



RESEARCH ARTICLE

Concentration of a widespread breeding population in a few critically important nonbreeding areas: Migratory connectivity in the Prothonotary Warbler

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ABSTRACT

One of the greatest challenges to informed conservation of migratory animals is elucidating spatiotemporal variation in distributions. Without such information, it is impossible to understand full-annual-cycle ecology and effectively implement conservation actions that address where and when populations are most limited. We deployed and recovered light-level geolocators ($n = 34$) at 6 breeding sites in North America across the breeding range of a declining long-distance migratory bird, the Prothonotary Warbler (*Protonotaria citrea*). We sought to determine migratory routes, stopover location and duration, and the location of overwintering grounds. We found that the species exhibits a large-scale, east–west split in migratory routes and weak migratory connectivity across its range. Specifically, almost all individuals, regardless of breeding origin, overlapped in their estimated wintering location in northern Colombia, in an area 20% the size of the breeding range. Additionally, most of the individuals across all breeding locations concentrated in well-defined stopover locations in Central America while en route to Colombia. Although error inherent in light-level geolocation cannot be fully ruled out, surprisingly much of the estimated wintering area included inland areas even though the Prothonotary Warbler is considered a specialist on coastal mangroves in winter. Based on these results, conservation efforts directed at very specific nonbreeding geographical areas will potentially have benefits across most of the breeding population. Our findings highlight the importance of using modern technologies to validate assumptions about little-studied portions of a species' annual cycle, and the need to distribute sampling across its range.

Keywords: Colombia, full annual cycle, geocator, migration, stopover

Reproductivas de importancia crítica: Conectividad migratoria en *Protonotaria citrea*

RESUMEN

Uno de los desafíos más grandes para la conservación de los animales migratorios es determinar las variaciones espacio temporales en sus distribuciones. Sin esta información, es imposible entender la ecología del ciclo anual completo y la implementación efectiva de acciones de conservación que establezcan dónde y cuándo las poblaciones están más limitadas. Colocamos y recuperamos geo-localizadores de nivel de luz ($n = 34$) en seis sitios reproductivos en América del Norte a lo largo del rango reproductivo de un ave migratoria de larga distancia en disminución, *Protonotaria citrea*. Buscamos determinar las rutas migratorias, la localización y duración de las paradas, y la localización de los sitios de invernada. Encontramos que la especie muestra una división este-oeste a gran escala en las rutas migratorias y una débil conectividad migratoria a lo largo de su rango. Específicamente, casi todos los individuos, más allá del origen reproductivo, se superpusieron en su ubicación estimada de invernada en el norte de Colombia, en un área de un 20% del tamaño de su rango reproductivo. Adicionalmente, la mayoría de los individuos a través de todas las localidades

reproductivas se concentraron en localidades de parada bien definidas en América Central mientras estaban en camino a Colombia. Aunque el error inherente en los geo-localizadores de nivel de luz no puede ser totalmente eliminado, sorprendentemente la mayoría del área estimada de invernada incluyó áreas tierra adentro, aunque *Protonotaria citrea* es considerada una especie especialista de los manglares costeros en invierno. Tomando estos resultados como base, los esfuerzos de conservación dirigidos a áreas geográficas no reproductivas específicas tendrán potenciales beneficios para la mayor parte de la población reproductiva. Nuestros hallazgos subrayan la importancia de usar tecnologías modernas para validar los supuestos sobre aspectos poco estudiados del ciclo de vida anual de una especie, y la necesidad de distribuir el muestreo a través de su rango.

Palabras clave: ciclo anual completo, Colombia, geo-localizador, migración, parada

INTRODUCTION

The need for a full-annual-cycle approach to animal conservation is increasingly being recognized (Marra et al. 2015a). However, the lack of detailed knowledge on dynamic geographic distributions across the annual cycle is a major obstacle to applying effective broad-scale conservation actions for migratory species. Migratory populations can redistribute themselves in various ways throughout their annual cycle, ranging from remaining discrete (strong migratory connectivity) to mixing extensively (weak migratory connectivity; Webster et al. 2002, Cohen et al. 2018a). Differential patterns of connectivity can exist during migration itself (Cohen et al. 2018b) or between breeding and nonbreeding grounds. Without an understanding of links between breeding, stopover (i.e. migratory refueling), and wintering locations, researchers and managers cannot determine the environmental conditions and anthropogenic challenges to which populations are exposed throughout the year (e.g., Negret et al. 2017). Thus, estimating the strength of migratory connectivity is a critical first step in identifying the scale at which conservation efforts should occur for species of concern. For example, if strong connectivity between breeding and wintering grounds exists, this may warrant managing each population segment separately, but if connectivity is weak, a unified (i.e. species- or range-wide) approach may be more appropriate. In addition, knowledge of the timing and routes of migration, including fidelity to and duration of use of stopover locations, is critical to conservation yet is largely lacking for many songbirds (Moore et al. 2005). Because mortality rates can be highest during migration (Sillett and Holmes 2002, Klaassen et al. 2014), detailed information during that phase can improve conservation of migratory species by revealing risks and vulnerability to anthropogenic change along their migratory pathways (e.g., climate change; Culp et al. 2017). Finally, information on migratory behavior may also reveal the underlying structure of populations, such as the existence of migratory divides (e.g., Delmore and Irwin 2014, Hobson et al. 2015).

Research on migratory connectivity in large-bodied animals can rely on accurate and precise, often real-time

measures from ARGOS satellite (e.g., Battley et al. 2012) and GPS technologies (e.g., Hallworth and Marra 2015). For small (<20 g) animals such as many songbirds (Order: Passeriformes), however, the best available technology is archival light-level geolocators (hereafter geolocators; Stutchbury et al. 2009, Bridge et al. 2013). These use photo-period and sun position to give accurate (Hallworth et al. 2013) though imprecise (Lisovski et al. 2018) estimates of the locations of tagged individuals during stationary portions of their annual cycle. Although these devices have provided a large amount of new spatial data on migratory songbirds in a short amount of time (McKinnon et al. 2013a), projects have been largely limited in the scale of deployments. For example, most projects using geolocators have either deployed tags at a single site (e.g., Heckscher et al. 2011, Nelson et al. 2016) or at a small number of sites, representing, for instance, 2 sides of a migratory divide (e.g., Delmore and Irwin 2014, Cormier et al. 2016). Likely because of logistical and financial limitations, relatively fewer studies have attempted to deploy geolocators at sites distributed across the entire breeding or nonbreeding range of a migratory bird species (e.g., Fraser et al. 2012, Hallworth et al. 2015, Stanley et al. 2015, Ouwehand et al. 2016, Haché et al. 2017).

