



RESEARCH ARTICLE

Fall migratory patterns of the Blackpoll Warbler at a continental scale

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ABSTRACT

Blackpoll Warblers (*Setophaga striata*) breed across Canada and the northern United States and fly across the Atlantic Ocean to South America in fall. Studies of fall migration in this species have centered on the extensive overwater flights but have ignored other aspects of this migration, including potential geographic variation. We used Blackpoll Warbler banding records from 3 coastal (Atlantic seaboard) sites and 9 inland sites to study the fall migration. The sites covered a wide range of the species' geographic distribution during breeding and fall migration in North America. The data spanned the years 1967–2013, though the particular years sampled varied considerably among the stations. We found that the Blackpoll Warbler's fall migration is occurring later by ~ 1 day decade⁻¹. Young birds generally moved through western sites before adults, whereas at eastern sites the reverse was generally true, which suggests that young birds are taking longer on migration. We also found that young birds were in poorer condition than adults, which may lead to an overall decreased rate of migration due to shorter flights and/or longer stops. Wing chords differed between western birds (longer wings) and eastern birds (shorter wings), and wing chords from the 2 more southerly coastal sites may reflect mixing of these groups. Birds were captured at coastal sites >10 days later than at inland sites, even when at similar latitudes. The heaviest individuals and those with the most fat were found at the 2 more southerly coastal sites from late September to mid-October. These results suggest that Blackpoll Warblers from the west move toward the east, where they develop the energy stores needed for their extensive overwater flights.

Keywords: age, Blackpoll Warbler, condition, fall migration, *Setophaga striata*, timing

Patrones migratorios de otoño de *Setophaga striata* a escala continental

RESUMEN

La especie *Setophaga striata* se reproduce a lo largo de Canadá y del norte de Estados Unidos y realiza un extenso vuelo transoceánico (i.e. sobre el Océano Atlántico) durante la migración de otoño para llegar a América del Sur. Sin embargo, los estudios de la migración de otoño de esta especie se han centrado en estos vuelos sobre el agua y han ignorado otros aspectos de la migración de otoño, incluyendo la potencial variación geográfica. Estudiamos la migración de otoño de *S. striata* usando registros de anillado provenientes de 12 sitios diferentes, 3 costeros (en el litoral Atlántico) y 9 tierra adentro, cubriendo un amplio rango de la distribución geográfica durante la reproducción y la migración en América del Norte. La migración de otoño de *S. striata* está ocurriendo ~ 1 día más tarde por década. Las aves jóvenes generalmente se mueven a través de los sitios del oeste antes que las aves adultas, mientras que en los sitios del este ocurre generalmente lo contrario, sugiriendo que las aves jóvenes están tardando más en la migración. También encontramos que las aves jóvenes presentaban una condición más baja que los adultos, lo que podría llevar a una tasa global decreciente de migración a partir de vuelos más cortos y/o paradas más largas. El patrón geográfico que observamos relacionado a la cuerda alar mostró diferencias entre las aves del oeste (alas más largas) y las aves del este (alas más cortas), y que las cuerdas alares de nuestras ubicaciones costeras más al sur pueden reflejar la mezcla de estos grupos. Las aves fueron capturadas en los sitios costeros más de 10 días después que en los sitios del interior, aun estando a latitudes similares. Las aves más pesadas y las aves con la mayor cantidad de grasa fueron encontradas en los dos sitios costeros más al sur desde fines de septiembre a mediados de octubre. Estos resultados sugieren que los individuos de *S. striata* del oeste se mueven hacia el este, donde desarrollan las reservas de energía necesarias para sus extensos vuelos sobre el agua.

Palabras clave: condición, edad, migración de otoño, *Setophaga striata*, sincronización

INTRODUCTION

Blackpoll Warblers (*Setophaga striata*) migrate between boreal forests spread across North America and forests in northern South America (DeLuca et al. 2013). They have the longest migratory route of any parulid. During fall migration they may double their mass prior to long-distance overwater flights (Drury and Keith 1962, Nisbet et al. 1963, 1995, Nisbet 1970). Most individuals initiate this trans-Atlantic crossing from the Canadian Maritime Provinces and New England and fly nonstop over the western North Atlantic Ocean to the Caribbean or South America (Nisbet 1970, Williams et al. 1978, DeLuca et al. 2015). Thus, Alaskan breeders may migrate almost twice the total distance of some eastern breeders, but half of their route may be overland.

Much of the study of Blackpoll Warbler migration has focused on a debate about the extensive transoceanic flight during fall. Nisbet (1970) reviewed observations of avian mortality events and capture at banding stations and suggested that the species made an extended overwater flight originating in the northeast. Ralph (1981) used age ratios at coastal sites to provide additional support for the idea of a western trans-Atlantic route. Murray (1989) summarized data on abundance, timing, and mass and argued that Blackpoll Warblers did not depart from the Maritime Provinces and New England but instead began their migration in the southeastern United States. However, Nisbet et al.'s (1995) summary of multiple lines of evidence, including radar data, led to general acceptance that the trans-Atlantic route likely was used, and this has now been confirmed unequivocally by DeLuca et al. (2015) using geolocators.

