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RESEARCH ARTICLE

Drivers of variation in migration behavior for a linked population of long-distance migratory passerine

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ABSTRACT

Despite advances in tracking technologies, migration strategies remain poorly studied for many small-bodied passerines. Understanding variation within a migration strategy is important as variation impacts a population's resilience to environmental change. Timing, pathway, and stopovers vary based on intrinsic and extrinsic factors that impact individual migration decisions and capacity. Here, we studied drivers of variation in migration across a linked population of Golden-winged Warbler (*Vermivora chrysoptera*) using data from 37 light-level geolocators. We tested if behaviors vary in response to extrinsic factors: season, year, and proximity to a large geographic barrier—the Gulf of Mexico—and intrinsic factors: age and wing chord. Spring migration was nearly twice as fast as fall migration, with tightly correlated arrival and departure dates that were consistent among years, in contrast to no correlation or consistency in fall. This aligns with predictions for selection to minimize time spent migrating in spring and a relaxation of that pressure in fall. Twenty-nine birds staged for multiple days (mean: 7.5, SE: 0.6) in stopover habitats before crossing the Gulf of Mexico in spring, but 6 individuals overwintering closer to the Gulf coast forewent the stopover and completed migration 8 days faster. These findings suggest birds capable of crossing the Gulf without a stopover may experience a selective advantage by minimizing total migration time. After crossing the Gulf, individuals reduced travel speed and stopover duration, indicating constraints on movement differ before and after the barrier. Wing chord, but not age, positively predicted the total distance and duration of migration, and neither varied with timing, suggesting migration distance impacts morphology, but strategies do not vary with age. Ultimately, we find undescribed stopover locations south of the Gulf are important for most of the population, while high variation in migration behaviors suggest potential resilience to changing environmental conditions.

Keywords: geographic barrier, geolocator, Golden-winged Warbler, migration strategy, migratory connectivity, optimal migration, stopover, *Vermivora*

Causantes de variación en el comportamiento migratorio para una población vinculada de un paseriforme migratorio de larga distancia

RESUMEN

A pesar de los avances en la tecnología de rastreo, las estrategias migratorias siguen estando poco estudiadas para muchas aves paseriformes de cuerpo pequeño. Entender la variación dentro de una estrategia migratoria es importante ya que la variación impacta en la resiliencia de una población al cambio ambiental. El momento de migración, los corredores y los sitios de parada varían en base a factores intrínsecos y extrínsecos que impactan las decisiones y las capacidades individuales de migración. En este trabajo, estudiamos los causantes de variación en la migración de una población vinculada de *Vermivora chrysoptera*, usando datos provenientes de 37 geo-localizadores de nivel de luz. Evaluamos si los comportamientos varían en respuesta a factores extrínsecos: estación, año y proximidad a una gran barrera geográfica—el Golfo de México, y a factores intrínsecos: edad y cuerda alar. La migración de primavera fue casi dos veces más rápida que la migración de otoño, con fechas de arribo y partida estrechamente correlacionadas que fueron consistentes entre

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los años, en contraste a una falta de correlación o consistencia en el otoño. Esto se condice con las predicciones de la selección para minimizar el tiempo gastado migrando en primavera y una relajación de dicha presión en el otoño. Veintinueve aves permanecieron por varios días (media: 7.5, EE: 0.6) en los hábitats de parada antes de cruzar el Golfo de México en primavera, pero seis individuos que invernaron más cerca de la costa del golfo se anticiparon a la parada y completaron la migración ocho días más rápido. Estos hallazgos sugieren que las aves que son capaces de cruzar el golfo sin una parada pueden tener una ventaja selectiva al minimizar el tiempo total de la migración. Luego de cruzar el golfo, los individuos redujeron la velocidad del viaje y la duración de las paradas, indicando que las limitantes en el movimiento son diferentes antes y después de la barrera. La cuerda alar, pero no la edad, predijo positivamente la distancia total y la duración de la migración, y ninguna varió con el momento de migración, sugiriendo que la distancia de migración afecta la morfología, pero que las estrategias no varían con la edad. En definitiva, encontramos que los lugares de parada no descriptos hasta la fecha al sur del golfo son importantes para la mayoría de la población, mientras que la alta variación en los comportamientos migratorios sugiere una resiliencia potencial a las condiciones ambientales cambiantes.

Palabras clave: barrera geográfica, conectividad migratoria, estrategia migratoria, geo-localizador, migración óptima, parada, *Vermivora chrysoptera*

INTRODUCTION

Birds are one of the best-studied migratory taxa, with a rich literature that provides insights into factors that shape migratory patterns (Berthold 2001). Over the past decade, full-annual movement patterns of many long-distance migratory landbirds have been described due to advances in lightweight individual tracking technologies (Stutchbury et al. 2009, Bridge et al. 2011). These studies show that landbirds commonly employ a migration strategy of rapid passage between only a few stopover sites (Bayly et al. 2018) that play a critical role in a bird's ability to fuel, cross dangerous geographic barriers, and complete migration (Gómez et al. 2017, Moore 2018). Especially fascinating is that many recent studies reveal variation in migration speed, pathway, and stopover duration within populations (Stanley et al. 2012, Cohen et al. 2014, Kramer et al. 2017, Cohen et al. 2018). Yet despite the recent proliferation in migration tracking studies, we still have a limited understanding of the drivers of individual variation within population-level migration strategies, especially for small-bodied passerines (McKinnon and Love 2018). This is a critical knowledge gap, as plasticity in migratory behaviors may impact the potential of a population to adapt to environmental changes during migration (Charmantier and Gienapp 2014, Bayly et al. 2019).