The Prothonotary Warbler (*Protonotaria citrea*) is a Nearctic–Neotropical migratory songbird that specializes on bottomland hardwood/forested wetland habitat in the eastern United States for breeding (Petit 1999). Prothonotary Warblers nest in cavities and readily use nest boxes, and thus they have been intensively studied during the breeding season (e.g., Petit and Petit 1996, Hoover 2003, Cooper et al. 2009, Bulluck et al. 2013, McKim-Louder et al. 2013, Slevin et al. 2018). Due largely to loss and degradation of breeding habitat and population declines during the 20th century, this species has been included on many watch lists (e.g., Butcher et al. 2007), listed as a species of concern in many states and nationally in the United States (U.S. Fish and Wildlife Service 2008, Rosenberg et al. 2016), and is considered endangered in Canada (COSEWIC 2016). Research on Prothonotary Warblers on the nonbreeding grounds has been very limited compared to that on the breeding grounds (but see Lefebvre and Poulin 1996, Warkentin and Morton 2000, Wolfe and Ralph 2009, Calvert et al. 2010). The warbler

may be even more threatened by habitat loss and degradation on its wintering grounds, as it is thought to specialize on mangroves (Petit 1999), one of the rarest and most endangered forest types globally (Sandilyan and Kathiresan 2012). Mangroves represent a fraction of the world's forest cover (<1% of tropical forest), and <30% of mangroves are found in the Americas, where they occur along the coastlines of Caribbean Islands and Central and South America. In addition to their already limited coverage, mangroves are being removed at an alarming rate (FAO 2007). Future losses are expected to greatly increase because of sea level rise induced by climate change (reviewed in Sandilyan and Kathiresan 2012). Nonbreeding habitat for Prothonotary Warblers may exist only in narrow, rapidly declining strips that cross many geopolitical boundaries. Thus, it is critical that managers and stakeholders understand the nonbreeding distributions and habitats relevant to different parts of the breeding population.

The first step toward developing an understanding of when and where Prothonotary Warblers are limited within their annual cycle is to determine the strength of migratory connectivity. We formed a range-wide collaboration of individuals from academic institutions, federal agencies, and nongovernmental organizations with the goal of coordinated research to advance conservation (Prothonotary Warbler Working Group; <https://www.prowwg.wixsite.com/home>). Although the Prothonotary Warbler's breeding range covers >2,000,000 km² spanning 19.5 degrees of latitude (Ridgely et al. 2003), local populations are often highly disjunct, being tightly associated with riparian corridors or seasonally flooded forests. Furthermore, breeding areas in the Atlantic Coastal Plain and the Mississippi Basin are divided by a major geographic feature, the Appalachian Mountains. The species' nonbreeding distribution is poorly understood and based largely on opportunistic observations by citizen scientists (Sullivan et al. 2009). We sought to quantify the strength of migratory connectivity in this species by deploying geolocators at 6 locations distributed across the breeding range. We used data from retrieved geolocators to estimate migratory routes, stopover locations, migration phenology, and wintering locations to provide a quantitative measure of migratory connectivity (Cohen et al. 2018a). Our findings provide information critical to the conservation of this species and, more broadly, highlight the importance of determining migratory connectivity at a range-wide scale to prioritize conservation actions.

METHODS

Study Sites

This study occurred at 6 locations across the breeding range of the Prothonotary Warbler, including locations east and west of the Appalachian Mountains in both

coastal and inland areas (Figure 1, Appendix Table 2). Habitats varied in composition across breeding locations and included seasonally flooded cypress swamp, riparian forest, and hardwood floodplain forest. Our sample populations comprised individuals nesting either exclusively in nest boxes (Virginia, Louisiana) or in a combination of nest boxes and natural cavities (Arkansas, Ohio, South Carolina, Wisconsin).

Geocator Deployment and Retrieval

We captured birds at each site either in a hand net placed over the nest opening (females) or in mist nets (males and females). For field identification, we fitted each bird with a unique combination of a USGS aluminum band and 1–3 plastic color bands. We determined age and sex based on plumage features (Pyle 1997) and collected standard morphometrics. Using a modified leg-loop harness (Rappole and Tipton 1991), we fitted each bird with either a stalkless model Intigeo-P50Z11 (Migrate Technology, Coton, Cambridge, UK) or a stalked model ML6140 (Lotek Wireless, Newmarket, Ontario, Canada) geocator that weighed <4% of the bird's body mass. In total we deployed 149 geolocators across our 6 sites (Appendix Table 2). One year following deployment, all returning birds carrying geolocators were captured in the same manner and tags were removed for data retrieval. In some cases, geolocators were retrieved but the tag failed to collect any data. In addition, due to battery life of retrieved tags and gaps in light data around the vernal equinox, we were not able to include data on spring migration (see Appendix Table 2 for all details on geocator deployment and retrieval). We have archived all location and movement data from this study on Movebank (Tonra et al. 2019).