Blackpoll Warblers must accumulate substantial fat reserves to fuel their extensive migratory flights, but the geographic locations where they accumulate fat and the points of departure for their overwater flights are not well known (Nisbet et al. 1963, DeLuca et al. 2013). Previous studies of Blackpoll Warbler mass at coastal stopover sites during fall migration have reported fewer individuals with extensive fat stores than might be expected (e.g., Murray 1979, Morris et al. 1996, Davis 2001). Murray (1979) showed that average mass generally increased throughout the migratory season, such that the heaviest birds tended to be among the later captures at a site in coastal New Jersey. However, most of the work on Blackpoll Warblers during fall migration has been limited to eastern coastal sites, which represent a narrow portion of the species' broad range. Given that its long fall overwater flight begins on the eastern seaboard, the species' migration and stopover ecology is presumably different (e.g., in timing of migration, duration of stay, and energetic changes) at these eastern coastal sites. A comparison of birds at inland and coastal sites is warranted because their aggregation

along coastlines may have biological meaning besides the simple effect of geographic distance from the wintering grounds. Additionally, comparison of morphological measures across sites may provide insight into whether groups of birds at a migratory stopover site include individuals from several different breeding areas.

Although there has been extensive discussion of the Blackpoll Warbler's trans-Atlantic flights, most other aspects of its migratory behavior in fall are understudied. The extensive breeding range of this species and the genetic structuring across that range (Ralston and Kirchman 2012) make it well suited for a broad-scale study investigating both spatial and temporal patterns of migration. Research has shown that migration can differ between eastern and western populations of songbirds, but this has not been studied in the Blackpoll Warbler. Examples include differences in migratory routes of eastern and Pacific coast Swainson's Thrushes (*Catharus ustulatus*; Ruegg and Smith 2002) and differences in the timing and migration routes of eastern and western breeding Wilson's Warblers (*Cardellina pusilla*; Ruegg et al. 2014). Furthermore, investigations of possible differences between age groups have focused on site-specific patterns of timing and energetic condition, for example on the Gulf Coast (Woodrey and Moore 1997) and in Maine (Morris et al. 1996).

Given the unusual migratory route of this species and the breadth of its breeding range, from Alaska to Newfoundland, we decided to study the fall migration of Blackpoll Warblers at a continental scale. We were interested in potential differences between coastal (i.e. Atlantic seaboard) and inland birds, differences related to migration distance, and differences among age groups. Specifically, we examined (1) temporal patterns of migration; (2) potential differences in migration related to location, age, and/or size (i.e. wing chord); and (3) how condition varied both temporally and geographically.

METHODS

Field Sites and Data Collection

We used Blackpoll Warbler fall banding data collected over the past 40 yr from 12 different sites in the United States and Canada, 3 along the east coast of North America and 9 inland (Table 1 and Figure 1). Our analysis includes data from the period 1967–2013, but the particular years sampled varied considerably among the stations (Table 1).

Each station captured birds in mist nets that, weather permitting, were opened at or just before dawn during days of operation and remained open for ≥ 6 hr. Stations provided us with data on age, wing chord, and mass for each individual that was trapped during the banding process. Most stations also provided fat scores. Age and sex were determined by plumage and skull pneumatization,

TABLE 1. Banding sites and dates of Blackpoll Warbler data in this study.

Banding site ^a	Distance to wintering range (km) ^b	Years ^c	Overall early capture date ^d	Median early capture date ^e	Overall median capture date ^f	Median late capture date ^g	Overall late capture date ^h
ABO	4,719	1996–2012	241.0	252.5	272.0	286.0	298.4
ALAS	9,391	1992–2013	216.1	223.9	233.5	246.0	262.6
BBBO	4,848	1991–2013	241.0	253.7	260.5	271.0	285.6
BI	4,505	1967–2013	251.0	267.0	277.0	288.0	305.6
DEMA	6,259	1992–2008	219.4	242.0	250.0	261.6	269.0
GMNP	5,470	2000–2005	203.0	218.0	235.0	252.0	255.0
IWBS	7,143	1995–2012	229.1	235.6	247.0	258.5	271.2
LPBO	4,835	1990–2013	237.0	248.3	258.0	274.0	283.5
LSL	7,477	1994–2013	200.0	213.1	226.0	240.9	258.0
PARC	4,556	1990–2013	243.7	256.6	266.2	278.5	310.2
PFBO	4,975	1971–2012	236.0	249.8	260.0	272.4	284.2
TCBO	5,700	1991–2013	221.2	243.0	252.0	263.7	277.0

^a ABO = Atlantic Bird Observatory, Nova Scotia, Canada; ALAS = Alaska Bird Observatory, Alaska, USA; BBBO = Braddock Bay Bird Observatory, New York, USA; BI = Block Island, Rhode Island, USA; DEMA = Delta Marsh Bird Observatory, Manitoba, Canada; GMNP = Gros Morne National Park, Newfoundland, Canada; IWBS = Inglewood Banding Station, Alberta, Canada; LPBO = Long Point Bird Observatory, Ontario, Canada; LSL = Lesser Slave Lake Bird Observatory, Alberta, Canada; PARC = Powdermill Avian Research Center, Pennsylvania, USA; PFBO = Pittsfield Bird Observatory, Michigan, USA; TCBO = Thunder Cape Bird Observatory, Ontario, Canada.

^b Calculated by the great-circle distance from the station to the approximate centroid of the species' winter range (66°W, 1°N).

^c First and last year of banding data included in this study.

^d "Overall early capture date" is the earliest date by which 5% of individuals had been captured in any year (q5).

^e "Median early capture date" is the median across years of q5, the date by which 5% of individuals in any year had been captured.

^f "Overall median capture date" was calculated by taking the median of each year's median date of capture.

^g "Median late capture date" is the median across years of q95, the date by which 95% of individuals in any year had been captured.