Optimal migration theory provides a framework for interpreting how migration routes and refueling stopovers balance selective pressures to migrate quickly, minimize energy expended, and minimize risk of predation or starvation (Clark and Butler 1999, Alerstam 2011). Optimal strategies may differ among species and between seasons and sexes. For example, passage time is substantially shorter in spring than fall for many species that breed in the northern hemisphere—especially songbirds and swifts—consistent with a time-minimizing strategy in spring driven by a stronger selective pressure to establish breeding territories than overwintering territories (reviewed in Nilsson et al. 2013 and Schmaljohann 2018). Conversely, spring migration strategies for some species—notably most waterfowl and "capital breeders" that amass breeding energy reserves during migration—prioritize low energy expenditure, and these migrants accordingly travel at a slower pace and refuel more frequently (Alerstam 2011, Nilsson et al. 2013, Schmaljohann 2018). In theory, a time-minimizing strategy should be riskier than an energy-minimizing strategy, as time-minimizing individuals may run the risk of depleting fuel reserves and starving between stopovers (Newton 2004, Baker et al. 2004, Gómez et al. 2017). The extent to which selection for passage-time minimization mediates mortality risk is unknown, but recent demographic work shows that survival of long-distance migrants is lowest during the spring (Klaassen et al. 2014, Lok et al. 2015, Rushing et al. 2017), suggesting the common spring time-minimization strategy may carry a survival cost.

Within a population, the migratory movement behaviors of individuals—including pathway, speed, and use of stopover sites—can vary within an overall migration strategy. Date of migration initiation has been shown to be under endogenous control with little to no individual plasticity in most obligate, long-distance migrants (Gwinner and Helm 2003, Gill et al. 2014), but migration pathways and speed are thought to be relatively flexible at both the individual and population level (e.g., Stanley et al. 2012, Cohen et al. 2014, La Sorte and Fink 2017). These movement behaviors may be influenced by intrinsic factors such as morphology (e.g., wing size and shape; Arizaga et al. 2006), age class (e.g., McKinnon et al. 2014), sex (e.g., Dierschke et al. 2005), and condition (e.g., Dossman et al. 2016, Wright et al. 2018). Simultaneously, extrinsic factors such as habitat quality and precipitation at overwintering sites (e.g., Studds and Marra 2005, 2011; Akresh et al. 2019, Bayly et al. 2019) and synoptic weather patterns and events (e.g., Richardson 1990, Kranstauber et al. 2015, Dossman et al. 2016, Wright et al. 2018) may influence the timing and duration of migration and stopovers. Understanding the drivers of variation in migratory behaviors is important,

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as a population's flexibility to respond to future changes in resources or threats along a migratory route depends in large part on the variation present in migratory pathway, timing, and stopovers (Charmantier and Gienapp 2014). Furthermore, interpreting these behaviors in the context of an optimal migration strategy may reveal constraints on the timing, speed, and pathways employed by a migrating population. Understanding these constraints is especially important during high-risk periods such as the crossing of geographic barriers—large, inhospitable areas over which no options for resting or refueling exist.

We use data from light-level geolocators to study the drivers of individual variation in migratory behaviors for a linked population of Golden-winged Warbler (*Vermivora chrysoptera*) that breeds in the Great Lakes region of United States and Canada and overwinters in Central America. Previous research on the small (8–10 g) and declining Golden-winged Warbler showed that these breeding and wintering regions are occupied by a strongly linked population that crosses (or occasionally circumvents) the Gulf of Mexico during spring and fall migration (Kramer et al. 2017, 2018). The Gulf of Mexico is a major geographic barrier for Neotropical migrants that breed in eastern North America, requiring either >1,000 km of sustained over-water flight or lengthy overland circumvention, and migrating birds regularly perish in the crossing (Drymon et al. 2019). For migrating passerines, survival over the Gulf and decisions about route and departure timing depend on a combination of wind favorability and accumulated fat levels (Deppe et al. 2015, Ward et al. 2018). For Golden-winged Warblers, we expected the population migrates under a time-minimizing strategy in spring, given pressure to establish breeding territories as early as possible (Nilsson et al. 2013). Under this strategy, departure and arrival dates should be tightly correlated with little to no variation between years, indicating that Golden-winged Warblers travel as fast as physically possible to arrive on an optimal date (McWilliams et al. 2004, Alerstam 2011). We had no a priori prediction about whether Golden-winged Warblers would optimize time or energy during fall migration, given evidence in some species that pressure to establish nonbreeding territories drives rapid fall migration (e.g., Cooper et al. 2017), while most passerines travel at a significantly slower pace in fall than spring, suggesting a relaxation of time-minimizing selection (Nilsson et al. 2013, Schmaljohann 2018). Golden-winged Warblers maintain fixed territories throughout the nonbreeding season (Chandler et al. 2016), but it is unknown if competition for overwinter territory establishment (described in Bennett 2018) drives rapid fall migration.

Within the context of a population-level migration strategy, we tested if individual migratory behaviors vary in response to 4 factors: season, wing length, age, and spatial proximity to the Gulf of Mexico. Evidence exists that longer and more pointed wings increase the efficiency of migratory flights (Norberg 1995, Corman et al. 2014, Lam et al. 2015) and that adults and juveniles segregate during migration such that adult individuals cross the Gulf of Mexico and arrive on the breeding grounds before first-year individuals (e.g., McKinnon et al. 2014, Cohen et al. 2018). We therefore tested if migration timing, distance, and duration varied with age or wing length. Given the inherent risks of trans-Gulf migration for our study population, we examined differences in migration speed and stopover duration before and after individuals crossed the barrier. We predicted that Golden-winged Warblers would spend more time at stopover sites before crossing the Gulf of Mexico, given the need to deposit enough fuel to make a nonstop flight of ~1,200 km. We had no a priori prediction about how flight speed or proportion of days spent moving would change after birds crossed the Gulf, given potential phenological constraints in resources or weather (Kelly et al. 2016).