Light-level Geolocation Analysis

Light-level geolocation capitalizes on known variation in day length and time of solar noon across the planet to estimate geographic coordinates from observed times of sunrise and sunset (Hill and Braun 2001). We used raw light data collected via geolocators to estimate geographic coordinates (latitude and longitude) with the Solar/Satellite Geolocation for Animal Tracking package (SGAT; Sumner et al. 2009, Wotherspoon et al. 2013) in program R (R Core Team 2017). We used a light threshold of 1 to assign the time of sunrise or sunset (twilight events). We considered sunrise the time at which the ambient light level recorded by the geocator rose above the user-defined threshold, and sunset the time at which the light level fell below the threshold value. To determine the time of sunrise/sunset, we used the findTwilights function in the TwGeos package (Wotherspoon et al. 2016). We set the minimum time between sunset and sunrise to 6.5 hr, which filtered out spurious sunrise/sunset times caused by shading or light

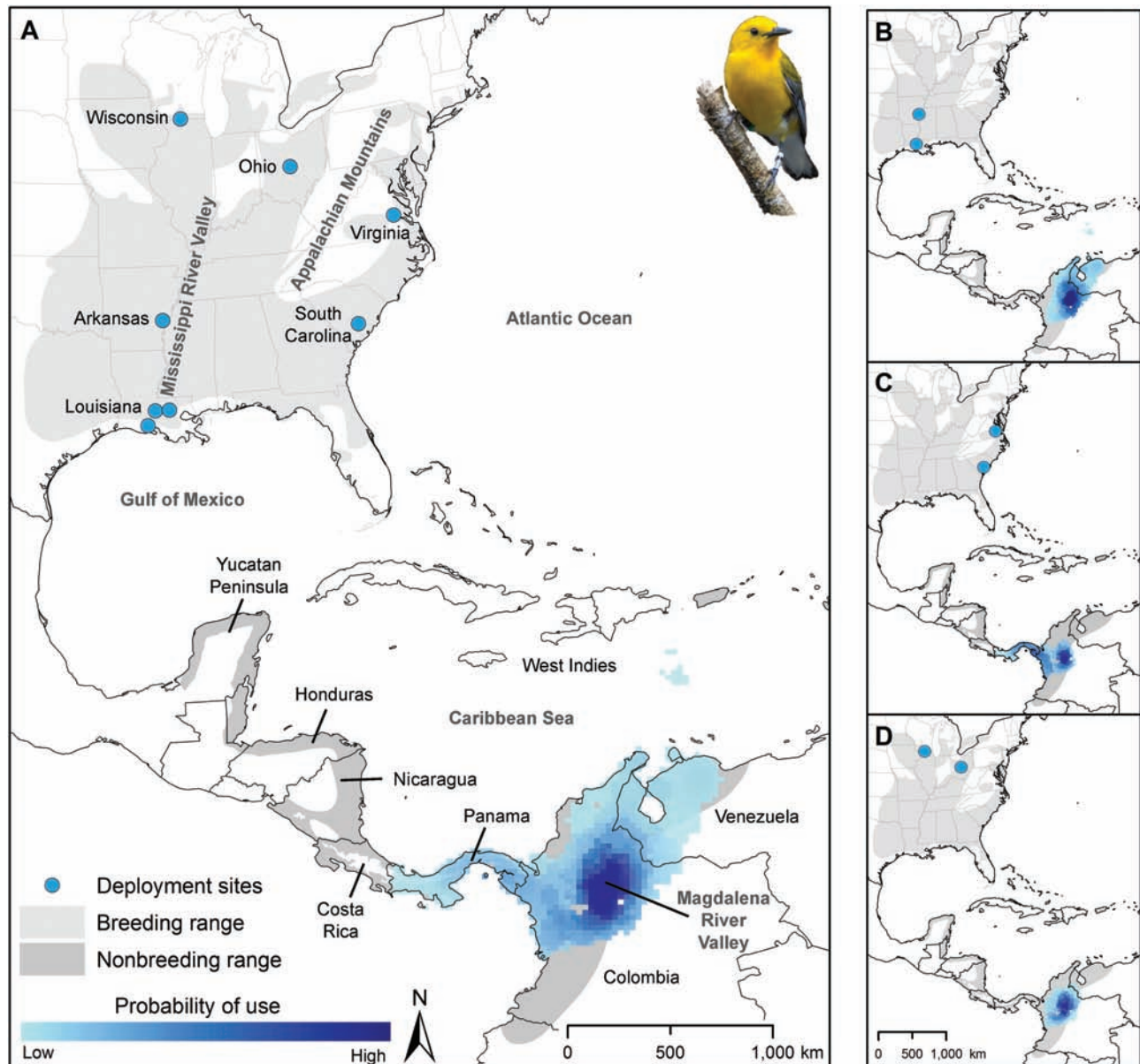


FIGURE 1. Wintering distribution of Prothonotary Warblers determined using light-level geolocators deployed during the 2013–2016 breeding seasons at 6 breeding locations. (A) Heat map of wintering locations (95% credible interval) of all individuals during the winter stationary period (November–February) from 6 breeding-season deployment sites (blue dots). Areas with a higher probability of use are shown in darker blue. Right panel shows heat maps of wintering locations of the same individuals from deployment sites in the (B) southwestern, (C) eastern, and (D) northern portions of the breeding range. The range of the Prothonotary Warbler (Ridgely et al. 2003) is shown in light gray (breeding) and dark gray (nonbreeding).

pollution. To edit or remove incorrect sunrise/sunset times with the twilightEdit function, we used the following criteria: (1) the sunrise/sunset time had a time difference of 35 min or greater from sunrise/sunset times within 2 days on either side of the suspected outlier, and (2) the sunrise/sunset times of those 4 days (2 days on either side) occurred within 25 min of one another.

The SGAT package estimates geographic locations while incorporating the error inherent in light-level

geolocation through use of Markov Chain Monte Carlo (MCMC) simulations. For each individual, we specified a model that included the raw locations derived using the threshold method: a model that described the error distribution between estimated and known sunrise and sunset times, a gamma-distributed behavioral model that described potential flight speeds (km hr^{-1} , shape = 0.7, rate = 0.08), and a land mask that constrained stationary periods but not migratory flights to land masses. We