^h "Overall late capture date" is the latest date by which 95% of individuals in any year had been captured (q95).

following keys in the North American *Bird Banding Manual* (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1977), Wood (1969), Pyle et al. (1987), and/or Pyle (1997). Birds with complete skull pneumatization and/or adult plumage characteristics were aged as "after-hatch-year" and were likely to have been among the breeding population (hereafter "adults"). Birds that were designated as "hatch-year" had incomplete skull pneumatization and were considered young-of-the-year (hereafter "young"). Stations that quantified the amount of subcutaneous fat used different scoring systems. To account for this methodological variation, we converted all scales to fit a 0–4 scale (Appendix Table 3). Only 1 station, PARC (abbreviations are defined in Figure 1), used a single category for both no fat (0 in our consolidated scale) and trace of fat (1 in our consolidated scale). We chose to keep these 2 categories separate for the rest of the stations to avoid loss of potentially important details affecting our analysis of condition. Although there is variation in the scoring of fat, we chose to include it here as a second proxy for condition, because differences in mass do not necessarily equate to differences in fat, and fat is the energy used to fuel migratory flights (Blem 1990).

We chose to exclude some information from our analyses when necessary to avoid bias. We did not use sex data, because sex was typically determined from morphological measures, which meant that only large or

small birds were sexed. Data from IWBS, LSL, and TCBO were excluded from analyses that included fat scores because they either did not provide that information (TCBO) or had fat scores for only a small proportion of birds (IWBS and LSL). We excluded data on recaptured birds.

Statistical Analysis

Overall approach. We were interested in examining the relationship age, distance from overwintering grounds (see models below), and setting (whether a station is along the Atlantic coast or not) to 3 response variables in Blackpoll Warblers: timing of migration, size (wing chord), and condition. To address condition, we included mass in all models, using wing chord as a covariate to control for variation in size. Although we report only models that use mass to represent condition, we also investigated patterns of fat scores, because differences in mass do not always reflect differences in fat.

We used 3 approaches to investigate the timing of migration. We used day of year (days since January 1) as the response variable in each. The first approach investigated the relationship between the predictors of interest and the median passage date of individuals through a site (hereafter "median capture date"). The second approach explored early arrival dates by using the value of the 5th quantile of the distribution of capture

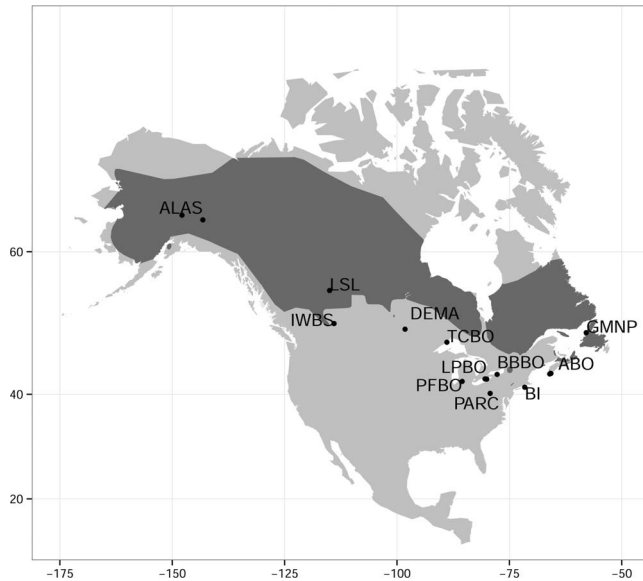


FIGURE 1. Location of banding sites included in this study of Blackpoll Warbler migration. We used data from 3 coastal sites: Gros Morne National Park, Newfoundland, Canada (GMNP); Atlantic Bird Observatory, Nova Scotia, Canada (ABO); and Block Island, Rhode Island, USA (BI). We also used data from 9 inland sites: Alaska Bird Observatory, Alaska, USA (ALAS); Lesser Slave Lake Bird Observatory, Alberta, Canada (LSL); Inglewood Banding Station, Alberta, Canada (IWBS); Delta Marsh Bird Observatory, Manitoba, Canada (DEMA); Thunder Cape Bird Observatory, Ontario, Canada (TCBO); Pittsfield Bird Observatory, Michigan, USA (PFBO); Braddock Bay Bird Observatory, New York, USA (BBBO); Long Point Bird Observatory, Ontario, Canada (LPBO); and Powdermill Avian Research Center, Pennsylvania, USA (PARC). The shape file for the Blackpoll Warbler breeding range was provided by BirdLife International and NatureServe (2014).

dates (i.e. the date by which 5% of individuals had been observed in any given year; Van Buskirk et al. 2009) at any given site in any given year as the response (hereafter “early capture date”). The third approach explored late arrival dates by using the value of the 95th quantile of the distribution of capture dates (i.e. the date on which 95% of individuals had been observed in any given year; Van Buskirk et al. 2009) at any given site in any given year as the response (hereafter “late capture date”). This allowed us to explore how the predictors were related to the arrival time among sites and years while limiting the effects of extremely early or extremely late captures. To explore potential differences in passage time among years, we pooled birds across age categories because of the low annual numbers of adults captured.

Models. All models were fit as linear mixed-effects models, and the overall fit of all models was examined using residual plots. We modeled each response by the great-circle distance between the banding site and the approximate centroid of this species’ wintering grounds

(66°W, 1°N; near where the borders of Brazil, Columbia, and Venezuela meet; Deluca et al. 2013), setting (coastal or inland), and age. Great-circle distance is the shortest distance between 2 points on the surface of the earth. Actual migratory routes (and specific wintering locations) for individual Blackpoll Warblers are not known, but our estimate of migratory distance from each banding station provides a reasonable approximation of distance to the wintering grounds and includes an overwater component, which we know is used by this species during fall migration. In addition to distance, we included a dichotomous variable called “setting” to determine whether sites along the Atlantic coast were different from inland sites, thereby investigating the possibility of differences as this species stages before beginning overwater flights. Site and year were included as separate random effects in each model to account for within-year variation across all sites and within-site variation across all years, except in analyses investigating whether birds were arriving earlier or later over the decades, in which case year was included as a linear effect. When investigating year as a linear effect, we used a truncated data set including all data since 1990, which would reduce the potential influence of the 2 data sets that were much longer than the others (BI and PFBO). By fitting site with a random intercept and fitting year with a random intercept and with random slopes for age, any modeled relationship between a fixed effect and the response would have the same slope among sites but could have different slopes among years. Differences in the slopes of the relationships among sites are accounted for by the interaction between great-circle distance and age.

