

Geocator reveals migratory and winter movements of a Prothonotary Warbler

Jared D. Wolfe^{1,2,3,4,6} and Erik I. Johnson^{1,2,5}

¹*School of Renewable Natural Resources, Louisiana State University Agricultural Center, Louisiana State University, 227 RNR Building, Baton Rouge, LA 70803, USA*

²*Louisiana Bird Observatory, Baton Rouge Audubon Society, P. O. Box 67016, Baton Rouge, Louisiana 70896, USA*

³*U.S.D.A. Forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, California 95521, USA*

⁴*Klamath Bird Observatory, P. O. Box 758, Ashland, Oregon 97520, USA*

⁵*Audubon Louisiana, National Audubon Society, 6160 Perkins Road, Suite 135, Baton Rouge, Louisiana 70808, USA*

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ABSTRACT. Prothonotary Warblers (*Protonotaria citrea*) are Nearctic-Neotropical migrants that have experienced declining populations over the past 50 yr. Determining their migration routes and wintering areas are critical steps in identifying habitats used by species and populations of conservation concern. We captured a male Prothonotary Warbler on its breeding territory in Louisiana in June 2013 and attached a geocator. We recaptured this male in March 2014 and analysis of the geocator data revealed that the male traveled an estimated 7950 km through seven countries. Fall migration was characterized by movements south into Central America on 13 August 2014, then east to the Greater Antilles for about 1 mo, followed by a second movement south to Panama or Colombia on 15 November 2014 where the male remained for the rest of the winter. Spring migration occurred rapidly, with the bird leaving its southern wintering area on 4 March 2014 and returning to its breeding territory on 23 March 2014. The movements of this male Prothonotary Warbler add to accumulating evidence that many migrant birds exhibit either prolonged stopover behavior or secondary migratory movements. Factors contributing to prolonged stopover behavior or additional migratory movements of the Prothonotary Warbler in our study warrant further investigation.

RESUMEN. Geocalizador revela los movimientos migratorios y durante el invierno de *Protonotaria citrea*

La Reinita anaranjada (*Protonotaria citrea*) es un migratorio neártico-neotropical cuyas poblaciones se han ido reduciendo en los últimos 50 años. El determinar sus rutas migratorias e identificar las áreas en donde pasan el invierno son pasos críticos en la identificación del hábitat utilizado por dichas especies y las preocupaciones para la conservación de la especie. Capturamos un macho de Reinita anaranjada en su territorio reproductivo en Luisiana en junio de 2013 y le colocamos un geocalizador. Recapturamos a dicho espécimen en marzo del 2014 y el análisis de los datos en el geocalizador revelaron que el individuo viajó 7950 km a través de siete países. La migración otoñal se caracterizó por movimientos hacia el sur de Centro América para agosto 13, 2014, luego se movió hacia el este, hasta las Antillas Mayores, y permaneció en estas por cerca de un mes, seguido de otro movimiento al sur de Panamá o Colombia en noviembre 15, donde paso el resto del invierno. La migración primaveral ocurrió rápidamente, dejando el ave su lugar invernal en marzo 4, y llegando a su territorio reproductivo el 23 de marzo de 2014. Los movimientos de este individuo macho añaden, a la evidencia ya acumulada, que muchos migratorios exhiben conducta prolongada de permanecer en lugares de parada o de exhibir movimientos migratorios secundarios. Los factores que contribuyen a permanecer por periodos prolongados en lugares de parada o movimientos migratorios adicionales merecen ser investigados.

Key words: intratropical migration, overwinter movement, *Protonotaria citrea*, stopover, trans-Gulf

Prothonotary Warblers (*Protonotaria citrea*) are New World warblers that breed in swamps, bottomland forests, and other forested wetlands in the southeastern, midwestern, and eastern United States (Petit 1999). Highly migratory, Prothonotary Warblers leave breeding areas

between mid-July and September and arrive in wintering areas in the Caribbean, Central America, and northern South America between late August and October (Janssen 1987, Ridgely and Gwynne 1989, Stiles and Skutch 1989, Walkinshaw 1991, Robbins and Easterla 1992). In wintering areas, Prothonotary Warblers use mangrove and coastal scrub habitat where they can switch from a predominantly insectivorous diet to one that includes fruit (Petit 1999,

⁶Corresponding author. Email: jdw@klamathbird.org

Wolfe et al. 2014). Prothonotary Warblers often successfully breed in degraded and fragmented habitats in temperate areas (Lee and Clark 1985) so precipitous declines of some populations suggest that events occurring outside their breeding range may be limiting population growth (Sauer et al. 2014).

