

## RESEARCH ARTICLE

**Rapid recovery by fat- and muscle-depleted Blackpoll Warblers following trans-oceanic migration is driven by time-minimization**Nicholas J. Bayly,<sup>1,\*</sup> Kenneth V. Rosenberg,<sup>2,3</sup> D. Ryan Norris,<sup>4,5</sup> Philip D. Taylor,<sup>6</sup> and Keith A. Hobson<sup>7,8</sup><sup>1</sup> SELVA: Investigación para la Conservación en el Neotrópico, Bogotá, Colombia<sup>2</sup> Cornell Lab of Ornithology, Ithaca, New York, USA<sup>3</sup> American Bird Conservancy, Washington, DC, USA<sup>4</sup> Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada<sup>5</sup> Nature Conservancy of Canada, Toronto, Ontario, Canada<sup>6</sup> Biology Department, Acadia University, Wolfville, Nova Scotia, Canada<sup>7</sup> Environment and Climate Change Canada, Saskatoon, Saskatchewan, Canada<sup>8</sup> Department of Biology, University of Western Ontario, London, Ontario, Canada\* Corresponding author: [nick.bayly@selva.org.co](mailto:nick.bayly@selva.org.co)

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**ABSTRACT**

Nonstop endurance flights are a defining characteristic of many long-distance migratory birds, but subsequent recovery phases are not typically distinguished from fueling phases (collectively “stopovers”), despite endurance flights inducing marked physiological changes including flight muscle atrophy and gastrointestinal tract reductions. Here, we hypothesize that recovery requires unique behavioral adaptations, leading to departures from the predictions of optimal migration theory for time-minimizing migrants. We predict that recovering birds will (1) select (moist) food-rich habitats on arrival; (2) have slow initial fueling rates due to decreased gastrointestinal capacity; (3) show a negative correlation between stopover duration and arrival condition instead of a negative correlation with fuel deposition rate (FDR); (4) stopover longer than required to store energy reserves for subsequent flights; and (5) show evidence of rebuilding flight muscles. To test these predictions, we studied Blackpoll Warblers (*Setophaga striata*) in northern Colombia following trans-oceanic flights >2,250 km. Birds selected dry seasonal habitats, despite the proximity of moist forests, and among 1,227 captured individuals, 14–21% were emaciated and 88% had atrophied flight muscles. We recaptured 74 individuals, revealing net positive mass gains and, contrary to prediction (2), no evidence for slow initial recovery rates. Contrary to prediction (3), stopover duration was only weakly correlated with arrival condition and birds with high FDR (4.9% lean body mass day<sup>-1</sup>) had shorter durations (3 days) relative to birds with slower rates (7 days): both groups accumulated sufficient fuel to reach nonbreeding (over-wintering) grounds 500–1,000 km away. Mass increases were largely attributable to fat deposition but some birds improved flight muscle condition (31.9%), consistent with prediction (5). Together these results reveal a strong selection for time-minimization in the decisions made by Blackpoll Warblers following trans-oceanic flights, likely mediated through advantages to early arrival on nonbreeding grounds, contrary to our hypothesis of recovery imposing unique selection pressures.

**Keywords:** Colombia, endurance flights, fuel deposition rate, La Guajira, optimal migration theory, physiology, *Setophaga striata*, stopover duration

**LAY SUMMARY**

- Following trans-oceanic flights, migratory landbirds often arrive in an emaciated state and must balance the need to immediately replenish energy reserves against finding optimal foraging conditions, rebuilding digestive organs and flight muscles consumed during flight, and a timely arrival at their final destination.
- We studied Blackpoll Warblers arriving in South America following trans-Atlantic flights, many of which had severely depleted fat reserves and flight muscles, to understand how birds balance these needs.
- Remarkably, Blackpoll Warblers took just 3–7 days to rebuild their energy reserves and continue migrating, implying a strong time pressure for reaching their nonbreeding (wintering) grounds as quickly as possible.
- High densities of birds and rapid refueling rates revealed the importance of xeric habitats on the Guajira Peninsula of Colombia for this steeply declining species, uncovering a previously unknown aspect of the species' migratory journey.

## La rápida recuperación de músculo y grasa en individuos de *Setophaga striata* después de su migración transoceánica está determinada por la hipótesis de minimización del tiempo

Los vuelos de larga distancia sin escalas son característicos de muchas especies de aves migratorias, pero la fase de recuperación posterior a los vuelos casi nunca se diferencia de la fase de acumulación de energía (colectivamente llamados “paradas”), a pesar que este tipo de vuelos causan cambios fisiológicos importantes incluyendo la atrofia muscular y la reducción del tracto intestinal. Aquí ponemos a prueba la hipótesis de que la recuperación física tras vuelos largos requiere de adaptaciones comportamentales que se alejan de las predicciones de la teoría de migración óptima para especies que minimizan el tiempo. Predicimos que las aves en recuperación: (1) seleccionan hábitats húmedos ricos en alimento al llegar; (2) tienen tasas iniciales de acumulación de combustible lentas debido a su capacidad gastrointestinal reducida; (3) muestran una correlación negativa entre la duración de la parada y la condición física al llegar, en lugar de una correlación negativa entre la duración de la parada y la tasa de acumulación de energía; (4) paran por más tiempo del requerido para acumular las reservas necesarias para el siguiente vuelo; y (5) muestran signos de recuperación del músculo de vuelo. Para poner a prueba nuestras predicciones, estudiamos individuos de *Setophaga striata* a su llegada en el norte de Colombia, luego de un vuelo transoceánico de >2,250 km. Las aves seleccionaron hábitats secos estacionales a pesar de la cercanía a bosques húmedos, y de 1,227 individuos capturados, 14–21% estaban demacrados y 88% tenían el músculo pectoral atrofiado. Recapturamos 74 individuos que mostraron aumento de peso y, contrario a nuestra predicción (2), no mostraron evidencia de tasas de acumulación inicial lentas. Contrario a la predicción (3), la duración de la parada solo tuvo una correlación débil con la condición física al llegar, y las aves con tasas de acumulación altas (4.9% de la masa magra diaria<sup>-1</sup>) mostraron duraciones más cortas (3 días) que las aves con tasas más lentas (7 días). Además ambos grupos (lentos y rápidos) acumularon suficientes reservas para llegar a sus sitios de invierno situados entre 500–1,000 km de distancia. El aumento de peso se atribuyó principalmente a la acumulación de grasa, pero algunos individuos también mostraron mejoría en la condición muscular (31.9%). Estos resultados revelan que hay una fuerte presión de selección para la minimización del tiempo en las decisiones que individuos de *Setophaga striata* toman luego de sus vuelos transoceánicos, probablemente mediados por ventajas de llegar temprano a los sitios de invierno, y contrario a nuestra hipótesis sobre la recuperación física imponiendo presiones diferentes.

**Palabras clave:** Colombia, vuelos de larga distancia, tasa de acumulación de combustible, La Guajira, teoría de migración óptima, fisiología, *Setophaga striata*, duración de parada migratoria

## INTRODUCTION

Long-distance migratory birds face many challenges during their annual cycle, none more so than migration itself (Newton 2006, Egevang et al. 2010, Moore 2018). Migration is especially challenging in species that undertake endurance flights to overfly vast inhospitable areas (Hedenström 2010). Overcoming such challenges can eliminate energetically costly detours, while getting it wrong, such as making inadequate preparations for flights, can result in mortality (Newton 2007, Ward et al. 2018). How birds attain energy reserves prior to crossing the Sahara Desert, Caribbean Sea, or Atlantic Ocean, for example, has been well studied (Nisbet et al. 1995, Fransson et al. 2001, Bayly et al. 2013). In contrast, few studies have examined behavioral decisions following endurance flights or the selection pressures acting on recovery phases (Jenni-Eiermann 2017). Here, we make a theoretical distinction between stopovers involving recovery and those used primarily for refueling, based on expected physiological and behavioral differences between birds. We hypothesize that behavioral decisions and refueling capacity in “recovering” birds will diverge from that expected under a time-minimization model of optimal stopover behavior (Alerstam and Lindström 1990). To examine this hypothesis, we studied Blackpoll Warblers (*Setophaga striata*) in northern Colombia following trans-oceanic flights.