used a relative abundance layer derived using the Spatio-Temporal Exploratory Model (STEM) for citizen-science observations from eBird.org (Fink et al. 2010, Fink et al. 2013, Johnston et al. 2015) as a spatial mask to constrain stationary periods. Using relative abundance to constrain stationary periods is analogous to using relative abundance as a prior for making stable-hydrogen isotope assignments (Rubenstein and Royle 2004) while still allowing for open-water crossing. The error distribution between estimated and known sunrise followed a lognormal distribution and was created from light-data during the time when Prothonotary Warblers were known to be at the capture location. We removed incubation periods (distinct visible pattern in light image) when determining the error distribution for females as this could skew the error distribution (Supplementary Material Figure S1). On the breeding grounds, we obtained calibration data from tags carried by warblers during times when individuals were known to be at the deployment site. We obtained calibration data from the wintering grounds from one stalked and one stalkless geolocator, which were tied in tree branches at a height of approximately 2 m in mangrove and lagoon forests along the northern coast of Colombia (Appendix Table 3). We rotated 1 tag between 2 sites for 16.9 days and 3.1 days each, while we rotated the other tag among 5 sites for an average of 2.9 days each. We determined the average sun zenith angles from each deployment. Based on these calibration data, we used 2 sun zenith angles (angle of the sun with respect to vertical when light-data crosses a specified threshold) for each individual to estimate locations throughout the year (McKinnon et al. 2013b, Hallworth et al. 2015): one during the breeding season (92.5°N) and one during the nonbreeding season (90.9°N). We ran the model 3 times with 5,000 MCMC iterations on 3 chains per run, with the first 2 runs as burn-in. In between each run, we collapsed the chains and summarized location estimates, and used the resulting median daily location to initialize the subsequent run. We kept every 10th iteration from the posterior distribution, from which we drew our geographic inference.

Estimating Migratory Routes and Timing

We used location estimates drawn from the posterior distribution to determine migratory routes and migration timing. Migratory routes and timing were derived using the MigSchedule function included in the LLMig package (<https://github.com/MTHallworth/LLMig.git>). The MigSchedule function uses natural changes (the optimal change points based on mean values) in latitudinal and longitudinal estimates to determine stationary locations. The posterior location estimates and accompanying uncertainty were used to assign geographic locations during stationary periods that lasted >1 day. The MigSchedule

function is similar to the commonly used ChangeLight function in the GeoLight package (Lisovski and Hahn 2012); however, the MigSchedule function incorporates uncertainty in location estimates. Because the effect of shading events is exacerbated during the autumnal and vernal equinoxes, we removed latitudinal movements that occurred within 5 days on either side of each. During that period, we only used changes in longitude to make inferences about migratory movements. To generate the most probable migration route, we used the median location weighted by the location uncertainty of each stationary period. We used the summation of the great-circle distances along the migration route as migration distance. We report values as means \pm standard error (SE).

Quantifying Migratory Connectivity

We calculated the strength of migratory connectivity (MC) between breeding and wintering locations with the estMC function in the MigConnectivity package (Cohen et al. 2018a, Hostetler and Hallworth 2017) using 1,000 bootstrap samples and 1,000 simulations. MC defines the distances between individuals in the following ways: negative MC values indicate weaker migratory connectivity (i.e. individuals living in close association in one season are far apart during another season), while positive MC values indicate stronger migratory connectivity (i.e. individuals maintain similar distances between seasons). The estMC function requires predefined origin and target locations, deployment and nonbreeding locations, respectively. We defined the origin locations as the individual states where the geolocators were deployed and target locations as the countries that fall within the known nonbreeding distribution. Therefore, we had 6 origin locations and 15 potential target locations.

The estMC function also incorporates relative abundance into the MC metric (Cohen et al. 2018a). Because we deployed all geolocators during the breeding season, we used the relative abundance within each state estimated from the STEM eBird abundance map. We summarized the weekly STEM results when Prothonotary Warblers are known to be stationary and breeding (June 1–July 24). We then extracted abundance within each of the deployment states and converted it to relative abundance.

We also incorporated geographic uncertainty inherent to geolocation by light into the MC metric. We calculated location bias (intercept = 1.67 km, latitude = 31.03 km) and location error (intercept = 25.55 km, latitude = 222.08 km) by determining the distance (in meters) between the deployment location and the derived locations from the posterior distribution while individuals were known to be at the capture site. Location bias and error were then used in the estMC resampling function when calculating MC.

RESULTS

We retrieved 44 geolocators 1 yr after deployment. Due to tag failure, however, we were able to acquire data from only 34 tags (8 from Arkansas, 13 from Louisiana, 3 from Ohio, 3 from South Carolina, 4 from Virginia, and 3 from Wisconsin), and obtained tracking data that included wintering location from 33 tags (excluded one from Arkansas that had fall migration but not winter data). All tag failures occurred in the Lotek ML6140 models. A detailed summary of tag deployments and retrievals can be found in [Appendix Table 2](#).

Migratory Connectivity

Regardless of breeding location, almost all Prothonotary Warblers that were recaptured had wintered in Colombia (91%, 30 of 33; [Figure 1](#)). The remaining individuals most likely had wintered in neighboring Panama and Venezuela ([Table 1](#); see [Supplementary Material Figure S2A–F](#) for individual maps with associated uncertainty). The area represented by the winter locations of all tracked individuals included less than a third (31%) of the Prothonotary Warbler's described wintering distribution ([Ridgely et al. 2003](#)). The confluence of individuals in Colombia from all deployment locations resulted in low migratory connectivity (MC mean = 0.07; 95% CI: -0.07 to 0.28) despite individuals from the same breeding location wintering in close proximity (i.e. low population spread). The median nonbreeding distance between individuals from the same breeding site was shortest for the Ohio site (180 km; 95% CI: 177–280 km), followed by Louisiana (226 km; 152–385 km), Wisconsin (267 km; 209–306 km), South Carolina (319 km; 262–448 km), Arkansas (320 km; 114–523 km), and Virginia (400 km; 129–681 km).

Migratory Routes and Timing

Migration routes differed among breeding sites despite most individuals wintering in the same region of northern South America ([Figure 2](#)). Individuals breeding in Louisiana, Arkansas, and Wisconsin most likely migrated through the Mississippi Alluvial Valley and crossed the Gulf of Mexico onto the Yucatan Peninsula. Individuals

breeding in Ohio most likely migrated south through peninsular Florida before crossing the Gulf of Mexico onto the Yucatan Peninsula. Birds from both Virginia and South Carolina breeding sites most likely migrated through the Bahamas and/or the West Indies before making landfall in Central America along either the Honduras/Nicaragua border or farther south along the Costa Rica/Panama border.

