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A boreal songbird's 20,000 km migration across North America and the Atlantic Ocean

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Migration is one of the most fascinating natural history events on the planet, and our understanding of these seasonal movements continues to rapidly increase with the advancement of tracking technology. For the 12 g Blackpoll Warbler (*Setophaga striata*; hereafter, Blackpoll; Fig. 1), the ability to follow year-round movement is essential given that they are one of the fastest declining songbirds in North America (Rosenberg et al. 2016). Although the study of Blackpoll migration has a long history and their non-stop flight over the Atlantic Ocean is often highlighted as a flagship example of remarkable songbird migrations (Gill 2007), much of this history has been anecdotal or based on indirect evidence (reviewed in DeLuca et al. 2015). Using small geolocator tracking devices, DeLuca et al. (2015) documented Blackpolls from breeding populations in the Maritimes and New England, at the southeastern margins of their range, depart from the northeast Atlantic coast and embark on a nonstop transoceanic flight of up to 3 d and 2,770 km on their way to overwintering grounds in South America. Yet, because their breeding range spans the entirety of North America's boreal forest, questions remain about the migration of Blackpolls from central and western breeding populations. Specifically, how does the phenology, duration, and routes of southward and northward migration vary geographically and do central- and western-breeding Blackpolls undertake similar overwater flights to eastern-breeding birds? Answers to these lingering questions can contribute vital natural history information for this declining species and provide insight into the physiological and ecological constraints that may limit extreme migration strategies.

We deployed archival light-level geolocators (Biotrack model MK-6; Biotrack, Wareham, UK, http://www.biotrack.co.uk/m-series.php; ~0.5 g with harness, 12-month battery life) on male Blackpolls at four locations across the boreal forest in 2016: Churchill, Manitoba, Canada (58°46′ N, 94°09′ W; $n = 31$), Whitehorse, Yukon Territory, Canada (60°43′ N, 135°03′ W; $n = 30$), Denali National Park, Alaska, USA (63°06′ N, 151°11′ W; $n = 20$) and Nome, Alaska (64°30′ N, 165°24′ W; $n = 30$; Fig. 2). We recovered a total of 27 tags (Churchill, $n = 12$; Whitehorse, $n = 5$; Denali, $n = 5$; Nome, $n = 5$) in 2017, of which 14 recorded data for southward and northward migration, 7 recorded data for some or all of southward migration only, and 6 failed before migration. We described timing and spatial information for three stages of southward migration: (1) cross-continent movement from the breeding grounds to the Atlantic coast of the United States; (2) stopover along the Atlantic coast; and (3) transoceanic movement toward the overwintering grounds (Appendix S1: Fig. S1). For northward migration, we extracted the timing and duration of migration from South America to the southeastern United States and the breeding grounds as well as the locations of multiday stopover locations. Northward migration routes were reconstructed using both latitude and longitude

FIG. 1. Western-breeding Blackpoll Warblers (*Setophaga striata*) undergo one of the most amazing migratory feats on the planet, crossing North America before flying over the Atlantic Ocean to South America. Pictured is a breeding male in Churchill, Manitoba, Canada on 21 June 2016 with a geolocator (only the light-level sensing stalk is visible on the back). (Photo by Christian Artuso).

estimates, whereas southward migration routes were reconstructed primarily using longitude estimates due to extensive overlap with the autumnal equinox (see Appendix S1 for detailed methods).

Blackpolls from the westernmost breeding locations (Nome and Denali) left the breeding grounds earlier than those farther east (Whitehorse and Churchill), but arrived in South America at similar times (mean ± SE; 30 October ± 2 d, Appendix S1: Fig. S2). After crossing North America in 18 ± 1.9 d (range = 7–29 d), individuals stopped over along the Atlantic coast for 26 ± 1.3 d (range = 18–41 d; Fig. 2a, Appendix S1: Fig. S1). This extended coastal stopover is similar to that found for Blackpolls further north along the Gulf of Maine (Brown and Taylor 2017, Smetzer and King 2018). All Blackpolls then embarked on a transoceanic movement to the north coast of South America that took an average of ~ 60 h (range = 48–96 h) to complete (Appendix S1: Table S1). Departure from the Atlantic coast exhibited some degree of synchronicity with 11 Blackpolls (52%) departing on 9 or 10 October and 6 departing on 21 or 22 October (Appendix S1: Table S1). With the possible exception of one bird, individuals completed the transoceanic movement without stopping (Fig. 2b). Based on estimated coastal departure locations from Rhode Island to Florida, minimum flight distances from the Atlantic coast to Venezuela ranged between 2,250 km and 3,400 km (Fig. 2, Appendix S1: Table S1). Overwintering sites were located primarily in the northern Amazon Basin (Fig. 2). Total minimum southward migration distances based on great circle routes ranged from 10,700 km for birds breeding in Nome, Alaska to 6,900 km for birds breeding in Churchill, Manitoba, and the average duration of southward migration was 60 ± 2 d (range = 45–78 d).