Physiological studies of migratory landbirds following endurance flights have revealed remarkable adaptations, including partial consumption of the gastrointestinal tract and extensive flight muscle catabolism, which provide essential components of fat metabolism, emergency fuel and facilitate dehydration avoidance (Biebach 1998, McWilliams and Karasov 2001, Schwilch et al. 2002, Biebach and Bauchinger 2003, Gerson and Guglielmo 2011). These physiological changes, coupled with oxidative stress (Jenni-Eiermann et al. 2014), often result in migrants arriving in an emaciated state (Rogers and Odum 1966, Newton 2006). We hypothesize that associated reductions in digestive capacity and flight muscle efficiency (McWilliams and Karasov 2001, Gerson et al. 2020), coupled with the slower speed at which lost protein can be replaced relative to fat stores (Smith and McWilliams 2010), will induce behavioral changes in emaciated birds to facilitate the rebuilding of essential protein structures and repair oxidative damage (Eikenaar et al. 2020; for alternative strategies, see Weber and Hedenström 2001). Indeed, constraints birds face while undergoing “physiological recovery” could override the selection pressures typically acting on stopovers as described by optimal migration theory (Alerstam and Lindström 1990, Alerstam 2011). We therefore use the latter theoretical framework to generate testable predictions comparing and contrasting recovery and refueling phases.

Stopover habitat selection and diet, for example, could be influenced by nutrient requirements, with recovering birds seeking habitats with protein-rich food sources that accelerate recovery of the gastrointestinal tract (Muñoz-García et al. 2012) and other protein structures. In contrast, birds building energy reserves for flights often select lipid- or carbohydrate-rich foods, such as fruit (Parrish 1997, Bairlein 1998, Smith et al. 2007). In Neotropical ecosystems, precipitation drives both fruit and insect abundance (Poulin et al. 1992, Smith et al. 2010), and increasing precipitation has been linked to habitat quality in migratory landbirds in the Neotropics (Sherry and Holmes 1996). Following endurance flights, Blackpoll Warblers might therefore select habitats only favoring physiological recovery or those where a diet of both insects and fruit promotes the simultaneous rebuilding of atrophied protein structures and fat stores (Lindström 2003).

How behavior differs between recovering birds and fueling birds will depend on the evolutionary pressures shaping migratory strategies (Alerstam and Lindström 1990). To date, energy (transport costs), time, and predation risk have all been considered as currencies that could be minimized during migration. If, as with almost all long-distance migrants studied to date (Hedenström 2008, Briedis et al. 2018, Schmaljohann 2018, Anderson et al. 2019), individuals are time-minimizers, they should only stop long enough to gain sufficient energy reserves for onward flights (Lindström and Alerstam 1992). This leads to a negative correlation between stopover duration and fuel deposition rate (FDR), and, for example, shorter stopovers in years or in habitats supporting higher rates (Weber et al. 1998, Bayly et al. 2019). Stopover duration is also expected to be unrelated or only loosely correlated with a bird's arrival condition under time-minimization, even if emaciated birds are present in the stopover population.

Conversely, if rebuilding of digestive organs and lost muscle are selected for, favoring energy assimilation efficiency and reducing transport costs during onward flights (Bauchinger and Biebach 2001), stops involving physiological recovery should be longer than predicted by time-minimization—rebuilding the digestive tract, for example, can take 2–3 days (Muñoz-García et al. 2012). Accordingly, stopover duration should be negatively correlated with arrival condition and increases in muscle mass (especially flight muscle) should contribute significantly to mass change. Further, if the digestive machinery is partly consumed, as commonly occurs during nonstop flights (McWilliams and Karasov 2001), fueling rates are expected to be negative or slower at the initiation of stopover.

The Blackpoll Warbler has an unusual migration strategy among migratory landbirds in the Americas, involving prolonged stopovers on the Atlantic coast of North America prior to traveling over the Atlantic

Ocean and Caribbean Sea to South America (Nisbet et al. 1995, DeLuca et al. 2019). This journey may involve daytime stops on Caribbean islands (Latta and Brown 1999) or longer stopovers in individuals from northeastern breeding populations (DeLuca et al. 2015) but most birds likely fly direct to South America (76% of geolocator tracks suggest direct flights; DeLuca et al. 2015, 2019). This physiologically demanding strategy entails nonstop flights lasting 70 hr on average and covering 2,250–3,400 km (DeLuca et al. 2019). The arrival of birds in northern South America therefore represents an ideal model system for studying behavioral decisions during recovery.

To examine the predictions arising from hypothesized behavioral differences between recovery phases and fueling stopovers laid out above, we tested (1) whether Blackpoll Warblers arriving in Colombia selected regions with high precipitation and if habitat choice led to a protein-rich diet conducive to recovery; (2) if fueling rates were influenced by arrival condition, with emaciated birds showing slower rates, as predicted if gastrointestinal tract atrophy occurs during flight; (3) if stopover duration was negatively correlated with arrival condition, as expected if recovery is selected for, or if durations were negatively correlated with FDR as expected under time-minimization; (4) if stopover durations exceeded the expected time required to accumulate sufficient reserves for onward flights; and (5) if there was evidence for flight muscle mass contributing to body mass gains. By assessing stopover use by Blackpoll Warblers in South America, our study also contributes to our knowledge of this steeply declining, long-distance migrant (Rosenberg et al. 2019).

## METHODS

### Habitat Selection and Diet

To examine the role of humidity and other factors in shaping where Blackpoll Warblers settled having made landfall along the southern coast of the Caribbean Sea, we used data from multispecies occupancy surveys (Mackenzie and Royle 2005) carried out across northern Colombia and Panama under the Neotropical Flyways Project (<https://neotropicalflyways.com>). The dataset consisted of surveys completed from September to November in 2016 (northern Colombia) and 2017 (Panama) across 21 study sites with associated vegetation data. Collection and analysis of occupancy data are described elsewhere (Gómez et al. 2019) and in the [Supplementary Material](#). For the results presented here, 5,748 repetitions of 264 individual transects were used. Using the R package *Unmarked* (Fiske and Chandler 2011), we modeled how occupancy rate varied with (1)

**TABLE 1.** Occupancy rates for Blackpoll Warblers across Panama and northern Colombia were positively correlated with longitude (Long) but negatively related to autumn precipitation (Rain), such that birds were more likely to occupy and remain in dry eastern sites. Occupancy rate decreased with elevation (Elev) and canopy height (CanH), reflecting the occupation of lowland sites dominated by tropical thorn scrub.  $k$  = number of parameters,  $w_i$  = AIC weight. Protocol = passive transects vs. playback points; Long = longitude; Rain = fall precipitation; Elev = elevation; CanH = canopy height; NatV = %natural vegetation.

