There's no place like home: tropical overwintering sites may have a fundamental role in shaping migratory strategies

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Migration theory has largely overlooked the role of overwintering grounds and yet many migratory animals spend most of the annual cycle there. High winter site familiarity could confer considerable advantages on animals preparing for subsequent migration phases, enabling them to maximize migration speed and minimise the use of unknown stopover sites. Despite this, quantitative studies of the magnitude of fuel stores attained at such sites are lacking. To evaluate the energetic contribution of an overwintering site to spring migration, we used manual and automated telemetry to estimate departure date, departure fuel load, flight range and breeding destination of blackpoll warblers (*Setophaga striata*) wintering in Colombia. Relative to overwinter mass, warblers increased body mass (a surrogate for fuel stores) by an average of 59% prior to departure from the overwintering site. Flight range (mean 2710 km, range 2110−3380 km, $N = 6$) and detections at automated telemetry stations in North America suggest movements to Cuba/southeastern US, before refuelling and then continuing towards breeding grounds in eastern Canada (total duration ~ 30 days). Total migration length was ~ 5350 km and energy acquired at the overwintering site was sufficient to cover 39−63% (mean = 50%), demonstrating the major contribution tropical wintering grounds can make to migration. It follows that varying the extent of fuelling prior to departing overwintering sites may provide animals with a mechanism for balancing their exposure to risk during migration, while simultaneously allowing for flexibility in migratory schedules in a changing world.
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To understand the organization of and decision-making processes during migration, optimal migration theory has largely focused on stopover sites, where the fuel for powering movements is attained (Alerstam, 2011). However, breeding and stationary nonbreeding sites ('overwintering sites' hereafter) could also provide a disproportionate amount of the energy reserves required to migrate (Klaassen, Alerstam, Carlsson, Fox, & Lindström, 2011) and therefore strongly influence key elements of migratory strategies, such as departure date, route, and the frequency and duration of stopovers. Despite their theoretical importance, the decisions made

at overwintering sites and their contribution to migratory behaviour are largely unknown (Lindström, Alerstam, & Hedenström, 2019).

Migration exposes animals to a wide range of potential threats, in part because they must typically stop at several, often unfamiliar, sites en route to refuel (Alerstam & Lindström, 1990; Hedenström, 2008). Site fidelity at refuelling/stopover sites is surprisingly low in birds (Catry et al., 2004), for example, and thus each time a bird stops, it is believed to lose time through search and settling costs, and to experience heightened predation risk in unfamiliar environments (Alerstam & Lindström, 1990). To offset such costs, migratory birds and other animals may reduce the number of stops required by seeking resource-rich sites where they can maximize energy stores (Hedenström, 2010; Klaassen et al., 2011; Sawyer &

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Kauffman, 2011). However, such a strategy entails other risks, including increasing mass-dependant predation risk as fuel stores increase (Kullberg, Jakobsson, & Fransson, 2000; Lind, 2004) and being dependent on locating resource-rich stopover sites that facilitate extensive fuelling (Bayly, Rosenberg, Gómez, & Hobson, 2019; Bibby, Green, Pepler, & Pepler, 1976). Furthermore, annual fluctuations in resource levels probably make this strategy costly in years when resource levels are below average (Baker et al., 2004).

An alternative strategy is to maximize energy stores prior to departing on the first migratory flight and to cover as much of the migration route as possible using fuel gained at breeding or overwintering sites. This strategy may be advantageous because animals presumably gain considerable knowledge by occupying these sites for several months at a time (Cuadrado, 1997) and can therefore locate resources and avoid predators with greater efficiency than at less familiar stopover sites (Cimprich, Woodrey, & Moore, 2005; Forrester, Casady, & Wittmer, 2015; Slagsvold & Wiebe, 2018). Furthermore, tropical overwintering sites may provide abundant resources, especially if the premigratory period overlaps with peaks in or increasing precipitation (Studds & Marra, 2007). Combined, these advantages may translate into higher fuelling rates, faster migration speed, dependence on a smaller number of stopover sites (Gómez et al., 2017) and an overall reduction in predation risk and possibly increased survival rates during migration (Hebblewhite & Merrill, 2011).

Despite the advantages of extensive fuelling at breeding/overwintering sites and its potential to allow animals to adjust their migratory schedules in the face of climate change (Lindström et al., 2019), few studies have evaluated the extent or consequences of this strategy (Neto, Encarnação, Fearon, & Gosler, 2008; Risely, Blackburn, & Cresswell, 2015). Indeed, this phase of migration is often ignored (Lindström et al., 2019), such that the role of tropical overwintering habitats in the great migrations of birds, for example, remains largely unknown. This uncertainty applies to overwintering sites used by long-distance migratory birds in the Neotropical region covering Central and South America and the Caribbean (Bayly et al., 2018). Studies from sub-Saharan Africa have revealed a mixture of strategies with some species apparently storing sufficient fuel at overwintering sites to cross the Sahara (Bayly, Atkinson, & Rumsey, 2012), while others abandon territories used over 6 months to fuel elsewhere (Risely et al., 2015). These mixed findings may be linked, in part, with the overlap of the initiation of migration and the tail end of the dry season at well-studied locations in sub-Saharan Africa (Bayly & Atkinson, et al., 2012; Risely et al., 2015) and the Caribbean, where, for example, dry conditions cause a 60% reduction in insect abundance (Cooper, Sherry, & Marra, 2015).

