BIOLOGY LETTERS

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Cite this article: DeLuca WV, Woodworth BK, Rimmer CC, Marra PP, Taylor PD, McFarland KP, Mackenzie SA, Norris DR. 2015 Transoceanic migration by a 12 g songbird. *Biol. Lett.* **11**: 20141045.
http://dx.doi.org/10.1098/rsbl.2014.1045

Received: 9 December 2014
Accepted: 1 March 2015

Subject Areas:
ecology

Keywords:
Atlantic Ocean, blackpoll warbler, geolocator, *Setophaga striata*

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2014.1045 or via http://rsbl.royalsocietypublishing.org.

THE ROYAL SOCIETY PUBLISHING

Animal behaviour

Transoceanic migration by a 12 g songbird

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Many fundamental aspects of migration remain a mystery, largely due to our inability to follow small animals over vast spatial areas. For more than 50 years, it has been hypothesized that, during autumn migration, blackpoll warblers (*Setophaga striata*) depart northeastern North America and undertake a non-stop flight over the Atlantic Ocean to either the Greater Antilles or the northeastern coast of South America. Using miniaturized light-level geolocators, we provide the first irrefutable evidence that the blackpoll warbler, a 12 g boreal forest songbird, completes an autumn transoceanic migration ranging from 2270 to 2770 km (mean $\pm$ s.d.: 2540 $\pm$ 257) and requiring up to 3 days (62 h $\pm$ 10) of non-stop flight. This is one of the longest non-stop overwater flights recorded for a songbird and confirms what has long been believed to be one of the most extraordinary migratory feats on the planet.

1. Introduction

Birds are renowned for accomplishing remarkable migratory feats [1,2] but for many species, particularly small songbirds, we have a surprisingly poor understanding of the migratory routes that connect temperate breeding grounds to tropical wintering areas [3]. The blackpoll warbler (*Setophaga striata*, hereafter 'blackpoll') is a small (approx. 12 g) songbird that breeds throughout the boreal forest in North America and winters in northern South America [4]. In spring, evidence suggests that blackpolls migrate northward overland through North America after one or more short overwater flights from South America [4]. By contrast, it has been hypothesized for more than 50 years that, on their autumn southward migration, blackpolls depart from northeastern North America and undertake a single non-stop flight over the Atlantic Ocean to either the Greater Antilles or the northeastern coast of South America [5–7]. Depending on exact departure and arrival locations, this flight could cover distances of 2700–4500 km. This migratory pattern is supported by several lines of evidence, including radar studies showing departure orientations of blackpolls in northeastern North America directed over the Atlantic [5], a paucity of blackpoll observations and captures in the southeastern US during autumn [8], as well as observations of migrating blackpolls in Bermuda [5] and on offshore vessels in the Atlantic [9]. Despite this circumstantial evidence, others have questioned its validity, suggesting instead that blackpolls more likely follow overland routes in autumn, similar to those used during spring migration [10,11].