Model ~ detection ~ occupancy	$k$	AIC	$\Delta$ AIC	$w_i$
~Protocol ~ Long + Rain + Elev + CanH + NatV + Period	12	795.65	0	0.82
~Protocol ~ Long + Rain + CanH + NatV + Period	11	798.62	2.97	0.18
~Protocol ~ Elev + Rain + CanH + NatV + Period	11	887.75	92.11	0.00
~Protocol ~ Elev + CanH + NatV + Period	10	888.83	93.18	0.00
~Protocol ~ Long + Period	8	892.28	96.63	0.00
~Protocol ~ CanH + NatV + Period	9	923.63	127.98	0.00
~Protocol ~ CanH + Period	8	985.34	189.69	0.00
~Protocol ~ Elev + Period	8	1,017.66	222.02	0.00
~Protocol ~ NatV + Period	8	1,054.23	258.59	0.00
~Protocol ~ Rain + Period	8	1,099.34	303.70	0.00
Null (~Protocol ~Period)	7	1,107.34	311.69	0.00

autumn precipitation, elevation, and longitude and (2) between study sites supporting different habitats. For both analyses, we created a model set to evaluate the main effects of interest (autumn precipitation and site) by comparing Akaike's information criterion (AIC) and  $\Delta$ AIC values (Table 1), while correcting for local vegetation structure. We used the top model from the second analysis to estimate the occupancy rate at each of the 21 study sites and describe habitat associations.

To evaluate diet during stopover (e.g., fruit vs. invertebrates), we carried out foraging observations on 88 focal birds encountered at random within El Pantano Reserve (see below). For each individual, we counted the number of attacks made with the bill before the bird was lost to view and classified attacks as being directed at invisible prey (insects), caterpillars, or fruit. We present the proportion of attacks on each prey item.

### Capture of Blackpoll Warblers Following Trans-Oceanic Flights

To examine predictions regarding Blackpoll Warbler behaviors following endurance flights, a constant effort mist-netting station was established on the Guajira Peninsula in the El Pantano Reserve located 3.5 km south of Colombia's Caribbean coast (11.2931, -73.2182 WGS84; Figure 1). We selected this region based on the occupancy surveys described above. The reserve, managed by the Iguaraya Foundation (<https://www.fundacioniguaraya.org/>), was selected for the presence of multiple conserved vegetation types covering 270 ha, including tropical thorn scrub and tropical dry forest.

Mist-netting was carried out daily from September 22 through November 8, 2017 and from October 3 to November 5, 2018. A maximum of 15 (12-m long, 30-mm mesh size) mist-nets were operated across 2 habitats: 9 nets in tropical thorn scrub close to a seasonal lagoon

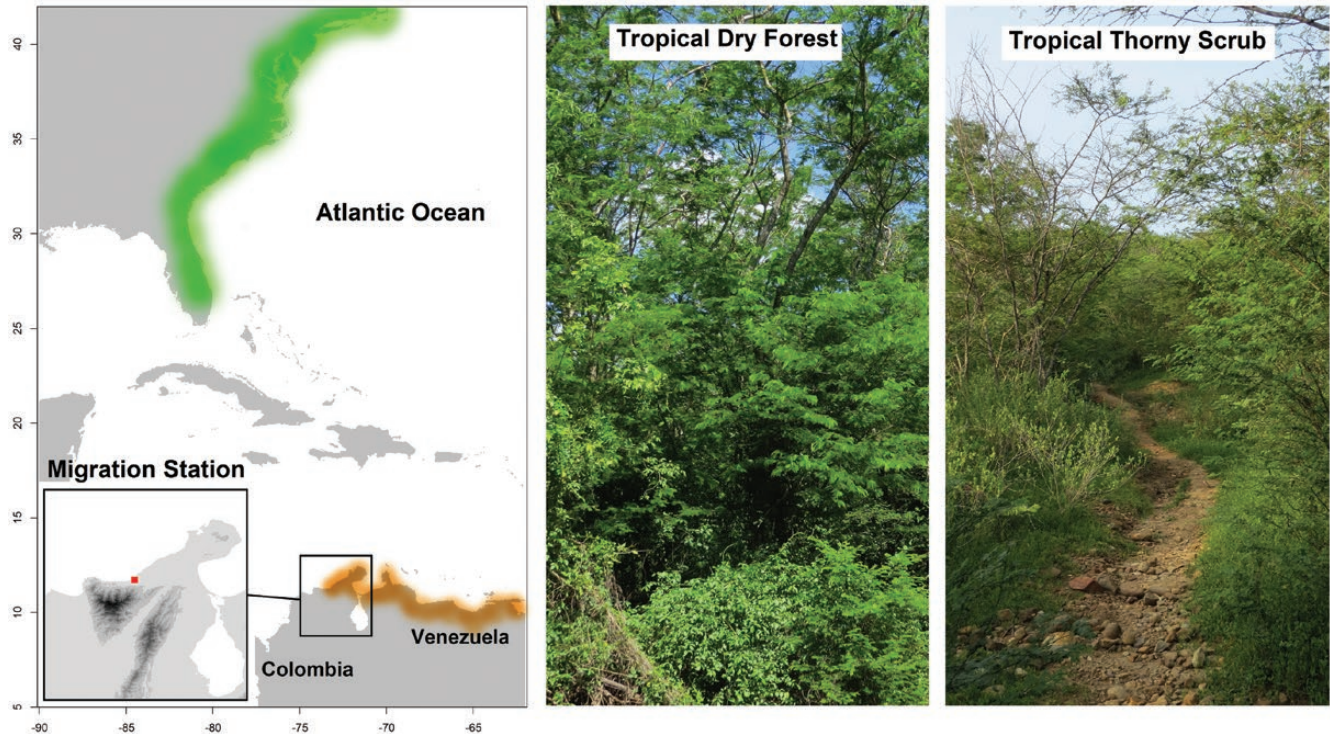
with an average canopy height of 3.7 m (range: 1–6 m; based on 2 measurements 5 m either side of each net) and 4–6 nets in tropical dry forest with an average canopy height of 8.8 m (range: 5–12 m) (Figure 1), ~1 km from the first net array. Nets were opened from dawn for up to 6 hr.

All captured Blackpoll Warblers were fitted with a uniquely numbered Porzana-made aluminum ring (reporting address: [www.aselva.co](http://www.aselva.co)) and the following data were collected prior to release: date and hour captured; mist-net number; age and sex (Pyle 1997); fat score on a 9-point scale from 0 to 8 (Kaiser 1993); muscle score on a 4-point scale from 0 to 3 in 2017 (Redfern and Clark 2001) and on a 7-point scale in 2018 (by including intervals of 0.5); unflattened wing chord; and body mass (nearest 0.1 g). The same data were collected for birds recaptured at least 3 hr after first capture ( $n = 5$ ), in order to provide mass change data over the first day of capture.

Capture data are used to describe the phenology of migration at our mist-netting site, summing captures by day and by age class (immature vs. adult) and plotting against date without correction for daily mist-net effort, given near constant effort across days. We also calculated the total number of captures by year, habitat, and age group and provide a correction for capture effort by calculating the capture rate per 100 mist-net hours, where a mist-net hour is equivalent to one 12-m mist-net open for 1 hr.

### Arrival Condition

To evaluate the degree of protein catabolism and percentage of "emaciated" individuals on arrival, we calculated the percentage of new captures with (A) fat score 0; (B) muscle score 0; and (C) muscle score 1. A fat score of 0 indicates likely total consumption of fat reserves. We consider muscle scores <2 as evidence of protein catabolism,



**FIGURE 1.** Location of the migration monitoring station (red square in inset) on the Guajira Peninsula, northeastern Colombia, relative to departure (green) and arrival regions (orange) of Blackpoll Warblers making trans-oceanic flights following DeLuca et al. (2019). The two dominant habitat types at the station are illustrated by photos.

given that 94% ( $n = 33$ ) of a sample of nonbreeding birds in Colombia had muscle score 2 (N. J. Bayly personal observation, captures in January and February). We also estimated the percentage of birds with body mass below lean body mass (LBM), based on two LBM estimates: (A) the fat-free mass (11.2 g) reported by Nisbet et al. (1963) following fat extraction of tower kills in Michigan; and (B) size-dependent LBM based on a regression of mass against wing length for birds with fat score 0 and muscle score 1 captured in this study (Ellegren 1992).