Blackpoll warblers, *Setophaga striata*, are known for making one of the longest nonstop flights (> 2500 km) described in a small migratory landbird (< 12 g; DeLuca et al., 2019; DeLuca et al., 2015), which they achieve by fuelling for southbound transoceanic flights at stopover sites along North America's Atlantic seaboard (Nisbet, Drury, & Baird, 1963). How they fuel the reverse journey from South to North America, however, is not known. Remote tracking suggests a potential role for overwintering sites (DeLuca et al., 2019), and given that the wet season arrives over 1 month prior to the initiation of migration across much of the species' South American range, we predict that associated increases in resources could facilitate extensive fuelling prior to departure. To evaluate the extent of fuelling at a tropical overwintering site, we captured and fitted blackpoll warblers with radiotransmitters in Colombia, enabling us to estimate departure body mass in birds with known departure date. To fully understand the contribution of accumulated energy stores to migration, it is necessary to evaluate them in the context of the total migratory journey and its duration (Bayly, Gómez, Hobson, González, & Rosenberg, 2012). To do so, we estimated flight ranges and tracked warblers carrying transmitters north through the Motus automated telemetry array (Taylor et al., 2017) and inferred the use of stopover sites, breeding locations and total migration distance through resulting intercontinental detections. Ultimately, by combining the multiple lines of evidence, we estimate the percentage of the total migration distance coverable using energy stores attained at an overwintering site and discuss the implications for migration theory.

METHODS

Study Site, Captures and Seasonal Variation in Body Mass

We studied blackpoll warblers at the Barcelona campus of the Universidad de los Llanos near the city of Villavicencio, Colombia, close to the foothills of the Eastern Andes (04°04′24″N, 73°34′53″W; 390 m elevation). The study site consisted of fragments of native forest (< 1 ha), riparian strips, live fences, citrus and cocoa plantations and experimental plots. To describe seasonal variation in body mass, we captured warblers during two periods, January/February and late April/early May, equating to (1) the overwintering period and (2) the initiation of fuelling for spring migration, over 2 years (2017 and 2018). Birds were captured using ground-level and canopy mist nets (mesh size = 30 mm nets, length = 12 or 18 m), changing net positions daily to target individual birds. Canopy nets consisted of two 10–15 m high bamboo poles dug approximately 1 m into the ground and rigged with a pulley system to raise and lower nets. We used recordings of blackpoll warbler song and chip calls to draw birds towards nets.

All captured birds were fitted with a numbered aluminium ring (Porzana Ltd., reporting address www.aselva.co) and a unique combination of plastic colour rings for future resightings. Birds were aged and sexed following criteria in (Pyle, 1997). We measured unflattened wing chord (mm) and body mass to the nearest 0.1 g using an electronic balance.

Overwinter Site Fidelity

To confirm overwinter residency and fidelity, we searched for colour-ringed birds every 10 days from December through April in 2017/2018 and 2018/2019. Of 18 birds marked in early 2017, seven individuals (39%) were resighted in 2017/2018 and three were resighted in 2018/2019. Of 11 individuals marked in 2018, two were resighted in the winter of 2018/2019 (18%). Returning birds included six individuals fitted with miniature radiotransmitters (Lotek NTQB-2 Nanotags, programmed at 17.89 s between pulses, battery life 60 days; Lotek Wireless Inc., Newmarket, ON, Canada) in 2017 (see below), with opportunistic resightings occurring in late October/early November.

Departure Date and Estimated Departure Mass

To determine departure date, 11 birds were fitted with nanotags in 2017 and six birds were fitted with nanotags in 2018 in late April/early May (one tag failed in 2017, such that $N = 16$). Nanotag weight was < 0.4 g complete with a leg-loop harness (Naef-Daenzer, 2007), which was equivalent to 3.8% of the mean overwintering body mass of blackpoll warblers at our study site. To track birds until departure, we used both a manual Lotek receiver (SRX800) with a 3-element Yagi antenna and a Motus automated telemetry tower installed within 1 km of capture locations. The tower was fitted with two 9-element Yagi antennas with a potential detection range of 15 km. We examined automated detections of individual birds to identify night-time departures following (Taylor et al., 2017).

To estimate departure mass it was necessary to first determine departure date through radiotelemetry. Using known departure dates, we then (1) carried out a bootstrap regression with 1000 replicates of body mass against the number of days birds were captured prior to departure, to provide a population mean and 95% confidence intervals for the daily increase in body mass (Fig. 1) and (2) multiplied the mean daily increase by the number of days each tagged individual remained at the study site postcapture and added it to body mass at the time of capture to give a departure body mass. For one individual whose nanotag failed, we used mass at first capture, as it was the heaviest bird in our sample (18.3 g).

Flight Range from Overwintering Site

Flight ranges were estimated by simulating migratory flights in Program Flight 1.22 (Pennycuick, 2008). We assumed that, at the end of a migratory flight, minimum body mass would be equivalent to the lower quartile (25th percentile) of masses recorded during January and February in Colombia (10.2 g) and that any mass above this value was available fuel (note that 35% of 599 blackpoll warblers captured following transoceanic flights in autumn had a body mass of < 10.2 g; Bayly, Norris, Taylor, Rosenberg, & Hobson, 2020). To simulate flights, we entered a wing span of 0.2108 m (mean of 11 live measurements from northeastern Colombia), a wing area of 0.0080 m^2 (mean of 11 wings plus body area traced on graphical paper; see Flight 1.22 manual) and a flight muscle fraction of 0.156 (mean of muscle fractions reported for the closely related bay-breasted warbler, *Setophaga castanea*, and blackburnian warbler, *Setophaga fusca*; Graber & Graber, 1962). 'Fat fraction' was calculated following the 'find fat fraction' guidelines in the Flight 1.22 manual, using a minimum mass (m_{min}) of 10.2 g. During simulated flights birds could convert both stored fat and muscle to fuel.