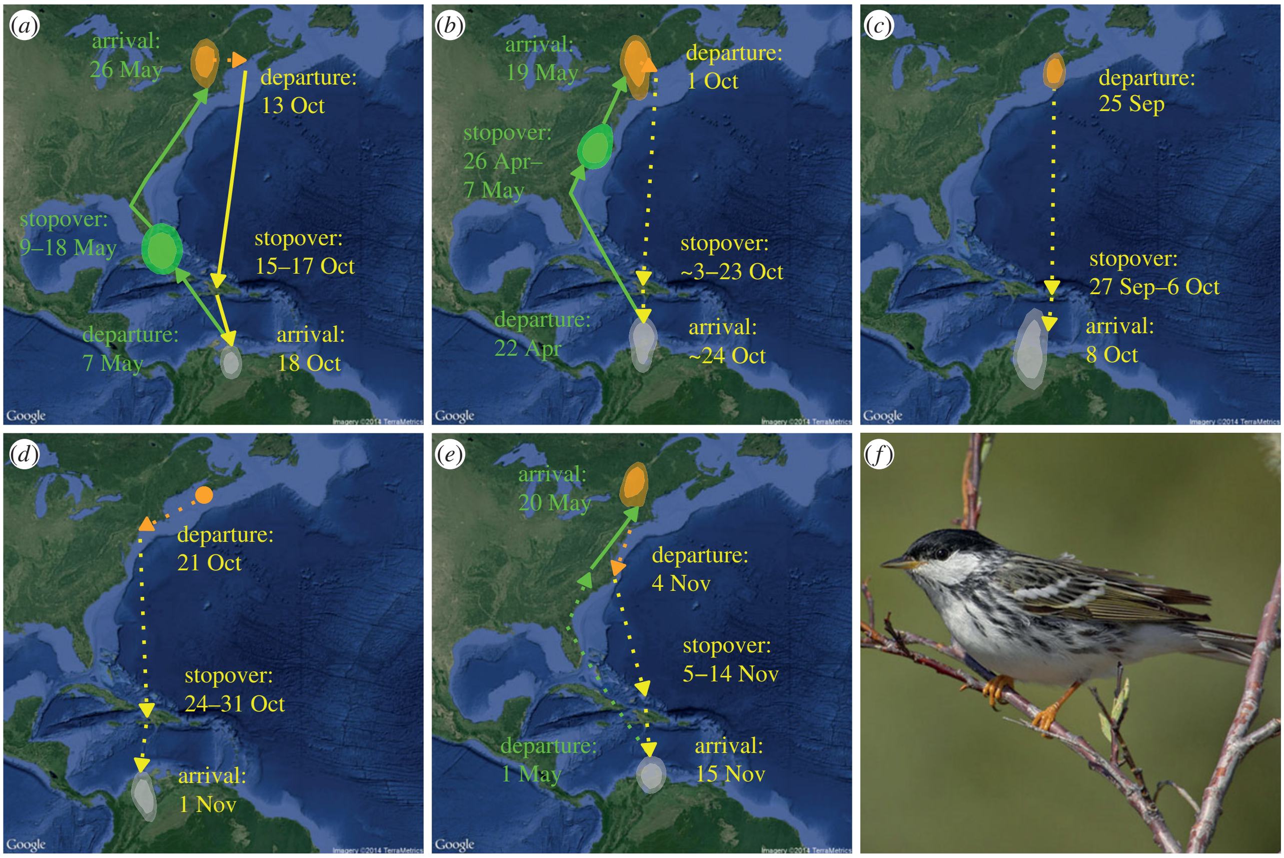

Figure 1. Migration routes, stopover locations and winter distributions of five blackpoll warblers (*a–e*) breeding in northeastern North America, as inferred from light-level geolocators. Lines represent migratory (yellow: autumn migration; green: spring migration) and premigratory (orange) movements. Dashed lines show movements when latitude estimates were poor, typically close to the equinoxes. Lines illustrate minimum distance routes based on longitudinal estimates and are not intended to represent the precise migratory pathway. Kernel densities (estimated using the R package 'adehabitatHR' [17]) encompass 30 and 50% of positions estimated during the breeding season (orange; 13–18 June to autumnal equinox), winter (grey; 15 December to 15 February) and spring stopovers of at least seven days (green). For stopovers of less than 7 days or when latitude estimates were poor, kernels were not estimated but arrows point to estimated stopover locations. (*f*) An adult male blackpoll warbler in breeding plumage. (Photograph by Robert Royse.) Maps (courtesy of Google Earth) were created using the R package 'ggmap' [18].

Here, we use miniaturized archival light-level geolocators [12] to directly test whether blackpolls embark on a trans-oceanic flight during autumn migration. We then use a flight range equation to confirm that the blackpoll's non-stop flight distance is physiologically possible given observed fuel loads and then compare the non-stop flight distances of blackpolls with those documented in other landbird species while controlling for body mass.