We had large sample sizes and few parameters to estimate for all models, so we used a likelihood ratio approach for model selection (Bolker et al. 2009). We first fit a full model (i.e. all main effects and both 2- and 3-way interactions). We then compared that model to a simpler model without the 3-way interaction. In almost all cases, there was evidence for the 3-way interaction. To aid in interpretation of effects, we therefore split the data into coastal and inland situations and fit new models assessing the 2-way interactions separately for each situation. For these models, we also used likelihood ratio tests to assess whether there was support for the 2-way interaction. Finally, we used the *t* values (assuming infinite degrees of freedom; i.e. “anticonservative”) to assess the robustness of parameter estimates in the simplest model (Bates 2010). Our focus here is on the biological effects (i.e. the magnitude and direction of the coefficients) of these parameters, given their presence in a supported model. When we present information from linear mixed-effects models, we present the results of the likelihood ratio test, the estimates and SE of each specific effect, and the *t*-statistic associated with that effect. We use plots of raw data to examine the direction and relative strength of these

TABLE 2. Sample sizes (*n*), age demographics, and proportion lean by age from Blackpoll Warbler data used in this study. For names and locations of banding sites, see Table 1.

Banding site	<i>n</i> ^a	Unknown age ^b (%)	Young ^c (%)	Young lean ^d (%)	Adult lean ^d (%)	Young wing chord ^e (mm)	Adult wing chord ^e (mm)	Young mass ^e (g)	Adult mass ^e (g)
ABO	2,166	3.9	76.7	26.2	23.9	70.3 ± 2.3	71.4 ± 2.6	13.6 ± 2.5	14.4 ± 2.8
ALAS	1,274	0.5	87.7	79.9	50.4	73.0 ± 2.4	74.4 ± 2.9	12.4 ± 0.8	13.0 ± 1.1
BBBO	3,038	4.0	74.0	86.0	80.9	72.0 ± 2.6	73.3 ± 2.8	12.2 ± 1.5	12.6 ± 1.8
BI	1,209	3.9	91.8	53.7	29.8	70.8 ± 2.8	72.0 ± 2.6	13.1 ± 2.7	15.0 ± 3.9
DEMA	540	13.5	88.9	74.4	70.7	72.6 ± 2.8	73.7 ± 3.1	12.0 ± 0.9	12.2 ± 0.9
GMNP	955	0.8	90.9	39.4	0	70.3 ± 2.5	70.7 ± 2.8	12.0 ± 0.8	12.4 ± 0.9
IWBS	144	1.4	85.2	n/a	n/a	73.1 ± 2.6	72.9 ± 2.8	12.2 ± 1.0	12.3 ± 1.1
LPBO	9,112	0.3	70.8	67.0	75.5	72.1 ± 2.6	73.8 ± 2.8	12.0 ± 1.0	12.0 ± 0.9
LSL	181	2.2	92.7	n/a	n/a	71.8 ± 2.8	72.8 ± 3.2	12.0 ± 0.7	12.2 ± 0.7
PARC	792	0.0	79.6	55.9	40.1	72.4 ± 2.5	74.0 ± 2.6	12.0 ± 1.8	13.1 ± 2.6
PFBO	1,396	0.1	81.9	86.8	83.1	72.1 ± 2.6	73.2 ± 2.6	12.0 ± 1.2	12.3 ± 1.3
TCBO	1,488	0.6	92.8	n/a	n/a	72.1 ± 2.6	73.1 ± 2.8	11.4 ± 0.9	11.6 ± 0.9

^a Sample sizes reflect all birds captured at the banding sites during the years of this study.

^b Percentage of birds captured that were of unknown age. These birds were excluded from all analyses of age.

^c Percentage of known-age birds that were aged as young (hatch-year).

^d Lean birds were those with fat scores of 0 or 1 on our 5-point scale (referring to no fat or a trace of fat).

^e We present means ± SD for wing chord and mass.

higher-order effects in relation to the main effects. We used R version 3.0.2 (R Development Core Team 2014) for all data analysis, including linear mixed-effects modeling using package lme4 (Bates et al. 2014). We present the parameter estimate ± SE of the estimate for results from modeling. We present the mean ± SD for comparisons of wing chords among different samples.

RESULTS

We analyzed fall banding data from 22,295 individuals (fewer individuals were included in some specific analyses, as noted). Most of the individuals were categorized as either adult (after-hatch-year) or young (hatch-year) at each site (98.3% overall; range among individual stations: 86.5–100%). After removing the birds of unknown age, the overall proportion of young was 76.6%, ranging from 70.8% at LPBO to 92.8% at TCBO (Table 2).

Timing of Passage

We found a significant effect of the 3-way interaction between distance to wintering grounds, setting, and age on the timing of passage through the sites ($\chi^2 = 17.4$, $P < 0.001$). Because the interaction between distance and age depended on setting (coastal or inland), we fit separate models for coastal and inland sites. Overall, individuals moved through sites more distant from the wintering grounds earlier in the year at both coastal and inland sites (Figure 2). The median capture date at coastal sites was >10 days later than that of birds captured at inland sites at similar latitudes (e.g., day 272 at ABO vs. day 258 at LPBO; or day 277 at BI vs. day 266 at PARC; Table 1). At inland sites, we found a significant interaction between age and distance to wintering grounds

on passage date ($\chi^2 = 133.0$, $P < 0.001$). Young birds generally moved through western sites (which were farther from the wintering grounds) before adult birds, whereas at eastern sites (which were closer to the wintering grounds) the reverse was generally true. Among coastal sites, we did not find an interaction between age and distance to wintering grounds ($\chi^2 = 0.0$, $P = 0.92$). Both age and distance were related to passage time at coastal sites (age: -45.3 ± 3.3 , $t = 3.4$; distance: 3.6 ± 1.1 , $t = -13.9$) and, as at eastern inland sites, adults moved through before young birds, and birds moved through more distant sites earlier.