To prioritize conservation strategies, determining where breeding populations spend the non-breeding season is a critical step toward protecting core areas of habitat use. For the past several years, migration routes and wintering areas of migratory birds have been identified using light-sensitive data-loggers, or geolocators (e.g., Stutchbury et al. 2009, Lemke et al. 2013). Our primary objective was to use a geocator to monitor the migratory movements and identify wintering areas of a Prothonotary Warbler that nested in Louisiana. Previous studies suggest that Prothonotary Warblers are not territorial during the winter and may exhibit long-distance movements (Lefebvre et al. 1992). Although they may move between areas during the winter, Prothonotary Warblers are known to exhibit strong site fidelity within and between years (Warkentin and Hernández 1996, Wolfe et al. 2013). Thus, our secondary objective was to examine the movements of a Prothonotary Warbler during the non-breeding season.

METHODS

We studied Prothonotary Warblers breeding in Bluebonnet Swamp Nature Preserve located within the city limits of Baton Rouge, Louisiana (30.37 N, -91.11 W). Bluebonnet Swamp is a 41.7-ha preserve comprised of bald cypress-tupelo swamp with an adjacent lowland deciduous hardwood forest. Three 0.5-g geolocators (Model MK6740, Lotek, Ontario, Canada) were deployed using 1-mm stretch-bead cord (Stretch Magic, Pepperell Braiding Company, Pepperell, MA) in June 2013 on one SY (second-year) and two ASY (after-second-year) male Prothonotary Warblers at Bluebonnet Swamp. One of the ASY males dropped his geocator prior to fall migration, and the SY male was never seen again after initial capture. The remaining ASY male with a geocator was last observed at Bluebonnet Swamp on 12 August 2013. The same bird was resighted on 23 March 2014 near the same nest box used the previous year, and was recaptured on 25 March 2014 and the geocator was retrieved.

Data from the geocator were extracted and processed using BASTrak software (British Antarctic Survey, Cambridge, UK). Several software filters, time-corrections, and a transition light level of 12 were used to estimate the longitude and latitude of the bird throughout the year. Because errors associated with estimates of latitude and longitude often result from shading, such as vegetation and cloud cover, we calibrated the geocator by matching sunrise and sunset against 1 mo of light-level data collected while the geocator was on the free-living bird at the capture location. The position and standard error associated with the 1-mo calibration period were 30.308 ± 0.273 latitude and -90.884 ± 0.247 longitude, with an estimated sun elevation prior to departure of -2.47348° . This allowed us to estimate latitude and longitude under average conditions elsewhere throughout the year, although, as in other geocator studies, accuracy of each point was no more certain than 100–150 km. Latitudinal estimates within 20 d of the spring and fall equinox were ignored; dates included in the analysis, but nearer the fall and spring equinox, made positioning latitude within Central American relatively uncertain. More specifically, we excluded 27 d initially based on poor transitions and then another 52 that were considered outliers, including 28 d surrounding the fall equinox and 17 d surrounding the spring equinox. Despite uncertainties in estimating latitude near the spring and fall equinox, longitude could be readily estimated throughout the year (Stutchbury et al. 2009). During migratory movements near the equinox, some assumptions were made to position the bird latitudinally. We considered the direction of movement before and after the equinox as well as the associated longitudes during the 40-d equinox period and, using the calculated longitude, we assumed the latitude that placed the bird on the nearest coastline because these warblers typically use wet lowland forest and mangroves during the non-breeding season. During stationary periods, we averaged latitudinal and longitudinal estimates and these shifted mid-points (but not error estimates) when necessary to the nearest land mass.

