



RESEARCH ARTICLE

Nonbreeding isolation and population-specific migration patterns among three populations of Golden-winged Warblers

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ABSTRACT

Golden-winged Warblers (*Vermivora chrysoptera*) are Nearctic–Neotropical migrants experiencing varied regional population trends not fully explained by breeding-grounds factors such as nest success. A lack of detailed information on the nonbreeding distributions, migration routes, or timing of migration among populations hampers our ability to identify population processes outside the breeding period. We used geolocators to track annual movements of 21 Golden-winged Warblers from 3 North American breeding locations experiencing varying population trends to investigate the potential for nonbreeding site factors to influence breeding populations. We used the template-fit method to estimate locations of individual warblers throughout the year. Geocator-marked warblers exhibited significant isolation among populations during migration and the nonbreeding period. During the nonbreeding period, Golden-winged Warblers from Minnesota, USA ($n = 12$) occurred in Central America from southern Mexico to central Nicaragua; warblers from Tennessee, USA ($n = 7$) occurred along the border of northern Colombia and Venezuela; and warblers from Pennsylvania, USA ($n = 2$) occurred in north-central Venezuela. Warblers travelled at slower rates over more days in fall migration than spring migration. Fall migration routes at the Gulf of Mexico were population-specific, whereas spring routes were more varied and overlapped among populations. Golden-winged Warblers from Pennsylvania migrated 4,000 and 5,000 km yr⁻¹ farther than Tennessee and Minnesota warblers, respectively, and spent almost twice as long migrating in the fall compared to Minnesota warblers. Our results reveal nearly complete temporal and geographic isolation among 3 populations of Golden-winged Warblers throughout the annual cycle, resulting in opportunities for population- and site-specific factors to differentially influence populations outside the breeding period. Our findings highlight the need for monitoring multiple populations of migratory species to understand and better inform conservation strategies.

Keywords: geolocators, isolation, migration, nonbreeding period, template-fit method, *Vermivora chrysoptera*

Aislamiento durante el período no reproductivo y patrones migratorios específicos entre tres poblaciones de *Vermivora chrysoptera*

RESUMEN

Vermivora chrysoptera es una especie migrante Neártica–Neotropical que está experimentando tendencias poblacionales diferentes a nivel regional, las cuales no se explican acabadamente por factores propios de los sitios reproductivos, como el éxito reproductivo. La falta de información detallada de las distribuciones no reproductivas, de las rutas migratorias o de las fechas de migración entre las poblaciones dificulta nuestra habilidad para identificar los procesos poblacionales por fuera del período reproductivo. Utilizando geo-localizadores para seguir los movimientos anuales de 21 individuos de *V. chrysoptera* provenientes de tres localidades reproductivas de América del Norte que están experimentando diferentes tendencias poblacionales, investigamos el potencial de los factores de los sitios no reproductivos de influenciar las poblaciones reproductivas. Empleamos el método de ajuste de plantilla para estimar las localizaciones de los individuos a lo largo del año. Los individuos marcados con geo-localizadores mostraron un aislamiento significativo entre las poblaciones durante la migración y el período no reproductivo. Durante el período no reproductivo, los individuos de *V. chrysoptera* provenientes de Minnesota, EEUU ($n = 12$) estuvieron presentes en

América Central desde el sur de México hasta el centro de Nicaragua; los individuos provenientes de Tennessee, EEUU ($n = 7$) estuvieron presentes a lo largo de la frontera del norte de Colombia y Venezuela; y los individuos provenientes de Pennsylvania, EEUU ($n = 2$) estuvieron presentes en el norte-centro de Venezuela. Durante la migración de otoño, las aves viajaron a tasas más lentas y por más días que durante la migración de primavera. Las rutas migratorias de otoño del Golfo de México fueron específicas de cada población, mientras que las rutas de primavera fueron más variadas y se superpusieron entre poblaciones. Los individuos de Pennsylvania migraron entre 4,000 y 5,000 km año⁻¹ más lejos que los de Tennessee y Minnesota y gastaron casi el doble migrando en el otoño comparado con los individuos de Minnesota. Nuestros resultados revelan un aislamiento temporal y geográfico casi completo entre las tres poblaciones de *V. chrysoptera* a lo largo del ciclo anual, lo que permite la existencia de factores específicos de las poblaciones y de los sitios que puedan influenciar diferencialmente a las poblaciones por fuera del período reproductivo. Nuestros resultados resaltan la necesidad de monitoreo de múltiples poblaciones de especies migratorias para entender y mejorar las estrategias de conservación.

Palabras clave: aislamiento, geo-localizadores, método de ajuste de plantilla, migración, período no reproductivo, *Vermivora chrysoptera*

INTRODUCTION

Conserving and managing migratory species is inherently complicated due largely to their reliance on multiple landscapes at different stages of their annual cycle. The combination and degree to which each life stage (e.g., nascence through independence from adult care), geographical location (e.g., a large estuarine stopover site), or portion of the annual cycle (e.g., the nonbreeding period) influence a population is often unknown; thus, resulting conservation strategies are often built with information representing a limited portion of a migratory species' annual range (e.g., Roth et al. 2012). This trend is concerning as recent studies demonstrate the influence of poorly studied life stages (e.g., the post-fledging period; Cohen and Lindell 2004, Streby and Andersen 2011) and carryover effects (e.g., habitat quality and food availability influencing subsequent productivity; Norris et al. 2004, Legagneux et al. 2012) on population dynamics of migratory species. Previous research suggests that, like other migratory taxa, global populations of many migratory birds are declining at alarming rates (Robbins et al. 1989, Sauer et al. 1996, Sanderson et al. 2006), presenting an important and time-sensitive opportunity to develop full life-cycle conservation and management plans and identify and mitigate key factors driving population declines.

The value of identifying migration routes, nonbreeding sites, and habitats used by migratory birds outside of the breeding period is not a new frontier in ornithology (e.g., Lincoln 1921, Hanson and Smith 1950), but one that is only recently being considered across taxa beyond waterfowl and shorebirds. The recent increase in efforts to develop informed, full life-cycle management and conservation plans is likely explained by technological advances that allow for tracking and monitoring most migrant bird species throughout the annual cycle (Webster et al. 2002, Holmes 2007, Stutchbury et al. 2009, Faaborg et al. 2010, Streby et al. 2015b). These technologies provide

avenues to identify nonbreeding sites, migratory pathways and connectivity, and population overlap away from the breeding grounds with finer spatial and temporal resolution than previously attainable using other methods (e.g., stable isotope analysis and/or band recoveries; Dunn et al. 2006, Macdonald et al. 2012, Hobson et al. 2016), though tradeoffs exist among available methods.

The Golden-winged Warbler (*Vermivora chrysoptera*) is a small (~9 g) Nearctic–Neotropical migrant currently experiencing one of the most dramatic declines of any North American songbird (Buehler et al. 2007). Trajectories for breeding populations of Golden-winged Warbler vary by region with sustained severe declines in southern Appalachian states such as Tennessee, USA (–7.88% annually from 1966 to 2013, 95% CI [–11.62, –4.70]), severe and recently accelerating declines in northern Appalachian states such as Pennsylvania, USA (–7.08% annually from 1966 to 2003, 95% CI [–9.1, –4.78]; –8.36% annually from 2003 to 2013, 95% CI [–15.27, –2.15]), and stable trends for populations in western Great Lakes states such as Minnesota, USA (0.81% annually from 1966 to 2013, 95% CI [–0.52, 2.18]; Sauer et al. 2014). Most studies attribute these declines to breeding-grounds factors; namely, the loss or lack of available nesting habitat and low productivity (i.e. nest success) often in combination with competition and the effects of hybridization with a closely related sister species, the Blue-winged Warbler (*Vermivora cyanoptera*; Gill 1980, 1997, Confer and Knapp 1981, Buehler et al. 2007, Bulluck and Buehler 2008, Confer et al. 2010). Despite extensive prior research on the breeding grounds, including recent genomics work suggesting Golden- and Blue-winged warblers comprise a single, polymorphic species (Toews et al. 2016), there is no consistent evidence that any single factor, or combination of factors, from the breeding grounds provides a complete and parsimonious explanation for the differential population trends observed in this species across its breeding distribution (Confer and Knapp 1981, Klaus and Buehler 2001, Gill 2004, Vallender et al. 2007, Bulluck et al. 2013).

