days (4-day model), and departure day and the previous 6 days (7-day model). **Figure S8.** Violin plots of the absolute value of residuals (log-scale) of geolocator-derived light data during three periods on randomly selected days (gray) and on full light pattern (FLP)-anomaly days when individuals initiated trans-Gulf flights (green). Residuals calculated as the sum of absolute value of deviations from a quadratic equation fit to light data (dawn, dusk) or deviations from maximum light (daytime). Black lines are group means. Asterisks denote significant differences between light conditions on random days versus FLP-days for a given period based on a two-way ANOVA and subsequent Tukey post-hoc test at $p < 0.05$. The lack of evidence for statistical differences is denoted by "NS".

Figure S9. Exploratory regression plots displaying the linear relationship between the 50% passage date (i.e., ordinal day by which 50% of individuals crossed the Gulf of Mexico) and three population-specific spatial factors: average breeding latitude, average nonbreeding latitude, and average nonbreeding longitude. Colored points represent individual populations of *Vermivora* warblers and population-level metrics used for explanatory variables were derived as an average of individuals within a given population. Dashed lines show the results of linear regressions with gray lines indicating no statistically significant relationship (i.e., $p > 0.05$) and black lines indicating a statistically significant association between predictor variables and 50% passage date.

Figure S10. Boxplots of predicted favorability of weather conditions (predicted probability of departure ≥ 0.50) by population (based on Bird Conservation Regions [BCR]). We tested for differences among groups using one-way ANOVAs and Tukey HSD ($p < 0.05$). Bold text indicates significant differences among groups based on ANOVAs and letters over bars indicate specific differences. Golden-winged warblers from breeding sites in the Boreal Hardwood Transition BCR (GW BHT), Appalachian Mountain BCR (GW AM) are represented with yellow and orange shades, respectively. Blue-winged warblers from breeding populations in the Prairie Hardwood Transition BCR (BW PHT), Central Hardwoods BCR (BW CH), or Appalachian Mountain BCR (BW AM) are represented by different shades of blue.

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