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Research Paper

Light-level geolocation reveals moderate levels of migratory connectivity for declining and stable populations of Black-throated Blue Warblers (*Setophaga caerulescens*)

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ABSTRACT. Black-throated blue warbler (*Setophaga caerulescens*) populations have been declining at the southern edge of the breeding range in North Carolina over the past two decades. Determining the causes of population declines in migratory species requires knowledge of the threats faced throughout the entire annual cycle, necessitating accurate information about the migratory routes and non-breeding areas used by birds. We used light-level geolocators to identify the fall migratory routes and non-breeding distributions of adults breeding at the southern edge of the range in North Carolina ($n = 5$), where populations are declining, and at the core of the range in New Hampshire ($n = 8$), where populations are stable. The strength of migratory connectivity was moderate (mean = 0.42). New Hampshire birds used non-breeding areas broadly distributed across the Caribbean, whereas North Carolina birds used a restricted non-breeding area largely in the Dominican Republic. Suitable forest cover declined at a higher rate from 2000 to 2019 in the Dominican Republic than in other Caribbean countries (8.4% vs. 2–4% loss), exposing birds from the trailing edge to significantly higher suitable habitat loss on the non-breeding grounds compared with range-core birds. Birds from the two study populations also exhibited differing migratory routes, with North Carolina birds migrating south through Florida and many New Hampshire birds performing an overwater flight from the Carolinas to the Caribbean. Our results suggest the possibility that, at least for this species, forest loss on the island of Hispaniola could be exacerbating population declines at the southern edge of the breeding range in North Carolina.

La géolocalisation fondée sur le degré de lumière révèle un niveau modéré de connectivité migratoire chez des populations stables et en diminution de Parulines bleues (*Setophaga caerulescens*)

RÉSUMÉ. Les populations de Parulines bleues (*Setophaga caerulescens*) ont diminué à la limite sud de l'aire de reproduction en Caroline du Nord au cours des deux dernières décennies. Pour déterminer les causes du déclin de populations d'espèces migratrices, il faut connaître les menaces qui pèsent sur celles-ci tout au long du cycle annuel, et donc avoir accès à des informations précises sur les routes de migration et les aires hors reproduction utilisées par les oiseaux. Nous avons utilisé des géolocalisateurs munis de photorécepteurs pour identifier les routes de migration d'automne et la répartition hors reproduction d'adultes nichant à la limite sud de l'aire de répartition en Caroline du Nord (n = 5), où la population est en diminution, et au cœur de l'aire de répartition dans le New Hampshire (n = 8), où la population est stable. Le degré de connectivité migratoire était modéré (moyenne = 0,42). Les oiseaux du New Hampshire ont fréquenté des aires hors reproduction très réparties dans les Caraïbes, tandis que les oiseaux de Caroline du Nord ont utilisé des aires hors reproduction restreintes, principalement en République dominicaine. Le couvert forestier adéquat a diminué à un taux plus élevé de 2000 à 2019 en République dominicaine que dans les autres pays des Caraïbes (8,4 % contre 2-4 % de perte), exposant les oiseaux nichant à la limite de l'aire de reproduction à une perte d'habitat significativement plus élevée sur les aires hors reproduction que les oiseaux nichant au cœur de l'aire de répartition. Les oiseaux des deux populations étudiées présentaient également des itinéraires de migration différents, ceux de Caroline du Nord migrant vers le sud par la Floride et de nombreux oiseaux du New Hampshire effectuant un vol au-dessus de l'eau depuis les Carolines jusqu'aux Caraïbes. Nos résultats indiquent la possibilité que, au moins pour cette espèce, la perte de forêt sur l'île d'Hispaniola pourrait exacerber les diminutions de population à la limite sud de l'aire de reproduction en Caroline du Nord.