Fall migration distance ranged from about 3,000 to 5,000 km, and because most birds wintered in a similar region in Colombia, migration distance was highly correlated with breeding latitude ($r = 0.84$, $t = 8.4$, $df = 30$, $P < 0.001$). The average duration of fall migration (from departure from breeding area to arrival on nonbreeding area) was 65 ± 4 days, which resulted in a mean migration rate of 69 ± 4 km day⁻¹. The mean breeding season departure date ranged from July 24 (ordinal date: 205 ± 9) in Wisconsin to August 25 (238 ± 8) in Virginia. There were 2 general winter arrival periods. One was in late September that spilled over into early October and consisted of individuals from South Carolina (ordinal date: 273 ± 5), Arkansas (274 ± 6), and Wisconsin (277 ± 18). The other was in late October and consisted of individuals breeding in Ohio (290 ± 2), Louisiana (293 ± 7), and Virginia (300 ± 11). It should be noted that deployment occurred in only one year at most sites and that this year was not consistent among sites (see [Appendix Table 2](#)). Thus, we cannot account for the possibility that some of the variation in migration phenology was due to annual variation in environmental conditions, and caution should be taken in interpreting these descriptive data. The mean migratory stopover duration in the fall was 21 ± 10 days and all individuals had at least one stopover that lasted 10 days or longer. The longest stopover durations occurred in southern Mexico, along the border between Guatemala and Honduras, and in central Nicaragua ([Figure 3A](#)). A few locations, such as the Yucatan Peninsula and the border between Honduras and Nicaragua, were used by the vast majority of individuals at some point during their journey south ([Figure 3B](#)). In fact, at least one individual from all 6 deployment locations used stopover locations along the border

TABLE 1. Estimated probabilities that Prothonotary Warblers from each breeding site overwintered in identified nonbreeding locations, based on location data from geolocators. The number of individuals with geolocators retrieved with data from each breeding site (n) is shown along with the mean transition probability (95% CI) for each nonbreeding location for those individuals.

Breeding site	n	Nonbreeding location		
		Panama	Colombia	Venezuela
Arkansas	8	0	0.74 (0.33–1.00)	0.26 (0.00–0.67)
Louisiana	13	0	1.00 (1.00–1.00)	0
Ohio	3	0	1.00 (1.00–1.00)	0
South Carolina	3	0.08 (0.00–1.00)	0.92 (0.00–1.00)	0
Virginia	4	0.25 (0.00–0.75)	0.75 (0.25–1.00)	0
Wisconsin	3	0	1.00 (1.00–1.00)	0

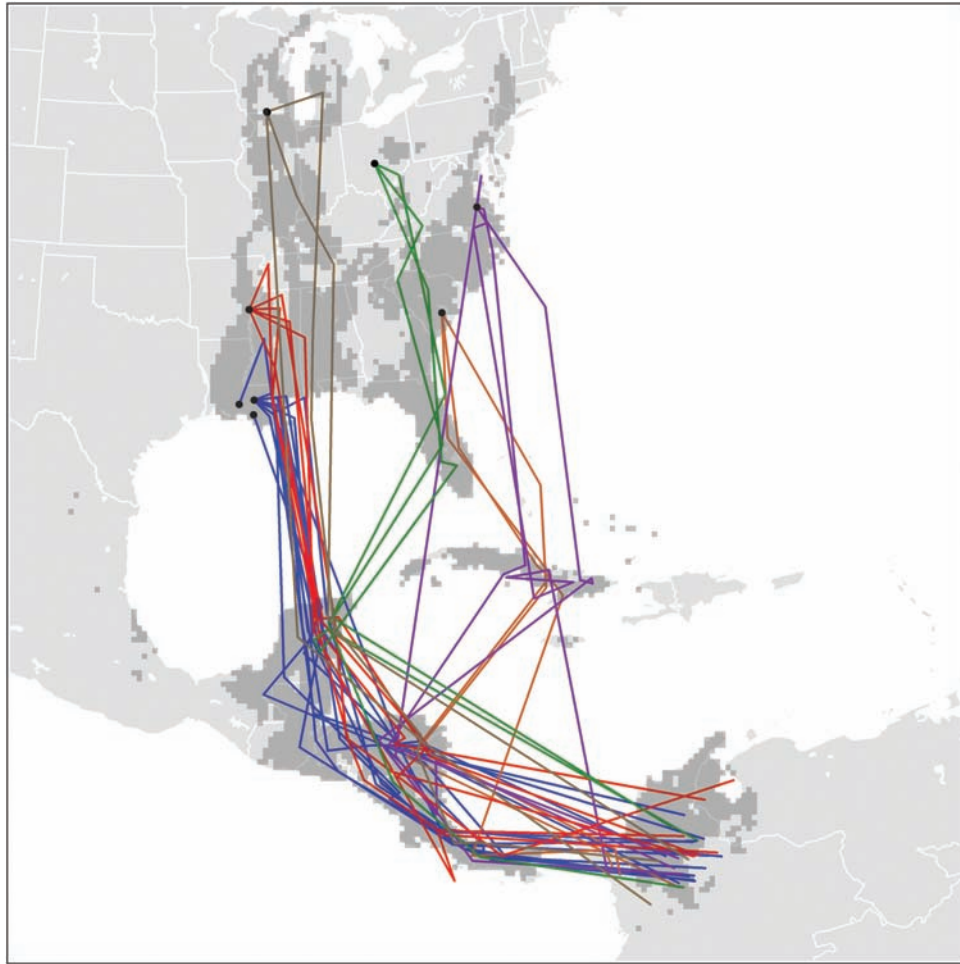


FIGURE 2. Most probable fall migration route (colored lines) and associated uncertainty (gray shading) of breeding Prothonotary Warblers from 6 breeding locations across the breeding range. Each line represents a different individual ($n = 36$) and each color represents a different breeding site ($n = 6$). In some instances, location uncertainty included bodies of water. Therefore, the median location, weighted by location uncertainty, that was used to generate the most probable migration route may occur over water. As such, some routes may appear to have “stationary” locations over water.

between Honduras and Nicaragua and another stop-over location in southern Costa Rica/northern Panama (Figure 3C).