METHODS

Data Collection

During the overwintering season of 2015–2016 (November 15 to March 15) we deployed geolocators on 123 Golden-winged Warblers at 8 sites in Central America (Table 1). While migration strategies may differ between sexes (Dierschke et al. 2005), we restricted this study to males due to low capture rates and small body size of females. Golden-winged Warblers were captured with a 30 mm mist net and fitted with a Lotek ML6040 stalkless geolocator attached to the leg-loop harness described by Streby et al. (2015). We recorded age, wing chord (length from carpal joint to longest primary; Pyle et al. 1987), and weight (g) of all captured birds, and affixed a single color band to aid in resighting. We recovered geolocators during the following nonbreeding season, beginning on October 15, 2016, and performed at least 3 area searches within a 500 m radius of each initial deployment location using male broadcast vocalizations to increase probability of resighting individuals (Chandler and King 2011). We resighted 26 of 123 Golden-winged Warblers and successfully recaptured 22 in mist nets. Because 2 geolocators failed within their first day of activation, we included only 20 units from this field effort in the analysis.

We supplemented our sample with published geolocator data from 6 Golden-winged Warblers tagged during January and February 2015 at El Jaguar, Nicaragua (Larkin et al. 2017), and 11 individuals tagged between May 2013 and June 2014 at Rice Lake National Wildlife Refuge, Minnesota (Kramer et al. 2016, 2017). We excluded

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TABLE 1. Deployment and recovery locations for light-level geolocators placed on male Golden-winged Warblers at 9 sites in the linked Central America–Great Lakes population and analyzed in this study, with season and year of deployment.

Site	Latitude	Longitude	Year deployed	Season deployed [a]	Number deployed	Number analyzed
Cerro de La Muerte, Costa Rica	9.56	−83.79	2016	N	2	0
Monteverde, Costa Rica	10.26	−84.69	2016	N	20	1
Finca Esperanza Verde, Nicaragua	12.94	−85.78	2016	N	21	4
El Jaguar, Nicaragua	13.24	−86.05	2016	N	9	4
Catacamas, Honduras	13.78	−86.03	2016	N	27	5
Pico Pijol, Honduras	15.14	−87.44	2016	N	27	2
Sierra Caral, Guatemala	15.37	−88.67	2016	N	20	4
Mountain Pine Ridge, Belize	16.95	−88.82	2016	N	2	0
El Jaguar, Nicaragua [b]	13.24	−86.05	2015	N	NA	6
Rice Lake, Minnesota [c]	46.5	−93.33	2014	B	NA	3
Rice Lake, Minnesota [c]	46.5	−93.33	2013	B	NA	8

[a] N = nonbreeding (November–March), B = breeding (May–July).
[b] Data from Larkin et al. (2017).
[c] Data from Kramer et al. (2016).

one geolocator that was part of the Rice Lake dataset (RL3) because light data were significantly distorted by mud caked on the light sensor (Kramer et al. 2016). For Nicaragua birds, we also acquired associated morphological data for all individuals that returned with a geolocator (Larkin et al. 2017). Our total sample therefore included 37 male Golden-winged Warblers, tagged at breeding or overwintering sites, and provided data across 3 spring and 4 fall migration seasons (Table 1).

Geolocator Analysis

We analyzed 37 geolocators carried by male Golden-winged Warblers, first unpacking data with BASTrack software and then refining position estimates in a Bayesian framework with package SGAT version 3.3.0 (Wotherspoon et al. 2016) in program R (R Core Team 2017). Our code directly followed the online tutorial available at http://scbi-migbirds.github.io/Geolocator_SGAT.html. All geolocators recorded light on the same arbitrary 0–64 scale. To create starting locations for the Bayesian models, we defined sunrise and sunset times using a threshold value of 1.25 on the arbitrary 0–64 light scale with the "preprocessLight" function in package SGAT. We did not alter any of the defined sunrise and sunset values as the modeling process corrects data outliers. For geolocators deployed at overwintering sites, we calculated average solar zenith and defined a log-normal density distribution of error in sunrise and sunset values between deployment and March 15, as Golden-winged Warblers are known to remain on winter territories until late March or early April (Rosenberg et al. 2016, Bennett et al. 2017). For 3 geolocators deployed after March 10, we extended the calibration period to April 1 after checking raw light data for evidence that no obvious migratory movement occurred before that date. For geolocators deployed on the breeding grounds in Minnesota, we calculated average solar zenith and a log-normal error distribution between deployment and June 25. The solar zenith angle recorded by a geolocator is known to vary among habitat types and life stages, which can have a profound effect on location estimates (McKinnon et al. 2013, 2015). We tested and accounted for changes in solar zenith throughout the year (described in Supplemental Material Methods).

We incorporated a behavioral model that assumes birds are usually stationary but capable of moving long distances during migration (gamma distribution with shape = 0.7 and scale = 0.08). We constrained locations around the spring and fall equinoxes with a spatial mask in ArcGIS 10.5 that was bounded by 7° latitude at the south, as all birds overwintered in Central America, and by a 250 km buffer above the northern edge of the Golden-winged Warbler breeding range, which we delineated with a polygon around the northern edge of all eBird.com records from the months of June and July over the past 10 yr. We did not constrain locations to occur over land, as land masks have been shown to bias the predicted location of birds that occur on islands or near large bodies of water (Cooper et al. 2017). Using these priors, we refined location estimates with the "estellemetropolis" algorithm in package SGAT. We ran 3 independent chains each with 50,000 iterations for burn-in and tuning, drew 5,000 iterations per chain for posterior analysis, and visually inspected convergence.