Key Words: *Black-throated Blue Warbler; light-level geolocator; migratory connectivity; migratory songbird; non-breeding forest loss*

INTRODUCTION

Almost three billion birds breeding in North America have been lost over the past 50 years (Rosenberg et al. 2019). Declines vary by habitat type and have been broadly observed across many taxonomic groups, but many of the strongest declines have been documented in long-distance migrants (Robbins et al. 1989, Ballard et al. 2003, Rosenberg et al. 2019). The pattern of decline for most species varies across the entire range, with populations decreasing in some regions and increasing or remaining stable in others (Sauer et al. 2017). Understanding the causes of these declines is complicated by the fact that migratory birds are

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subjected to a wide range of conditions and threats throughout their annual cycle (Rappole and McDonald 1994, Sherry and Holmes 1995, Faaborg et al. 2010, Sergio et al. 2019). Conditions on the non-breeding grounds and during migration can affect breeding-season demographic rates and population dynamics (Marra et al. 1998, Norris et al. 2004, Sanderson et al. 2006, Hewson et al. 2016), and conditions experienced throughout the annual cycle likely interact to drive population dynamics (Sherry and Holmes 1995, Sillett et al. 2000, Runge and Marra 2005). Threats experienced during the non-breeding season are most likely to cause regional population declines on the breeding grounds if migratory connectivity is strong, such that birds from declining populations use broadly discrete non-breeding areas or migratory pathways compared with birds from stable or increasing populations (Finch et al. 2017, Kramer et al. 2018). Thus, quantifying the strength of migratory connectivity is critically important for understanding the causes of population declines in migratory birds (Webster et al. 2002, Webster and Marra 2005).

Many species of long-distance migratory birds that breed predominantly in Canada and the northern USA reach the southern edge of their breeding distributions in the Appalachian Mountains of Georgia and North Carolina. These species are restricted to high-elevation forests of the Southern Appalachians, where conditions are cooler, wetter, and more similar to conditions further north within the core of the breeding range (Merker and Chandler 2021). Many of these species are declining at the southern limit of their range in North Carolina (Sauer et al. 2017), with population declines being associated with abandonment of low-elevation breeding habitats and upslope range shifts for at least some species (Stodola et al. 2013, Merker 2017, Lewis et al. 2023). Due to the elevational range shifts, we refer to populations in this region as trailing edge populations. This strong elevational pattern shown by several species suggests that climate change on the breeding grounds is a primary driver of their trailing edge population declines in North Carolina (Lewis et al. 2023); however, breeding declines could be exacerbated by threats encountered on the non-breeding grounds. Currently, information about specific migratory routes or non-breeding areas is lacking for most of these trailing edge populations breeding in North Carolina, thereby precluding an understanding of how threats encountered during the non-breeding season may influence these populations.

One such trailing-edge species is the Black-throated Blue Warbler (*Setophaga caerulescens* [BTBW]). Black-throated Blue Warblers are small (9–11 g), sexually dimorphic songbirds that spend the non-breeding season primarily in the Caribbean and breed predominantly in the northern USA and southeastern Canada, with a trailing distribution in the Southern Appalachians (Holmes et al. 2017). Over 1.4 million BTBW are estimated to have been lost since 1970 (Rosenberg et al. 2019), although population trajectories vary regionally (Sauer et al. 2017). Since 2002, BTBW breeding demography has been extensively studied at research stations located at the trailing edge of the breeding range in North Carolina and within the core of the breeding range in New Hampshire (hereafter, trailing edge and range core sites, respectively). Populations have been declining over the past two decades at low elevations at the trailing edge site, but populations have remained relatively stable at the range core site (Lewis et al. 2023). Furthermore, population dynamics at the research stations appear to be representative of patterns in the broader region, i.e., western North Carolina and central New Hampshire (Sillett and Holmes 2005, Holmes 2011, Doser et al. 2022, Lewis et al. 2023). Lewis et al. (2023) suggested that climate change on the breeding grounds is the most likely driver of this regional pattern of population declines; however, threats encountered during the non-breeding season could also contribute to breeding-ground declines if migratory connectivity is strong. Previous research provides some support for the hypothesis that non-breeding-season threats could exacerbate regional breeding-ground declines in BTBW. Using stable-hydrogen isotope signatures from BTBW feather samples collected across the breeding and non-breeding ranges, Rubenstein et al. (2002) found that birds breeding in the Southern Appalachians predominantly spend the non-breeding season further east in the Caribbean than do more northern-breeding birds. Stable isotope analyses, however, provide very broad-scale estimates of migratory connectivity and do not provide information about migratory routes. More precise data on migratory pathways and non-breeding areas for specific breeding populations are required to disentangle the effects of threats encountered throughout the annual cycle on population declines. Here, we use light-level geolocators to determine migratory routes, calculate the strength of migratory connectivity, and assess forest loss on the non-breeding grounds for BTBW breeding in North Carolina and New Hampshire.