DISCUSSION

Determining how distributions of migratory species change over time relies upon sampling across population segments and tracking their movements throughout the year. Recent advances in tracking technology have led to an increase in studies of migratory birds throughout the annual cycle, and this study adds to this growing body of knowledge. We examined the strength of migratory connectivity in the declining Prothonotary Warbler and determined that connectivity at the scale of the breeding range is weak due to high mixing and low population spread on the nonbreeding

range (Finch et al. 2017, Cohen et al. 2018a). Regardless of the breeding sites we sampled, the majority (91%) of recaptured Prothonotary Warblers had wintered in northern Colombia, concentrating in an area roughly 20% the size of the breeding range. Further, individuals from across the breeding range used 2 well-defined Central American regions for protracted migratory stopover. Although we did not sample every portion of the breeding range, our results suggest these specific nonbreeding regions are critically important to any full-annual-cycle conservation approach (cf. Hostetler et al. 2015, Marra et al. 2015a). The coordinated range-wide deployment of geolocators was integral to determining the importance of these regions to the species, as single-site deployments would have been unable to predict confidently the scale at which these regions are used.

Understanding the spatial distribution of species throughout the annual cycle is vital to determining

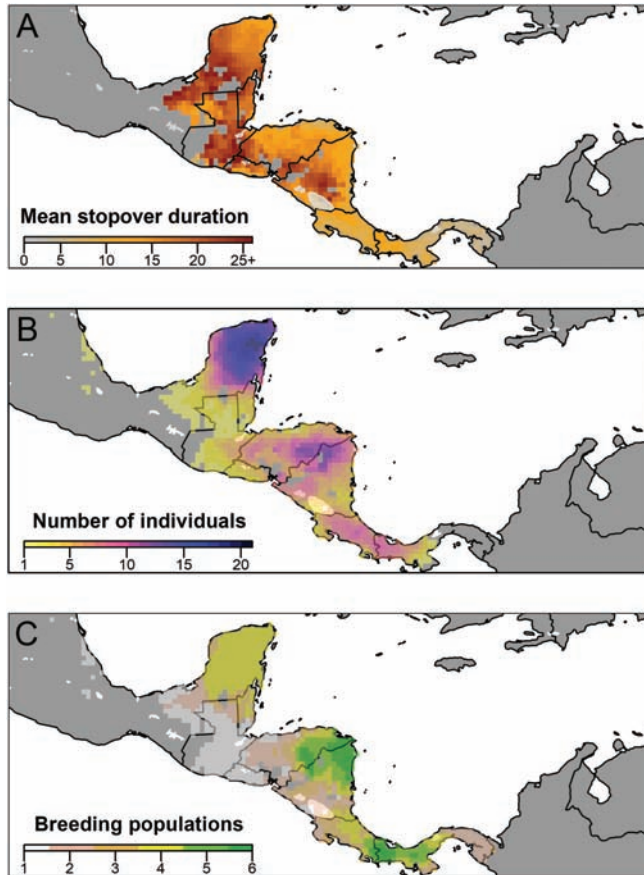


FIGURE 3. Heat maps depicting important fall migration stopover areas for Prothonotary Warblers tagged with geolocators at 6 different locations across the breeding range. (A) Mean stopover duration in days, (B) the estimated number of individuals using locations during fall migration, and (C) the estimated number of breeding populations (i.e. of 6 locations) from which one or more tagged individuals used the location during fall migration.

exposure to threats. For example, the apparent, newly described importance of Colombia to Prothonotary Warblers allows us to link the conservation of the species to land-use change and conservation policy in this nation. This is complicated by the fact that Colombia has only recently emerged from a 50-yr civil war that displaced millions of residents away from rural areas (Zafra 1997, Colombian National Information Network 2016). The Caribbean region of Colombia, where most Prothonotary Warblers wintered, has the least remaining forested land and second-highest deforestation rate in the nation (Armenteras et al. 2013). During the conflict, deforestation was driven largely by the planting of illicit crops, conversion to livestock pasture, and establishment of a large human population in the region (Armenteras et al. 2013). Economic development following the end of the conflict is likely to put increased pressure on natural resources, with negative consequences

for wildlife habitat, especially without informed conservation planning such as effective environmental zoning plans (Negret et al. 2017). This will likely be the case for many forest types, including mangroves in Colombia, which have already experienced losses resulting from development, altered hydrology, insect outbreaks, and their interactive effects (Elster et al. 1999). Thus, conservation of the Prothonotary Warbler will rely on collaboration among the Colombian government, natural resource managers, and conservation organizations to protect habitats in the region.

The lack of variation in wintering locations of Prothonotary Warblers is surprising, given they are known to be fairly abundant in regions other than those identified by our geolocator deployments. For instance, in mangroves that bookend the Panama Canal (Lefebvre and Poulin 1996), mangroves in northeastern Venezuela (Lefebvre et al. 1992), and tropical broadleaf forest in northeastern Costa Rica (Wolfe et al. 2013), research has documented seemingly high abundance in coastal areas. Our results did suggest that a small percentage of birds likely winter in Panama and Venezuela but that a substantially higher percentage winter in Colombia. Standardized surveys across the nonbreeding range to document region- and habitat-specific relative abundance patterns would provide greater detail on the differences between Colombia and other portions of the range. Further studies may also be warranted to determine if the pattern of weak connectivity can be extrapolated to areas not predicted as wintering locations by geolocators, but are known wintering areas, such as coastal regions of Costa Rica, Panama, Venezuela, and Colombia (Lefebvre and Poulin 1992, Lefebvre et al. 1992, Wolfe et al. 2013; L. P. Bulluck, C. Viverette, and J. Reese personal observations). For example, birds from high-density breeding sites that were not sampled in this study (e.g., southern Illinois; Hoover 2003) may be disproportionately using these coastal wintering areas. Range-wide efforts on the wintering grounds to quantify migratory connectivity through either geolocator deployment or intrinsic markers (e.g., stable isotopes; Hobson and Wassenaar 2008) would be useful to determine if this is the case. Regardless, it appears that most of the breeding population of this species, or at least that from the areas we sampled, may converge on a wintering area that is a small fraction of the size of the breeding range, as previously found in a grassland specialist (Bobolink [*Dolichonyx oryzivorus*]; Renfrew et al. 2013) and an aerial insectivore (Purple Martin [*Progne subis*]; Fraser et al. 2012).