We estimated flight ranges for two data sets: (1) extrapolated departure mass in 16 individuals fitted with nanotags and (2) body mass of 20 birds at the time of capture, to verify/refute extrapolated

values from 1. For the second data set, we calculated flight range for the mean, upper quartile (75th percentile) and maximum body mass, which we expected would approximate to the range of departure masses in our population, given that birds departed 5–13 days after initial capture (Fig. 1).

Location of Likely Stopover Regions and Migration Speed

To determine the location of likely stopovers and migration speed in blackpoll warblers, we downloaded detections of nanotags within the Motus automated telemetry array (Taylor et al., 2017). We first filtered detections for those with a minimum of three consecutive hits (runLen $\geq$ 3), before manually examining each one to check for the characteristic parabola shape of flyby detections (Fig. A1) and ensure that date and geographical location were biologically plausible. Next we combined estimated flight range with the mean flight bearing of all birds detected in the southeastern United States (346°, $N = 3$), for each of 16 blackpoll warblers fitted with nanotags, to determine where they would most likely run out of fuel and require a stopover. To simulate natural variation in flight direction within the population, we assigned bearings of 5° on either side of the mean (from 341° to 351°) at random to each of the 16 birds (support for an initial flight northwest towards the southeastern United States is provided by birds tracked with geolocators; DeLuca et al., 2015, 2019). We then determined the coordinates where birds would run out of fuel by entering flight range and bearing into a web-based destination calculator (Movable Type, 2019). Finally, we generated a kernel density plot of destinations using the KernSmooth package in Program R (R Development Core Team, 2017) to represent the most likely locations of stopover sites.

To estimate migration speed (calculated here as 'overall migration speed following departure' to facilitate comparison with other studies, although actual migration speed should be calculated including the fuelling period prior to departure; see Discussion and Lindström et al., 2019), we first calculated the great-circle distance between the study site and detections of tagged blackpoll warblers to the north during spring migration (Table A1). We then fitted a linear regression model of distance flown (km) against the number of days since departure for 10 blackpoll warblers detected in northern Colombia and North America by Motus automated telemetry stations and used the coefficient of the slope to estimate average migration speed.

Contribution to Total Migratory Journey

To understand the contribution of energy stored at our overwintering site to the entire spring migration of blackpoll warblers, we combined flight ranges, stopover locations and detections within the Motus array to calculate the percentage of the migratory journey coverable using fuel stored in Colombia (Bayly & Gómez et al., 2012). We estimated the total distance (5350 km) covered between Colombia and the breeding grounds, as the distance between our study site and the most northerly detection of a bird within the known breeding grounds of the blackpoll warbler (Quebec; Table A1), when assumed to be following a route via the southeastern United States (see above). To visualize the spring migration of warblers from Colombia, we mapped the kernel density plot of most likely stopover locations (see above) using the Raster package in Program R and overlaid the locations of the telemetry towers where birds were detected away from the study site, connecting detections of individual birds with a straight line.
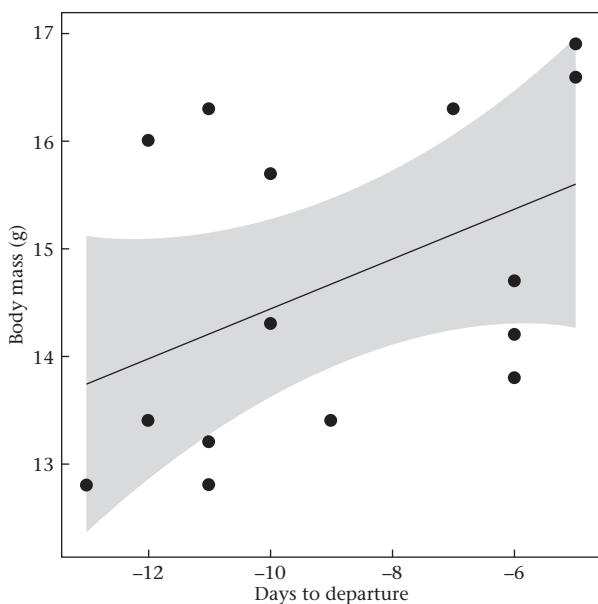
Figure 1. Body mass relative to the number of days before known departure in 15 blackpoll warblers fitted with nanotags and tracked until departing on migration from an overwintering site in Colombia. Two birds fitted with tags were excluded, one because of tag failure and a second because it was not detected at the study site postrelease, and thus, departure date or use of the study site was uncertain. Regression equation: body mass = 0.23 × days predeparture + 16.79 (regression: $F_{1,13} = 3.27$, $R^2 = 0.201$, $P = 0.09$).

Animal Welfare Note

All captures realized in this study were carried out under permit from the ANLA, Colombia, (Resolution number 0597 in 2014, 0189 in 2016, and 00874 in 2018) following internationally recognized protocols and standards for the capture and marking of birds. All birds were released after processing, and where birds were fitted with radiotransmitters, transmitters complete with harness were equivalent to 3.8% of body mass and within the recommended range (< 5%). To minimize stress during the capture and handling process, nets were checked at least every 30 min, but in most cases, nets were watched constantly through binoculars given that we were target-netting individual birds. Handling times were kept below 5 min by preparing radiotransmitters and harnesses in advance and activating transmitters prior to removing birds from holding bags. Each individual fitted with a radiotransmitter was carefully checked prior to release to ensure that there was sufficient give (~ 0.5 cm) in the elastic thread to allow for 'fattening' (measured by inserting the tip of a finger between the transmitter and back), that movement of legs or wings was in no way hindered by the harness and that as few body feathers as possible were displaced/trapped by the transmitter and harness.