Because breeding-grounds factors fail to fully explain the variation in local and regional population trends throughout the breeding distribution, it is logical that these trends may be linked to factors outside the breeding period along migration routes, at nonbreeding sites, or both. Little is known about the Golden-winged Warbler away from North American breeding sites (Chandler and King 2011, Bennett 2012, Chandler et al. 2016) and, although the distribution of Golden-winged Warbler at sites outside the breeding period is approximately delineated, no detailed information exists on the assortment and distribution of breeding populations away from the breeding grounds (Buehler et al. 2007). Recent evidence from the stable isotope analysis of feathers collected from Golden-winged Warblers at nonbreeding sites indicates nonbreeding warblers sampled during migration in South America likely breed in the Appalachian region and nonbreeding warblers sampled in Central America likely breed at more northern latitudes in the Great Lakes region; however, these data suggest possible population overlap as some Central American warblers sampled in Honduras may have Appalachian breeding origins (Hobson et al. 2016). The extent to which Golden-winged Warbler breeding populations segregate on nonbreeding sites, use different migratory pathways, or use the same pathways but at different times of the year (or any combination of the above), affects the likelihood of site-specific factors (e.g., land-cover change, chemical exposure) to influence populations independently of each other and contribute to the trends observed in regional populations on the breeding grounds.

Here we identify migration routes and connectivity, nonbreeding sites, and distribution of breeding populations away from the breeding grounds in 3 breeding populations of Golden-winged Warblers. We were particularly interested in quantifying nonbreeding overlap among breeding populations. Based on available information, we predicted Appalachian breeding populations (i.e. Tennessee and Pennsylvania) winter in South America, and Great Lakes populations winter in Central America during the nonbreeding period (Hobson et al. 2016).

METHODS

Study Area and Field Methods

We attached 84 geolocators (model ML6240, 2-min light-sampling regime; 0.40 g stalkless and 0.47 g with 5-mm light-stalk; Biotrak, Wareham, UK; see Streby et al. [2015b] for detailed attachment methods and Peterson et al. [2015] for discussion of geocator effects) to adult male Golden-winged Warblers at 3 sites in the eastern USA during April–May of 2013 and 2014. We marked 43 individuals (2013: $n = 20$; 2014: $n = 23$) at Rice Lake National Wildlife Refuge, Aitkin County, Minnesota (hereafter Rice Lake;

46.58°N, 93.38°W), 21 individuals (2013: $n = 20$; 2014: $n = 1$) at North Cumberland Wildlife Management Area, Campbell County, Tennessee (hereafter Cumberland Mountains; 36.28°N, 84.28°W), and 20 individuals (2014: $n = 20$) at Delaware State Forest, Monroe County, Pennsylvania (hereafter Delaware Forest; 41.38°N, 75.18°W). We marked all warblers within ~15 km of one another at each site.

We captured territorial male Golden-winged Warblers in mist nets using broadcasts of conspecific and congeneric songs and calls. We observed Blue-winged Warblers and phenotypic hybrids at or near all of our sites but only marked phenotypically pure Golden-winged Warblers, although it is possible that some birds were cryptic hybrids (Vallender et al. 2007). We banded each geocator-marked individual with a standard U.S. Geological Survey band and 1–3 plastic color bands. In 2014 and 2015 we systematically and opportunistically searched for returning geocator-marked Golden-winged Warblers within 500 m of their original capture location (see Peterson et al. [2015] for details on recapture methods and analysis of geocator effects). At Rice Lake we expanded our 2015 search radius to 2.5 km after forest management caused abandonment by Golden-winged Warblers of our primary study area and an outward redistribution of birds.

Sites in the Cumberland Mountains were composed of mixed hardwood forests at an average elevation of 780 m; some sites were managed for timber production and others were reclaimed mountaintop-mining sites (Bulluck and Buehler 2008). Rice Lake is in east-central Minnesota in the northern hardwood forest transition zone at an average elevation of ~350 m. Land cover consisted of a mosaic of upland and wetland forest, shrubland, and grassland surrounded by small amounts of agriculture (Ford et al. 2007). Delaware Forest is in Pennsylvania on the Pocono Plateau and land cover was composed of forested hills and valleys with swamps and peat bogs at an average elevation of ~300 m (Bakermans et al. 2015). Rice Lake is ~1,300 km north-northwest of the Cumberland Mountain site and ~1,600 km northwest of the Delaware Forest site. The Delaware Forest site is ~1,000 km northeast of our Cumberland Mountain site.

Statistical and Geocator Data Analysis

We extracted and unpacked data from recovered geolocators using BASTrak software (Biotrak, Wareham, UK). We performed subsequent geocator data analysis in R (v. 3.3.0; R Core Team 2016). We used the BASTag package (Wotherspoon et al. 2013) to automatically identify transition periods (i.e. sunrises and sunsets) using a light threshold value of 2. We calibrated our data in FLIGHTR (v. 0.3.6; Rakhimberdiev and Saveliev 2015) using transitions recorded for geocator-marked warblers known to be on breeding sites (i.e. 1–2 days following deployment

through July 1 of the deployment year, and from the date of first resighting to the date of recovery in the following spring). We used FLIGHTR to estimate the spatial likelihood of occurrence for all twilights using the template-fit method (Ekstrom 2004, Rakhimberdiev et al. 2015). We chose a program using the template-fit method over the more commonly employed threshold method (Hill and Braun 2001) because it has been demonstrated to be more accurate and less sensitive to potential shading error than currently available threshold models (Ekstrom 2007, Rakhimberdiev et al. 2016). The template-fit method of light-level analysis also provides an inherent estimate of uncertainty with each location estimate unlike the threshold method (Ekstrom 2007).

FLIGHTR estimates the tracks of migratory animals equipped with geolocators by combining 2 component models: (1) a physical model that estimates the geographic location of the geocator on the globe for each transition (i.e. sunrise or sunset) using light data analyzed with the template-fit method, and (2) a movement model employing a hidden Markov chain model constrained by predetermined spatial and behavioral masks (Rakhimberdiev et al. 2015). We used the physical, template-fit model in FLIGHTR with a land mask to estimate location likelihoods for each transition but did not use the movement model to link location estimates together because FLIGHTR failed to estimate biologically reasonable migration tracks using our data (e.g., location tracks never approached South or Central America, warblers apparently began migrating while they were known to be on the breeding grounds, warblers constantly changed locations throughout the breeding and nonbreeding period; G.R. Kramer, personal observation, E. Rakhimberdiev, personal communication).