During northward migration, Blackpolls from the three western breeding sites departed South America on average two weeks earlier (21 April ± 1 d) than Blackpolls from Churchill (6 May ± 4 d), but arrived at the breeding grounds at similar times (1 June ± 1 d; Appendix S1: Fig. S2). The average total duration of northward migration was 34 ± 2 d (range = 17–49 d), slightly more than one-half the duration of southward migration. From South America, birds crossed the Caribbean Sea to the southeastern United States in ~ 3.4 ± 0.3 d (range = 2.5–6.0 d; n = 14), before stopping over in the central United States directly south of Lake Superior (39.1° ± 0.2° N, 91.9° ± 0.1° W, n = 108; Fig. 2c). Seven of eight Blackpolls from the three western populations and one Blackpoll from Churchill utilized this area, stopping there for 6.7 ± 0.7 d (n = 8), before quickly moving through the upper midwest states and prairie provinces, into northwest Canada. Blackpolls took 17.8 ± 1.8 d to reach western breeding sites from the central United States (Fig. 2c). Blackpolls destined for Churchill made one to three extended stopovers south of the Great Lakes and east of the stopover region used by western Blackpolls.

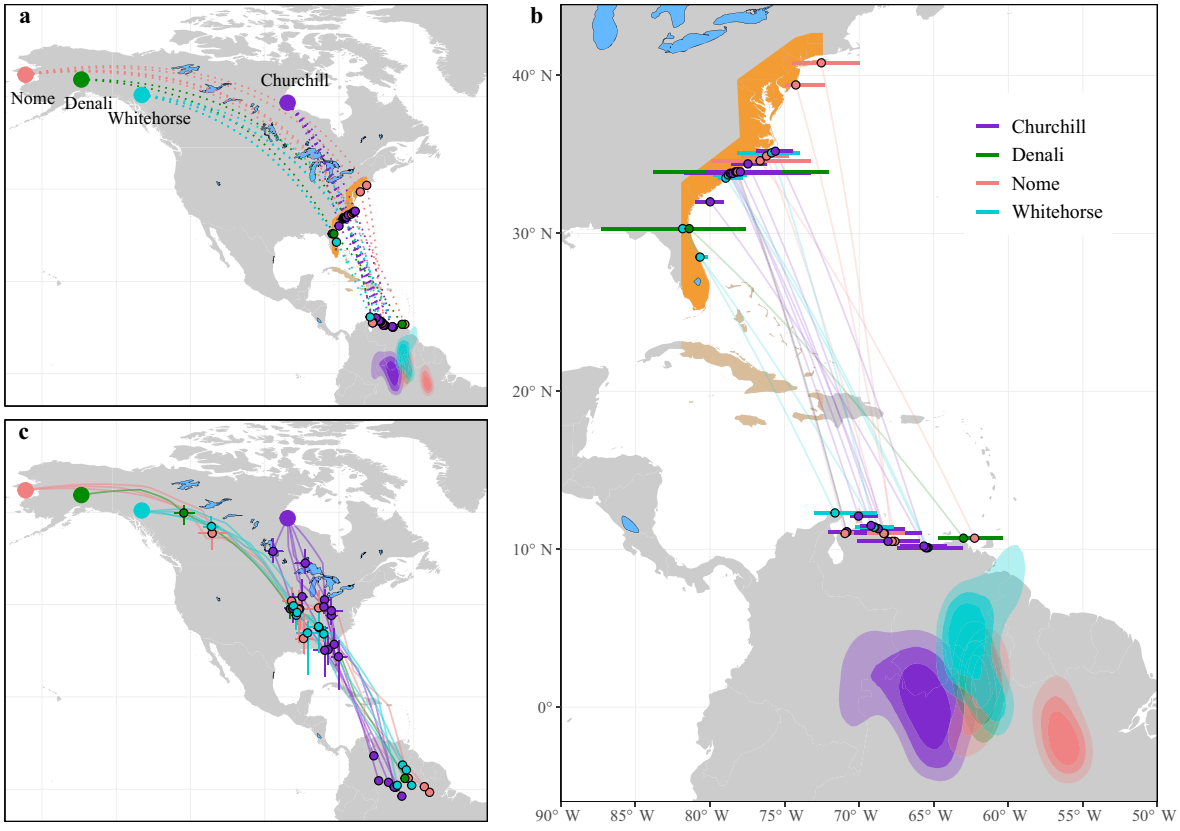

FIG. 2. (a, b) Southward and (c) northward migration of Blackpoll Warblers from four breeding sites in Nome, Alaska, USA; Denali, Alaska; Whitehorse, Yukon, Canada; and Churchill, Manitoba, Canada. (a) Great circle routes between breeding sites, estimated departure locations from the stopover region along the Atlantic Coast of the USA (dark orange), and the estimated overwintering grounds in South America. (b) Estimated longitudes of departure from the coast of North America and arrival along the coast of Venezuela. We highlighted the western Greater Antilles (light orange) to acknowledge the possibility that some Blackpolls could have moved directly south from the Atlantic coast (dark orange) to the western Greater Antilles without changing longitude before later departing for South America. (c) Northward migration routes for 14 individuals, with points in North America showing areas (mean ± 95% quantiles of latitude and longitude estimates) where individuals stopped over for 4 days or longer.

Our results show that Blackpolls across their boreal breeding range, travel thousands of kilometers eastward across North America before making a continuous flight over the Atlantic Ocean, to their overwintering grounds in South America, then migrate back to their breeding grounds along what is close to the most direct route. This represents one of the longest recorded round-trip migrations for a small songbird, up to 21,600 km in total for Blackpolls from Nome (~1,800 km/g; but see Sokolovskis et al. 2018). Moreover, some of the Blackpoll overwater flight