### Fuel Deposition Rates and Evidence for Reduced Digestive Capacity

To describe temporal changes in FDR as evidence for reduced digestive capacity, we modeled body mass change as a function of number of days elapsed between captures in 74 Blackpoll Warblers captured and weighed more than once (26 and 48 in 2017 and 2018, respectively), following methods described in Bayly et al. (2012). We created a model set in which mass change followed a linear or quadratic relationship with days since first capture, while also testing for the influence of arrival mass, arrival date, age, and the interaction of vegetation type and year with days since first capture (Table 2). To account for differences in time of capture, we included the difference in capture hour as an additive

variable in models. To evaluate model support, we used AIC and  $\Delta$ AIC, and employed 95% coefficient intervals (CIs) around coefficients to assess the relative importance of variables. All modeling was carried out in R (R Development Core Team 2017).

### Stopover Duration in Relation to Arrival Condition, Time-Minimization Predictions, and Onward Flights

We calculated 2 estimates of stopover duration: (1) minimum stopover duration and (2) “total stopover” (see Bayly et al. 2012). Minimum stopover duration was calculated as the number of days recaptured birds were known to have stayed at the study site. To estimate “total stopover” and test for correlations between stopover length and arrival condition, we ran a survival analysis in the program MARK (9.0) following Schaub et al. (2001). Given the small number of recaptures (2017: 27 of 602 captures, 4.5%; 2018: 47 of 624 captures, 7.5%), we fitted models without time dependence. We included arrival body mass, age, and vegetation type as variables and examined their influence on survival or seniority probabilities by comparing and contrasting appropriate models through (quasi)-Akaike’s information criterion (QAIC<sub>c</sub>) and  $\Delta$ AIC<sub>c</sub> values (Supplementary Material Table S1), while structuring models to account for transients in the population (Efford 2005). To test for goodness of fit, we calculated  $\hat{c}$  for the best-fitting model

**TABLE 2.** Model set examining the factors influencing fuel deposition rates and recovery of body mass by Blackpoll Warblers following trans-oceanic flights. Year and vegetation type had an overriding effect on mass change, with limited evidence for the role of arrival mass, capture date, and age. There was also strong support for a quadratic relationship between mass change and days, with rates decreasing in time.  $k$  = number of parameters,  $w_i$  = AIC weight.

Model	$k$	AIC <sub>c</sub>	ΔAIC	$w_i$
Days * Year * Habitat + Days <sup>2</sup> * Year * Habitat + Arrival mass + Hour	10	146.14	0	0.68
Days * Year * Habitat + Days <sup>2</sup> * Year * Habitat + Date + Hour	10	148.73	2.59	0.19
Days * Year * Habitat + Days <sup>2</sup> * Year * Habitat + Age + Hour	11	149.74	3.59	0.11
Days * Year * Habitat + Days <sup>2</sup> * Year * Habitat + Hour	9	153.33	7.19	0.02
Days * Year + Days <sup>2</sup> * Year + Hour	6	168.27	22.13	0.00
Days + Days <sup>2</sup> + Hour	4	218.23	72.09	0.00
Days + Hour	3	249.02	102.88	0.00
Days	2	272.07	125.93	0.00
Null	2	286.91	140.77	0.00

without a transient structure and adjusted AIC values of all models for the resulting values of  $\hat{c}$  ( $\hat{c}$  was <1.5 for models from both years).

To determine whether stopover durations were longer than those predicted by a time-minimizing model, we ran 3 variations of equation 3 in [Hedenström and Alerstam \(1997\)](#) in which we varied:  $t_o$  = the time cost of stopping over expressed in whole days, including values of 0.1, 1, and 2 days;  $f_o$  = the energy cost of stopping over, expressed as a percentage of LBM, fixed at 0.01; and  $k$  = FDR, expressed as the proportion of LBM accumulated per day, including values of 3.06% and 4.9% (see results). We compared the resulting values for  $t$  to our estimated stopover duration values.

To determine whether stopover durations were longer than necessary to accumulate the fuel for on-ward flights, we estimated departure mass and flight range (see [Supplementary Material](#); see also [Bayly et al. 2012](#)) and compared them with the distance to likely final nonbreeding destinations.

### Relationship Between Fuel Deposition Rate and Stopover Duration

To test whether stopover duration was negatively correlated with FDR as expected under time-minimization, we utilized the variation in FDR between vegetation types and years at our study site to perform a linear regression using estimated mean FDR and “total stopover” duration for each vegetation type and year of study. To generate FDR values from mass change models, we entered the mean stopover duration of 6 days into the top model (see above) and expressed the total expected mass change as a daily rate. To present FDR as a percentage of LBM (see [Fransson 1998](#)), we used the equation:  $FDR = (\text{daily mass change}/LBM) \times 100$ , where LBM was calculated as described above.

### Contribution of Muscle to Mass Gains

To assess the relative contribution of increases in the protein mass of flight muscle to mass gains, we carried out

linear regressions of mass change against changes in both muscle and fat score in R.

## RESULTS

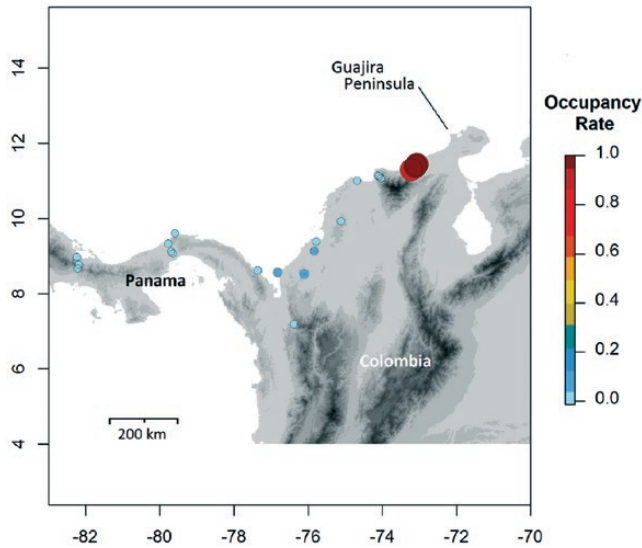
### Habitat Selection and Diet

We recorded 865 Blackpoll Warblers during occupancy surveys, with nearly all records from xeric habitats (Caribbean dry thorn scrub and tropical dry forest) on the Guajira Peninsula in northeastern Colombia. Correspondingly, occupancy rate increased with longitude (coefficient  $\pm$  SE top model =  $3.12 \pm 0.43$ ; [Table 1](#)) and decreased with elevation (coefficient  $\pm$  SE =  $-1.70 \pm 0.92$ ) and canopy height (coefficient  $\pm$  SE =  $-0.90 \pm 0.24$ ). Contrary to our prediction, occupancy decreased with increasing autumn precipitation (coefficient  $\pm$  SE =  $-0.18 \pm 0.53$ ), although the 95% CI for precipitation included zero. Site-based analyses revealed high occupancy rates (>0.8) at 3 sites on the lower Guajira Peninsula ([Figure 2](#)) and low rates (<0.03) in nearby humid forests between 500 and 2,000 m in the Sierra Nevada de Santa Marta mountains (see [Supplementary Material Figure S2](#)).