RESULTS

Seasonal Variation in Body Mass

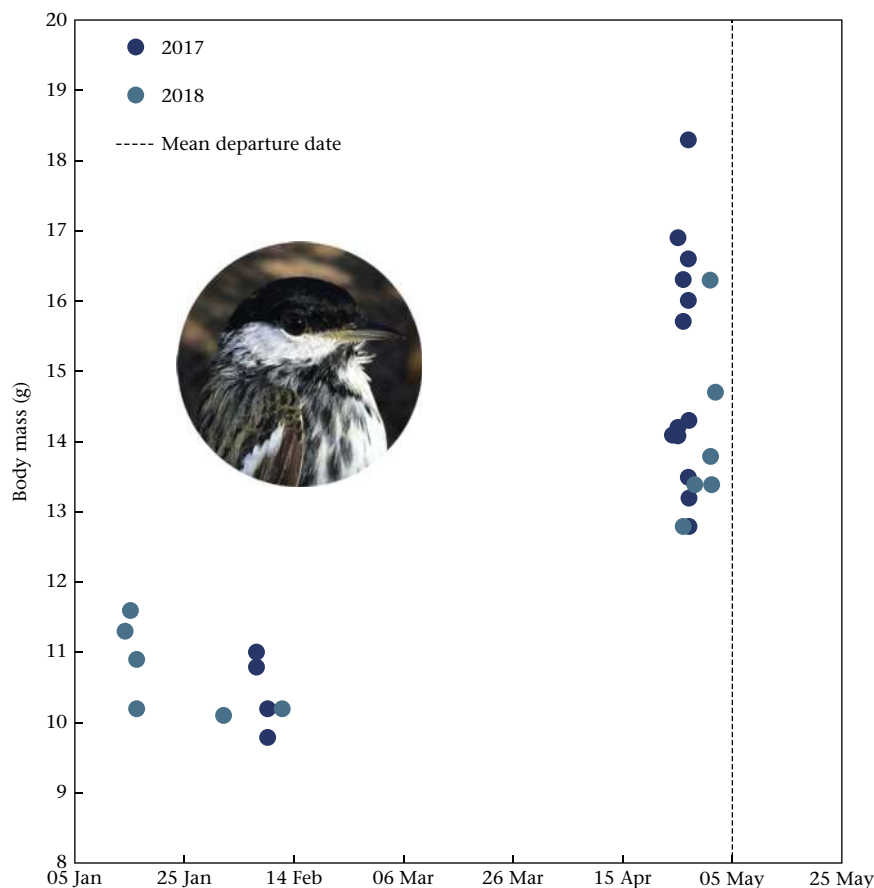Average body mass (± SD) of blackpoll warblers captured during the mid-overwintering period (January–February) was 10.6 ± 0.59 g (range 9.8–11.6 g, $N = 10$; Fig. 2). In late April and early May, body mass increased dramatically by an average of 40% (mean ± SD = 14.8 ± 1.55 g, range 12.8–18.3 g, $N = 20$), and the highest recorded mass (18.3 g) was equivalent to a 73% increase.

Departure from Overwintering Site

Based on automated and manual detections of birds with nanotags, the earliest individuals departed on 25 April and the latest on 12 May (mean = 5 May, SD = 4.2 days, $N = 16$; Table 1). In both years, multiple birds departed on the same night (e.g. three birds departed on 6 May 2018). Tagged birds remained at the study for 5–13 days postcapture. Mean daily mass gain was estimated at 0.23 g per day (95% CI -0.05, 0.46) (Fig. 1), equivalent to a fuel deposition rate of 2.3% lean body mass/day (Lindström, 2003), which gave rise to extrapolated departure masses in tagged birds between 15.2 and 18.9 g (mean ± SD = 16.9 ± 1.64 g, $N = 16$; Table 1).

Flight Range from Overwintering Site

Based on extrapolated departure masses, estimated flight ranges of tagged birds ranged from 2110 to 3380 km (mean ± SD = 2710 ± 451 km, $N = 16$; Table 1). Birds of known body mass but captured 8 days (average for tagged birds) prior to initiating migratory flights, had similar ranges, varying from 2000 km for a bird of mean body mass (14.8 g) to 3170 km for a bird with the maximum recorded mass (18.3 g).

Figure 2. Variation in body mass between the overwintering period and immediately prior to northward (spring) migratory flights in blackpoll warblers captured at an overwintering site near Villavicencio, Colombia (dashed vertical line shows average departure date in birds tracked through radiotelemetry).

Table 1
Estimated departure mass and flight range for blackpoll warblers fitted with nanotags at an overwintering site in Colombia immediately prior to northward migration

Tag no.	Year	Capture date	Departure date	Body mass on capture (g)	Days to departure	Est. departure mass (g)	Flight range (km)
64	2017	25 Apr	30 Apr	14.2	6	15.6	2270
66	2017	25 Apr	29 Apr	16.9	5	18.1	3140
67	2017	26 Apr	06 May	16.3	11	18.9	3380
68	2017	26 Apr	05 May	15.7	10	18.0	3110
20	2017	27 Apr	09 May	12.8	13	15.8	2350
65	2017	27 Apr	Unknown	18.3	Unknown	18.3	3170
69	2017	27 Apr	07 May	13.2	11	15.8	2350
70	2017	27 Apr	01 May	16.6	5	17.8	3040
71	2017	27 Apr	08 May	16	12	18.8	3340
72	2017	27 Apr	06 May	14.3	10	16.6	2630
05	2018	26 Apr	06 May	12.8	11	15.4	2190
06	2018	28 Apr	06 May	13.4	9	15.5	2230
09	2018	01 May	06 May	13.8	6	15.2	2110
10	2018	01 May	12 May	13.4	12	16.2	2520
11	2018	01 May	07 May	16.3	7	17.9	3060
12	2018	02 May	07 May	14.7	6	16.1	2470