The median capture date increased across years, with birds arriving 0.11 days later per year (~1 day later per decade; $t = 2.2$, $P = 0.03$). A similar pattern was found for the date by which the bulk of individuals (the 95th percentile) moved through (0.17 days later per year; $t = 3.0$, $P = 0.003$) but not for the earliest arrivals (5th percentile; $t = -0.2$, $P = 0.84$).

Size (Wing Chord)

We found support for an effect of the 3-way interaction of distance to wintering grounds, setting, and age on wing chord ($\chi^2 = 4.3$, $P = 0.04$). Adult wing chords were longer than those of young (adult: $n = 5,478$, 73.4 ± 9.5 mm; young: $n = 19,755$, 71.8 ± 5.5 mm), and inland birds had slightly longer wings than coastal birds (coastal: $n = 6,000$, 70.8 ± 2.9 mm; inland: $n = 19,640$, 72.6 ± 7.2 mm). Generally, wing chord increased with distance from the wintering grounds among inland birds, although among coastal birds wing chord was greater at the sites closer to the wintering grounds. Individuals with the smallest average wing lengths were from GMNP, the most northerly coastal site.

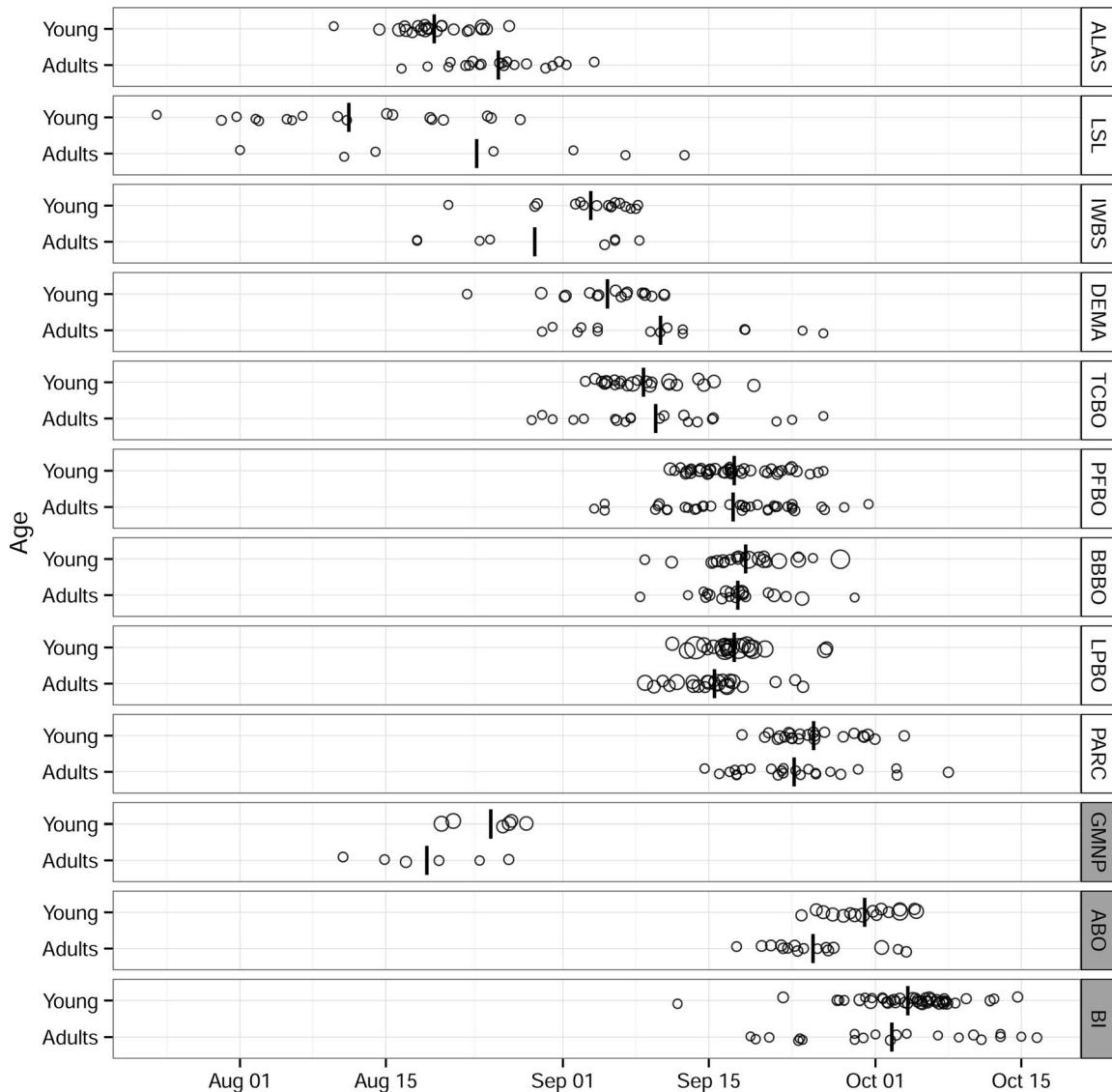


FIGURE 2. Average date of capture of Blackpoll Warblers by age during fall migration. Points are annual average capture dates (size of point reflects annual sample size), and the vertical line reflects the overall average capture date. Circle size is proportional to the square root of the annual sample size. Western sites generally had earlier capture of young birds during the fall, whereas eastern sites generally had earlier capture of adults. Site labels for the 3 eastern sites are shaded gray. For names and locations of banding sites, see Figure 1.