RESULTS

We estimated that the Prothonotary Warbler traveled a minimum of 7950 km and visited



Fig. 1. Estimated migratory routes of a Prothonotary Warbler fitted with a geolocator at Bluebonnet Swamp, Baton Rouge, Louisiana. Locations are labeled with associated dates and durations. Fall and spring migration are indicated by dashed and solid lines, respectively.

at least seven countries in a single calendar year. The warbler left Baton Rouge on 26 July 2014, briefly staged on the Gulf Coast in southwest Louisiana until 12 August 2014, then flew south across the Gulf of Mexico making landfall in Mexico on 13 August 2014. The male then moved east through the Yucatan and across the Caribbean to southern Cuba or Jamaica, remaining in the Greater Antilles from

9 October to 14 November (Fig. 1). The male then flew south on a nonstop flight over the Caribbean Sea, arriving in southeastern Panama or northwestern Columbia on 15 November and staying there until 4 March 2014.

The Prothonotary Warbler left Panama on 4 March 2014, heading north–northwest and making short westward movements over the next three weeks. However, estimating latitude

near the spring equinox made positioning the bird in Central America relatively uncertain. The male remained in Central America for approximately 3 weeks before making a final movement north across the Gulf of Mexico on 22 March and arriving at Bluebonnet Swamp on 23 March.

DISCUSSION

Spring migration by the Prothonotary Warbler in our study was rapid, leaving Panama on 4 March 2014 and returning to Bluebonnet Swamp on 23 March 2014. Prothonotary Warblers are one of the earliest-arriving migrant warblers in the Americas (Ridgely and Gwynne 1989), and this male was one of the first of its species to arrive at Bluebonnet Swamp in spring 2014. Fall migration by the Prothonotary Warbler included movement south into Central America, then east to the Greater Antilles for about 1 mo (11 October to 14 November), followed by a movement south to Panama/northwest Columbia for the duration of the winter. These movements suggest three possible scenarios.

First, the Prothonotary Warbler exhibited a secondary migratory movement during the overwinter period thereby spending considerable time at two locations. Lefebvre and Poulin (1996) pointed out that several investigators have reported a decline in migrant abundance in the West Indies (Emlen 1980, Wunderle 1995, Sherry and Holmes 1995) and Central America (Galindo et al. 1963, Greenberg 1984, Blake and Loiselle 1992) over the non-breeding season. In contrast, some habitats in South America support an increasing number of migrants throughout winter (Johnson 1980, Hilty 1980, Lefebvre and Poulin 1996), suggesting a second southerly migration. More recent geolocator studies have provided additional evidence of secondary migratory movements during the overwinter period from a number of bird species both in the New and Old World (Heckscher et al. 2011, Delmore et al. 2012, Fraser et al. 2012, Macdonald et al. 2012, Stach et al. 2012, Jahn et al. 2013a, b). The second migratory movement southward by the Prothonotary Warbler in our study may have been driven by shifting food resources during the overwinter period (Lefebvre and Poulin 1996, McKinnon et al. 2013).

A second possibility is that the Prothonotary Warbler in our study spent considerable time during stopover prior to reaching its main wintering area in mid-November. Previous studies have provided no evidence of such a protracted fall migration by Prothonotary Warblers (Janssen 1987, Walkinshaw 1991, Robbins and Easterla 1992). However, more recent studies relying on geolocators have noted prolonged stopover periods for a number of bird species in the New and Old World (Bächler et al. 2010, Stutchbury et al. 2011, Åkesson et al. 2012, Tøttrup et al. 2012); in fact, the results of these studies have begun to call into question previously held ideas of what constitutes stopover and migratory behavior (McKinnon et al. 2013). Given recent evidence supporting prolonged stopover in a diversity of migrant species, we cannot dismiss the possibility that the Prothonotary Warbler in our study exhibited similar behavior.

Yet another possible explanation for our results is that errors in geolocator data acquisition resulted in erroneous estimates of locations. This seems unlikely, however, given our robust data validation routine and the precision of longitudinal estimates.

The Prothonotary Warbler in our study exhibited either prolonged stopover behavior or a secondary migratory movement during the overwinter period. Of course, with a sample size of one, our ability to differentiate between stopover behavior and additional migratory movements, or to generalize about the prevalence of such behaviors, is limited. The degree to which prolonged stopovers and secondary migratory movements are exhibited by other Prothonotary Warblers, or other species of New World warblers (Parulidae), are not known and merit additional study.