We used FLIGHTR to create likelihood surfaces for each transition throughout the year. We multiplied the likelihood surface derived from an individual transition by the likelihood surfaces of the 5 subsequent transitions to produce a joint likelihood surface reflecting the most likely location of the geocator at the third transition (i.e. the approximate midpoint) of the 6-transition product string. The joint likelihood surface for any given transition is therefore informed by the 2 preceding, and 3 subsequent, transitions and has a pixel size $\sim 0.5^\circ$. Multiplying likelihood surfaces together is necessary to achieve location estimates because a likelihood surface derived from a single sunrise or sunset is curvilinear and does not provide enough information to estimate a location by itself (Rakhimberdiev et al. 2015). Likelihood surfaces estimated from single transitions produce swaths of likelihoods across the hemisphere at nearly perpendicular angles depending on whether the transition is a sunrise or a sunset, thus necessitating the multiplication of multiple likelihood surfaces to identify areas with the

highest likelihood of occurrence during both sunrise and sunset.

We assumed geocator-marked warblers did not move between these 6-transition periods (i.e. 3 sets of consecutive sunrises and sunsets), though there are likely times that geocator-marked birds in our study spent < 3 days at a particular site. We chose a 6-transition window to balance the smoothing effect of multiplying likelihood surfaces together with a relatively short period to identify movements. The lack of certainty around any particular point is reflected in the overall probability of occurrence over those 6 twilights; therefore, individuals that remained stationary during a particular period should produce location estimates with higher probabilities and smaller core areas of the highest probabilities than moving or migrating individuals. Notably, Golden-winged Warblers are primarily nocturnal migrants and therefore most likely to make long-distance migratory flights from sunset to sunrise (i.e. a maximum of 3 movements per 3-day, 6-transition, period). We transformed each joint likelihood surface into a utilization distribution (i.e. probability distribution function) by dividing the likelihood in each cell of a given joint likelihood surface by the sum of the likelihoods across all cells of the surface. This allowed us to directly compare utilization distributions between and among individuals and populations. We extracted the coordinates of the cell with the highest probability of utilization and assigned those coordinates and the associated probability to the third transition (i.e. sunrise or sunset) of the multiplication string used to calculate that utilization distribution. Following the extraction of coordinates and associated maximum probabilities for each transition in the dataset, we plotted the coordinates as points and reviewed them in QGIS (QGIS Development Team 2015). We averaged points when there was a location estimate from a sunrise transition and a sunset transition on the same date resulting in only one location estimate per date. If there was only one estimate for any given date (e.g., if one of the twilights was excluded as an outlier during processing in FLIGHTR), we used that estimate as the location point estimate.

Identification of Migration Routes

We treated our template-derived points as previous studies treated threshold-derived location estimates (e.g., Delmore et al. 2012). To delineate general fall migratory routes, we used points from July 2 to October 31 and deleted points arbitrarily north of the breeding site and > 150 km from land (i.e. outside the range of expected location error). We defined the onset of fall migration as the first point in a string of ≥ 5 that were $> \pm 1^\circ$ longitude from the breeding site (i.e. east or west) and > -3 to -5° latitude from the breeding site (i.e. south). Longitude estimates are highly accurate using the template-fit method whereas latitude

estimates are less accurate (Rakhimberdiev et al. 2016). We developed these criteria based on the ability of FLIGHTR to place geolocator-marked warblers at their breeding sites when they were known to be there and we adjusted these criteria depending on the characteristics of the individual geolocator (e.g., if estimates during the period of known location were consistently biased north or south). We relied primarily on longitudinal movements to identify the beginning of migratory periods as our method allows for a bird to travel straight south for about 300–500 km within a 100-km buffer east and west of the study site before being characterized as a migrant. For this reason, we acknowledge that our estimates of the onset of fall migration may be later than when warblers initiated migration. We marked the end of fall migration as the date an individual crossed an imaginary plane $\pm 1^\circ$ longitude and $\pm 4^\circ$ latitude from its estimated nonbreeding site (calculated below).

To delineate general spring migration routes, we selected points from March 1 to the end of a geolocator's tracking period and defined the onset of spring migration as the first point in a string of ≥ 5 consecutive points for which the longitude of the bird was $> 1^\circ$ west of its estimated nonbreeding site (calculated below). We marked breeding-site arrival as the first point in the spring period $< \pm 1^\circ$ longitude (i.e. east or west) from the study site and < -3 to -5° latitude (i.e. south) from the breeding site and confirmed breeding-site arrival with field observations (Peterson et al. 2015). We recreated spring and fall migratory pathways by linking single points, or clusters of points (i.e. > 2 consecutive points separated by < 150 km), together chronologically. We disregarded nonsensical, low-probability points at this stage, which were rare (i.e. usually < 5 points per bird per migration; for example, if an individual appeared to move back and forth across the Gulf of Mexico, we considered the first movement to be the true movement and assumed the bird did not traverse the Gulf of Mexico twice in 2 consecutive days). Migration routes are to be interpreted as general migratory trajectories and not as exact paths.

We investigated migration-route directness by dividing the great circle (i.e. direct) route distance directly linking an individual's breeding site to its estimated nonbreeding site by the distance travelled along generalized spring and fall migration routes. A perfect value of one would occur if an individual migrated along the great circle route from its breeding site to its nonbreeding site (and vice versa). Warblers deviating from a great circle route travel a greater distance than is required (assuming no physiological or physical barriers) and receive a lower, less efficient estimate of directness. We acknowledge that there are likely energetic advantages to not migrating along direct routes, so our estimates of directness are simply an aid to compare migration pathways among breeding populations. We characterized spring and fall migration routes as

crossing the Gulf of Mexico (i.e. overwater routes crossing the Gulf of Mexico directly in one flight), island hopping (i.e. routes with stopover sites associated with islands in the western Caribbean), or circumventing the Gulf of Mexico (i.e. primarily overland movements with stopovers along the eastern coast of Mexico). We tested for population-level differences in broad-scale migration-route characteristics using a Fisher's exact test.

Identifying Nonbreeding Sites of Warblers

We estimated the nonbreeding sites of individual warblers by deriving a utilization distribution for the entire period during which Golden-winged Warblers are resident in Central and northern South America. We multiplied each likelihood surface for transitions (i.e. sunrises and sunsets) spanning January 1–February 28 together and divided the likelihood in each cell in the resulting surface by the sum of likelihood across the entire surface to derive a utilization distribution representing the probability of residency during the nonbreeding period (Appendix Table 2). We selected these dates to avoid location-error issues known to occur in some cover types and species during the tropical wet season (McKinnon et al. 2013) and because Golden-winged Warblers defend a single territory between fall and spring migration (Chandler and King 2011).

We estimated the effective overlap between populations at nonbreeding sites by averaging nonbreeding utilization distributions for all warblers of a given population. The resulting utilization distribution represents the probability of a warbler from that population occupying any cell during the nonbreeding period. We then quantified overlap among populations during the nonbreeding period by multiplying their nonbreeding utilization distribution (as calculated, above) together. The sum of the product surface is the probability that sampled warblers from both populations occupied the same cells during the nonbreeding period. This process does not measure geographic or area overlap, but instead results in a statistical representation of overlap. The probability of an individual from a population occupying any given cell during the period January 1–February 28 is multiplied by the probability of an individual from a different population occupying the same cell over the same period providing a scaled estimate of overlap.

We produced a single point estimate for the nonbreeding site of each warbler by averaging the latitude and longitude of point estimates from November 1 to February 28 occurring within 250 km of the delineated nonbreeding range of Golden-winged Warblers (U.S. Geological Survey Gap Analysis Program) to limit the effect of outliers while allowing geolocator-marked warblers to occur outside their predetermined range (Appendix Table 3).