At the El Pantano Reserve, we recorded foraging sequences lasting from 10 to 175 s for 88 Blackpoll Warblers (total 90.3 min of foraging observations). Of 320 attacks observed, 78% were towards unidentifiable (insect) prey, 21% towards caterpillars, and <1% towards fruit. Proportions were extremely similar across habitats.

### Captures of Blackpoll Warblers Following Trans-Oceanic Flights

Blackpoll Warblers began arriving at the mist-netting station from late September and were largely absent when the station was closed in November. The main arrival began in mid-October continuing through till the end of the month ([Supplementary Material Figure S1](#)). Arrivals were accompanied by rapid increases in capture rates and loose groups of up to 25 Blackpoll Warblers involved in



**FIGURE 2.** Site-based occupancy rates for Blackpoll Warblers were highest at the base of the Guajira Peninsula in northeast Colombia during fall migration. Fewer than 5 birds were recorded at 3 sites in northwestern Colombia, while no birds were recorded in Panama. Occupancy rate is reflected in the size and color of the points. Sites are plotted over a grayscale base map showing elevation (light gray <250 m; black >4,000 m).

morning flight over the study site. Totals of new captures were similar between years (2017: 603 individuals, 2018: 624) despite a 10% decrease in effort in 2018 (2,472 and 2,248 mist-net hours, equivalent to 24.4 and 27.8 birds per 100 mist-net hours, respectively). Capture totals varied by vegetation type, with tropical dry forest accounting for 41% (249 birds) of captures in 2017 (equivalent to 75.0 birds per 100 mist-net hours) but just 11% (70 birds) in 2018 (13.1 birds per 100 mist-net hours). In dry thorn scrub, capture rates increased in 2018 with 32.3 birds per 100 mist-net hours relative to 16.5 birds per 100 mist-net hours in 2017. Immature birds were more abundant than adults in both years (ratio of immatures to adults 3.4:1 in 2017 and 1.5:1 in 2018).

### Arrival Condition: Evidence for Fat and Muscle Depletion

Of 603 individuals captured in 2017 (Figure 3), 14% were fat-depleted (fat score = 0) and 87% had reduced flight muscles, having either a severely reduced muscle (12% with muscle score = 0) or a reduced muscle relative to nonbreeding birds in Colombia (75% with muscle score = 1). Fat scores were lower in 2018, with 21% of 624 birds being fat-depleted. Birds showing both fat and muscle depletion (emaciated birds) accounted for 14% and 21% of birds in 2017 and 2018, respectively.

Compared to the mean fat-free mass reported by Nisbet et al. (1963), 77% and 70% of birds had arrival masses <11.2 g in 2017 and 2018, respectively. The lowest recorded mass,

8.3 g, was 2.9 g below fat-free mass (Figure 3). Our regression equation for 49 birds with fat score = 0 and muscle score = 1 ( $LBM = 0.09 \times \text{wing length} + 3.39$ ) estimates a mean LBM of 9.9 g. When calculated for each individual, 21% and 17% of birds were classed as below expected LBM in 2017 and 2018, respectively.

### Fuel Deposition Rates and Evidence for Reduced Digestive Capacity

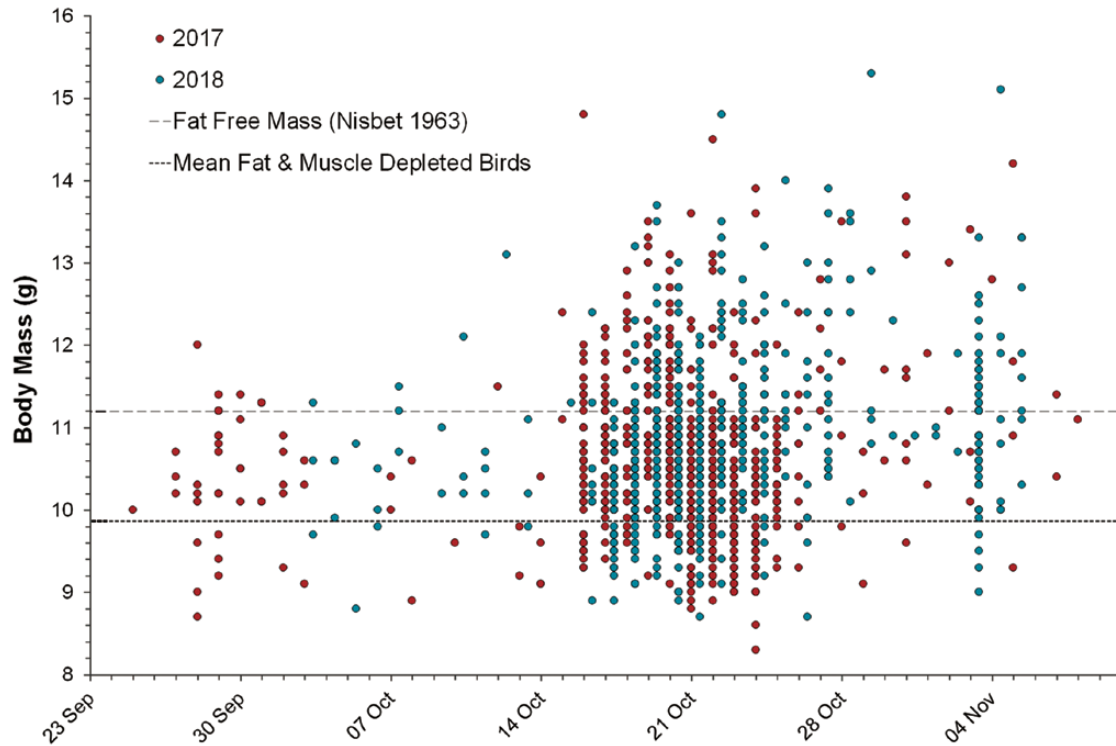
We found support for a nonlinear increase in body mass from birds that were recaptured ( $n = 74$ ). However, contrary to our prediction of reduced digestive capacity upon arrival, rates decreased, not increased, over time (see Figure 4). Further, there was limited support for a correlation between mass change and arrival condition, in which birds in poorer condition tended to fuel faster (coefficient  $\pm$  SE =  $-2.539 \pm 0.835$ ; Table 2). Rates of mass change were strongly influenced by year and vegetation type (Table 2, Figure 4). Rates were fastest in tropical thorn scrub in 2018 ( $0.48 \text{ g day}^{-1}$  or  $4.90\% \text{ LBM day}^{-1}$ ), followed by tropical dry forest in 2017 ( $0.30 \text{ g day}^{-1}$  or  $3.06\% \text{ LBM day}^{-1}$ ), and slowest in tropical thorn scrub in 2017 ( $0.08 \text{ g day}^{-1}$  or  $0.82\% \text{ LBM day}^{-1}$ ; NB). FDR could not be estimated for tropical dry forest in 2018.