Our results also highlight the importance of tracking movements of tagged individuals to test long-held assumptions of a species' ecology that were based on limited (and potentially biased) data. For instance, it was previously thought that Prothonotary Warblers typically specialized

on mangrove forests in the winter (Lefebvre and Poulin 1996, Petit 1999) and only occasionally used other habitats (e.g., Wolfe et al. 2013), an example of habitat matching between breeding and winter. Contrary to expectations, however, the region of highest overlap of wintering locations was not centered on the coast. Similar assumptions about other habitat specialists have also been found to be inaccurate (e.g., Louisiana Waterthrush [*Parkesia motacilla*]; Hallworth et al. 2011). Some researchers have sampled the Prothonotary Warbler in other habitats during stopovers (e.g., in tropical lowland forest; Wolfe and Ralph 2009). Use of inland forested wetland habitats could also be considered habitat matching, and our work confirms that there is a critical need for understanding use of alternative wintering habitats by this species. A recent study using a network of long-term monitoring stations (Monitoreo de Sobrevivencia Invernal, MoSI) across the southern United States, Central America, and northern South America found that Prothonotary Warblers have low residency rates, particularly at lower latitudes, suggesting that they may shift among habitats during the wintering period (Ruiz-Gutierrez et al. 2016). If they do in fact use multiple habitat types, identifying the relative quality and importance of alternative wintering habitats may be key to predicting and mitigating the effects of the loss of mangroves due to climate change (i.e. sea level rise, drying trends) or anthropogenic conversion (Sandilyan and Kathiresan 2012). As mangroves decline, either the warblers will need to shift to alternative habitats or their densities in preferred habitats will need to increase, which could have detrimental density-dependent consequences for fitness (cf. Marra et al. 2015b).

A caveat to our conclusion that Prothonotary Warblers heavily use interior, noncoastal sites in Colombia is that location uncertainty associated with light-level geolocation is relatively high (Fudickar et al. 2012, Bridge et al. 2013), on the scale of hundreds of kilometers (305 ± 40 km). For example, if individuals routinely traveled between diurnal foraging locations in closed-canopy mangrove forest to more open evening roost sites, as do some other species that winter in mangrove forests (e.g., Northern Waterthrush [*Parkesia noveboracensis*]; Smith et al. 2008), our location estimates could be biased south. There is some evidence, however, that substantial numbers of Prothonotary Warblers overwinter in inland portions of northern Colombia, since recent, preliminary surveys have found that abundance in the Magdalena River valley appears to be similar to that in regions along the coastline of Colombia (L. P. Bulluck personal observation).

Distribution-wide tracking of tagged individuals is also critical for determining population-specific exposure to threats during movement phases of the annual cycle (e.g., anthropogenic structures; Hager et al. 2017) and

for predicting the impacts of spatially variable environmental change (e.g., habitat alteration; Studds et al. 2017). Prothonotary Warblers exhibit a disjunct breeding distribution (Ridgely et al. 2003), which increases the likelihood of variable migratory routes. Although Prothonotary Warblers could be perceived to exhibit a large-scale migratory divide between the western and eastern parts of their breeding range (e.g., Hobson et al. 2015), we would not strictly define the observed pattern as such, given the high level of mixing in the wintering range (Fraser et al. 2013). However, more westerly breeding individuals (i.e. from the Mississippi Valley) crossed the Gulf of Mexico from the Mississippi Delta to the Yucatan Peninsula, whereas more easterly breeders (i.e. from the Atlantic coast) migrated down the Florida Peninsula and passed through the West Indies. Interestingly, although geographic features often drive such divides (e.g., the Rocky Mountains; Delmore and Irwin 2014), Prothonotary Warblers breeding in central Ohio appeared to cross over a prominent physical feature, the Appalachian Mountains, and migrate along the same route as the Atlantic coast birds in the fall. For some species, variation in migratory orientation may be genetically based (e.g., Berthold 1991, Pulido 2007, Delmore and Irwin 2014), which suggests that Prothonotary Warblers breeding in Ohio may be more genetically similar to eastern than to western breeding populations. This possibility warrants examination of genetic structure among population segments in this species (DeSaix et al. 2019). Weather patterns could also explain why Prothonotary Warblers from Ohio apparently took a more circuitous route south. A recent study by Kranstauber et al. (2015) demonstrated that the shortest migratory routes in terms of distance to wintering destinations are rarely the quickest; instead, prevailing wind patterns determine the most energetically efficient and fastest routes. Regardless of the cause, our results show that there is spatial variation in exposure to environmental hazards during migration based on breeding location. This highlights the importance of range-wide examination of migratory routes, even when wintering locations have a high degree of similarity. Our finding of separate migration routes converging on a common wintering area was highly unusual compared to that of other systems, wherein divergent southbound routes tend to lead to different wintering areas (e.g., Delmore et al. 2012, Hallworth et al. 2015, Hobson et al. 2015; but see Fraser et al. 2013). Because the migratory period is often considered the portion of the annual cycle with the greatest mortality risk (e.g., Sillett and Holmes 2002), population-specific migratory routes can be important in elucidating regional variation in population trends. Analysis of the relationship between population-specific routes and corresponding trends will be necessary to determine if this is the case for Prothonotary Warblers.

Geographic “bottlenecks” during migratory stopover are increasingly being documented for small landbirds (Bayly et al. 2018). Here, in addition to admixture of wintering birds from various breeding locations, there was consistent use among populations of stopover regions in Central America. In particular, 2 large regions centered on the Honduras/Nicaragua border and the Costa Rica/Panama border were likely used during fall stopovers by birds from every breeding location sampled in this study despite the variability in migratory routes. In addition, the typical use of stopover sites for extended periods of time (>20 days) provides further evidence of the importance of these regions to the species. This migratory strategy appears analogous to the “staging” patterns of some shorebirds (families Charadriidae and Scolopacidae; Warnock 2010), and recently documented in a songbird (Wright et al. 2018), and is similar to a multi-site wintering strategy (e.g., Renfrew et al. 2013, Stutchbury et al. 2016). The documentation of these areas as more than brief refueling sites may prove to be critical for their conservation. Recent studies have shown continuous declines in mangrove habitats in Honduras because of activities such as shrimp farming (e.g., Chen et al. 2013). Among mangrove forests worldwide, those along the Pacific and Caribbean coasts of Central America have the greatest estimated extinction risk (Polidoro et al. 2010). Thus, in addition to surveying wintering locations in Colombia, future efforts should aim to understand habitat selection during the migratory period (e.g., Wolfe and Ralph 2009) and the ecological drivers of long stopover durations (Bayly et al. 2018) to identify specific threats the population may face during this phase of the annual cycle.