We evaluated differences between populations using one-way ANOVA and post-hoc Tukey HSD tests in R (R

Core Team 2016) unless noted otherwise. We used multiple linear regression to evaluate relationships between variables and used *t*-tests to determine if regression coefficients were significantly different from zero. Results of all tests were considered statistically significant at $\alpha = 0.05$. All means are presented \pm SD.

RESULTS

We recovered geolocators from 15 Golden-winged Warblers in 2014 ($n = 9$, Rice Lake; $n = 6$, Cumberland Mountains). Three of 15 (20%) geolocators recovered in 2014 at Rice Lake collected data for only a portion of the year. Two of these geolocators malfunctioned (one in January, one in February), and one functional geocator was recovered with mud caked on the light sensor and stopped recording reliable data in early November 2013. In all 3 cases, we recovered adequate data to estimate fall migration and nonbreeding sites; however, it was not possible to estimate initiation of spring migration or arrival at breeding areas from those geolocators. In 2015, we recaptured and recovered geolocators from 8 Golden-winged Warblers marked in 2014 ($n = 3$, Rice Lake; $n = 1$, Cumberland Mountains; $n = 4$, Delaware Forest). Two geolocators (50%) recovered at the Delaware Forest in 2015 malfunctioned and failed to record data after \sim 2 months following deployment, and we censored those units from all analyses. Consequently, we analyzed light-level data from 21 geolocators deployed on 20 individual Golden-winged Warblers (we recovered a geocator from an individual at Cumberland Mountains in both 2014 and 2015). Eighteen of 21 (86%) geolocators contained data for the full year whereas the remaining 3 geolocators (14%) contained data for fall migration and a portion of the nonbreeding period. We recovered fewer geolocators in 2015 than in 2014 due to vegetation management efforts resulting in cover-type changes that caused Golden-winged Warblers to occupy breeding territories outside of the core of our Rice Lake study site (G.R. Kramer, personal observation).

Nonbreeding Sites and Population Overlap

Golden-winged Warblers marked at Cumberland Mountains ($n = 7$) wintered in the border region of northern Colombia and Venezuela (Figure 1, Table 1). Warblers breeding at Rice Lake ($n = 12$) wintered at sites in Central America ranging from southern Mexico to south-central Nicaragua (Figure 1, Table 1) and were on average >200 km farther apart from each other than Cumberland Mountain warblers (397 ± 288 km vs. 166 ± 69 km, $n = 66$ and $n = 21$, respectively, one-way ANOVA, $F_{2,86} = 9.5$, $P = 0.001$). Golden-winged Warblers marked at Delaware Forest ($n = 2$) wintered at sites in Venezuela (Figure 1, Table 1). All 3 populations used areas during the

nonbreeding period at significantly different longitudes (Table 1, Figure 1) but latitude of these areas only differed between Rice Lake and both Delaware Forest and Cumberland Mountain populations ($P < 0.001$ for both comparisons, post hoc Tukey test; Table 1, Figure 1). The 3 breeding populations we marked exhibited no effective range overlap ($<0.01\%$ for all comparisons; Figure 1) during the nonbreeding period.

Migration Routes and Timing

The average fall departure date from the breeding grounds did not differ among the 3 breeding populations we marked (Table 1, Figure 2), although there were differences in characteristics of fall migration routes among these populations (Fisher's exact test, $P < 0.001$). All 12 (100%) Golden-winged Warblers migrating from Rice Lake traversed the Gulf of Mexico, whereas only 29% (2/7) of warblers from Cumberland Mountains and 0% (0/2) of warblers from Delaware Forest crossed the Gulf of Mexico during fall migration (Figure 3). Golden-winged Warblers migrating from Cumberland Mountains and Delaware Forest island hopped through the western Caribbean (5/7 [71%], Cumberland Mountains; 1/2 [50%], Delaware Forest) or circumvented the Gulf of Mexico to the west (0/7 [0%], Cumberland Mountains; 1/2 [50%], Delaware Forest; Figure 3). Golden-winged Warblers that crossed the Gulf of Mexico arrived at nonbreeding sites 19 ± 7 days earlier than warblers that island hopped, and 38 ± 7 days earlier than warblers circumnavigating the Gulf of Mexico, controlling for breeding population and fall departure date ($F_{3,17} = 17.2$, $P < 0.001$). Golden-winged Warblers from Delaware Forest migrated along routes $>2,000$ km longer than Rice Lake and Cumberland Mountain warblers during fall migration (Table 1, Figure 1).

Warblers from all 3 breeding populations migrated at similar average daily rates during fall migration (Table 1), regardless of migration route ($F_{3,17} = 0.5$, $P = 0.7$), but warblers that left their breeding sites later in the season migrated faster, with the average daily rate of migration increasing by 2.5 ± 0.4 km day⁻¹ for each day that a bird deferred the onset of fall migration (two-tailed *t*-test, $t_{16} = 5.8$, $P < 0.001$), controlling for breeding population and migration route ($F_{4,16} = 9.4$, $P < 0.001$). The duration of fall migration differed among the Golden-winged Warbler breeding populations we monitored with Delaware Forest warblers migrating over a longer period than Rice Lake warblers (Table 1, Figure 2). Rice Lake warblers arrived at nonbreeding sites one month earlier than warblers from Delaware Forest (Table 1, Figure 2) and also initiated spring migration 20 and 25 days after both Delaware Forest and Cumberland Mountain warblers, respectively (Table 1, Figure 2). As a result, Rice Lake warblers spent 20% and 29% more days at nonbreeding sites than