### Stopover Durations in Relation to Arrival Condition, Time-Minimization Predictions, and Onward Flights

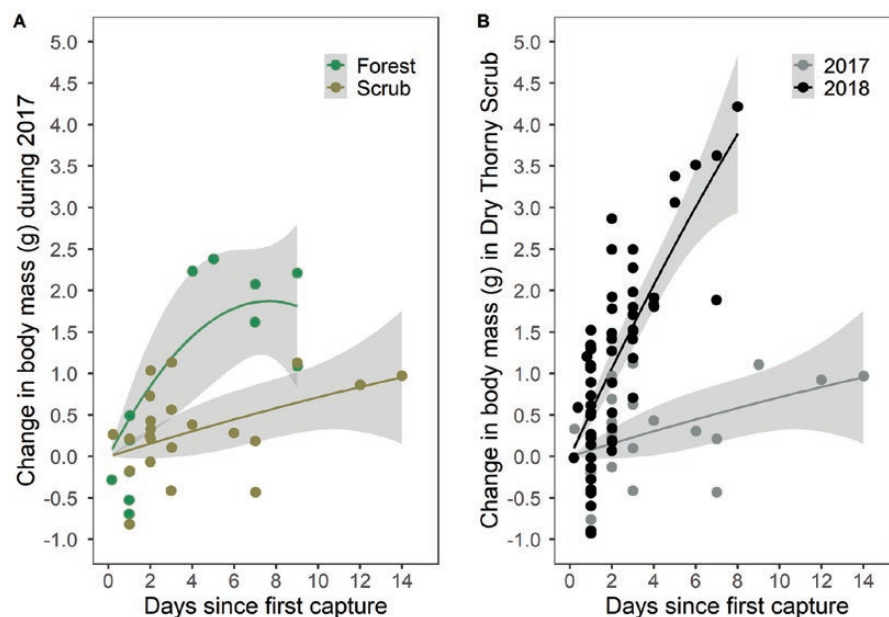
Twenty-seven of 603 Blackpoll Warblers were recaptured in 2017 and 47 of 624 birds were recaptured in 2018. Minimum stopover durations varied between 2 and 15 days, with mean values of 5.3 days and 3.2 days in 2017 and 2018, respectively (Table 3). “Total stopover” duration was estimated at 7.1 days in 2017 and 3.1 days in 2018. Top models explaining variation in stopover duration included a transient structure and an effect of arrival mass and vegetation (Supplementary Material Table S1). Although birds arriving at lower masses were predicted to stay longer in both years (coefficient  $\pm$  SE; 2017 =  $-0.097 \pm 0.194$ ; 2018 =  $-0.041 \pm 0.188$ ), 95% CI around coefficients included zero and effect sizes were small (e.g., maximum difference of 2 days between an arrival mass of 8.3 g vs. 14.8 g in 2017 and 0.3 days between arrival mass of 8.7 and 15.3 g in 2018).

When compared to the predictions from a time-minimizing model, stopover durations were shorter than expected when a time cost of 1 or 2 days were included (prediction: 8–10 days in 2017 and 6–8 days in 2018). However, durations were in good agreement with the model predictions when only a minimal time cost of 0.1 days was included (5 days for 2017 and 3 days for 2018).

Based on estimated stopover durations, predicted flight ranges were similar between years but not habitats (Table 3), with most birds likely capable of a flight >1,000 km on departing from the study site under still air



**FIGURE 3.** Majority of Blackpoll Warblers arrived on the Guajira Peninsula during fall migration at body masses below reported fat-free mass (upper dotted line, 11.2 g) and with many birds below the lean (*minimum*) body mass calculated in this study (lower line, 9.9 g). Birds below the lower line typically had muscle scores of 0 (where 0 = severely depleted) and no visible fat (fat class 0).



**FIGURE 4.** Recovery and fueling following trans-oceanic flights, as measured through fuel deposition rates, was strongly affected by (A) the vegetation type Blackpoll Warblers occupied during autumn 2017, and by (B) variation between years within the same vegetation type, such that refueling conditions were most favorable in tropical thorn scrub (Scrub). Each symbol in the graphs represents the change in mass recorded in individual Blackpoll Warblers between successive captures. Fitted lines and 95% confidence intervals (gray shadow) were based on predictions from the general linear model:  $\text{Mass change} = \text{Days} \cdot \text{Year} \cdot \text{Habitat} + \text{Days}^2 \cdot \text{Year} \cdot \text{Habitat} + \text{Hour}$  (see Table 3).

**TABLE 3.** Stopover durations in Blackpoll Warblers on fall migration on the Guajira Peninsula of Colombia varied markedly between years but led to similar departure mass and flight range as a result of annual variation in fuel deposition rate, with the exception of flight ranges from tropical thorn scrub in 2017.

Stopover estimate method	Year	Mean duration (95% CI), days	Estimated departure mass, g	Potential flight range, km
Minimum stopover	2017	5.3 (3.8–6.8)	Forest <sup>a</sup> 12.50	1,210
			Scrub <sup>b</sup> 11.21	611
“Total stopover”	2018	3.2 (2.7–3.7)	Scrub 12.46	1,186
	2017	7.1 (5.3–9.7)	Forest 12.67	1,281
			Scrub 11.33	670
	2018	3.1 (2.5–3.9)	Scrub 12.41	1,116

<sup>a</sup>Tropical dry forest.

<sup>b</sup>Tropical thorn scrub.

conditions (sufficient to reach final nonbreeding [overwintering] destinations; see Discussion).

### Relationship Between Fuel Deposition Rate and Stopover Duration

To examine the relationship between FDR and stopover duration, we first estimated “total stopover” duration by vegetation type and year, giving rise to durations of 7.6 days (95% CI: 5.4–11.0) and 5.5 days (95% CI: 3.3–9.7) in thorn scrub and dry forest, respectively, in 2017 and a duration of 3.1 days (95% CI: 2.5–3.9) and <1 day in thorn scrub and dry forest, respectively, in 2018 (Figure 5). FDR could not be calculated for dry forest in 2018 due to a lack of recaptures (Figure 5). Stopover durations decreased as FDR increased (Figure 5; as supported by a linear regression but note that only 3 data points were available,  $F_{1,2} = 152.3$ ,  $P = 0.05$ ,  $R^2 = 0.98$ ), implying that birds present in different habitats and years adjusted their durations to experienced FDR.