METHODS

We assessed the migratory routes and non-breeding areas of BTBW by deploying archival light-level geolocators on breeding adults at two range positions: the trailing edge of the range within the Nantahala National Forest in the Appalachian Mountains of North Carolina (35°6′ N, 83°24′ W), and within the range core at the Hubbard Brook Experimental Forest in New Hampshire (43°56′ N, 71°45′ W). Both sites are composed of contiguous hardwood forest that has experienced little in the way of land use change over the past few decades. We deployed geolocators on males at both range positions, although we also deployed some units on females at the range core site in 2017–2018. We captured territorial males with mist nets using conspecific playback, and we captured females passively or by flushing them off of nests. We banded birds upon capture with a USGS aluminum leg band and unique combination of three colored leg bands. We fit birds with a 0.36 g Intigeo P30Z11-7-DIP geolocator (Migrate Technology, Cambridge, UK) using a leg-loop harness made of elastic beading cord (Naef-Daenzer 2007). Archival light-level geolocator data can be used to infer the daily longitude and latitude of the unit during the previous year. Although accuracy is much lower than with satellite and GPS tags (expected accuracy of geolocators is ca. 200 km; Fudickar et al. 2012, Lisovski et al. 2012), geolocators currently provide the best method for assessing migratory connectivity of small birds. The combined mass of the geolocator and harness was <5% of warbler body mass. We deployed 36 geolocators at the trailing edge site between 2018–2019 and 83 at the range core site in 2015, 2017, and 2018. We recovered geolocators in the subsequent year by searching areas near deployment locations and netting returning birds.

We performed all analyses in program R v. 4.0.4 (R Core Team 2020). We used the solar/satellite geolocation for animal tracking (SGAT) program to estimate geographic positions and associated error from the light data (Wotherspoon et al. 2013). We assigned twilight events (i.e., sunrise, sunset) with the TwGeos package (Lisovski et al. 2015, Lisovski et al. 2020) using a light threshold of one and a minimum time between sunset and sunrise of 8 h. Light data from a few birds showed extreme and variable shading on the breeding grounds, which occurs when light is blocked from reaching the light sensor (e.g., the bird is in thick vegetation or flight feathers obstruct the sensor). In these cases, we used a light threshold of 1.5. We manually edited twilights if (1) they differed by at least 30 min from the corresponding twilight events on the previous and subsequent days, and (2) they did not occur during periods when the bird was likely to have been migrating. We performed calibration from ambient light recorded when birds were known to be at the deployment location (e.g., deployment date until 1 August). We extended the calibration period for one unit until 31 August because it was not deployed until early August, and light levels indicated that the bird did not leave the deployment area until September. Calibration infers error associated with light recordings by calculating a reference zenith angle (position of the sun relative to the vertical plane at twilight) for the period when the bird was known to be stationary. Some birds exhibited different zenith angles between the breeding and non-breeding grounds, likely due to differences in weather, topography, or habitat between areas (Lisovski et al. 2012, Hallworth et al. 2015). In these instances, we calculated a separate zenith angle for the non-breeding season using the GeoLight package (Lisovski and Hahn 2012, Lisovski et al. 2020).

The SGAT program estimates locations from the light-level data using raw estimates of geographic position from the threshold analysis, a behavioral model describing likely flight speeds, and a spatial model restricting stationary periods to land. We defined the behavioral model with separate flight speeds for stationary and migratory periods (Hallworth et al. 2021). Similar to Tonra et al. (2019), we generated a spatial mask using BTBW occurrence data across the entire annual cycle from the Spatio-Temporal Exploratory Model (STEM) from eBird (Fink et al. 2020). The spatial mask reduces the likelihood of positions falling outside the normal range of BTBW. We ran models three times with Markov Chain Monte Carlo (MCMC) simulations, using three chains of 3,000 iterations. Each subsequent model was initialized with the median estimates of longitude and latitude from the previous run (Lisovski et al. 2020). Stationary periods were determined from location estimates generated from the MCMC posterior distribution, using the MigSchedule function from the LLmig package (https://github.com/MTHallworth/LLmig; Tonra et al. 2019). We estimated the migratory distance traveled by each bird by summing the great circle distance (shortest distance between points on a sphere) between the median longitude and latitude estimates for successive stationary periods during migration. We summed the great circle distances traveled along each leg of the migratory journey to calculate the total length of the migratory journey. The assumptions of parametric statistical tests could not be met, so we assessed differences in migratory route length between range positions with a Mann-Whitney U test.