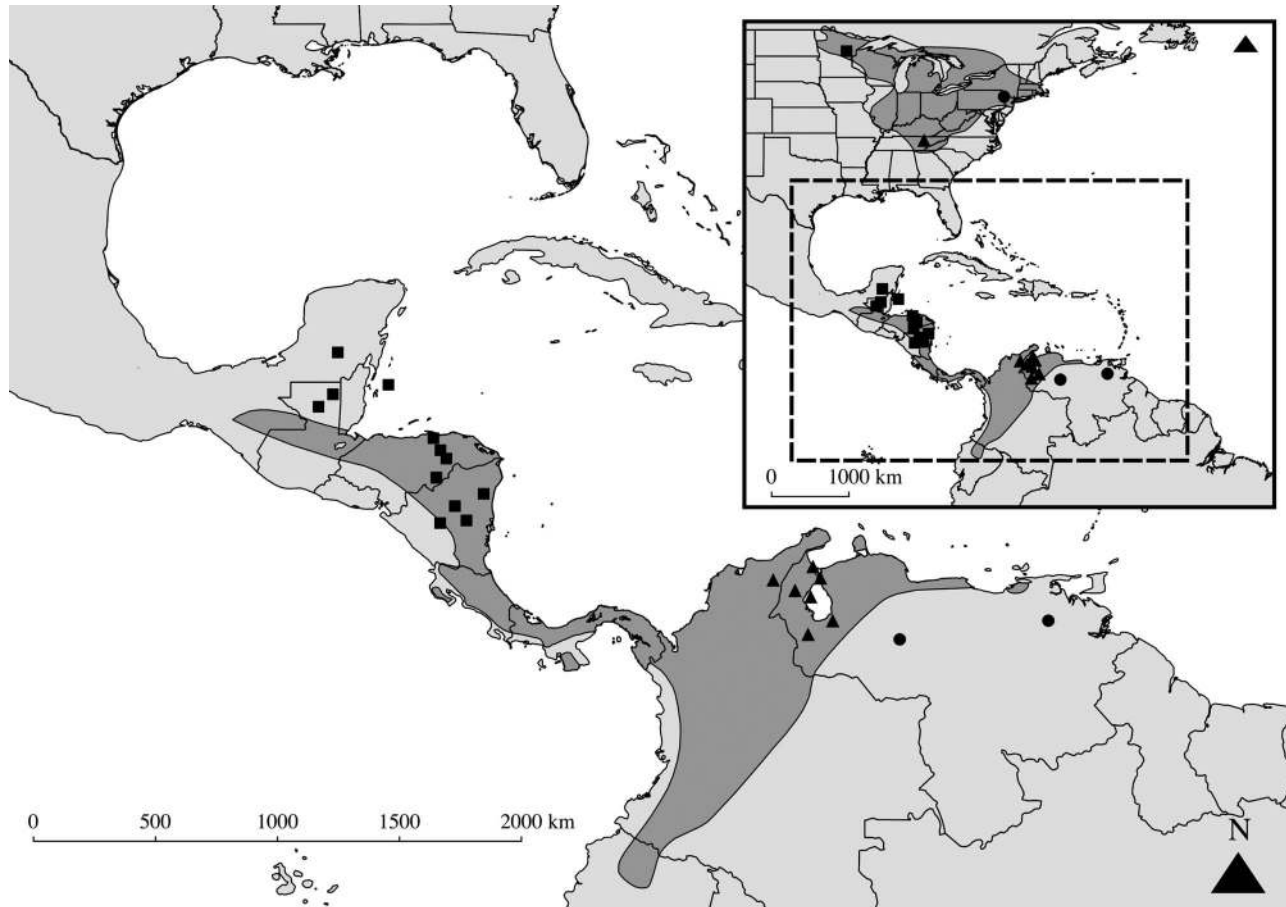


FIGURE 1. Estimated location during the nonbreeding period for 21 male Golden-winged Warblers from 3 breeding populations derived from light-level geolocators. Gray shading represents Golden-winged Warbler distribution. Inset shows breeding distribution and deployment/breeding sites. Squares ($n = 12$) represent Golden-winged Warblers breeding at Rice Lake National Wildlife Refuge, Minnesota, USA; triangles ($n = 7$) represent Golden-winged Warblers breeding at North Cumberland Wildlife Management Area, Tennessee, USA; and circles ($n = 2$) represent Golden-winged Warblers breeding at Delaware State Forest, Pennsylvania, USA. Range maps provided by U.S. Geological Survey Gap Analysis Program.

Cumberland Mountain and Delaware Forest warblers, respectively (Table 1, Figure 2).

Golden-winged Warblers from Cumberland Mountains arrived at their breeding areas 22 ± 4 days before Rice Lake warblers (Table 1). Date of onset of spring migration was not a significant predictor of arrival date on breeding areas after controlling for breeding population (two-tailed t -test, $t = 1.7$, $P = 0.11$). The duration of spring migration did not differ among the 3 breeding populations we monitored (Table 1, Figure 2) and showed no relationship to the type of route used to navigate the Gulf of Mexico (i.e. crossing, island hopping, or circumnavigating) when we controlled for breeding population effects ($F_{3,14} = 1.0$, $P = 0.41$); however, warblers that migrated longer distances did so at a faster rate ($\bar{x} = 0.03 \pm 0.01$ km day⁻¹ for each km travelled along their spring migration route, $t = 2.2$, $P = 0.04$) after controlling for breeding population effects. The type of route used by individual warblers to navigate the

Gulf of Mexico during fall migration did not predict the type of route used during spring migration when controlling for breeding population ($F_{3,17} = 1.3$, $P = 0.29$) and we found no evidence of population-level differences in the frequencies of routes used by individuals during spring migration (Fisher's exact test, $P = 0.14$). The Cumberland Mountains warbler with 2 years of tracking data took the same general route during both fall migrations (island hopping route) but used different routes each year during spring migration (circumnavigating route, spring 2014; crossing route, spring 2015).

We found no difference in the average daily rate of spring migration among breeding populations (Table 1). The date of onset of spring migration did not predict the daily average rate of migration in spring ($R = 0.14$, $F_{3,14} = 2.0$, $P = 0.17$) nor did the type of route used to navigate the Gulf of Mexico when controlling for breeding population ($F_{3,14} = 0.5$, $P = 0.70$). Spring-migrating Golden-winged

TABLE 1. Mean values (SD) of migration and nonbreeding period characteristics of Golden-winged Warblers from breeding populations in Minnesota (Rice Lake National Wildlife Refuge; RL), Tennessee (Cumberland Mountains; CM), and Pennsylvania (Delaware Forest; DF), USA, derived from geolocator data. *P* values are given for one-way ANOVA, and superscript letters indicate a significant difference between breeding populations for Tukey's HSD post hoc test using $P < 0.05$. See text for definitions of terms.

Nonbreeding-period factor	Population			<i>P</i>
	RL (<i>n</i> = 12)	CM (<i>n</i> = 7)	DF (<i>n</i> = 2)	
Nonbreeding-period longitude	84.41°W ^a (2.07)	71.95°W ^b (0.70)	65.82°W ^c (3.87)	<0.001
Nonbreeding-period latitude	15.31°N ^a (2.07)	8.71°N ^b (0.90)	9.99°N ^b (0.49)	<0.001
Migration factor				
Fall departure date	Jul 24 (8)	Jul 22 (10)	Jul 16 (2)	0.39
Fall migration termination date	Sep 21 ^a (14)	Oct 5 (20)	Oct 28 ^b (12)	0.02
Spring migration departure date	Apr 10 ^a (10)	Mar 16 ^b (3)	Mar 21 ^b (2)	<0.001
Breeding-site arrival date	May 16 ^{a,1} (6)	Apr 24 ^b (9)	May 6 (8)	<0.001
Fall migration duration (days)	59 ^a (20)	75 (28)	104 ^b (10)	0.03
Nonbreeding (resident) period duration (days)	200 ^a (20)	169 ^b (20)	143 ^b (14)	<0.001
Spring migration duration (days)	36 ¹ (8)	38 (8)	46 (6)	0.26
Fall migration distance (km)	4,144 ^b (369)	4,710 ^b (277)	6,748 ^a (1,808)	<0.001
Spring migration distance (km)	4,575 ^{b,1} (616)	5,228 ^b (513)	7,212 ^a (216)	<0.001
Total migration distance (km)	8,702 ^{a,1} (963)	9,938 ^b (604)	13,959 ^c (1,592)	<0.001
Fall migration average daily rate (km day ⁻¹)	76 (18)	73 (35)	64 (11)	0.83
Spring migration average daily rate (km day ⁻¹)	132 ¹ (12)	141 (40)	158 (15)	0.64
Fall migration-route directness	0.86 ^a (0.04)	0.68 ^b (0.04)	0.57 ^b (0.15)	<0.001
Spring migration-route directness	0.78 ^{a,1} (0.07)	0.61 ^b (0.06)	0.52 ^b (0.02)	<0.001
Great circle distance between breeding and nonbreeding period location (km)	3,552 ^b (263)	3,172 ^a (105)	3,742 ^b (40)	0.002

¹*n* = 9

Warblers from Delaware Forest took routes >2,600 km longer than warblers migrating to Rice Lake and >1,900 km longer than warblers migrating to Cumberland Mountains (Table 1, Figure 3). Golden-winged Warblers from Cumberland Mountains travelled farther than Rice Lake warblers during spring migration although this difference was not statistically significant (Table 1).