All mean locations and standard deviations were summarized from the 15,000 retained posterior iterations. Migration departure and arrival were defined as the date the mean location pathway moved out of with returning or into without leaving the 90th quantile of breeding and wintering locations, calculated with the "slice" function in SGAT. We calculated breeding location for each bird between the breeding grounds arrival date and June 25 and overwintering location between winter grounds arrival date and February 10 to avoid incorporating any latitudinal

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skew from the equinox or from light level changes during habitat shifts (Supplemental Material Methods). We defined landfall after trans-gulf migration as the date the mean pathway entered the continental United States along the Texas or Louisiana coastline during spring migration. Following Cooper et al. (2017), we defined stopover dates using package GEOLIGHT, a position change probability of 0.87, and stopover duration of 1 day, and summarized the mean location and standard deviation for the bird during those dates. Spring migration distance was measured as the shortest great circle distance connecting the breeding and wintering centroids and passing through each successive stopover location with package GEOSPHERE (Hijmans et al. 2017). Shortest great circle distance and direction (bearing along the rhumb line) between the mean wintering and breeding locations was also calculated with package GEOSPHERE. We defined prolonged refueling stopovers as any stopover lasting more than 2.5 days in order to decrease the probability of confusing "rest or roost" stops with stops where a bird is actively depositing fat to fuel subsequent migration (Bayly et al. 2018). We calculated movement speed as the average km/day traveled during unique movement periods defined by GEOLIGHT and calculated the average speed between migration departure, all prolonged refueling stops, and arrival on the breeding grounds. We note that this speed should be interpreted as a relative rather than exact speed, given the low precision of geolocator data and the influence of the position change probability value we selected in GEOLIGHT. Due to uncertainty in latitudinal positions around the fall equinox, we did not attempt to define specific stopover locations during the fall migration, calculate total distance traveled, or calculate the date at which birds crossed the Gulf of Mexico.

Statistical Analysis

We compared the relationships between all metrics of migratory timing including dates of spring departure, post–Gulf migration landfall, spring arrival, fall departure, fall arrival, duration of fall and spring migration, and the mean location of breeding and wintering areas with Pearson's correlations. We used a 2-sample *t*-test to determine if distance between overwinter centroid and mean Gulf Coast departure point (18.72°, −91.67°) differed for birds employing or foregoing a pre-Gulf stopover. To investigate the impact of wing chord on migration, we regressed wing chord against the shortest distance between breeding and wintering sites, total distance traveled in spring migration, duration of fall and spring migration, and average travel speed in spring migration. For all linear models, we calculated Cook's distance to identify points with disproportionate influence on the regression. For any points determined to be influential (using common cutoff of Cook's $D > 0.5$; Cook 1977), we removed the point to examine if its exclusion changed the trend or significance of the regression and reported statistics for the model with the point included and excluded (Aguinis 2013). We used 2-sample *t*-tests to determine if the distance between breeding and wintering sites, the departure, arrival, and landfall dates, the duration of fall and spring migration, and the average rate of spring migration differed significantly between age classes. We compared wing chord and age with a 2-sample *t*-test to ensure no interaction existed. To test for variation in behavior around a geographic barrier, we compared average travel speed, number of days spent at multi-day stopovers, and proportion of days moving vs. stopped before and after birds crossed the Gulf of Mexico using 2-sample *t*-tests. We also compared date of post-Gulf arrival with average post-Gulf travel speed to test if early migrators slow their migration in response to leaf-out phenology. Variance between groups was assessed with *F*-tests and determined not to differ significantly prior to conducting all *t*-tests.

RESULTS

All 37 Golden-winged Warblers overwintered in Central America and spent the breeding season in the western Great Lakes region, as expected for members of this linked population (Supplemental Material Figure S1 and Table S1). Distance and direction between individual overwintering and breeding centroids were normally distributed with a mean straight-line distance of 3,472 km (48 SE) and a mean direction of 351° (1 SE); average spring pathway was longer, however, at 4,093 km (60 SE). Breeding latitude and longitude did not correlate with overwintering latitude ($r = 0.29$, $P = 0.14$) or longitude ($r = 0.22$, $P = 0.29$), respectively. Of the 37 geolocators we analyzed, 35 recorded spring migration and 36 recorded fall migration. Individuals migrated south and crossed the Gulf of Mexico along a more easterly route in fall and migrated north along a more westerly route in spring (Supplemental Material Figure S2). All birds crossed the Gulf of Mexico during fall migration. In spring, 33 of 35 birds flew across the Gulf of Mexico, and 2 individuals migrated along the eastern Mexico coastline with mean pathways occurring near or over land.

Migration Duration, Timing, and Distance

Across years, birds spent 16–39 days (mean = 27, SE = 1) migrating north in spring, whereas fall migration took nearly twice as long (range: 30–78 days, mean = 48, SE = 2). For individual Golden-winged Warblers, neither spring and fall departure dates ($r = 0.20$, $P = 0.34$) nor durations ($r = 0.27$, $P = 0.19$) were correlated. Spring departure date was positively correlated with arrival date on the breeding grounds ($r = 0.56$, $P = 0.003$), but fall departure and arrival dates were not correlated ($r = 0.25$, $P = 0.22$). Number

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of days spent in spring migration was positively correlated with actual distance traveled (r = 0.52, P = 0.001), but neither number of days spent in spring (r = 0.20, P = 0.26) nor fall (r = −0.18, P = 0.30) migration was correlated with the shortest distance between breeding and wintering locations. Mean spring migration duration, departure date, Gulf landfall date, and arrival date were consistent among years (Table 2). Conversely, all metrics describing the timing of fall migration were highly variable among individuals and among years (Table 2).