2. Material and methods

(a) Study sites and field methods

Between May and August 2013, we captured 19 blackpolls on Mt Mansfield, Vermont, USA (44°31′ N, 72°48′ W; hereafter 'VT'), 10 blackpolls on Bon Portage Island, Nova Scotia, Canada (43°27′ N, 65°44′ W), and eight on Seal Island, Nova Scotia, Canada (43°24′ N, 66°01′ W; collectively referred to as 'NS'). Using a leg-loop harness [13], VT blackpolls (mean body mass: 11.8 g ± 0.6 s.d.) were fitted with Biotrack model MK-6 (0.5 g including harness) geolocators and NS blackpolls (12.3 g ± 1.0 s.d.) were fitted with Migrate Technology Ltd Intigeo-W50 (0.45 g including harness) geolocators. Five of the 37 geolocators were recovered in 2014 ($n = 3$ in VT, $n = 2$ in NS). An additional blackpoll was recaptured in VT but had lost its geolocator. We received ethical approval to conduct this study by the United States Geological Survey's Bird Banding Laboratory and Environment Canada's Bird Banding Office.

(b) Analysis of light data

Position estimates were derived from light-level recordings using the 'threshold method' [14], which we implemented using the GeoLight package [15] in R v. 3.0.2 [16] (electronic supplementary material, figure S1). Sunrise and sunset times were determined using threshold values of 3 (Intigeo) and 15 (Lotek). Erroneous sunrise and sunset times caused by shading events during the day or lighting events during the night were identified using a local polynomial regression and excluded from calibration and position estimation (see electronic supplementary material).

We excluded 21–45 days of latitude estimates surrounding the autumnal (22 September 2013) and vernal (20 March 2014) equinoxes because of similar day lengths across the globe. For all but one individual (figure 1*a*), this precluded estimating latitude to infer autumn migration routes. Instead, we simultaneously examined plots showing the quality of light transitions and corresponding shifts in longitude estimates, which were not obscured by the equinox (electronic supplementary material, figure S2). When individuals occupied shaded habitats prior to autumn migration, at stopover sites, and following arrival at wintering areas, sunset and sunrise transitions were noisy (i.e. nonlinear with numerous light peaks) and light levels varied widely throughout the day. By contrast, during a migratory flight, sunset and sunrise transitions were much cleaner and diurnal light levels were more consistent. Differences in the quality of light transitions were especially apparent for geolocators that recorded a full light range (electronic supplementary material, figure S2C,D), enabling us to estimate the timing and duration of extended migratory flights. Longitude estimates preceding, during and following periods of clean transitions allowed us to approximate departure and stopover areas for each individual, and to determine whether blackpolls migrated over the western Atlantic Ocean or coastal North America. Minimum non-stop overwater flight distances were estimated as the shortest distance between estimated departure and stopover locations. However, our mapped minimum distance routes are not intended to represent the precise migratory pathways of individual birds, rather to provide a general spatial estimate sufficient to differentiate between overland and transoceanic flyways.

3. Results and discussion

Our data provide irrefutable evidence that blackpolls fitted with geolocators in VT and NS made non-stop flights over the Atlantic Ocean and overwintered either in northern Columbia or Venezuela (figure 1). Four of five birds departed between September 25 and October 21 from western Nova Scotia to western Long Island/New Jersey and made landfall in either Hispaniola (figure 1*a*,*b*,*d*) or Puerto Rico (figure 1*c*). Minimum overwater flight distances ranged from 2270 to 2770 km (mean $\pm$ s.d.: 2540 $\pm$ 257; electronic supplementary material, table S1) and lasted between 49 and 73 h (62 $\pm$ 10; electronic supplementary material, table S1), which corresponded to flight speeds between 10.7 and 13.4 m s^{-1} (12.2 $\pm$ 1.2). The fifth bird departed the US mainland on November 4 from Cape Hatteras and landed in Turks and Caicos (figure 1*e*) 18 h later (electronic supplementary material, table S1), having flown an estimated overwater distance of 1500 km at an average speed of 23.1 m s^{-1}. However, it is possible that this bird took a different route to the wintering grounds that involved a shorter flight over water (see electronic supplementary material).

