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The mystery of the missing warbler

Migratory songbirds are among the most well-studied of vertebrates. Miniaturization of tracking devices as well as the popularity of online citizen science databases (e.g., www.ebird.org, www.wikiaves.com.br) are generating a wealth of data on many species, including those that migrate annually between hemispheres (Fraser et al. 2012, La Sorte et al. 2016). Here, we show that the 13 g Connecticut Warbler (*Oporornis agilis*; Fig. 1) makes a previously undocumented 2-d long open-ocean flight from the eastern coast of the US to the Greater Antillean islands. Until now, even basic year-round distribution has been unclear for this species, despite its membership in the well-studied wood-warbler family (Parulidae). Scant information on its breeding biology comes from the study of a single nest in 1960 (Walkinshaw and Dyer 1961). The paucity in breeding information for the Connecticut Warbler, named by the Scottish-American naturalist Alexander Wilson for a specimen collected in that state, likely stems from its preference for northern, boggy forests, where human population density is low and the logistics of fieldwork are difficult. Fall migration was assumed to occur along the eastern US coast, through the Antillean islands to putative nonbreeding grounds in South America. Records on the nonbreeding grounds for this species are rarer still. Of >25,000 Connecticut Warblers banded since 1955, only three were captured within the nonbreeding period (December–February); none were captured



FIG. 1. Connecticut Warblers (*Oporornis agilis*) are arguably one of the most understudied songbirds to breed in North America. (Photo by K. Bell). [Color figure can be viewed at wileyonlinelibrary.com]

within the expected nonbreeding range (Appendix S1). The fact that a recent capture of a single individual in Brazil was of scientific interest (Diniz et al. 2014) illustrates how elusive this species is outside of the breeding season. In effect, Connecticut Warblers have been “missing in action” for nearly all of fall migration as well as during the boreal winter.

Chapman (1907) noted Connecticut Warblers are “common in the Atlantic states” in fall, and that individuals were “excessively fat, no other warbler approaching them in this respect”. Generally, birds with excessive fat stores are preparing for very long migratory flights, often over water. The long-held hypothesis that the Blackpoll Warbler (*Setophaga striata*) migrates southward over the ocean in fall was recently confirmed via direct-tracking using light-level geolocators (DeLuca et al. 2015). We hypothesized that Connecticut Warblers may also use this ocean-crossing migratory strategy. Connecticut and Blackpoll Warblers both breed in northern forests and overwinter in South America; thus, selection may have favored a convergent fall migration strategy for these species. Further anecdotal evidence supports this idea. Connecticut Warblers, despite their overall rarity, are regularly recorded in fall on Bermuda, including a record of 75 individuals grounded during Hurricane Emily in September 1987 (Pitocchelli et al. 2012). There is also a detailed account of a flock of at least eight Connecticut Warblers attracted to the lights of a Caribbean cruise ship in 8 October 2002, between St. Thomas (British Virgin Islands) and Saint Martin (Netherlands Antilles) islands (G. Kunkel, www.bio.uma.edu/biology/kunkel/gjk/migration/migration.html). These records suggest that Connecticut Warblers are travelling primarily overwater, from the eastern Atlantic Coast of the US to the eastern Caribbean. The relative scarcity even of island records suggests some individuals may travel from the US directly to the northern coast of South America, by-passing the Caribbean islands altogether, thus avoiding all human detection.

To test this migratory-marathon hypothesis, we began by equipping individual Connecticut Warblers ($n = 29$) with migration-tracking geolocators at their breeding sites in Manitoba in June 2015. We used miniature (0.45 g) geolocators (MigrateTech MK50, 6-month battery life) tied with an individually sized harness. These tags do not transmit data, but must be recovered in the following year to retrieve migration information. In 2016 we successfully recaptured 4 of the 29 individuals and removed the tags (a suspected fifth returning bird evaded capture). We downloaded data from the tags, and processed these data using R packages designed for light data analysis (see Appendix S1). Briefly, sunrise and sunset times were used to estimate daily latitude and longitude. We ignored

latitude estimates during the equinox period (8 September–8 October) and concentrated on longitude estimates during this time, which are not affected by the equinox. Longitudes were examined for shifts indicating movements.

We found clear evidence that Connecticut Warblers migrate over the Atlantic Ocean in fall (Fig. 2) by using a minimum 48-h non-stop flight from the eastern coast of the US to landing points on Cuba or Hispaniola, a distance of 1,700–2,400 km. After a stop of 5–7 d, Connecticut Warblers again traveled over open water (the Caribbean Sea) in a single flight covering 600–800 km before travelling to their final nonbreeding sites in the Amazon basin. While an open-water crossing may seem extreme, wind patterns provide the necessary advantage. Westerlies initially carry birds out to sea towards

Bermuda, where northeastern trade winds push them southwards towards the Caribbean (Williams and Williams 1978). We estimated a flight speed of 9–14 m/s for the first ocean-crossing, similar to estimated flight speeds of Blackpoll Warblers (DeLuca et al. 2015). This is the first direct evidence of any other songbird using an open-ocean strategy to reach nonbreeding sites in South America. Warblers detected by radar off the Atlantic coast cannot be identified accurately to species, but are assumed to be Blackpolls (Williams and Williams 1978). We suggest that Connecticut Warblers and other species could be included in these nonspecific radar detections.