Effect of Age and Morphology on Migration

Thirteen of the birds for which we had age data were second-year (SY) birds undertaking their first spring migration, and 13 were after second-year (ASY) birds that had already completed at least one annual migration. No variation occurred between age classes for spring departure date (t_{24} = 0.79, P = 0.44), post-gulf landfall date (t_{23} = 1.6, P = 0.12), or spring arrival date (t_{24} = 0.38, P = 0.71). We did not test for age differences during fall migration, as all individuals were ASY during the fall. Wing chord did not vary with age (F_{24} = 0.36, P = 0.55). Birds with longer wing chords spent more days in both spring migration and fall migration and occupied overwintering sites farther from breeding sites than shorter-winged birds (Figure 1). Note that the bird with a 65 mm wing chord was determined to be an influential data point in regression with great circle distance (Cook's D = 0.6), and its exclusion changed the significance level (presented in Figure 1). Neither wing chord (F_{24} = 0.24, P = 0.63) nor age (t_{24} = 0.62, P = 0.54) predicted average travel speed in spring migration.

Stopovers and Travel Speed

During spring migration, 83% of individuals (n = 29) stopped over at least once before crossing the Gulf of Mexico at an average of 682 km (234 SD) from their overwintering sites, primarily in the region encompassing Guatemala and the states of Campeche and Chiapas, Mexico (Figure 2A). Six individuals (17%) crossed the Gulf of Mexico without a prolonged stopover (Figure 2B), traveling an average of 1,983 km (595 SD) before making their first multi-day stopover. Individuals that did not stop over before crossing the Gulf completed spring migration significantly faster (mean 20.5 days, 1.5 SE) than birds that stopped over south of the Gulf of Mexico (mean 28.5 days, 1.0 SE; 2-sample t_{33} = 3.94, P < 0.001). All 6 individuals that migrated without a pre-Gulf stopover overwintered in the northern and western half of the nonbreeding range, significantly closer to the Gulf Coast (mean 468 km, 144 SD) than individuals that stopped over (mean 806 km, 142 SD, 2-sample t_{33} = 5.30, P < 0.001; Figure 2B). No birds that overwintered in eastern Honduras, Nicaragua, or Costa Rica crossed the Gulf of Mexico without a multi-day stopover (Figure 2A). After crossing or circumventing the Gulf, 27 birds (77%) employed one or more additional multi-day stopovers within the United States throughout the spring migration pathway (Figure 2 and Supplemental Material Figure S2), which is closely aligned with the Mississippi River Valley. Eight birds (23%) migrated from the northern Gulf coast to their breeding grounds without employing an additional multi-day stopover.

Stopover durations and migration speed differed before and after birds crossed the Gulf of Mexico in spring migration. Prior to crossing the Gulf, individuals spent almost twice as long at stopover sites (mean = 7.5 days, SE = 0.6, range: 3–15) and spent fewer days moving (mean days moving/stopped = 0.24, SE = 0.03) than after crossing the Gulf (mean = 4.2 days in stopover, SE = 0.2; t_{72} = 5.8, P < 0.001; mean days moving/stopped = 1.00, SE = 0.15; t_{71} = 5.6, P < 0.001; Figure 2). Daily movement speed also declined by 44% after birds crossed the Gulf of Mexico (t_{106} = 4.8, P < 0.001; Figure 2 and Supplemental Material Table S2). Finally, date of post-Gulf landfall had no relationship with the subsequent speed of migration (r = −0.01, P = 0.97).

TABLE 2. Differences in timing and duration of spring and fall migration among years for 37 male Golden-winged Warblers in the linked Central America–Great Lakes population.

Year	Departure date [a]	Trans-Gulf landfall date [a]	Arrival date [a]	Days spent migrating
Spring				
2014 (n = 9)	10 (6)	20 (4)	38 (4)	28 (8)
2015 (n = 8)	10 (5)	26 (4)	39 (6)	29 (4)
2016 (n = 20)	13 (6)	25 (6)	40 (5)	27 (5)
P	0.28	0.07	0.51	0.74
Fall				
2013 (n = 9)	27 (5)	NA	71 (7)	44 (6)
2014 (n = 2)	15 (21)	NA	79 (1)	64 (20)
2015 (n = 6)	13 (11)	NA	69 (6)	56 (11)
2016 (n = 20)	20 (6)	NA	66 (7)	46 (7)
P	0.007*		0.02*	0.004*

[a] Spring dates presented as the mean (SD) number of days after first spring departure date, April 7; Fall dates presented as the mean (SD) number of days after first fall departure date, August 16.
*P significant at <0.05 in a one-way ANOVA test for difference across years.