We calculated the strength of migratory connectivity between breeding and non-breeding locations using the MigConnectivity package (Cohen et al. 2018) with 1,000 bootstrap runs. The strength of migratory connectivity describes the geographic link of populations in two or more phases of the annual cycle. Estimates range from -1 (birds close together in one season spread further apart in another season) to 1 (birds close together in one season staying close together in another season), with a 0 value representing no pattern. Black-throated Blue Warblers showed a general east/west divide during the non-breeding season (see Results), so we used two non-breeding target regions (Cuba and Jamaica vs. Hispaniola) for the migratory connectivity analysis. The estMC function incorporates location uncertainty and relative abundance of the study species between deployment regions, which we calculated from the eBird STEM models. To calculate relative abundance of the two range positions, we extracted BTBW breeding abundance for each Bird Conservation Region, subset down to the state in which each deployment region was located (North Carolina Appalachian Mountains and New Hampshire Northern Hardwood Forest). We classified the strength of migratory connectivity as either weak (0.333 or less), moderate (0.334–0.667), or strong (0.668–1) based on classifications in Hallworth et al. (2015).

As an ancillary analysis, we assessed whether non-breeding areas used by BTBW from the trailing edge site experienced higher levels of habitat loss over the past two decades compared with non-breeding areas of BTBW from the range core site. Black-throated Blue Warblers are primarily associated with forested habitat throughout the annual cycle (Holmes et al. 2017); therefore, forest loss in the Caribbean likely represents non-breeding habitat loss. We downloaded forest cover loss data from 2000–2019 for the entire Caribbean using the Global Forest Change data set (v. 1.7; Hansen et al. 2013). This data set provides a binary measure of change from forest to non-forest cover over the 2000–2019 period. Black-throated Blue Warblers predominantly spend the non-breeding season in higher-elevation forests in the Caribbean (Holmes et al. 1989, Wunderle and Waide 1993, Latta et al. 2003); therefore, we subset the forest loss data to only include forest loss at or above 100 m in elevation. We further refined our raster of BTBW non-breeding habitat loss by subsetting to only areas with at least 40% probability of BTBW occurrence during the stationary non-breeding season from the eBird STEM models (values range from ca. 0–80%). We refer to this distribution as "suitable areas" and "suitable forest cover loss." We then used the MCMC posterior distribution to extract the mean relative probability of non-breeding occurrence (1 December–1 March) for each bird. We multiplied the raster of BTBW habitat loss over the past two decades by the relative probability of occurrence during the non-breeding season of each bird. We then summed across the resulting cells to generate an index of habitat loss for the non-breeding areas of each bird. We used a one-tailed Mann-Whitney U-test to determine if this index of non-breeding habitat loss was higher for trailing edge birds compared with range core birds.

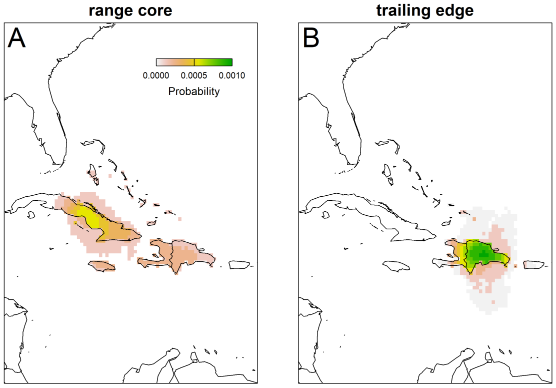
RESULTS

We recovered geolocators from five birds at the trailing edge site and eight birds at the range core site. Only one unit was recovered from a female. An additional four birds (two from each range position) were recovered without their geolocators; omitting these birds, recovery rates were 15% at the trailing edge site and 10% at the range core site. Recovery rates of tagged birds varied by year, from 7–20% at the trailing edge site and from 4–20% at the range core site. We collected tracking data from all 13 geolocators;

however, we could not determine fall migratory routes for three range core birds due to extreme shading resulting in biologically implausible stopover locations (e.g., in Amazonia or the Atlantic Ocean).