Condition

Mass varied with age, distance to wintering grounds, and setting ($\chi^2 = 17.4$, $P < 0.001$), with coastal birds being heavier than inland birds. Because of the 3-way interaction, we fit separate models for coastal and inland sites. Our models showed evidence of an interaction between distance and age for inland sites, but not for coastal sites. However, the effect was small and was largely driven by the most distant sites (e.g., ALAS and IWBS; Figure 3). At both inland and coastal sites, adult birds were heavier than young birds (coastal: $t = 4.0$; inland: $t = 4.3$), and this difference was greatest among the coastal sites closest to the wintering

grounds (Figure 3). The mass of inland individuals was slightly greater at the sites most distant from the wintering grounds; but the opposite was true of coastal individuals, the heaviest of which, on average, were captured at the coastal sites closer to the wintering grounds (Figures 3 and 4). At all locations, the heaviest individuals were in the highest fat category. The coastal sites showed the highest percentage of fat birds and the heaviest birds in both age categories (Table 2 and Figure 3). The greatest concentrations of heavy individuals were encountered from late September through mid-October at ABO and from early October through mid-October at BI (Figure 4).

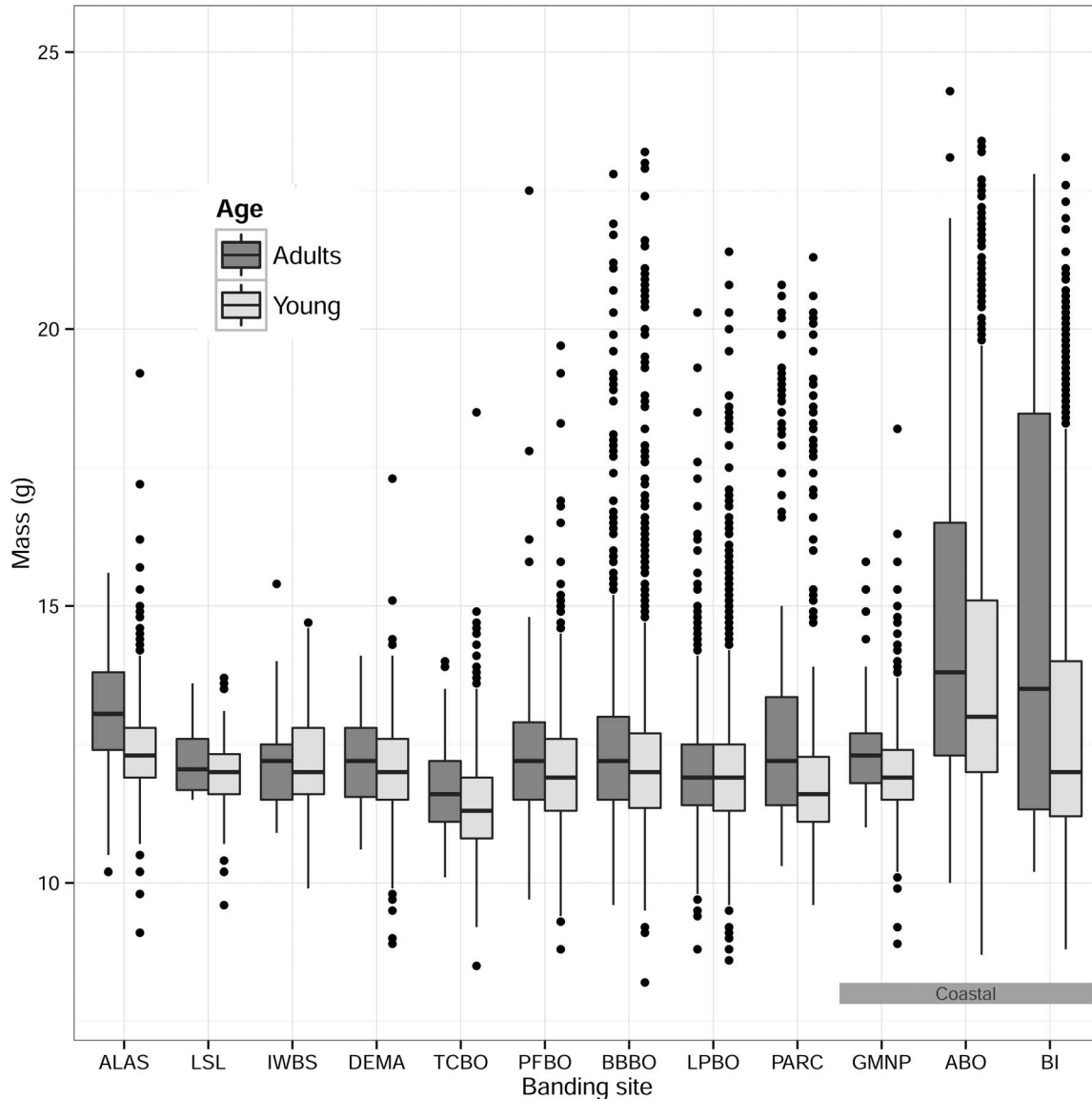


FIGURE 3. Boxplots of mass of Blackpoll Warblers by age during fall migration. Boxes show the first and third quartiles; the bar within each box is the median. Lines above and below boxes represent the highest and lowest data points that fall within 1.5 of the respective quartile range, and individual points fall outside these values. Adults were heavier than young birds, and the difference was greatest at our 2 southerly coastal sites. For names and locations of banding sites, see Figure 1.