### Contribution of Muscle to Mass Gains

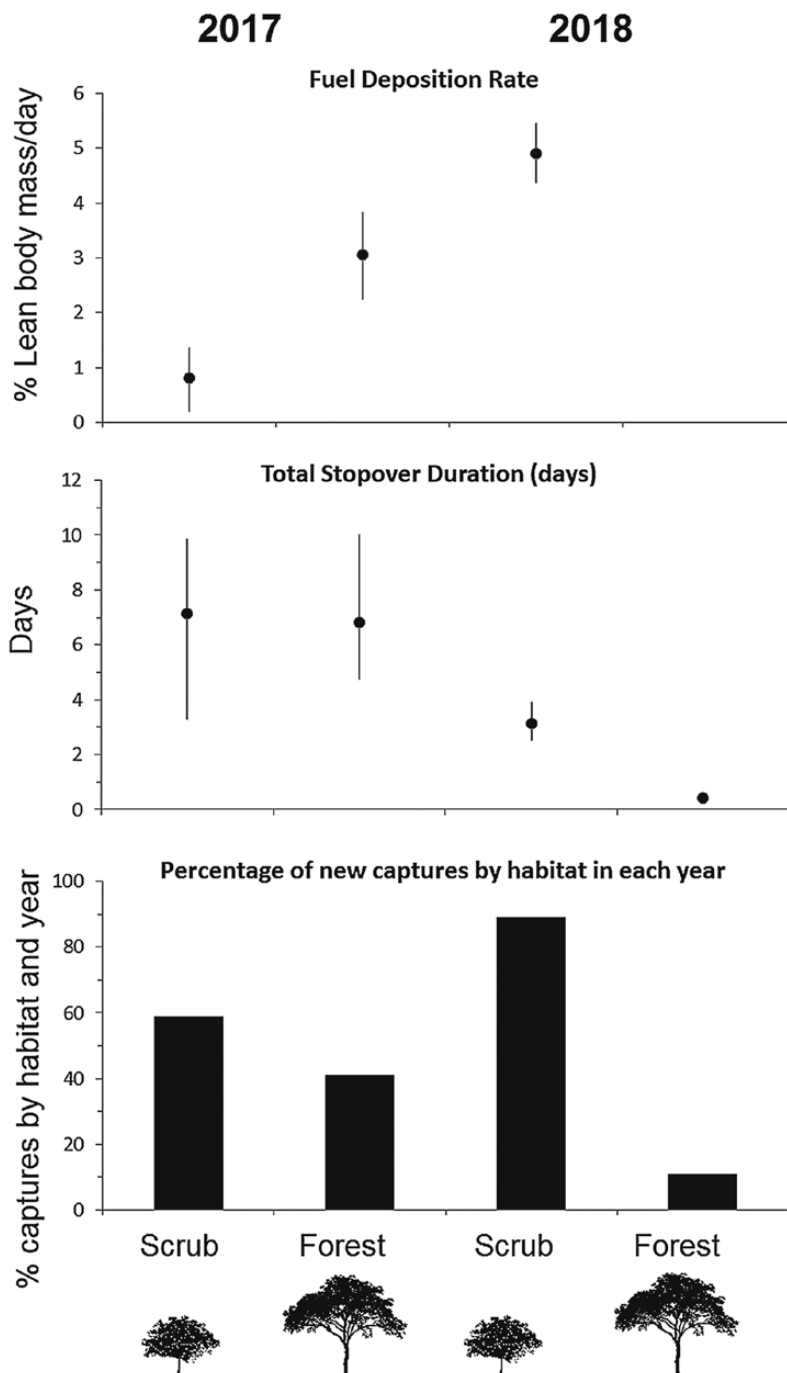
Observed mass changes were largely explained by changes in visible fat based on amount of variance explained by a linear regression of mass change against change in fat score ( $F_{1,92} = 122.5$ ,  $P < 0.005$ ,  $R^2 = 0.571$ ). Although less of a contribution to overall mass change, we observed changes in muscle scores among recaptured individuals ( $F_{1,92} = 9.86$ ,  $P < 0.002$ ,  $R^2 = 0.097$ ; Figure 6). Increases in fat and muscle scores were recorded in 46.8% and 31.9% of recaptures, respectively.

## DISCUSSION

Our study sought to determine whether recovery phases following endurance flights, during which birds consume vital protein structures (Bauchinger and Biebach 2001), result in different selection pressures and behavioral decisions compared with those expected during fueling stopovers under a time-minimization strategy (Alerstam and Lindström 1990). Contrary to our hypothesis that

recovery phases and fueling stopovers are biologically distinct processes requiring different behavioral responses, we found only limited evidence for behavioral adaptations in Blackpoll Warblers following extreme endurance flights (DeLuca et al. 2019), with decisions continuing to be driven by selection for time-minimization. Of our 5 predictions, the results for predictions (1) and (5) partially supported behavioral adaptations for recovery, whereas tests of predictions (2), (3), and (4) were contrary to our expectations for recovering birds. Patterns of habitat use, a largely protein-based diet, and high FDR may allow Blackpoll Warblers to ameliorate the physiological changes induced by endurance flights, as evidenced by rapid deposition of fat stores and also partial recovery of lost muscle mass.

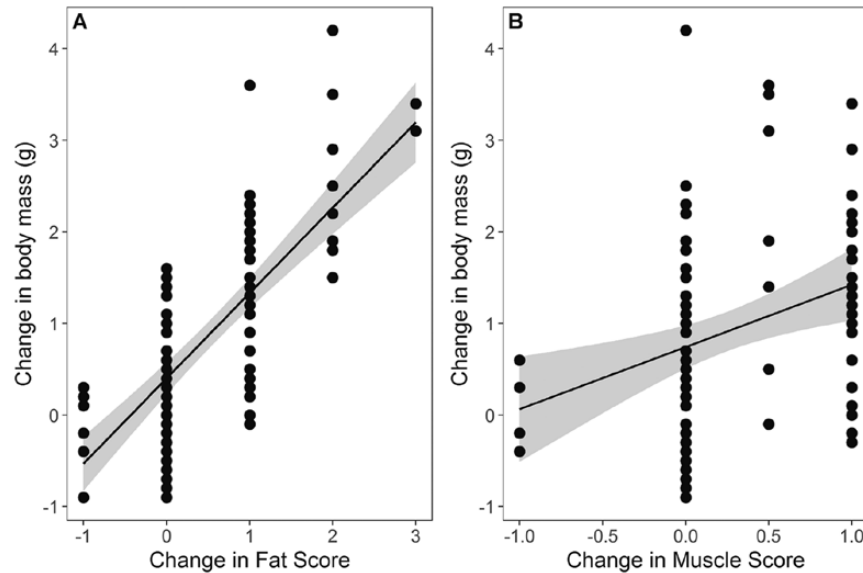
Following trans-oceanic flights, most birds arrived on the Guajira Peninsula with depleted flight muscles and 14–21% of birds arrived emaciated, with no fat reserves and severely depleted flight muscles. In spite of arrival condition, we found no evidence for a reduced gastrointestinal capacity (Tracy et al. 2010, Gerson et al. 2020), with FDR decreasing and not increasing with days since first capture (Schwlich and Jenni 2001). This finding suggests that fueling rates in recently arrived Blackpoll Warblers were not constrained by physiological changes occurring during flights. Further support for this conclusion comes from the weak relationship between arrival condition and stopover duration, which implies that rebuilding of the gastrointestinal tract either did not result in a time penalty for emaciated birds or did not occur, as seen in Blackcap (*Sylvia atricapilla*; Gannes 2002). Indeed, Blackpoll Warblers adjusted their stopover duration to experienced FDR, as would be expected under selection for time-minimization (Alerstam and Lindström 1990), resulting in average durations of just 3 days in 2018, when FDR (4.90% LBM day<sup>-1</sup>) were close to the upper limit recorded in migratory passerines (Lindström 2003). The close agreement between estimated stopover durations and the predictions of a time-minimizing model in which search and settling costs were set at 0.1 days also supports the conclusion that Blackpoll Warblers did not pay a time cost for physiological changes caused by endurance flights.



**FIGURE 5.** Fuel deposition rate (FDR), stopover duration, and number of captures varied by habitat (tropical thorn scrub and tropical dry forest) and by year (2017 and 2018) at a stopover site on the Guajira Peninsula, Colombia, such that stopover duration decreased with increasing FDR. The number of captures also appeared to respond positively to experienced FDR (in 2018, FDR was not estimated in forest for lack of recaptures).

Together our results point to time-minimization remaining a pervasive selection pressure (Hedenström 2008), even in birds showing clear signs of physiological stress. Concordantly, Blackpoll Warblers only remained long enough to accumulate sufficient fuel for onward

flights (estimated flight ranges would allow birds to reach core nonbreeding areas in the Orinoco basin 500–1,000 km away, Fink et al. 2020; see Table 3), similar to the final sprint strategy described in other long-distance migrants (Briedis et al. 2018). Our results also highlight



**FIGURE 6.** Mass increases between successive captures of individual Blackpoll Warblers were largely explained by increases in visible fat deposits (A) and to a lesser extent by visible changes in the shape of the flight muscle (B).

the importance of a previously undescribed stopover region on the Guajira Peninsula of Colombia for the steeply declining Blackpoll Warbler.