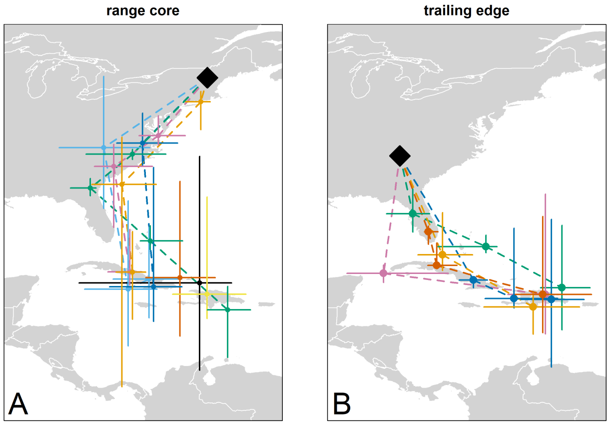
Black-throated Blue Warblers breeding at the two range positions showed a general longitudinal divide in their stationary non-breeding areas. Non-breeding areas of birds from the range core site were broadly distributed across the Caribbean, from Cuba to the Dominican Republic, but probability of occurrence peaked in central Cuba (Fig. 1A). Of the eight birds from the range core site, three spent the non-breeding season in central to eastern Cuba, two (including the lone recovered female) spent the non-breeding season in either Jamaica or southern Cuba, and three spent the non-breeding season on the island of Hispaniola. The specific country could not be determined for two birds on the island of Hispaniola, but the third bird appeared to spend the non-breeding season in the Dominican Republic. In contrast to the longitudinal spread of birds from the range core site, all five birds from the trailing edge site spent the non-breeding season on the island of Hispaniola, largely in the Dominican Republic (Fig. 1B). No returning birds spent the non-breeding season in Puerto Rico or western Cuba. The combination of a restricted non-breeding distribution for birds from the trailing edge site and diffuse non-breeding range of birds from the range core site resulted in moderate migratory connectivity (MC mean = 0.42, SE = 0.26).

Fig. 1. Non-breeding distribution (1 December–1 March) determined via light-level geolocation for Black-throated Blue Warblers (*Setophaga caerulescens*) breeding at the core of the range in New Hampshire (A, *n* = 8) and trailing edge of the range in North Carolina (B, *n* = 5). Geolocator deployment occurred from 2018 to 2019 at the trailing edge and in 2015, 2017, and 2018 at the range core. Heat maps show 95% credible intervals for non-breeding probability of occurrence (green = highest probability). Non-breeding probability of occurrence was calculated for each breeding range position by summing likelihood of occurrence across birds at each pixel and dividing by the sum of all likelihood values across birds. New Hampshire birds spent the non-breeding season in a broad area across the Caribbean, but probability of occurrence was centered in Cuba. North Carolina birds spent the non-breeding season in the Dominican Republic.



Estimated fall migratory routes differed between range positions. Black-throated Blue Warblers from the trailing edge site largely migrated south through Florida and Cuba before turning east to Hispaniola (Fig. 2B). In contrast, many birds from the range core site followed the coast southwest until reaching the Carolinas, after which they flew directly across the ocean to non-breeding areas in Cuba or Jamaica (Fig. 2A). This direct flight from the Carolinas to Cuba could have saved birds up to 300 km of flight distance compared with the overland route through Florida. Migratory routes were generally shorter for birds from the trailing edge site (mean = 2,545 km, SD = 271 km) than from the range core site (mean = 2,991 km, SD= 434 km), but this difference was not statistically significant (Mann-Whitney U-test, *p* = 0.056).

Fig. 2. Fall migratory routes of Black-throated Blue Warblers (*Setophaga caerulescens*) determined via geolocation for birds breeding at the core of the range in New Hampshire (A, *n* = 8) and trailing edge of the range in North Carolina (B, *n* = 5). Deployment locations are shown with black diamonds. Geolocator deployment occurred from 2018 to 2019 at the trailing edge and in 2015, 2017, and 2018 at the range core. Median longitude and latitude are shown for stationary periods for each bird, as well as 95% credible intervals. Different colors represent different birds and do not necessarily represent the migratory path taken. Migratory tracks could not be determined for three range core birds, although estimated non-breeding locations are shown. The light blue track from the range core (subfigure A) was from a female; all other tracks were from males. Successive stopover locations are connected with a dotted line, but this does not represent the actual flight path that the bird took.