DISCUSSION

Our continent-wide, multiyear study of Blackpoll Warblers revealed several patterns related to the timing of fall migration. First, the median capture date of Blackpoll Warblers during fall migration is getting later (~ 1 day per decade). Although we didn't find a corresponding change in the early capture dates at banding stations, we did find a change in the late capture dates, which suggests that the overall timing of migration is changing. Not only are the majority of birds migrating later, but the latest groups of migrants are moving later. A later fall departure provides

additional time on the breeding grounds. If this trend continues over several decades, the extra time could be used to attempt a second clutch if a first clutch were unsuccessful or even to attempt second broods, although the latter are apparently relatively uncommon in this species (DeLuca et al. 2013). Alternatively, this additional time prior to migration could allow birds more time for migratory preparations (e.g., molting, foraging, fat storage).

Blackpoll Warblers moved through sites more distant from the wintering grounds earlier in the fall. This result indicates not only that birds in the western portion of the breeding range have a prolonged migration in North

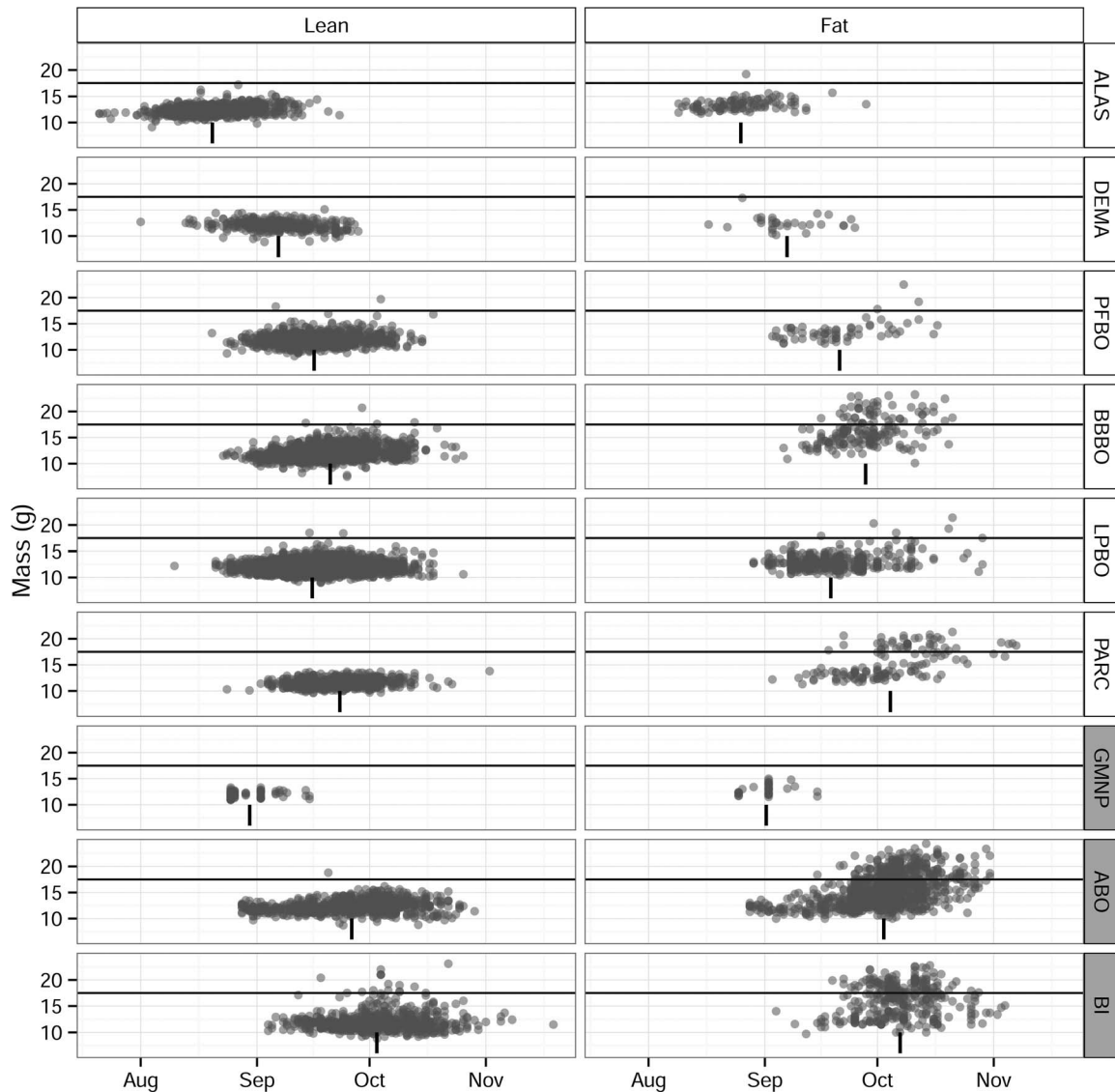


FIGURE 4. Comparison of Blackpoll Warbler mass during fall migration and date of capture. For reference, we include a line at 17.5 g and a vertical bar for the median capture date in each panel. Fat birds (fat scores ≥ 2 ; see Appendix Table 3) were most common at 2 of the coastal sites and later in the season. We excluded data from IWBS, LSL, and TCBO because of limited fat score data. For names and locations of banding sites, see Figure 1.