In conclusion, our results suggest that Prothonotary Warblers are likely more concentrated on the wintering grounds and at stopover sites than on the breeding grounds. This would imply that conservation actions and threats during these portions of their annual cycle could likely have disproportionate impacts (both positive and negative) on the species. A recent paper by Gilroy et al. (2016), which examined variation in breeding and nonbreeding dispersion in hundreds of European bird species, demonstrated that species with restricted winter distributions were more likely to be declining than those with greater population spread. Thus, conservation efforts directed toward Prothonotary Warblers wintering in a single country (Colombia), or those migrating through a small subset of stopover regions, would likely benefit individuals from across the breeding range. The benefits of such efforts, however, will depend on the role that factors on the nonbreeding grounds play in seasonal interactions (Marra et al. 1998, Harrison et al. 2011) and, ultimately, population dynamics. Such impacts could be measured through integrated population models (Schaub and Abadi 2011,

Hostetler et al. 2015). More broadly, our findings highlight the need to test long-held assumptions about a species' ecology (e.g., habitat specialization) and seasonal distributions. As new techniques and technologies open previously obscured areas of inquiry, new insights into spatial aspects of the annual cycle can often, as they have here, lead to further lines of research. Such research is critical to a more complete understanding of population structure, limitation, and adaptability.

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APPENDIX TABLE 2. Deployment and recovery locations for geolocators placed on Prothonotary Warblers at breeding sites in 6 states from 2014 to 2016. Numbers represent total birds (number of females) on which geolocators were deployed and recovered. Final column represents the number of birds that returned to the site but either eluded recapture or were recaptured but had lost their geolocators.

State	Site	Latitude	Longitude	Year of deployment	Number deployed	Number recovered	Number recovered with data	Number returned, but unrecovered or tag dropped
Arkansas	White River National Wildlife Refuge	34.26°N	91.10°W	2015	20(9)	7(2)	7(2)	0(0)
Louisiana	Atchafalaya National Wildlife Refuge	30.49°N	91.71°W	2014	4(0)	2(0)	2(0)	0(0)
	Bluebonnet Swamp Nature Center	30.37°N	91.11°W	2013	2(0)	1(0)	1(0)	0(0)
	Brownell Memorial Park	29.74°N	91.17°W	2014	3(2)	2(2)	2(2)	0(0)
	Butte Larose Biological Station	30.33°N	91.69°W	2016	4(2)	1(1)	1(1)	1(0)
	Cypress Island Preserve	30.20°N	91.90°W	2016	2(2)	1(1)	1(1)	0(0)
	Frenchtown Rd Conservation Area	30.48°N	90.99°W	2014	3(2)	0(0)	0(0)	0(0)
	Jean Lafitte National Historical Park & Preserve	29.81°N	90.14°W	2016	5(1)	2(0)	1(0)	0(0)
	Oak Hill Plantation	29.86°N	91.40°W	2016	1(0)	0(0)	0(0)	0(0)
	Palmetto Island State Park	29.86°N	92.15°W	2014	2(0)	0(0)	0(0)	0(0)
	Dittmann/Cardiff residence (private)	30.31°N	91.09°W	2016	7(3)	0(0)	0(0)	1(1)
	Sam Houston Jones State Park	30.29°N	93.26°W	2014	2(0)	1(0)	1(0)	1(0)
	Sherburne Wildlife Management Area	30.47°N	91.73°W	2014	1(0)	0(0)	0(0)	0(0)
Ohio	Hoover Nature Preserve	40.21°N	82.88°W	2015	5(1)	2(0)	2(0)	0(0)
South Carolina	Beidler Forest	33.22°N	80.35°W	2014	1(0)	0(0)	0(0)	0(0)
	Deep Bottom	37.41°N	77.30°W	2016	25(6)	7(2)	3(1)	0(0)
	Presquile National Wildlife Refuge	37.61°N	77.25°W	2014	1(0)	1(0)	1(0)	0(0)
	Avon Bottoms Natural Area	42.53°N	89.32°W	2014	8(2)	3(0)	2(0)	0(0)
				2014	13(7)	1(0)	1(0)	0(0)
				2014	12(12)	3(3)	3(3)	1(1)
Wisconsin				2016	22(0)	6(0)	3(0)	0(0)

APPENDIX TABLE 3. Location, date, and time of deployment and retrieval, and total duration of deployment, of 2 geolocators for calibration of location data on the wintering grounds in 2016. Geolocators were tied to tree branches at a height of ~2 m at 5 known wintering locations of Prothonotary Warblers along the northern coast of Colombia. Geolocator 1 was a stalked model ML6140 (Lotek Wireless) and Geolocator 2 was a stalkless model Intigeo-P50Z11 (Migrate Technology).

Geolocator	Location	Latitude	Longitude	Deployed		Retrieved		Deployment duration (days)
				Date	Hour	Date	Hour	
1	Salamanca	11.0063°N	74.6863°W	Jan 5	0545	Jan 21	0955	16.18
1	Flamencos	11.4201°N	73.1012°W	Jan 22	0630	Jan 25	0939	3.13
2	Salamanca	11.0063°N	74.6863°W	Jan 5	0545	Jan 9	0956	4.17
2	Marimonda	8.5691°N	76.8174°W	Jan 11	1109	Jan 13	1030	1.97
2	Bocas del Atrato	8.0892°N	76.8369°W	Jan 13	1633	Jan 16	0900	2.69
2	Cispata	9.3928°N	75.7839°W	Jan 17	2000	Jan 20	1045	2.60
2	Flamencos	11.4201°N	73.1012°W	Jan 22	0630	Jan 25	0939	3.13