Caribbean countries varied in their degree of suitable forest cover loss from 2000 to 2019. The greatest suitable forest cover loss was observed in the Dominican Republic with a loss of 1,924 km² (8.4% of suitable area), followed by Cuba (1,541 km², 2.7% of suitable area), Haiti (570 km², 2.9% of suitable area), and Jamaica (394 km², 3.9% of suitable area). Suitable forest cover loss was especially concentrated in the mountains of central Hispaniola and at the very eastern tip of Cuba. Due to their restricted non-breeding range in the Dominican Republic, BTBW from the trailing edge were exposed to significantly higher levels of suitable forest cover loss on the non-breeding grounds than were range core birds (Mann-Whitney U-test, *p* = 0.003).

DISCUSSION

Black-throated Blue Warblers exhibited moderate migratory connectivity between breeding and non-breeding areas; the non-breeding range of birds from the trailing edge site was centered on the island of Hispaniola, whereas the non-breeding range of birds from the range core site was centered further west, primarily in Cuba. Although breeding populations were not completely separate on the stationary non-breeding grounds, BTBW exhibited stronger migratory connectivity than has been observed in many other species of long-distance migratory birds (Finch et al. 2017, Cohen et al. 2019, Tonra et al. 2019, Hallworth et al. 2021, but see Hallworth et al. 2015, Kramer et al. 2018). The stronger migratory connectivity in BTBW could possibly be an artifact of the low sample size of returning birds (McKinnon and Love 2018); however, previous research using stable isotopes has also found longitudinal separation on the non-breeding grounds between BTBW from the southern and northern portions of the breeding range (Rubenstein et al. 2002). The geolocator data confirm the findings of Rubenstein et al. (2002), but also show that the size of the non-breeding range differs between breeding populations (Hallworth and Marra 2015). Birds from the range core site spent the non-breeding season across a broad region of the Caribbean, from central Cuba to eastern Hispaniola, whereas birds from the trailing edge site were concentrated on Hispaniola. These results suggest that BTBW from the trailing edge site not only spend the non-breeding season in somewhat different regions compared with birds from the range core site, but also have a greatly restricted non-breeding range.

The restricted non-breeding range of BTBW from the trailing edge site suggests that they may be particularly vulnerable to threats, such as habitat loss or hurricane activity, on the island of Hispaniola. This restricted range in the Dominican Republic is likely caused, at least partially, by the widespread loss of primary forest in Haiti (Hedges et al. 2018), thereby forcing birds that spend the non-breeding season on Hispaniola into the more intact forests of the Dominican Republic. This massive pre-2000 forest cover loss in Haiti likely explains why suitable forest cover loss from 2000–2019 was so much lower in Haiti than in the neighboring Dominican Republic. Despite retaining more forest cover than its neighbor, the Dominican Republic has experienced substantial forest cover loss over the past few decades, mainly attributable to fire and clearing for agriculture (Lloyd and León 2019). Although nearly 38% ($n = 3$ of 8) of birds from the range core site also spent the non-breeding season in Hispaniola, and thus should have been exposed to the same negative effects of deforestation, most used areas further west in the Caribbean. Conservation efforts have led to substantial recovery of forested land in Cuba (Goulart et al. 2018); therefore, the diffuse non-breeding range of BTBW from the range core site may have buffered against any population-level effects of deforestation in the eastern Caribbean. Our forest-loss analysis was necessarily conducted at a broad scale due to the inherent location uncertainty associated with light-level geolocation; however, our results suggest the possibility that habitat loss on the island of Hispaniola could have exacerbated observed trailing edge declines on the breeding grounds in North Carolina.