Open-water crossings impose strong selective pressures on songbird morphology and behavior (Corman et al. 2014). Comparative analyses of wing morphology of Connecticut and Blackpoll Warblers vs. related

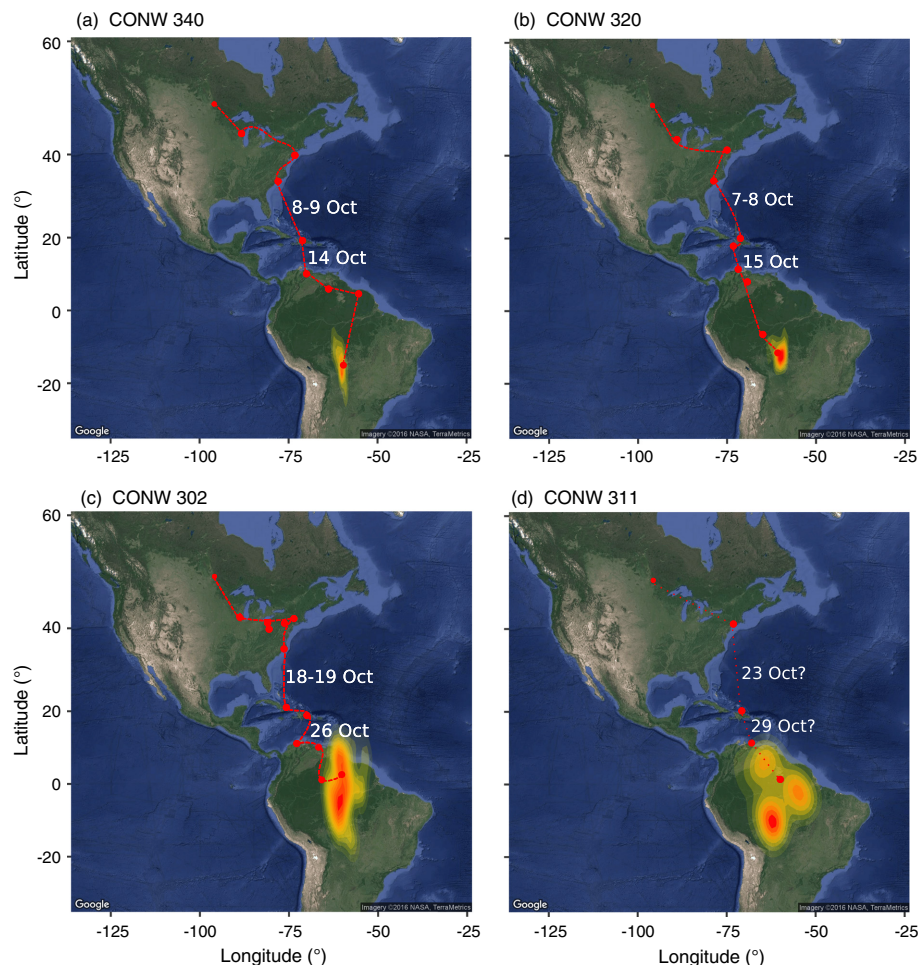


FIG. 2. Estimated fall migration routes of four male Connecticut Warblers from a breeding site in Manitoba, Canada. Each bird's estimated path is shown by a dashed line, with points indicating at least two consecutive days in the same location (based on longitudes), and estimates for the nonbreeding locations shown (kernel utilization distributions; high density of locations are red). Dates indicate the open-water flights, identified by examining the raw light data for days with no habitat shading (see Appendix S1). Light data from individual 311 (d) were very poor quality and thus the path is represented by a dotted line and dates with question marks. [Color figure can be viewed at wileyonlinelibrary.com]

species could provide insight into selection pressures for flight efficiency vs. selection for maneuverability in forested habitats where these species breed and overwinter. The fact that 2 of 4 of our Connecticut Warblers were over the Atlantic ocean on the exact same date (8 October; Fig. 2a, b) could be evidence of flexible tuning of take-off decisions to local conditions, or environmental canalization of overall migration timing (Pulido and Widmer 2005). Selection should have strongly favored behavior that would allow birds to avoid fall hurricanes and other inclement weather when they are embarking on a multiple-day over-water journey. More frequent or more severe hurricanes associated with warmer oceans could change the optimal timing for open-water flights for species such as the Connecticut Warbler; understanding proximate drivers of migration timing is an important area of research.

Many songbirds regularly cross the Gulf of Mexico between the US to the Yucatán peninsula of Mexico (e.g., Stanley et al. 2015); yet over-water flights of the Connecticut Warbler amount to 3× the distance covered by the typical trans-Gulf migrant. These marathon flights support the hypothesis that selection has favored a time-minimizing migratory strategy for Connecticut Warblers, which requires massive fuel loads but few en-route stops (Alerstam 2011). This strategy relies heavily on high-quality staging and stopover habitats, yet for most songbirds, migration habitat requirements remain one of the biggest knowledge gaps and a critical area for future research. This long-flight, few-stops strategy is much more typical of shorebirds, for which we know key staging areas are key to entire species' survival (e.g. Red Knots *Calidris canutus* Baker et al. 2004).

The main stopover sites for Connecticut Warblers appear to be on the island of Hispaniola, particularly on the western side in Haiti. This may explain why Connecticut Warblers are generally under-detected in the Caribbean; Hispaniola's landscape is rugged, and humanitarian crises have resulted in few bird surveys there in recent decades. If this is a major stopover for Connecticut Warblers,

it is cause for concern, as the forests of Haiti and the Dominican Republic are almost entirely gone (Latta 2005, Hansen et al. 2013). Breeding-range wide, Connecticut Warbler populations appear to be declining quite severely. In the core breeding range in Manitoba, abundance trends show 3.25% population loss per year (1996–2013; 95% CI –3.82 to –1.15; Sauer et al. 2014). Solving one mystery with respect to fall migration routes of this species has therefore opened up an even more pressing issue of conservation of critical habitat. Identifying nonbreeding habitat usage, particularly at major migratory stopovers and nonbreeding sites, is now a critically important step towards ensuring the conservation of this little-known warbler before it disappears altogether.

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