#### Arrival Condition

Most Blackpoll Warblers arrived on the Guajira Peninsula showing marked reductions in flight muscle and these compositional changes were reflected in the body mass of individual birds, with over 70% of birds arriving below typical masses reported elsewhere (Nisbet et al. 1963). Extreme values were 25% below the fat-free mass of a healthy bird and match historical reports of exhausted birds in the Caribbean and Venezuela (Wetmore 1939). Low body masses may partly result from dehydration but studies on several species suggest that water loss typically accounts for just 1% of mass loss following over-water flights or 5% in extreme cases (Leberg et al. 1996, Klaassen et al. 2000, Landys et al. 2000). Together, these findings suggest that Blackpoll Warblers may be especially elastic in their ability to catabolize muscle and gastrointestinal protein (if indeed Blackpoll Warblers catabolize their gut as other long-distance migrants do), and successfully recover afterwards (McWilliams and Karasov 2014). Alternatively, they may reflect a reduced capacity for Blackpoll Warblers to maintain their body mass in a rapidly changing world (Zurell et al. 2018).

#### Evidence for Behavioral Differences Between Recovery and Stopover

Several lines of evidence presented here point to selection for time-minimization shaping the decisions made by Blackpoll Warblers following endurance flights and not,

as we hypothesized, needs arising from the physiological stress of trans-oceanic flights. Namely, as has now been demonstrated in several long-distance migratory birds (Hedenström 2008), stopover durations decreased as FDR increased (Figure 5). Estimated durations in 2018 were half as long as those in 2017, with birds departing after just 3 days on average in 2018. Such short stopovers following a >2,250 km trans-oceanic endurance flight might come as a surprise but given the high FDRs experienced by birds in 2018 (4.9% LBM day<sup>-1</sup>; see Lindström 2003 for estimates in multiple species), a 3-day stopover was sufficient to lay down fuel reserves equivalent to a >1,000 km onward flight (see Supplementary Material and Table 3). Indeed, in spite of large differences in stopover duration between years, birds in tropical dry forest in 2017 and in tropical thorn scrub in 2018 were expected to attain similar departure fuel loads. We hypothesize that varying precipitation likely drives these differences between years in FDRs and stopover durations through its influence on food availability (Smith et al. 2010). Testing this hypothesis would provide valuable information on how climate change may affect the speed and success of migration, for example.

While stopover duration was negatively correlated with arrival condition, as we had predicted if emaciated birds remain longer to recover (Biebach et al. 1986), this may simply reflect differences in time between arrival day and when some birds were first captured (e.g., heavier birds were those captured one or more days after arrival). Indeed, predicted differences in duration between emaciated (<9 g) and “fat” birds (>14 g) were so small (<2 days) that there was no clear evidence for exhausted birds remaining longer to rebuild atrophied protein structures or counteract the effects of oxidative

stress (Jenni-Eiermann et al. 2014). Furthermore, stopover durations were in good agreement with the predictions of a time-minimizing model, suggesting that, on average, birds did not stay longer than was necessary to attain fuel for onward flights. Concordantly, the majority of mass gains could be explained by changes in fat score, with only a limited contribution from increasing flight muscle, as found in other species (Bauchinger and Biebach 2001). The limited rebuilding of muscle mass, as well as being a time-minimizing strategy, may also be related to the fact that the nonbreeding grounds were relatively close to our study site and, therefore, the energetic costs and predation risk associated with maintaining atrophied flight muscles are likely small.

### Migratory Strategy and Habitat Selection During Stopover

Blackpoll Warblers from opposite extremes of the North American continent converge on the Atlantic coast in fall prior to making trans-oceanic flights directly, in many cases, to northern South America (DeLuca et al. 2015, 2019). Our occupancy data and discovery that birds made multiday stopovers in northeastern Colombia, greatly increase the precision for the location of known stopovers and the habitats used on arrival in South America. Further, the finding that stopovers in northeastern Colombia were sufficient to fuel flights >1,000 km to nonbreeding grounds farther south, fills a key gap in our understanding of this species' fall-migration strategy. It is notable that in spite of the presence of suitable habitat for the species between the Guajira Peninsula and the nonbreeding grounds, average departure fuel loads in this study suggest that birds arriving on the Guajira likely did not use these habitats for additional stopovers.

Previous studies in Colombia have documented the importance of humid lowland and premontane forests in the nearby Sierra Nevada de Santa Marta for Nearctic–Neotropical migrants (Bayly et al. 2012, Gómez et al. 2015). In contrast, our results indicate that Blackpoll Warblers selected some of the driest habitats (<1,000 mm per year) available across northern Colombia (see [Supplementary Material Figure S2](#)), similar to findings in adjacent Venezuela (Bosque et al. 1987). These xeric habitats experience a growing period restricted to just 3 months between September and November, which is dependent on erratic rainfall (Ramírez and del Valle 2012). The arrival of Blackpoll Warblers coincided with the wettest month of the year in the region (October; [Supplementary Material Figure S3](#)), suggesting that they select this habitat to take advantage of a seasonal peak in food availability driven by precipitation. Indeed, even the normally leafless tropical thorn scrub was covered in fresh green foliage during our study period (see [Figure 1](#)). Our foraging observations of Blackpoll Warblers revealed a diet consisting primarily of small insects and caterpillars. Insects provide more protein

than fruit and the need to rapidly rebuild flight muscle, albeit partially, in arriving Blackpoll Warblers may explain why birds selected xeric habitats over moister habitats that may provide a more balanced (macronutrient) diet.

### Final Considerations

The study of recovery phases in free-living birds has considerable potential for understanding the decisions animals make when under physiological stress. While our study revealed that time-minimization may override other decision-making processes in Blackpoll Warblers, this may not be true in other species and several questions remain unanswered regarding this rarely addressed aspect of migratory behavior. For example, while mass gains in Blackpoll Warblers were largely explained by increases in visible fat reserves, there was also evidence for increases in flight muscle but it was not possible to determine whether birds with heavily depleted muscles were more likely to rebuild muscle or not. Using more advanced techniques to measure fat mass and muscle mass (e.g., muscle meters or quantitative magnetic resonance; Powell et al. 2021, Seewagen and Guglielmo 2011) could help us better understand the tradeoffs between rebuilding energy reserves vs. depleted protein structures. In a different vein, both FDRs and stopover durations imply that Blackpoll Warblers were subject to no or only limited search and settling costs, bringing into question once again why some species show evidence of such costs while others do not (Schwilch and Jenni 2001, Alerstam 2011).

Our results also draw attention to the use of unpredictable and seasonal resources by migratory birds that may render them especially vulnerable to climate change-driven effects that disrupt seasonal resource peaks (Jones and Cresswell 2010, Kellermann and van Riper 2015). Further exploration of the role that seasonal tropical habitats play in the migration of landbirds is therefore warranted, especially in northern South America and lower Central America, which serve as a potential bottleneck for millions of intercontinental migrants in both fall and spring (Bayly et al. 2018).

### SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

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**Ethics statement:** The capture of birds was undertaken following strict international protocols for the capture and marking of birds and the methods were approved by the Colombian Ministry of the Environment (Research permits approved by the ANLA under Resolutions 0597 of 2014, 0189 of 2016, and 00874 of 2018). Observations in protected areas were approved by the Colombian National Parks Service (Permit PIC-DCTA 001-16).

**Author contributions:** N.J.B. and K.V.R. conceived of and designed the occupancy surveys, N.J.B. conceived and designed the capture setup on the Guajira Peninsula, N.J.B. analyzed the data and led the manuscript writing, all authors contributed to the development of the ideas in the manuscript and reviewing of manuscript drafts.

**Data deposits:** Analyses reported in this article can be reproduced using the data provided by Bayly et al. (2021).

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