Departure mass was extrapolated from mass at first capture by multiplying the number of days that a bird remained at the study site by the mean daily mass gain within the population (0.23 g/day).
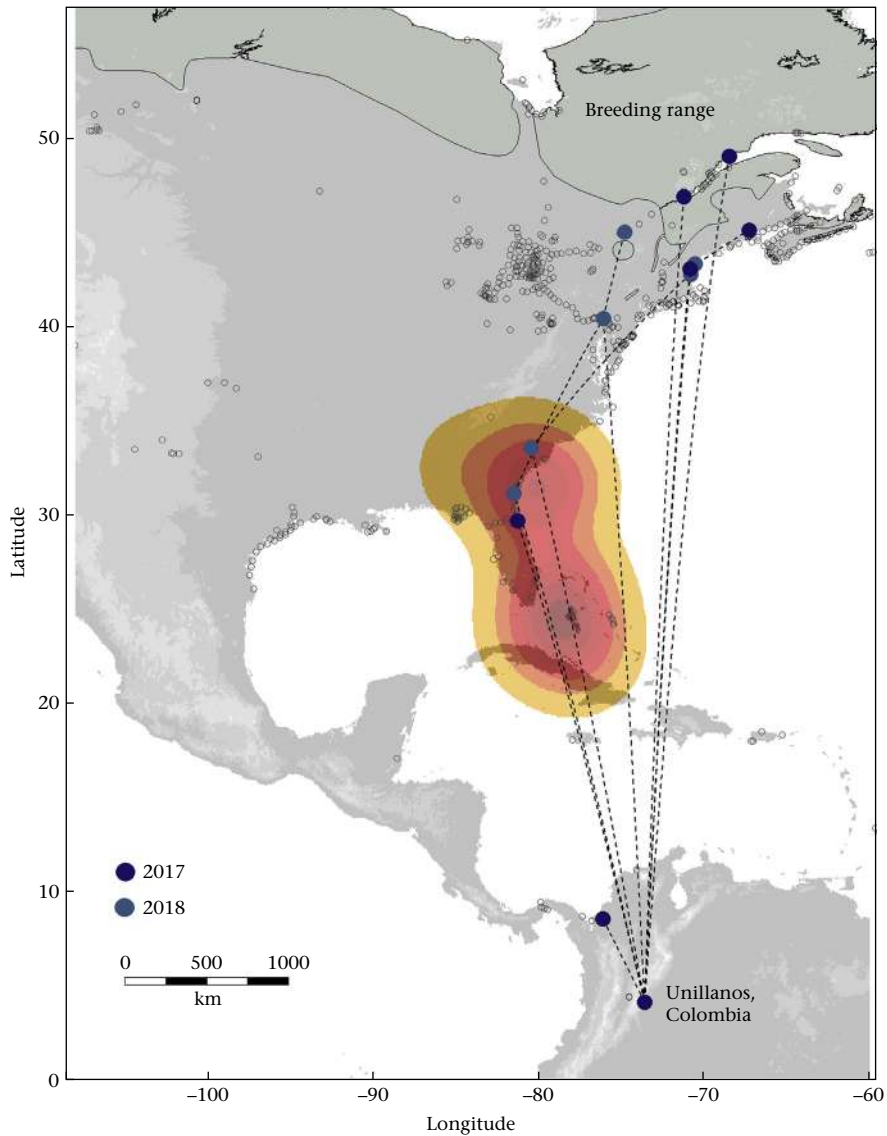
Figure 3. Detections of blackpoll warblers (blue circles) carrying radiotransmitters across the Motus automated telemetry array after departing on spring migration from a Colombian overwintering site. Estimated flight ranges from Colombia suggest that birds could reach Cuba, the Bahamas or Florida before refuelling (50% of journey): as indicated by a Kernel density plot of the most likely destination of 16 birds (probability decreases from red to orange). Dashed lines join successive detections of individual birds in Colombia and at Motus stations (open circles) active during the 2017 and 2018 migration periods (note: straight lines are not expected to reflect actual routes).

Location of Most Likely Stopover Regions and Migration Speed

Of 16 individuals fitted with nanotags in Colombia (excludes failed tag), 10 individuals were detected by automated telemetry stations beyond the study site (a detection rate of 62.5%; Table A1): two in northern Colombia, six in the United States and three in Canada (Fig. 3). Six individuals were detected on multiple occasions, including one bird first detected in South Carolina, then 6 days later in Massachusetts (1325 km), and subsequently in Maine 1 h later, as it flew past two coastal Motus stations 65 km to the northeast. A pattern of a NNW bearing from Colombia (mean of three birds = 346°, SD = 2.0°), followed by a NNE bearing in North America (mean of five birds = 28°, SD = 16.0°) was common to all tracked individuals.

Based on the flight ranges and flight bearings described above, and the simulation of flights from Colombia, birds were expected to run out of fuel and require a stopover in an area encompassing Cuba, the Bahamas, the Florida peninsula and, in rare cases, the southeastern United States (Fig. 3). For birds detected on or close to breeding grounds, straight-line distances from Colombia varied between 4050 km and 5000 km and were completed in 19—32 days, giving rise to a remarkably synchronized arrival over a week-long period between 30 May and 7 June. Based on the slope of a linear regression of distance flown against number of days, mean migration speed was 156 km/day (Fig. 4). Two birds detected within the known breeding range in Quebec, had total durations of 26 days 12 h and 27 days 2 h and a migration speed of 190 and 197 km/day, respectively.