Migration-route directness varied among breeding populations during both fall and spring migrations (Table 1, Figure 3). Routes taken by Rice Lake warblers during spring migration were more direct than routes taken by warblers from Delaware Forest and Cumberland Mountains (Table 1, Figure 3). We found no differences in fall migration-route length compared to spring migration-route length when we controlled for breeding population effects (two-tailed *t*-test, $\bar{x} = -467 \pm 164$ km, $t_{14} = 1.2$, $P = 0.27$). Golden-winged Warblers travelled at an average daily rate 77% faster in the spring than during fall migration controlling for breeding population effects (two-tailed *t*-test, $\bar{x} = 0.77 \pm 0.29$, $t_{14} = 2.6$, $P = 0.008$; Table 1).

DISCUSSION

We provide evidence for extensive spatial and temporal isolation during migration and the nonbreeding period among 3 breeding populations of Golden-winged Warblers. Differences in migratory patterns and nonbreeding

distribution among these breeding populations suggest that factors outside the breeding period could differentially influence population trends. Golden-winged Warblers exhibited low migration-route diversity during fall migration, similar to migration patterns in Purple Martins (*Progne subis*; Fraser et al. (2013). Golden-winged Warbler breeding populations used a variety of routes to traverse or circumnavigate the Gulf of Mexico in the spring (Figure 3), similar to eastern and western Veeries (*Catharus fuscescens*) and Barn Swallows (*Hirundo rustica*) (Hecksher et al. 2011, Hobson and Kardynal 2015, Hobson et al. 2015) but unlike Red-eyed Vireos (*Vireo olivaceus*) in which fall migration routes were more variable than spring routes (Callo et al. 2013). Interestingly, Wood Thrushes (*Hylocichla mustelina*) tracked for multiple seasons showed individual annual variation in migration routes, especially during spring, suggesting that seasonal variation in routes may be related to a combination of individual experience, weather, and/or energetic condition during migration (Stanley et al. 2012). We did not detect any effect of route type on arrival time or rate of migration during both fall and spring suggesting that route-type selection may not influence an individual's migratory schedule and such decisions may result from exogenous influences (e.g., weather). Higher variation in spring migration routes may also be explained by the shorter duration of spring vs. fall migration periods. In fall, migrating warblers may have more flexibility to wait for favorable conditions to

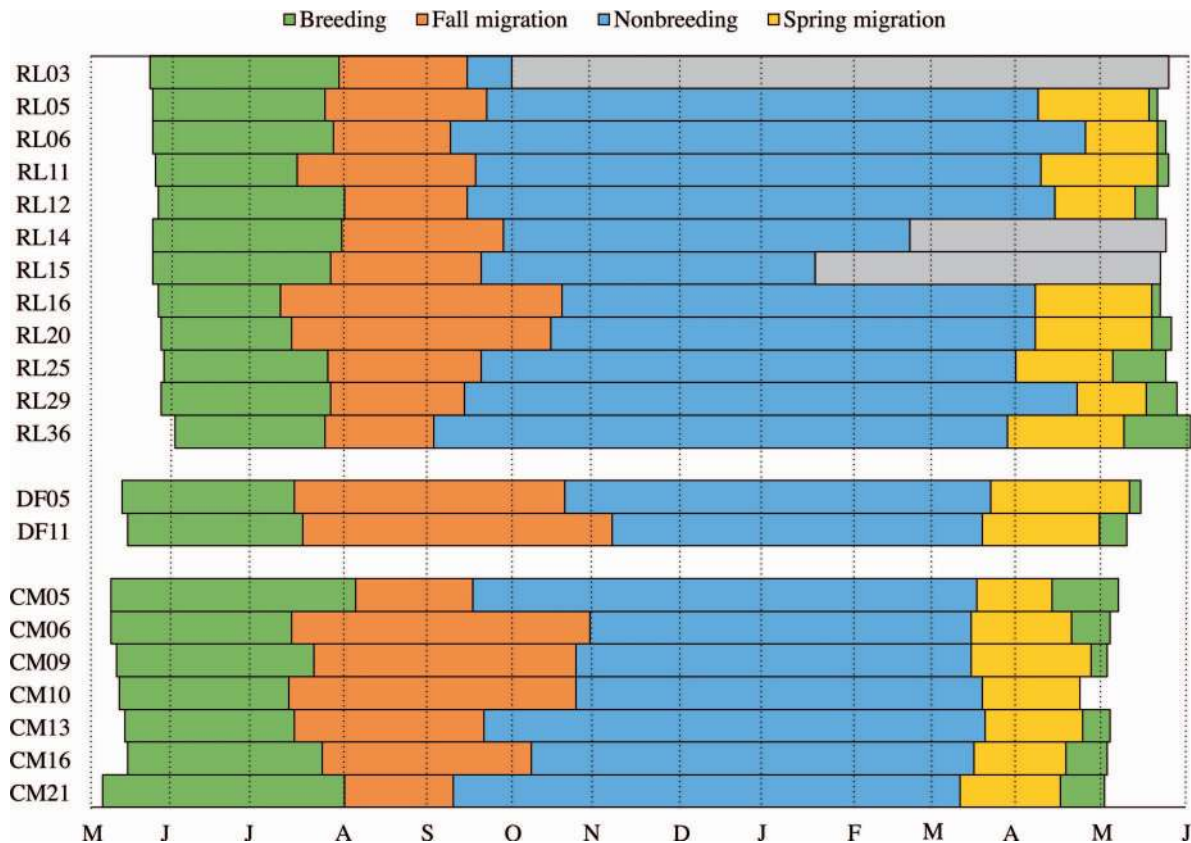


FIGURE 2. Estimated annual schedules ($n = 21$) by month for individual male Golden-winged Warblers ($n = 20$; CM13 and CM21 are the same individual marked in consecutive years) marked with geolocators at 3 breeding sites during 2013–2015. The color of each segment of a horizontal bar represents the status of an individual Golden-winged Warbler from geolocator deployment through recovery for warblers marked at Rice Lake National Wildlife Refuge, Minnesota, USA ($n = 12$; labeled “RL”), Delaware Forest, Pennsylvania, USA ($n = 2$; labeled “DF”), and Cumberland Mountains, Tennessee, USA ($n = 7$; labeled “CM”). Shading represents warblers at breeding areas (green), in fall migration (orange), at stationary nonbreeding areas (blue), and in spring migration (yellow). Periods without geolocator data are shaded in gray.

undertake their preferred route. In the shorter spring migration period warblers may be more likely to take variable routes depending on environmental conditions at the time they reach the Gulf of Mexico.

Golden-winged Warblers in our study all travelled at daily average rates that were similar among breeding populations during both fall and spring migrations with the general trend of travelling faster during spring than during fall. Golden-crowned Sparrows (*Zonotrichia atricapilla*; Seavy et al. 2012) and Northern Wheatears (*Oenanthe oenanthe*; Schmaljohann et al. 2012) exhibited similar accelerated migration rates in spring vs. fall. When we controlled for the effects of breeding population on migration rate, individuals travelling longer routes did so faster, similar to observations in Northern Wheatears (Bairlein et al. 2012). Moreover, we did not detect any relationship between spring departure and arrival on breeding areas when we controlled for breeding-population effects. Although our sample sizes are relatively small, this finding warrants further investigation as it contradicts

other research suggesting birds leaving nonbreeding sites earlier also arrive on the breeding grounds earlier and that early arrival confers some fitness benefit over late arrival and identifies high-quality individuals (e.g., Norris et al. 2004, Spottiswoode et al. 2006).