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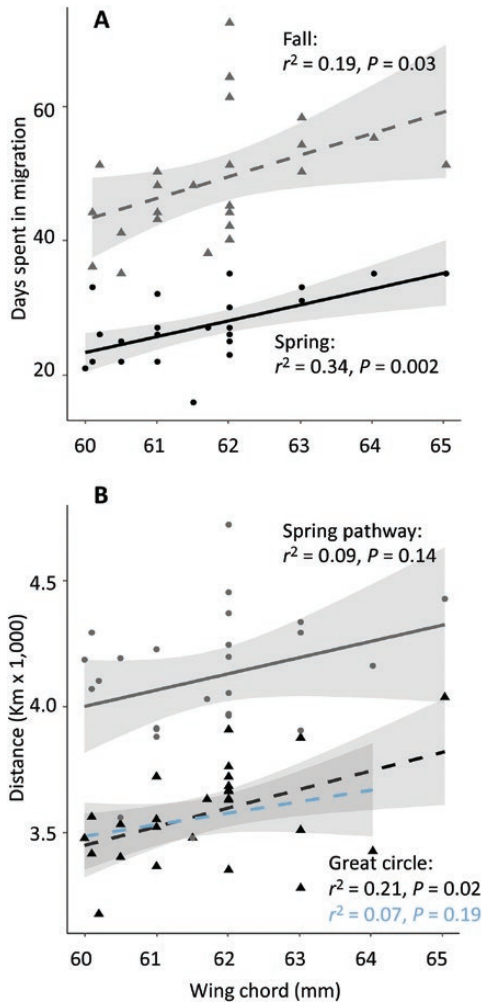

FIGURE 1. Linear regressions between wing chord and (**A**) number of days spent in fall migration (gray triangles, dashed line) and spring migration (black dots, solid line) and (**B**) distance traveled in spring migration (gray dots, solid line) and shortest great-circle distance between breeding and wintering sites (black triangles, dashed line). Data from 26 male Golden-winged Warblers tagged with light-level geolocators in Central America between January and March of 2015 and 2016. Blue regression line and statistics have influential point at 65 mm removed.

DISCUSSION

The seasonal patterns we observed are consistent with time-minimizing selection during spring and a relaxation of that pressure in fall. Across 3 spring migrations, the population departed Central America, landed on the northern Gulf coast, and arrived on the breeding grounds on approximately the same dates, despite individual variation in pathway and stopover behavior. The tight correlation between spring departure and arrival dates suggests that individuals traveled as fast as possible during that period (McWilliams et al. 2004) and matches expectations for a species under selection to arrive on the breeding grounds on an optimal date (Alerstam 2011). Fall migration conversely showed no consistency in timing between years, no relationship between arrival and departure date, and took nearly twice as long as spring migration. This suggests Golden-winged Warblers were under less pressure to establish overwinter territories on an optimal date and minimize time spent migrating in fall. While overwinter territory quality affects reproductive success in other warblers (e.g., Norris et al. 2004, Rushing et al. 2016), behavioral dominance rather than arrival timing mediates overwintering territory establishment in at least one warbler population (Marra 2000), which might lessen the pressure to arrive on an optimal date.

Within spring migration, movement behaviors varied before and after birds crossed the Gulf of Mexico. Movement speed, proportion of days spent at stopover, and stopover duration all decreased after birds crossed the Gulf. While migrants are known to have a flexible speed response to plant phenology and temperature (Marra et al. 2005, Kelly et al. 2016), we found no evidence that birds that crossed the Gulf of Mexico early in spring migration subsequently traveled at a slower speed than those that crossed at later dates. Rather, the change in travel speed and stopover use was consistent across dates and accompanied by a trend in a greater proportion of days spent moving rather than stopped, which suggests factors other than the progression of leaf-out drove this pattern. Individuals may spend less time at refueling stopovers in the United States because food resources generally become poorer or less reliable after crossing the Gulf, or because fuel reserves acquired at pre-Gulf stopovers are nearly sufficient to complete migration and only need to be topped up post-Gulf (e.g., Hedenström et al. 2007). Indeed, 8 individuals completed migration without any multi-day stopovers post-Gulf, indicating this is a possibility, although likely only for individuals in good condition that encountered stopovers with high food quality and availability (Bayly et al. 2018). However, data on fuel deposition rates and resource availability at stopovers will be necessary to discern between proximate mechanisms for this slowdown in migration speed.

Stopover behavior varied between individuals in spring migration with 2 major patterns emerging. Approximately 80% of individuals conducted at least one prolonged pre-Gulf stopover, while ~20% crossed the Gulf without a multi-day stopover and completed migration 8 days faster. Selection to minimize time spent in spring migration could favor individuals that are able to decrease total migration time by foregoing a pre-Gulf stopover. Only birds in the northern part of the overwinter range forewent a pre-Gulf stopover, thus time-minimizing selection could potentially drive a northward shift in the nonbreeding distribution that parallels the documented northward breeding range shift (Cristol et al. 1999, Rosenberg et al. 2016). It