Contribution to Total Migratory Journey

Assuming a route from Colombia to breeding areas in northeastern Canada (the most likely destination based on telemetry detections; Fig. 3) that went via the southeastern United States, we
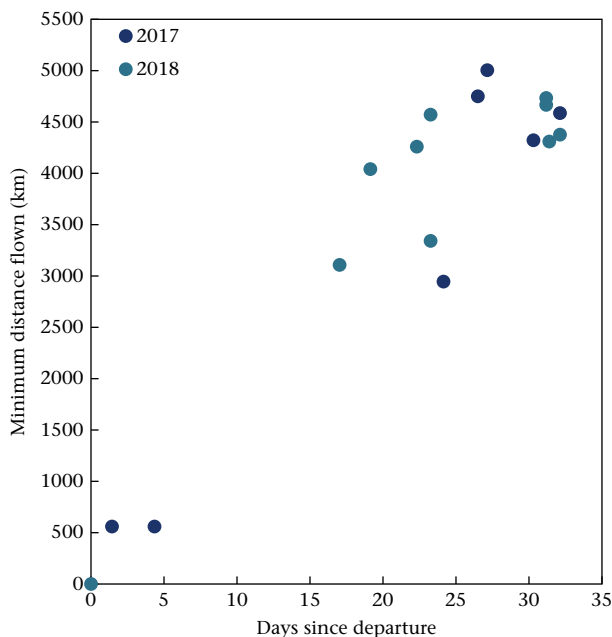
Figure 4. Minimum distance flown relative to the number of days since departure for 10 blackpoll warblers fitted with radiotransmitters at an overwintering site in Colombia and subsequently detected across the Motus automated telemetry array. Distances close to or greater than 5000 km equate to arrival in regions on or near the breeding grounds, suggesting that individuals could cover the distance between wintering and breeding grounds in ≈ 30 days.

estimated total migration distance to be 5350 km. The mean estimated departure mass of tagged blackpoll warblers from their Colombian overwintering grounds, would allow birds to cover 50.1% of the journey to the breeding grounds (range 39—63%). The highest recorded body mass in Colombia (18.3 g) equated to a flight range of 3170 km or 59% of the total migration distance.

DISCUSSION

Blackpoll warblers overwintering in Colombia showed dramatic increases in body mass (a surrogate for fuel stores) immediately prior to northward migratory flights, and estimated flight ranges imply that birds could cover 50% of their total migration distance (≈ 5350 km) without needing to refuel. Estimated flight ranges and detections of birds carrying nanotags suggest that birds flew to Cuba or Florida prior to refuelling and continuing to the breeding grounds, with the entire migration from South America to the boreal forest occurring in less than 1 month. Comparable data from other species wintering in South America show that blackpoll warblers had faster migration speeds (≈ 194 km/day) post-departure than red-eyed vireos, *Vireo olivaceus* (< 146 km/day; Callo, Morton, & Stutchbury, 2013), and Swainson's thrushes, *Catharus ustulatus* (111 km/day; Delmore, Fox, & Irwin, 2012), but slower migration speeds than veeries, *Catharus fuscescens* (247 km/day; Hobson & Kardynal, 2015), and eastern kingbirds, *Tyrannus tyrannus* (277 km/day; Jahn et al., 2013). Note, however, that true migration speed is lower, as overall speed should take into account days spent fuelling prior to departure (Lindström et al., 2019), and thus interspecies comparisons have limited value.

Combined, these results provide a unique quantitative demonstration of the energetic contribution of overwintering sites and highlight the critical role these sites can play in providing fuel for migration. It follows that destruction or degradation of overwintering sites may not only affect survival during the stationary nonbreeding period (Wilson et al., 2018) but would most likely carry over to have negative effects on the speed of migration (Gómez et al., 2017) and possibly survival en route to the breeding grounds (Newton, 2006). In the context of migration theory, being able to quantify the extent of premigratory fuelling is key to parameterizing optimal migration models and understanding how flexible migration strategies are in a changing world (Lindström et al., 2019).

Fuelling in Blackpoll Warblers

Long-distance migratory animals are known for their extreme phenotypic plasticity (Hedenström, 2008; McWilliams & Karasov, 2001; Piersma, 1998), and several bird species have been shown to accumulate energy reserves equivalent to 50% or more of their body mass (e.g. Bibby et al., 1976; Nisbet, McNair, Post, & Williams, 1995). Such major changes in body mass bring disadvantages, such as increasing mass-dependent predation risk (Hedenström, 2010; Jenni-Eiermann, 2017; Kullberg et al., 2000), but are believed to be offset by increases in flight range and a reduction in the dependence on unfamiliar stopover sites (Alerstam, 2011). Nonstop endurance flights have already been described in blackpoll warblers during their southward migration over the Atlantic Ocean and the Caribbean Sea to South America (DeLuca et al., 2015, 2019) but, despite this migratory feat, breeding areas do not contribute significantly to fuel requirements, with most energy being attained at stopover sites along the Atlantic seaboard (DeLuca et al., 2015; Nisbet et al., 1995). In contrast, we found that an overwintering site provided sufficient fuel for birds to cover between 39% and 63% of their total northward migration.

Despite not being able to record body mass on the day of departure, both our actual measurements and extrapolated departure masses were in general agreement and are also well within the range of values recorded prior to transoceanic flights from North America (20–23 g; Nisbet et al., 1963). Indeed, given the regular occurrence of birds weighing over 20 g in Massachusetts in September/October (Nisbet et al., 1963), it is possible that we underestimated true departure mass. Our estimate of daily mass gain (0.23 g/day) is similar to rates reported at stopover sites in Massachusetts ($\approx$ 0.2 g/day over 6–7 days; Nisbet et al., 1963) and is, therefore, likely to provide a reasonable estimate of departure mass in birds with known departure date. However, the decision to depart is typically an interaction between current fuel load, optimal departure date and climatic conditions, and may be delayed due to precipitation, for example (Deppe et al., 2015; Eikenaar, Klinner, Szostek, & Bairlein, 2014). Such delays could have resulted in our underestimating fuelling rate, if birds reached optimum departure mass several days prior to departure (see birds with mass > 16 .5 g in Fig. 1).