Golden-winged Warblers exhibited variation in migration-route lengths and directness. Delaware Forest warblers took the longest and least direct routes compared to Rice Lake and Cumberland Mountain warblers. Shorter, more direct routes may be more efficient in that birds travel less distance, but a tradeoff may exist when those routes are more dangerous, or more energetically demanding than longer, primarily overland routes. Golden-winged Warblers from the Delaware Forest population successfully migrated 4,000–5,000 km yr⁻¹ farther than Cumberland Mountain and Rice Lake populations suggesting that, at least, Cumberland Mountain and Rice Lake populations are not approaching limits of their physiology during migration. Additional evidence from Golden-winged Warblers suggests that Cumberland Mountain

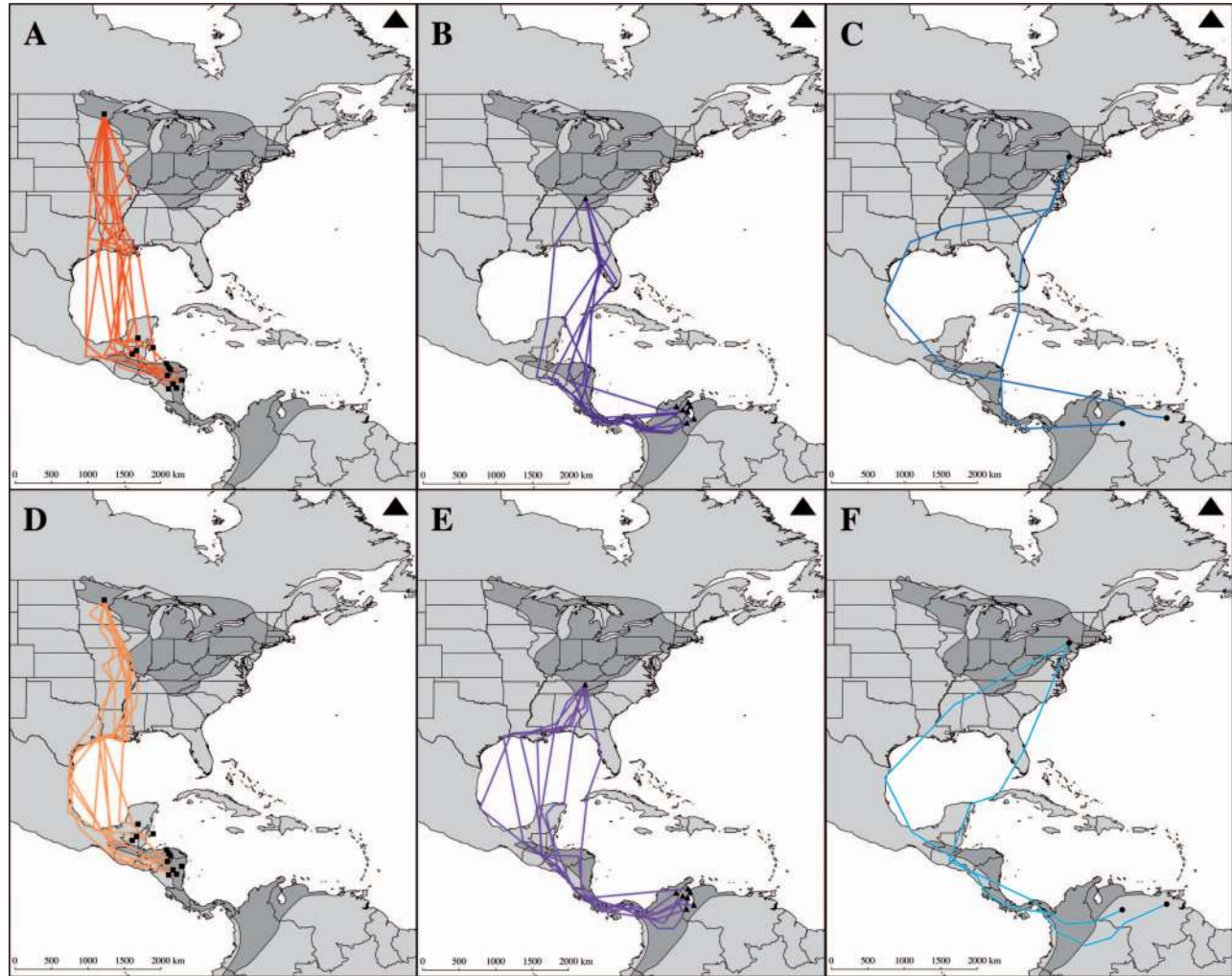


FIGURE 3. Estimated general migration routes for male Golden-winged Warblers marked at 3 breeding populations during 2013–2015. Orange tracks represent warblers marked at Rice Lake National Wildlife Refuge, Minnesota, USA (RL; $n = 12$ for fall migration [A]; $n = 9$ for spring migration [D]), purple tracks represent warblers marked at North Cumberland Wildlife Management Area, Tennessee, USA (CM; $n = 7$ for fall [B] and spring migration [E]), and blue tracks represent warblers marked at Delaware State Forest, Pennsylvania, USA (DF; $n = 2$ for fall [C] and spring migration [F]). Generalized range maps provided by the U.S. Geological Survey Gap Analysis Program delineate general breeding distribution and do not reflect abundance or dispersion.

warblers are capable of undertaking $\sim 1,500$ -km facultative migrations to avoid large, long-lasting tornadic storms immediately after completing a $\sim 5,200$ -km obligate migration (Streby et al. 2015a). Migration is purported to be among the most dangerous periods for migratory species (Sillert and Holmes 2002) and therefore may be a factor influencing population trends in Golden-winged Warbler populations travelling longer periods or greater distances relative to other populations. However, declines in abundance in recent decades could only be explained by migration-route distance if that distance has changed from periods of stable population numbers or a change in the birds' ability to complete the route.

We found complete isolation during the nonbreeding period among these 3 breeding populations as they used

sites along a general east–west gradient that reflected arrangement on the breeding grounds (Figure 1). Our findings support results of a recent isotopic analysis of nonbreeding Golden-winged Warblers, although we found no evidence of Appalachian Mountain warblers wintering in Central America suggesting more significant isolation among populations (Hobson et al. 2016). Sampling more individuals from these breeding and nonbreeding regions will provide more complete estimates of distribution and overlap; therefore, we suggest that additional sampling along a latitudinal gradient through the Appalachian Mountains and/or sampling along a longitudinal gradient through multiple regions in Central America might resolve the question of population overlap observed by Hobson et al. (2016). Our findings are similar to those reported in

western-breeding populations of Swainson's Thrushes (*Catharus ustulatus*; Delmore et al. 2012, Cormier et al. 2013), eastern- and central-breeding Gray Catbirds (*Dumetella carolinensis*; Ryder et al. 2011), and Ovenbirds (*Seiurus aurocapilla*; Hallworth et al. 2015), and unlike patterns observed in Wood Thrushes (Stanley et al. 2015) and Purple Martins (Fraser et al. 2012) in which breeding populations showed moderate to extensive overlap during the nonbreeding period, excluding migration. Unlike several other species of Nearctic–Neotropical migrant songbirds (e.g., Hecksher et al. 2011, Cormier et al. 2013), Golden-winged Warblers showed no evidence of long-distance movements within the nonbreeding period, corroborating evidence from radio-telemetry studies of Golden-winged Warblers in Costa Rica (Chandler and King 2011) and Nicaragua (Chandler et al. 2016). Smaller-scale, nonbreeding-grounds efforts may therefore be effective in conserving individual populations of this species. Conversely, the use of a relatively small area throughout the nonbreeding period implies a reliance on that location and the availability and quality of appropriate land cover in that region potentially suggesting sensitivity to moderate- or large-scale changes in land-cover types and composition in Golden-winged Warblers.