Fall migratory routes also differed between the breeding populations; trailing edge birds migrated south through Florida, whereas many birds from the range core made overwater flights from the Carolinas to the Caribbean. Because of the uncertainty associated with light-level geolocation, the locations of short-duration stopovers in Fig. 2 should be interpreted with caution. Most BTBW migrated during the fall equinox period when latitude cannot be reliably estimated; however, the differential migration routes between the range positions is not an artifact of location uncertainty. Longitude estimates are relatively unaffected by the equinox (Hallworth et al. 2015), and the 95% credible intervals of longitude estimates for only one range core bird overlapped Florida during fall migration. Geolocator tracking has revealed that Connecticut Warblers (*Oporornis agilis*; McKinnon et al. 2017, Hallworth et al. 2021) and, to a greater extent, Blackpoll Warblers (*Setophaga striata*; DeLuca et al. 2015) also undertake similar trans-Atlantic flights during migration. This overwater trip between the Carolinas and the Caribbean likely saved BTBW from the range core site one night of prolonged flight, plus any time that would have been spent at stopover sites in Georgia and Florida, which could provide a significant benefit if early arrival on the non-breeding grounds allows access to higher-quality habitats or other fitness benefits (Newton 2006).

Changing conditions along the differential migratory routes could affect trailing edge population declines in North Carolina (Baker et al. 2004, Hewson et al. 2016); however, several lines of evidence suggest that this may be unlikely. First, migration is the most energetically expensive and hazardous phase of the annual cycle, and the majority of annual mortality occurs during migration (Sillett and Holmes 2002, Klaassen et al. 2014, Paxton et al. 2017, Sergio et al. 2019). Longer migratory routes may therefore be associated with higher mortality, but routes tended to be longer for birds from the range core site. Second, birds from the trailing edge site predominantly migrated over land, whereas many range core birds made long transoceanic flights. Most birds likely can complete these long flights without incident, although prolonged overwater crossings may lead to heightened mortality risk if birds are physiologically unprepared or encounter inclement weather en route (Newton 2007, Ward et al. 2018). The prolonged overwater flight could convey fitness benefits for birds from the range core site compared with a longer overland route; however, the associated risks of overwater flight for these birds may lead to higher mortality during migration than experienced by birds from the trailing edge site. Finally, most birds from the trailing edge site made a stopover in Cuba, which is the primary non-breeding area for birds from the range core site. Any threats facing birds from the trailing edge site stopping in Cuba likely would have had a larger effect on the birds from the range core site. The longer migratory route and prolonged trans-Atlantic flight may explain why apparent survival is lower at the range core site than at the trailing edge site (Lewis et al. 2023), but conditions along the migratory routes are unlikely to be the primary drivers of trailing edge population declines in North Carolina.

Recovery rates of geolocator-tagged BTBW were low but similar to most other studies deploying geolocators on small birds (Salewski et al. 2013, DeLuca et al. 2015, Delancey et al. 2020, Hallworth et al. 2021, but see Peterson et al. 2015). Although this study was not designed to evaluate the fitness effects of geolocators, the low return rates may indicate that geolocators had a negative effect on BTBW apparent survival. Studies have reported conflicting results on the fitness consequences of geolocators (e.g., Arlt et al. 2013, Peterson et al. 2015, Raybuck et al. 2017), but a recent metanalysis found only minor effects of geolocators on apparent survival (Brlík et al. 2020). Several BTBW dispersed >100 m between years, and one bird was recaptured 750 m from its deployment location. Breeding dispersal has also been observed for geolocator-tagged Cerulean Warblers (*Setophaga cerulea*; Raybuck et al. 2017); therefore, geolocator return rates are likely to underestimate true survival. We currently do not have enough data to assess the effects of geolocator deployment on emigration; for example, if the extra weight left birds at a competitive disadvantage and forced dispersal to alternative breeding sites.