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LITERATURE CITED

- ÅKESSON, S., R. KLAASSEN, J. HOLMGREN, J. W. FOX, AND A. HEDENSTRÖM. 2012. Migration routes and strategies in a highly aerial migrant, the Common Swift *Apus apus*, revealed by light-level geolocators. *PLoS ONE* 7: e41195.
- BÄCHLER, E., S. HAHN, M. SCHAUB, R. ARLETTAZ, L. JENNI, J. W. FOX, V. AFANASYEV, AND F. LIECHTI. 2010. Year-round tracking of small trans-Saharan migrants using light-level geolocators. *PLoS ONE* 5: e9566.
- BLAKE, J. G., AND B. A. LOISELLE. 1992. Fruits in the diets of Neotropical migrant birds in Costa Rica. *Biotropica* 24: 200–210.
- DELMORE, K. E., J. W. FOX, AND D. E. IRWIN. 2012. Dramatic intra-specific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. *Proceedings of the Royal Society B* 279: 4582–4589.
- EMLEN, J. T. 1980. Interactions of migrant and resident landbirds in Florida and Bahama pinelands. In: *Migrant birds in the Neotropics: ecology, behavior, distribution and conservation* (A. Keast and E. S. Morton, eds.), pp. 133–143. Smithsonian Institution Press, Washington, D.C.
- FAO [FOOD AND AGRICULTURAL ORGANIZATION OF THE UNITED NATIONS]. 2007. *The world's mangroves 1980–2005*. FAO Forestry Paper 153, Food and Agricultural Organization of the United Nations, Rome, Italy.
- FRASER, K. C., B. J. M. STUTCHBURY, C. SILVERIO, P. M. KRAMER, J. BARROW, D. NEWSTEAD, N. MICKLE, N. B. F. COUSENS, J. C. LEE, D. M. MORRISON, T. SHAHEEN, P. MAMMENG, K. APPLGATE, AND J. TAUTIN. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proceedings of the Royal Society B* 279: 4901–4906.
- GALINDO, P., E. MENDEZ, AND A. J. ADAMES. 1963. Banding of migrant thrushes in Almirante, Panama. *Bird-Banding* 34: 202–209.
- GREENBERG, R. 1984. The winter exploitation systems of Bay-breasted and Chestnut-sided warblers in Panama. University of California Publications in Zoology 116: 1–124.
- HECKSCHER, C. M., S. M. TAYLOR, J. W. FOX, AND V. AFANASYEV. 2011. Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. *Auk* 128: 531–542.
- HILTY, S. L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. *Biotropica* 12: 292–306.
- JAHN, A. E., V. R. CUETO, J. W. FOX, M. S. HUSAK, D. H. KIM, D. V. LANDOLL, J. P. LEDEZMA, H. K. LEPAGE, D. J. LEVEY, M. T. MURPHY, AND R. B. RENFREW. 2013a. Migration timing and wintering areas of three species of flycatchers (*Tyrannus*) breeding in the Great Plains of North America. *Auk* 130: 247–257.
- , D. J. LEVEY, V. R. CUETO, J. P. LEDEZMA, D. T. TUERO, J. W. FOX, AND D. MASSON. 2013b. Long-distance bird migration within South America revealed by light-level geolocators. *Auk* 130: 223–229.
- JANSEN, R. B. 1987. *Birds in Minnesota*. University of Minnesota Press, Minneapolis, MN.
- JOHNSON, T. B. 1980. Resident and North American migrant bird interactions in the Santa-Marta highlands, northern Colombia. In: *Migrant birds in the Neotropics: ecology, behavior, distribution and conservation* (A. Keast and E. S. Morton, eds.), pp. 239–247. Smithsonian Institution Press, Washington, D.C.
- LEE, D. S., AND M. K. CLARK. 1985. Atypical nest site for a Prothonotary Warbler. *Chat* 49: 98–99.
- LEFEBVRE, G., B. POULIN, AND R. MCNEIL. 1992. Abundance, feeding behavior, and body condition of Nearctic warblers wintering in Venezuelan mangroves. *Wilson Bulletin* 104: 400–412.
- , AND ———. 1996. Seasonal abundance of migrant birds and food resources in Panamanian mangrove forests. *Wilson Bulletin* 108: 748–759.
- LEMKE, H. W., M. TARKA, R. H. KLAASSEN, M. ÅKESSON, S. BENSCH, D. HASSELQUIST, AND B. HANSSON. 2013. Annual cycle and migration strategies of a trans-Saharan migratory songbird: a geolocator study in the Great Reed Warbler. *PLoS ONE* 8: e79209.
- MACDONALD, C. A., K. C. FRASER, H. G. GILCHRIST, T. K. KYSER, J. W. FOX, AND O. P. LOVE. 2012. Strong migratory connectivity in a declining Arctic passerine. *Animal Migration* 1: 23–30.
- MCKINNON, E. A., K. C. FRASER, AND B. J. STUTCHBURY. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. *Auk* 130: 211–222.
- PETTIT, L. J. 1999. Prothonotary Warbler (*Protonotaria citrea*). In: *The birds of North America Online* (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- ROBBINS, M. B., AND D. A. EASTERLA. 1992. *Birds of Missouri: their distribution and abundance*. University of Missouri Press, Columbia, MO.
- RIDGELEY, R. S., AND J. A. GYNNNE, JR. 1989. *A guide to the birds of Panama*. Princeton University Press, Princeton, NJ.