Furthermore, conservation efforts targeting Golden-winged Warblers breeding in the western Great Lakes region might be most effective if focused on protecting appropriate nonbreeding sites throughout Central America. Such efforts would help conserve nonbreeding-site diversity of Golden-winged Warblers breeding within the western Great Lakes region. Conservation efforts targeting Golden-winged Warblers breeding in the Appalachian Mountains region might be most effective if focused on targeting appropriate nonbreeding sites in northern South America (i.e. Colombia and Venezuela). Targeted conservation efforts for Golden-winged Warblers breeding in the Appalachian Mountain region may be especially effective at appropriate sites along the border of Colombia and Venezuela where a high proportion of our sample of geolocator-marked Golden-winged Warblers that bred in the Appalachian Mountains region spent the nonbreeding period.

We documented spatial segregation among 3 populations of Golden-winged Warblers in their nonbreeding distribution and differences among breeding populations in migration routes and behavior highlighting the importance of identifying the full life-cycle movements of multiple populations of the same species. We found no evidence of Appalachian-breeding warblers wintering in Central America suggesting that sampling of additional Appalachian populations may be required to determine if any nonbreeding population overlap exists among Appalachian and Great Lakes Golden-winged Warbler populations in Central America (Hobson et al. 2016).

Additionally, future efforts may benefit from sampling both Golden- and Blue-winged warblers from additional populations across their respective distributions as the 2 likely constitute phenotypic morphs of the same species and a species-wide study focused on a single morph would be incomplete (Toews et al. 2016). Moreover, as many passerine populations are female-limited (i.e. some males are unpaired; Habib et al. 2007, Streby and Andersen 2011), it is critical that female migration and nonbreeding ecology are addressed by future studies of species of conservation concern. Finally, the nonbreeding population structure we describe suggests breeding population trajectories may be driven by population- or site-specific factors experienced by populations independently during the nonbreeding period or migration. Identifying those environmental factors associated with individual survival across the nonbreeding distribution and during migration might aid in the development of robust conservation strategies. Our findings suggest a need for a more comprehensive evaluation of the ecology and distribution of Golden-winged Warblers outside the relatively well-studied breeding period.

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Ethics statement: We captured, marked, and collected data from birds following Protocol No. 561, approved by the University of Tennessee Institutional Animal Care and Use

Committee and Protocol No. 1004A80575, approved by the University of Minnesota Institutional Animal Care and Use Committee.

Author contributions: HMS, DEA, DAB, PBW conceived of, designed, and supervised research. GRK, HMS, SMP, JAL, and DJM conducted research. GRK wrote the paper with input from all authors. GRK, HMS, DEA, and SMP developed methods. GRK analyzed the data. HMS, DEA, DAB, PBW, and JLL contributed substantial resources.

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APPENDIX TABLE 2. Number of nonbreeding transitions (i.e. sunrises and sunsets) derived from light-level geocator data used to calculate nonbreeding-site joint likelihood estimates for individual Golden-winged Warblers at 3 breeding sites across their breeding distribution. RL denotes individuals marked at Rice Lake National Wildlife Refuge, Minnesota, USA; DF denotes individuals marked at Delaware State Forest, Pennsylvania, USA; CM denotes individuals marked at North Cumberland Wildlife Management Area, Tennessee, USA. Transitions refer to the number of transition periods (sunrises and sunsets) used to create an individual's nonbreeding period probability density function (the probability that an individual bird was located at each possible location).

ID	Transitions	Date range	Year
RL03 ^{a,b}	28	Sep 14 to Sep 28	2013
RL05	114	Jan 1 to Feb 28	2013
RL06	107	Jan 1 to Feb 28	2013
RL11	115	Jan 1 to Feb 28	2013
RL12	110	Jan 1 to Feb 28	2013
RL14 ^b	103	Jan 1 to Feb 26	2013
RL15 ^b	20	Dec 27 to Jan 6	2013
RL16	112	Jan 1 to Feb 28	2013
RL20	116	Jan 1 to Feb 28	2013
RL25	116	Jan 1 to Feb 28	2014
RL29	115	Jan 1 to Feb 28	2014
RL36	117	Jan 1 to Feb 28	2014
DF05	111	Jan 1 to Feb 28	2014
DF11	117	Jan 1 to Feb 28	2014
CM05	117	Jan 1 to Feb 28	2013
CM06	116	Jan 1 to Feb 28	2013
CM09	115	Jan 1 to Feb 28	2013
CM10	117	Jan 1 to Feb 28	2013
CM13 ^c	110	Jan 1 to Feb 28	2013
CM16	115	Jan 1 to Feb 28	2013
CM21 ^c	116	Jan 1 to Feb 28	2014

^a Light sensor on geocator was covered in mud upon recovery, selected period was apparently before mud caused errors in light collection.

^b Geocator stopped recording data prematurely.

^c Same individual marked in subsequent years.

APPENDIX TABLE 3. Summary of points used to calculate mean estimated location of male Golden-winged Warblers during the nonbreeding period (with SD in parentheses). Points are transition-derived estimates of location calculated by multiplying the likelihood of 5 subsequent transitions with a given twilight and exporting the coordinates of the cell with the maximum likelihood. RL denotes individuals marked at Rice Lake National Wildlife Refuge, Minnesota, USA; DF denotes individuals marked at Delaware State Forest, Pennsylvania, USA; CM denotes individuals marked at North Cumberland Wildlife Management Area, Tennessee, USA. We averaged the latitude and longitude of transition-derived points from November 1 to February 28 falling within 250 km of the delineated nonbreeding distribution of Golden-winged Warblers to calculate a single nonbreeding site for each warbler.

ID	Points	Longitude	Latitude	Year
RL03 ^a	10	85.70°W (2.01)	13.48°N (2.66)	2013
RL05	116	85.73°W (1.77)	15.76°N (5.20)	2013
RL06	29	87.38°W (1.39)	17.72°N (3.13)	2013
RL11	141	85.48°W (0.94)	12.65°N (1.91)	2013
RL12	31	89.25°W (1.65)	18.92°N (2.56)	2013
RL14	5	83.88°W (2.17)	13.72°N (3.40)	2013
RL15	11	89.96°W (1.99)	16.92°N (2.80)	2013
RL16	65	85.25°W (2.15)	15.01°N (5.55)	2013
RL20	115	85.62°W (1.20)	14.31°N (4.56)	2013
RL25	80	84.51°W (1.75)	12.74°N (2.65)	2014
RL29	104	84.93°W (1.81)	13.27°N (5.08)	2014
RL36	97	89.43°W (0.83)	17.38°N (3.25)	2014
DF05	23	68.56°W (1.88)	8.36°N (2.61)	2014
DF11	3	63.08°W (1.90)	9.05°N (4.85)	2014
CM05	199	72.41°W (0.93)	10.17°N (1.97)	2013
CM06	80	73.22°W (0.89)	10.56°N (0.92)	2013
CM09	3	71.93°W (1.73)	8.55°N (2.61)	2013
CM10	37	71.84°W (1.82)	9.94°N (2.41)	2013
CM13 ^b	20	71.02°W (2.72)	9.05°N (1.75)	2013
CM16	92	71.75°W (1.01)	11.05°N (1.41)	2013
CM21 ^b	73	71.48°W (1.26)	10.63°N (2.26)	2014

^a Light sensor on geocator was covered in mud upon recovery, selected period was apparently before mud caused errors in light collection

^b Same individual marked in subsequent years