Tracked BTBW likely used non-breeding areas in Cuba, Jamaica, and Hispaniola, although we did not detect any birds spending the non-breeding season in Puerto Rico. Stable isotopes suggest that Puerto Rican BTBW are likely to breed in the Appalachians (Rubenstein et al. 2002). We found no evidence of this with the geolocator tracks; however, Puerto Rican birds may breed further north of the trailing edge study site (e.g., West Virginia or Pennsylvania), similar to patterns exhibited by Ovenbirds (*Seiurus aurocapilla*), another long-distance migrant spending the non-breeding season in Puerto Rico (Hallworth et al. 2015). We may not have detected any birds migrating to Puerto Rico for two reasons: (1) birds from the study populations did not spend the non-breeding season there; or (2) birds that spend the non-breeding season in Puerto Rico have higher mortality than other non-breeding locations and thus do not return to the breeding grounds (Rushing et al. 2021). Birds from the trailing edge site therefore may have spent the non-breeding period in Puerto Rico, but declining conditions on the island led to reduced survival and lower return rates to the breeding grounds. Forest cover has tripled in Puerto Rico since the 1970s (Yuan et al. 2017), but changes in habitat quality or other threats could have affected BTBW during the non-breeding season. A third possibility is that birds did spend the non-breeding season in Puerto Rico and returned to the study sites, but we did not recapture them. We spent considerable effort searching an expanded area around the study sites for returned birds and we recaptured all returning birds we located, but the observed breeding dispersal for some returning birds suggests that we likely did not recapture every bird that returned to the breeding sites. Deploying geolocators across the non-breeding grounds, especially in Puerto Rico, would be beneficial for refining estimates of BTBW migratory connectivity.

Our results support the possibility that non-breeding habitat loss may be contributing to breeding population declines at the trailing edge site; however, they do not imply that breeding-ground effects are unimportant for explaining trailing edge declines in North Carolina. Indeed, several lines of evidence suggest that environmental threats on the breeding grounds are a major driver of declines at the trailing edge site. If deforestation on the island of Hispaniola is driving breeding declines, then population declines should be observed across all breeding elevations in the Southern Appalachians. Instead, populations have remained stable at the highest elevations but declined at the lowest, warmest elevations in response to warming temperatures (Lewis et al. 2023). Furthermore, many trailing edge species are declining at the southern edge of their breeding range despite using very different non-breeding areas. For example, populations of Canada Warblers (*Cardellina canadensis*) and Veeries (*Catharus fuscescens*) are also declining at low elevations in North Carolina (Merker 2017); however, these species predominantly spend the non-breeding season in the Andes Mountains and Amazonia, respectively. For non-breeding habitat loss to be driving breeding declines in all these species, each would have to exhibit strong migratory connectivity with trailing-edge populations in North Carolina utilizing non-breeding areas with high rates of forest loss or other threats. These findings suggest that trailing edge declines in North Carolina are unlikely to be solely driven by non-breeding habitat loss. Instead, the migratory paths of BTBW suggest the possibility that habitat loss on the non-breeding grounds could be magnifying climate-induced population declines at the trailing edge site. Our results suggest that more intensive study is needed on the non-breeding grounds, particularly examining how non-breeding season conditions interact with breeding-ground climate change to drive population declines.

CONCLUSION

We found moderate migratory connectivity in BTBW. Birds breeding at a range core site in New Hampshire exhibited a broad non-breeding distribution across the Caribbean, whereas birds breeding at a trailing edge site in North Carolina exhibited a restricted non-breeding range on the island of Hispaniola. Deforestation rates have been accelerating in the Dominican Republic (Lloyd and León 2019), which could be disproportionately affecting BTBW from the trailing edge of the range in North Carolina. The island of Hispaniola also provides important non-breeding habitat for other species, such as the Bicknell's Thrush (*Catharus bicknelli*, McFarland et al. 2013); therefore, protecting forested land on Hispaniola should be a top conservation priority. Promoting sustainable agricultural practices, such as shade-grown coffee, may also provide suitable habitat for a variety of forest-dwelling species such as BTBW (Wunderle and Latta 1996, Wunderle 1999); however, sustainable agricultural practices generally support lower biodiversity than primary forest (Rappole et al. 2003, Chandler and Royle 2013). Sustainable agricultural practices should therefore be considered lower priority than conservation of native forest. Although population declines in North Carolina appear largely driven by climate change on the breeding grounds, our results suggest the possibility that deforestation in the Caribbean may be exacerbating these declines. Further work from elsewhere in the breeding and non-breeding range is needed to refine estimates of migratory connectivity in BTBW to determine the relative influence of threats experienced throughout the annual cycle on trailing edge population declines in North Carolina.

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Data Availability:

Raw light levels and processed locations from geolocators are accessible through Movebank (ID: 3043180186, Geolocator tracks of black-throated blue warblers [data from Lewis et al. 2023]).

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