America, but that they may have a shortened time on the breeding grounds. Coastal birds were captured later than inland birds, regardless of distance to the wintering grounds. Both of these findings are consistent with movement toward the coast prior to the extensive overwater flights of fall migration. The observed early departure from western sites would facilitate birds moving toward eastern North America in preparation for these nonstop flights. The heaviest birds were captured late in migration at BI and ABO, primarily in late September and throughout October (Figure 4), which is consistent with the results of Nisbet et al. (1963), who found higher average mass in late September and the first 2 wk of

October in Massachusetts; and with the radar studies of Williams et al. (1977), which showed that the bulk of transoceanic movement in the western North Atlantic occurred in early October to mid-October. Moreover, DeLuca et al. (2015) reported that Blackpoll Warblers departed between September 25 and November 4 from the north Atlantic coast for their trans-Atlantic flight.

We found several patterns in wing chord data across our study that may be related to migration. When considering wing chord data, it should be noted that given the migratory pattern in Blackpoll Warblers, more easterly stations are likely to capture and record data not only from individuals that breed in the east but also from some that breed in the

west. Therefore, data from easterly and southerly stations likely represent a mix of individuals from populations across the majority of the breeding range. Birds captured at inland sites that were more distant from the wintering grounds (i.e. western) had longer wings than birds captured closer to the wintering grounds (i.e. eastern), which supports geographic size variation in this species (e.g., Pyle 1997, DeLuca et al. 2013), especially given the likelihood that the birds captured at the more easterly stopover sites included some of the larger western individuals, which would dampen this effect. Ralston and Kirchman (2012) found evidence for 3 genetic groups within this species: western, eastern, and Newfoundland, reflecting the separation of the groups geographically. Longer wings among birds in the most distant populations might facilitate their longer migratory distance, either through wing morphology that could increase flight speed and/or flight efficiency or by compensating for more feather wear during the longer flight. The smaller average wing chord among birds captured at coastal sites than among those captured at inland sites is consistent with this geographic pattern of decreasing wing length from west to east. The increased wing chord of birds captured at more southerly coastal sites compared to northern coastal sites is counter to the supposition that longer wings would facilitate longer-distance flights. However, the more southerly coastal sites likely include birds from both western and eastern sites, resulting in average longer wing chords than in the northern coastal site, which likely reflects only Newfoundland breeders.

Although young birds preceded adults at our most westerly sites, adults preceded young at the eastern sites. These results may reflect differences in migratory behavior between the 2 age groups. Although the first prebasic molt occurs as part of the nestling stage, adults must molt after breeding. In this species, molt occurs on or near the breeding grounds (DeLuca et al. 2013). Thus, the later capture of adults in our more westerly inland locations may reflect their persistence near the breeding grounds and, thus, a later initiation of fall migration. However, given that adults are often captured earlier than young in the eastern sites, adults are likely moving more quickly after leaving the breeding grounds. Woodrey and Moore (1997) found that in 5 migrant species, young birds were often captured earlier than adults and that the range of capture dates was more compressed for adults than for young birds on the coast of Alabama during fall migration. This differs from the results of the present study, in which adult Blackpoll Warblers were captured earlier at coastal locations. Because adults had longer wing chords and were heavier than young birds in our study, it is possible that they were in better condition and thus able to migrate faster because of more efficient flight and/or more efficient fat deposition. Migration speed is a function of numerous variables, including flight speed, distance of individual flights, time spent at stopover sites

between flights, and route taken (Hedenström and Ålerstam 1997). Heise and Moore (2003) reported that adult birds were more efficient foragers at stopover sites, which would lead to an ability to more rapidly build or rebuild fat stores and, potentially, increase the speed of migration. Additional study is needed to determine the reasons for the patterns observed in our study.

We found that our heaviest birds were captured at 2 of our coastal sites, ABO and BI, during the second half of migration (Figures 3 and 4). Likewise, the fat birds that were captured at PARC, LPBO, BBBO, and PFBO, although far fewer than at ABO and BI, coincided temporally with those at ABO and BI. Additionally, these same 2 sites had the greatest difference in mass between age groups. These mass patterns may reflect differences in experience between the age groups. Higher proportions of young birds captured at banding stations along the coast have been shown previously (e.g., Murray 1966, Ralph 1981, Morris et al. 1996), and young birds have had lower mass than adults during fall migration (Morris et al. 1996, Woodrey and Moore 1997). However, the magnitude of the difference in mass between adults and young birds that we report from our 2 more southerly coastal sites and the fact that this difference was greater than the age-related difference at our inland sites are novel. Ralph (1981) reported a lower proportion of young Blackpoll Warblers in Bermuda than has been described along the northern Atlantic coast (including in the present study). Taken together, these results may indicate age-related differences in mortality during migration. The observed poorer condition of young birds compared with adults in the present study may lead to increased mortality among young birds during migration, which is particularly important because the migratory periods are responsible for the highest rates of mortality during the annual cycle (Sillert and Holmes 2002). Butler (2000) documented that abundance of Blackpoll Warblers in the breeding season was negatively correlated with storm frequency during the previous fall, providing further evidence of the impact of mortality during migration in this species. While many adults and some young birds have high energy stores, many young birds may not be adequately prepared to successfully cross the Atlantic Ocean en route to South America.

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APPENDIX TABLE 3. Blackpoll Warbler fat scale used in this study. For consistency, we used a single scale of fat scoring, which required converting some stations' data. The final 5-point scale ranged from 0 to 4. For names and locations of banding sites, see Table 1.

Banding site	Original station fat score				
	0	1	2	3	4
ABO	0	1	2	3	4
ALAS	0	1	2	3	4-7
BBBO	0	1	2	3	4-5
BI	0	1	2	3	4
DEMA	0	1	2	3	4-5
GMNP	0	1	2	3	4-7
LPBO	0	1	2	3	4-7
PARC	0		1	2	3
PFBO	0	1	2	3	4-5