Migration Theory and Behaviour

Estimated flight ranges, flight directions and detections of birds carrying nanotags suggest that blackpoll warblers flew NNW from Colombia to arrive in an area between southernmost Cuba, the Bahamas and the southeastern United States (Fig. 3). Flight bearings changed on arrival in North America, with birds heading NNE towards likely breeding areas in eastern Canada (note, however, that birds flying NW have a lower probability of detection in the Motus array). Blackpoll warblers breed across North America from Newfoundland to Alaska, which implies that birds from our study site showed strong connectivity to the eastern extent of the breeding range based on flight trajectories and the probability of detection in the Motus automated array (all detections north of 40° latitude occurred within 10° of longitude between -67° and -77°; there were an equal number or greater number of antennas 10° on either side of this band). Given that estimated flight ranges point to birds running out of fuel in an area between Cuba and Florida, we predict a stopover in this region for up to 2 weeks before continuing their migration. This prediction is supported by findings from geolocators, which revealed stopovers > 4 days in Florida and the southeastern United States in nine birds (DeLuca et al., 2019). Together, these studies imply that individual blackpoll warblers breeding in eastern Canada may complete their migration using energy reserves largely obtained at just two sites.

The evidence laid out above highlights the role of overwintering sites in fuelling a significant percentage of the migratory journey, as well as enabling individuals to overcome challenges en route like crossing the Caribbean Sea. The advantages of this strategy would appear to be many and yet it is not common to all avian species studied to date (Risely et al., 2015). Indeed, even within species there may be marked interindividual variation (Lindström et al., 2016). For some species, and the same might apply to individuals, resource availability may determine the strategy adopted (Atkinson et al., 2007), with access to abundant resources promoting extensive fuelling prior to the first migratory flight. Specifically, access to resources mediated through dominance hierarchies may explain why interindividual variation exists (Kirk & Gosler, 1994; Marra, 2000), perhaps explaining why in this study one individual departed the study site 'early' prior to attaining large energy reserves.

It follows that certain environmental conditions, such as the timing of dry and wet seasons (Rockwell et al., 2017) or spring greening (Merkle et al., 2016) relative to the initiation of migratory fuelling, could also shape how animals prepare for migration.

Tracking studies, for example, hint at long flight stages from South American overwintering sites in veeries and bobolinks, *Dolichonyx oryzivorus*, which, like blackpoll warblers, occupy regions where precipitation increases prior to spring migration (Hobson & Kardynal, 2015; Renfrew et al., 2013). Nevertheless, extensive fuelling at a likely overwintering site has also been recorded at the height of the dry season in the Sahel region of Africa (Bayly & Atkinson et al., 2012), suggesting that other factors such as optimal routes (Alerstam, 2001) or the location of barriers (Delingat, Bairlein, & Hedenström, 2007) may influence the extent of fuelling. Unlike blackpoll warblers at our study site, not all species or populations occupy a single overwintering site for up to 6 months (Knight et al., 2019; Mckinnon, Fraser, & Stutchbury, 2013). Thus, potential advantages accrued through site familiarity may not be common across all species and could contribute to the variation in strategies observed to date.

Conclusions

The role of overwintering sites in contributing to and shaping migratory strategies has received little attention in the past. The blackpoll warbler serves to highlight the enormous potential of such sites to influence all aspects of migratory behaviour from departure time, migration pace and duration, and the use of stopovers. We propose that extensive fuelling at overwintering sites should be the behavioural norm, given high site familiarity and the facility to find food and avoid predators, with the caveat that overwintering sites provide sufficient food resources and are occupied for months at a time. This result also adds to a growing body of evidence showing that in migratory birds, at least, the energy requirements for migration and therefore the decisions taken during migration depend on/occur at a small number of sites (Bayly et al., 2018; Klaassen et al., 2011; Mckinnon et al., 2013), which should now include overwintering sites as well as stopover sites. While such a strategy makes a steeply declining species like the blackpoll warbler (estimated loss of 92% over 44 years; Rosenberg et al., 2016) vulnerable to changes at tropical overwintering sites and stopover sites, it also makes managing for the species more practical, given the restricted extent of regions with the potential to drive demographic change (Rockwell et al., 2017; Sherry & Holmes, 1996).

Declaration of Interest

None.

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Appendix

Table A1

List of detections for 10 blackpoll warblers fitted with nanotags in Colombia and subsequently recorded across the Motus automated telemetry array

Tag no.	Year	Departure date	Detection date	Latitude	Longitude	Detection site	Days	Distance flown (km)
63	2017	25 Apr? [a]	19 May	29.6682	-81.2663	Favre-Dyke, Florida	24.1	2946
64	2017	30 Apr	05 May	8.5258	-76.0966	Las Palmeras, Colombia	4.3	565
67	2017	06 May	08 May	8.5258	-76.0966	Las Palmeras, Colombia	1.4	565
68	2017	05 May	01 Jun	49.0432	-68.4605	Pointe-aux-Outardes, Quebec	27.1	5008
70	2017	01 May	01 Jun	43.0752	-70.8393	Great Bay, New Hampshire	30.4	4329
70	2017	01 May	02 Jun	45.1257	-67.2661	Moosehorn NWR, Maine	32.1	4590
72	2017	06 May	02 Jun	46.8930	-71.2111	D'Estimauville, Quebec	26.5	4750
5	2018	06 May	30 May	33.5339	-80.4312	Santee NWR, South Carolina	23.3	3352
5	2018	06 May	06 Jun	42.7803	-70.8085	PKR Salt Pannes, Massachusetts	31.1	4678
5	2018	06 May	06 Jun	43.2819	-70.5817	Furbish 2018, Maine	31.2	4736
5	2018	06 May	06 Jun	43.3351	-70.5491	WNERR, Maine	31.2	4743
9	2018	06 May	07 Jun	42.7803	-70.8085	PKR Salt Pannes, Massachusetts	31.4	4312
9	2018	06 May	07 Jun	43.3351	-70.5491	WNERR, Maine	32.1	4377
11	2018	07 May	26 May	40.4107	-76.0796	Blue Marsh, Pennsylvania	19.1	4048
11	2018	07 May	30 May	45.0091	-74.7904	Saunders, Ontario	23.1	4570
12	2018	07 May	24 May	31.1228	-81.4777	GA_DNR_DOCK, Georgia	17.0	3119
12	2018	07 May	30 May	40.4107	-76.0796	Blue Marsh, Pennsylvania	22.2	4260