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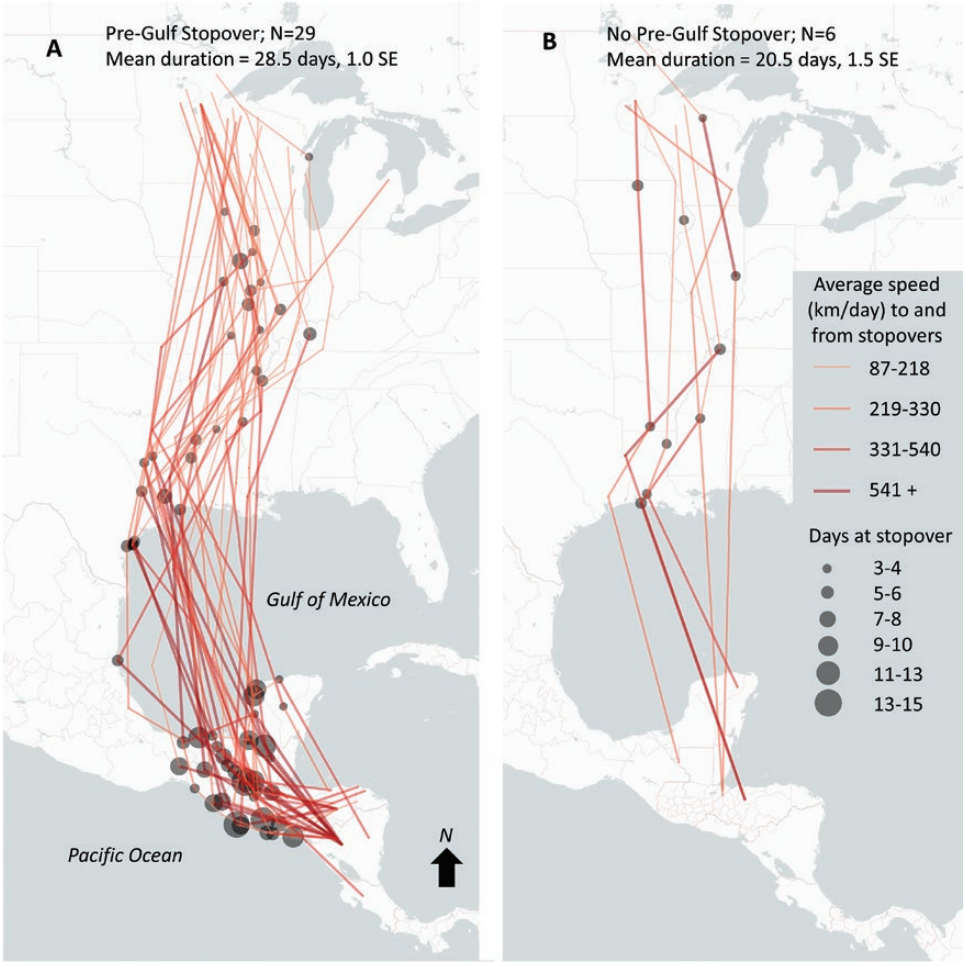

FIGURE 2. Stopover duration and average travel speed between stopovers in spring migration for 35 male Golden-winged Warblers that (**A**) conducted a multi-day stopover before crossing the Gulf of Mexico, or (**B**) forewent a pre-Gulf stopover and thereby spent significantly fewer days in migration. Across the population, travel speed and number of days spent at stopovers decreased significantly after birds crossed the Gulf of Mexico. Lines terminate at breeding and wintering locations and pass through all prolonged stopovers (dot radius indicates days stopped) and short stopover (1–2 days; no dot). Travel speed (km day^{-1} when bird is moving) is averaged for periods between migration departure, each subsequent stopover site, and breeding grounds arrival. Mean (SD) stopover locations reported in Supplemental Material Table S2. Data from light-level geolocators deployed from 2013 to 2016 at 9 sites in Central America and Minnesota.

is necessary to point out that our models were unlikely to detect changes in fueling behavior before the first migratory flights or short movements away from overwintering territories (e.g., only stopovers >200 km apart detected; see Supplemental Material Table S2). Time spent fueling before the first migratory flight is an important component of migration (Lindstrom et al. 2019) and may differ between individuals or groups. Indeed, evidence from Northern Wheatears (*Oenanthe oenanthe*) shows fuel loads amassed before the first migratory flight varied among individuals such that some individuals departed with insufficient fuel to cross a geographic barrier, thereby necessitating a refueling stop, while other individuals departed with sufficient reserves to cross the barrier (Delingat et al. 2008). It is possible the 6 Golden-winged Warblers that forewent a pre-Gulf stopover amassed greater fuel reserves before their first flight than the individuals that conducted a prolonged pre-Gulf stopover. However, future research on fueling rates will be necessary to determine if distance between overwintering territory and the Gulf of Mexico impacts fueling decisions before the first migratory flight. We also considered if stopover locations were masked by geolocator uncertainty for birds closer to the Gulf Coast. However, 5 of the 6 individuals that did not stop over had winter capture locations or mean estimated locations >450 km from the Gulf Coast, which is within one standard deviation of the mean distance at which we detected pre-Gulf stopovers. We have no reason to believe geolocator precision differed between birds that did or did not stop over before crossing the Gulf of Mexico, making us equally likely

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to overlook short movement for both groups. We therefore conclude there is a real difference in pre-Gulf stopover behavior that is correlated with proximity between overwintering territories and the Gulf coast.

Our data indicate some annual variation in the dates on which Golden-winged Warblers crossed the Gulf of Mexico, despite high year-to-year consistency in spring departure and arrival dates. Other migratory birds from Central America and the Caribbean are known to delay flights across the Gulf of Mexico by 2–3 days when spring conditions are dry (Cohen et al. 2015) or when weather conditions are unfavorable for sustained flight (Richardson 1990, Dossman et al. 2016). Anecdotally, we noticed extremely dry conditions in the springs of both 2015 and 2016 related to the El Niño phenomenon, and in both years Golden-winged Warblers crossed the Gulf on average later than in 2014. Low seasonal rainfall and declines in rainfall at the end of the winter season affect both departure date and annual survival of insectivorous migratory warblers (Faaborg et al. 1984, Studds and Marra 2011, Rockwell et al. 2017), and migrants are known to make landfall with extremely depleted fat and muscle reserves after crossing the Gulf of Mexico in El Niño years (Paxton et al. 2014). Thus, weather conditions likely contributed to this variation in timing of migratory flights across the Gulf during spring migration.