Our estimates of flight range (see electronic supplementary material) suggest that most blackpolls are capable of completing a non-stop trans-Atlantic flight, consistent with conclusions from previous studies [7,19]. A bird weighing 16.6 g, the mean weight of blackpolls captured with pre-migratory fat loads in Nova Scotia, is predicted to fly a maximum distance of 3800 km lasting 81 h. However, blackpolls in the lower 5% of observed weights (13.1 g) are likely able to migrate only 1660 km (40 h).

In contrast to autumn, spring migration tracks from three blackpolls show that they followed a more westerly route, moving northwest from their overwintering grounds to Cuba and Florida, and then travelling north along the eastern US seaboard before arriving on the breeding grounds in late May (figure 1*a*,*b*,*e*). Given our high degree of confidence in longitude estimates from geolocators (electronic supplementary material, figure S1, electronic supplementary material, table S2), there can be little doubt that the spring overland and autumn overwater migration routes of blackpolls are dramatically different.

Banding data support our findings that Hispaniola and Puerto Rico are used as autumn stopover sites by migrating blackpolls [20]. However, data from islands to the east, such as the British Virgin Islands [21] and Barbados [22] suggest that some blackpolls take a more easterly track, and possibly a direct flight to South America. It remains to be seen whether blackpolls breeding in other areas of North America, particularly further west, follow different routes to South America. Although some blackpolls appear to migrate through the southeastern US [6,10,11], our results support previous work suggesting that overland autumn routes are less common compared with transoceanic flights [5]. Individuals may be more likely to follow an overland autumn route when they are in poor body condition or during adverse weather conditions [6].

Compared with previously published non-stop flight estimates for other species, our data suggest that blackpolls undergo one of the longest distance non-stop overwater flights ever recorded for a migratory songbird. The extraordinary nature of this feat is underscored when overwater distance is scaled for body mass (233 km g^{-1} for blackpolls). By comparison, the northern wheatear (*Oenanthe oenanthe*, 25 g) travels an estimated non-stop distance of 3400 km from the Canadian Arctic to the UK [2], which is approximately 136 km g^{-1}. The ruby-throated hummingbird (*Archilochus colubris*), weighing only 3–4 g, is believed to migrate across the Gulf of Mexico [23], a minimum overwater distance of 850 km. Although this could be a longer distance than blackpolls given body size, no empirical tracking data exist to confirm the occurrence or distance of this putative overwater flight. Nevertheless, we provide direct evidence of a non-stop transoceanic flight in blackpoll warblers, finally confirming what has long been hypothesized as one of the most extraordinary migratory feats on the planet.

Data accessibility. The datasets supporting this article can be accessed in Dryad (http://dx.doi.org/10.5061/dryad.2f850).

Acknowledgements. We thank T. Brown, D. Bell, B. Collins, S. Faccio, T. Duclos, S. Hardy, N. Dodge, D. Giesbrecht, J. St-Amand, J. Smetzer, M. O'Brien, G. Thurber, and L. & C. Adams for assistance with field work.

Author contributions. W.V.D., C.C.R., P.P.M., P.D.T., K.P.M. and D.R.N. conceived and designed the study. W.V.D., B.K.W. and D.R.N. wrote the manuscript. C.C.R., P.P.M., P.D.T., K.P.M. and S.A.M. provided comments and reviewed the manuscript. B.K.W., D.R.N. and W.V.D. analyzed the data. C.C.R., B.K.W., W.V.D., K.P.M. and S.A.M. conducted the fieldwork. C.C.R., P.P.M., D.R.N., and P.D.T provided funding for this research. All authors have read and approve the final version of the manuscript.

Funding statement. This work was funded by the Smithsonian Migratory Bird Center (P.P.M.), University of Guelph (D.R.N.) and grants from the Norcross Wildlife Foundation (C.C.R., K.P.M), Vermont Monitoring Cooperative (C.C.R., K.P.M.), Natural Sciences and Engineering Research Council (D.R.N, P.D.T) and Bird Studies Canada.

Competing interests. We declare no competing interests.

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