- SAUER, J. R., J. E. HINES, J. E. FALLON, K. L. PARDIECK, D. J. ZIOLKOWSKI, JR., AND W. A. LINK [online]. 2014. The North American Breeding Bird Survey, results and analysis 1966 – 2012. Version 02.19.2014. Patuxent Wildlife Research Center, Laurel, MD. <<http://www.mbr-pwrc.usgs.gov/bbs/>> (Accessed July 2014).
- SHERRY, T. W., AND R. T. HOLMES. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence? In: *Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues* (T. E. Martin and D. M. Finch, eds.), pp. 85–120. Oxford University Press, New York, NY.
- STACH, R., S. JAKOBSSON, C. KULLBERG, AND T. FRANSSON. 2012. Geolocators reveal three consecutive wintering areas in the Thrush Nightingale. *Animal Migration* 1: 1–7.
- STILES, F. G., AND A. F. SKUTCH. 1989. *A guide to the birds of Costa Rica*. Comstock, Ithaca, NY.
- STUTCHBURY, B. J. M., E. A. GOW, T. DONE, M. MACPHERSON, J. W. FOX, AND V. AFANASYEV. 2011. Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proceedings of the Royal Society B* 278: 131–137.
- , S. A. TAROF, T. DONE, E. GOW, P. M. KRAMER, J. TAUTIN, J. W. FOX, AND V. AFANASYEV. 2009. Tracking long-distance songbird migration using geolocators. *Science* 323: 896.
- TERBORGH, J. 1989. *Where have all the birds gone?* Princeton University Press, Princeton, NJ.
- TØTTRUP, A. P., R. H. G. KLAASSEN, R. STRANDBERG, K. THORUP, M. W. KRISTENSEN, P. S. JØRGENSEN, J. FOX, V. AFANASYEV, C. RAHBK, AND T. ALERSTAM. 2012. The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society B* 279: 1008–1016.
- WALKINSHAW, L. H. 1991. Prothonotary Warbler. In: *The atlas of breeding birds of Michigan* (R. Brewer, G. A. McPeck, and R. J. Adams, Jr., eds.), pp. 430. Michigan State University Press, East Lansing, MI.
- WARKENTIN, I. G., AND D. HERNÁNDEZ. 1996. The conservation implications of site fidelity: a case study involving Nearctic-Neotropical migrant songbirds wintering in a Costa Rican mangrove. *Biological Conservation* 77: 143–150.
- WOLFE, J. D., M. D. JOHNSON, AND C. J. RALPH. 2014. Do birds select habitat or food resources? Nearctic-Neotropical migrants in northeastern Costa Rica. *PLoS ONE* 9: e86221.
- , ———, AND ———. 2013. Greater mass increases annual survival of Prothonotary Warblers wintering in northeastern Costa Rica. *Condor* 115: 163–167.
- WUNDERLE, J. M., Jr. 1995. Population characteristics of Black-throated Blue Warblers wintering in three sites on Puerto Rico. *Auk* 112: 931–946.