Distance flown represents the straight-line distance from an overwintering site in Colombia (Universidad de los Llanos, WGS84 4.07333, -73.58086), where a total of 17 birds were fitted with nanotags immediately prior to northward migration (one tag failed).

[a] Bird/tag not recorded following release at study site – departure date uncertain.
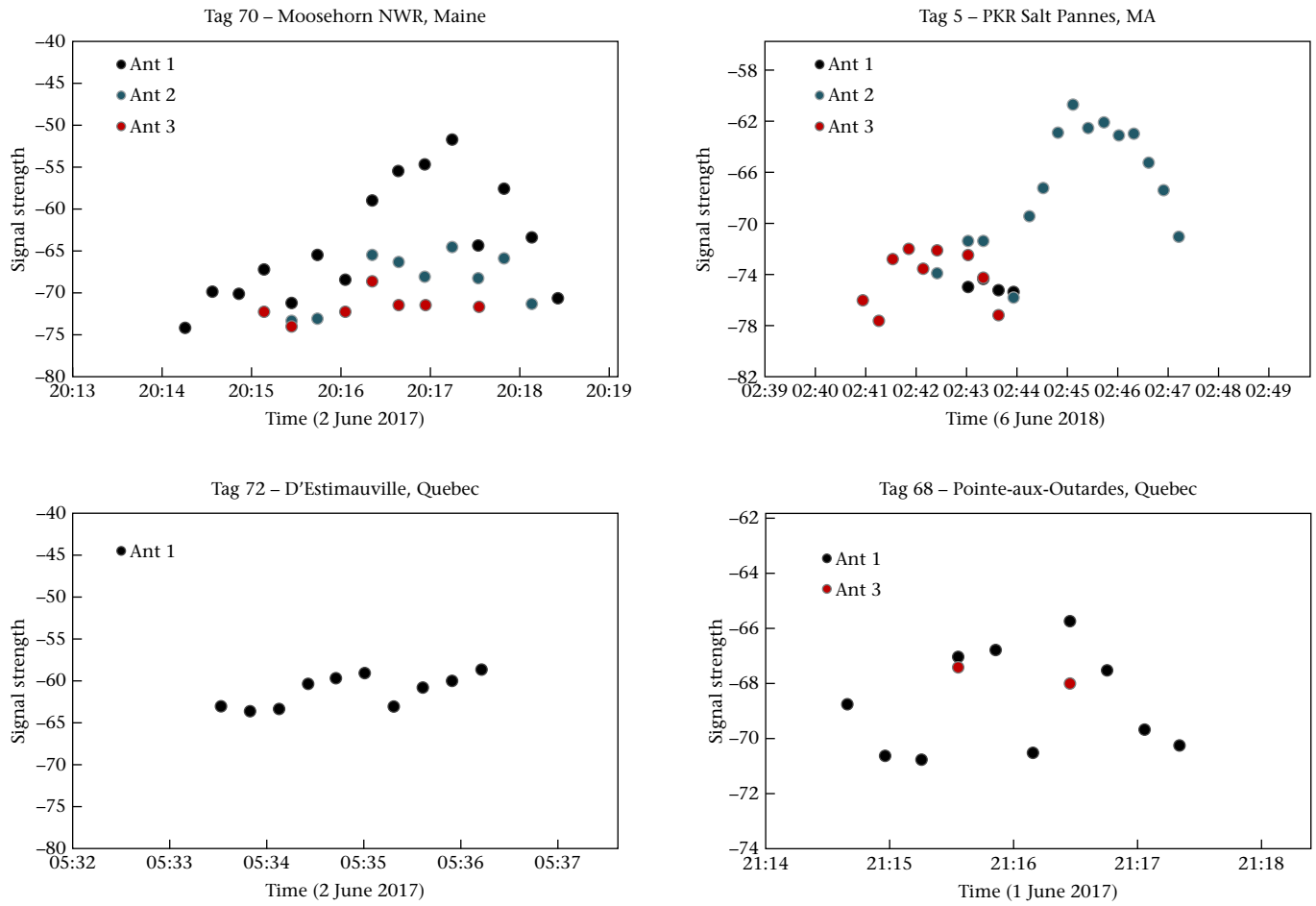
Figure A1. Plots of signal strength against time of day for a selection of blackpoll warblers fitted with nanotags at an overwintering site in Colombia and subsequently detected in North America at Motus automated telemetry stations. Detections of Tag 70 and Tag 5 show classic flyby parabola patterns for at least one antenna (Ant1 and Ant2, respectively). The detection pattern of Tag 72 is typical of a bird flying parallel to the antenna without any clear pattern in signal strength, while Tag 68 shows hints of a parabola pattern. Note that all detections occurred at night and relate to nocturnal migratory flights.