While migratory behavior is known to vary among age classes for some Neotropical migrants, we found no evidence that SY and ASY individuals differed in migration patterns. This was surprising as SY males are often subordinate to ASY birds (Piper 1997) and thus more likely to occupy suboptimal overwinter habitats and migrate later, as in American Redstart (*Setophaga ruticilla*; Marra 2000, Studds and Marra 2005). Our findings similarly contrast with migration patterns of Wood Thrush (*Hylocichla mustelina*), Ovenbird (*Seiurus aurocapilla*), and American Redstart, in which SY individuals cross the Gulf of Mexico later than ASY birds that have already completed at least one full migration (McKinnon et al. 2014, Cohen et al. 2018). Our results suggest that age class does not affect migration strategy and timing consistently across Neotropical migratory species. A possible explanation is that Golden-winged Warblers are unusual among migratory warblers in that HY birds obtain adult plumage prior to fall migration (Pyle et al. 1987) and thus resemble ASY birds when they arrive at the nonbreeding range. The apparent lack of an age-related plumage signal may mediate aggressive territorial encounters and dilute carryover effects both during overwintering and migratory periods (Rohwer 1975, Balph et al. 1979, Marra 2000). However, subtle plumage or behavioral differences between age classes may be detectable to individuals of the species despite not being readily apparent to human observers. Future research into interspecific variation in migratory strategies may help elucidate under what circumstances or in which taxonomic groups age class impacts migratory timing.

The strong relationship we found between male Golden-winged Warbler wing chord and migration duration and distance is surprising, given that we detected relatively little variation across the population in total migration distance and decision to cross the Gulf of Mexico. Studies of other migratory passerines demonstrate relationships between wing morphology and migratory behaviors among rather than within populations. Typically, populations that migrate longer distances or cross larger geographic barriers have longer and/or more pointed wings than more sedentary populations (Fitzpatrick 1998, Pérez-Tris and Tellería 2001, Arizaga et al. 2006, Provinciato et al. 2018). Long, pointed wings generally correspond to greater energy efficiency in long-distance flights (Norberg 1995, Pennycuick 2008), and long distance migrants accordingly experience selective pressures that favor aerodynamic wing shapes over wings with greater maneuverability (Pennycuick 2008, Corman et al. 2014). Our study makes a unique contribution by describing a relationship between wing chord and migration distance and duration within a linked population rather than between populations that differ in migratory pathway and distance. Indeed, wing chord was the only predictor we encountered for total distance between breeding and overwintering sites, which suggests the range of possible migration distances in this population depends on intraspecific variation in wing length. We offer 2 possible explanations for this pattern: longer-winged individuals had an aerodynamic advantage that allowed them to travel greater absolute distances (albeit over longer amounts of time), or longer wing chord indicated larger overall body size, which is known to decrease flight speed (Hedenström and Alerstam 1998) and could explain longer migration times. Although we cannot differentiate between these explanations with our data, we know of no other study that demonstrates a fine-scale relationship between wing length and migration distance and duration within a linked migratory population (but see Peiró 2003). It is necessary to point out that our sample was composed entirely of males, which have longer wings than females (Pyle et al. 1987) and likely face greater pressure to arrive early on the breeding grounds (Cristol et al. 1999, Dierschke et al. 2005). Future research should seek to establish the relationship between morphology (with more detailed wing morphometric data that accounts for wing loading, aspect ratio, and wing tip shape; e.g., Corman et al. 2014) and migratory distance for both males and females once tracking technologies are small enough to be supported by them.

Golden-winged Warblers are experiencing range-wide population declines (Rosenberg et al. 2016), as are many species of long-distance migratory birds across the globe

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(Sanderson et al. 2006, Sauer et al. 2017). Given the high mortality incurred by many migratory birds during spring migration (Sillett and Holmes 2002, Rushing et al. 2017, Rockwell et al. 2017), it is important to consider how migration patterns and strategies may impact the long-term conservation of these species. As our results match predictions for time-minimizing selection in spring, that period is likely more energetically costly and exposes migrants to greater risk from starvation and predation (Alerstam 2011). Fall migrants, in contrast, may have greater flexibility to minimize energy costs and avoid risks (Hedenström and Alerstam 1997, Alerstam 2011). Multi-day refueling stopovers are understood to be a critical factor in successful migration for long-distance migrants of multiple taxa (Alerstam and Lindström 1990, Taylor et al. 2011, McGuire et al. 2012, Gomez et al. 2017), yet conservation efforts are just beginning to effectively identify and prioritize these sites for migratory birds (Bayly et al. 2018, Tonra et al. 2019). The stopover region we identified between Guatemala and southern Mexico is likely of high importance to this population, as it was utilized by more than 80% of individuals and presumably provided the fuel reserves necessary to cross the only major geographic barrier in the migration pathway. In contrast, specific stopover regions within the United States may be of lower importance to Golden-winged Warblers, given that birds stopped over across a wider geographic area and spent fewer days at any particular site. Unfortunately, geolocators do not have the precision to identify specific sites or habitats used by the species within the migration pathway. On-the-ground research within the region will be necessary to understand migratory resource requirements, energetic constraints, and stopover habitat quality (Bayly et al. 2018). As land-use change is occurring rapidly within the Central America/Mexico stopover region we identified in this study (Hansen et al. 2013), it will be critical to describe and assess the quality of migratory stopover habitats to refine conservation strategies for the Golden-winged Warbler (Bennett et al. 2016) and other declining migratory birds.

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Ethics statement: Fieldwork followed all guidelines in Cornell IACUC permit #2013–029 and was conducted under the following national permits: Belize Forest Department No. 14/2000, Guatemala CONAP No. 2016–115096, Honduras ICF DE-MP-052-2016, Nicaragua MARENA DGPN/DB–IC–023–2016, and Costa Rica ACOPAC-INV-RES-010-15.

Author contributions: REB, ADR, KVR, and JL conceived the ideas and designed methodology. REB, RC, LCD, JG, DIK, and JL collected data. REB analyzed the data and led the writing of the manuscript.

Data depository: Data deposited in OSF data repository: https://osf.io/cek45/ doi:10.17605/OSF.IO/CEK45

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