distances (Appendix S1: Table S1) are on the edge of what was previously thought possible given the fuel requirements for a songbird weighing only ~12 g (Klaassen 1996). Other North American songbirds, for example, Bobolink (*Dolichonyx oryzivorus*, Perlut 2018) and Connecticut Warbler (*Oporornis agilis,* McKinnon et al. 2017), also make similar transoceanic flights, suggesting that transoceanic flights may be a strategy shared by more species than previously thought.

We still do not understand how extreme migrations may limit populations in the face of environmental change. During fall migration, prevailing westerly winds are predicted to increasingly facilitate transatlantic flights but wind assistance is expected to decrease over central and eastern portions of North America (La Sorte et al. 2018). Further complicating our understanding of how changing climate conditions may influence songbird migration are the potential changes in the frequency and intensity of extreme coastal weather events (Bender et al. 2010). Compared to Blackpolls from two eastern populations (DeLuca et al. 2015), western breeding Blackpolls appear to depart the Atlantic coast of North America farther south and fly straight to South America rather than stopping over in the Greater Antilles

(Fig. 2a). However, isotope analysis of feathers collected during migration in the Gulf of Maine region between 2007 and 2010 suggests that western-breeding Blackpolls also depart from coastal areas farther to the northeast (Holberton et al. 2015). It is possible that above-normal hurricane activity in the western Atlantic Ocean in 2016 (Beven 2017) could explain the more southwesterly coastal departure locations we observed. Tracks from individuals across the breeding range over multiple years could determine the extent to which migratory songbirds adapt their cross-continent and overwater flight routes to changes in wind conditions.

Our work begins to fill an important gap in the development of a range-wide migratory network for this species (Morris et al. 2015). Such networks are critical for not only identifying the location of major stopover and overwintering sites but also for determining the degree to which breeding populations mix during subsequent periods of the annual cycle (Taylor and Norris 2010). Connectivity information is key to linking habitat loss at breeding, overwintering and stopover sites to regional population fluctuations. For Blackpolls, our results suggest that loss or degradation of stopover habitat along the Atlantic coast of the United States, northern Venezuela, and the Great Lakes basin could result in disproportionately wide-ranging effects on Blackpoll abundance since they are used by individuals from across the breeding range.

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