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Age-Specific Differences In Fat Reserves And Migratory Passage Of Setophaga Striata (Blackpoll Warbler)

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Age-Specific Differences in Fat Reserves and Migratory Passage of *Setophaga striata* (Blackpoll Warbler)

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Abstract - Adequate fat reserves are vital for long non-stop transatlantic avian-migration movements, such as those made by *Setophaga striata* (Blackpoll Warbler). Over a 5-y period, we studied differences in preparedness (determined by presence of fat content and arrival time at stopover locations) between hatch-year (HY) and after hatch-year (AHY) Blackpoll Warblers at 3 stopover sites (Hancock and York counties in Maine, and Plymouth County in Massachusetts) covering 2.65° latitude along the Gulf of Maine. Migration timing varied across a latitudinal gradient and between age classes. In September, AHY Blackpoll Warblers were more abundant in the northern and central counties, but HY birds mostly passed through in October. Compared to AHY Blackpoll Warblers, our results suggest that HY birds migrated along a more northern route. After hatch-year birds had higher fat-content than HY birds at the northern and central sites. However, AHY birds had lower fat-content at the southern-most site. After hatch-year birds were more abundant than HY birds at the southern-most site. Overall, across our study region, our data illustrate that Blackpoll Warblers show age-related differences in fall-migration strategy; hatch-year birds may simply need more time at stop-over sites to build up fat reserves prior to large-distance flights.

Introduction

Migration is a dangerous and physically demanding period in the life cycle of migratory birds. Some species take long overseas flights, requiring them to have enough stored energy to reach their destination without stopping. Birds must deposit and metabolize sufficient levels of fat reserves to survive these long flights (Fusani et al. 2009, Hedenstrom 1993). Therefore, an individual bird's migration strategy must include the ability to accumulate fat reserves and to appropriately time their long flights in accordance with favorable weather conditions.

Migration strategy sometimes differs between age classes of birds. Several studies, but not all (see Deppe et al. 2015), suggest that after hatch-year (AHY) birds prepare better for migration than hatch-year (HY) birds (Brown and Taylor 2015, Nisbet et al. 1963, Woodrey and Moore 1997). For example, HY *Setophaga ruticilla* L. (American Redstart) arrived at their wintering grounds after AHY American Redstarts, and HY birds stayed longer at stopover sites than AHY birds (Francis and Cooke 1986, Morris 1994). The average fat reserves in after hatch-year *Setophaga striata* (Forster) (Blackpoll Warbler) are greater than those of HY Blackpoll Warblers at fall stopover locations, which may be a result of age-specific differences in migration timing because AHY warblers are better able to plan a migration suitable to obtaining efficient resources (Murray

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1979, Nisbet 1963). Multiple factors may be responsible for this AHY-related advantage in migration preparedness, including: (1) past experience, (2) reduced amount of excessive fat stored, and (3) increased social dominance that results in a competitive advantage in food acquisition (Brown and Taylor 2015, Francis and Cooke 1986, Marra et al. 1993, Mettke-Hofmann and Gwinner 2003, Woodrey and Moore 1997).

Blackpoll Warblers breed from the northeastern US to Alaska, and they are a locally common fall migrant in New England coniferous forests where they embark on a transoceanic flight to northern South America (Morse 1979, Murray 1979, Richardson 1972). Their migration route is the longest known of any New World warbler species, and one of the longest of all migratory songbirds (DeLuca et al. 2015, Morris et al. 2015). Individual Blackpoll Warblers fly up to 2770 km non-stop during autumn migration, which may require 3 days of continuous flight (DeLuca 2015). This unusual and remarkably long migration requires the deposition of suitable fat reserves (e.g., Cooke 1904) at key points along their migratory route—especially just prior to departing on their transatlantic flights (DeLuca et al. 2015, Nisbet et al. 1995). To complete these overwater flights, a Blackpoll Warbler needs to accumulate ≥50% of its body weight as fat (Davis 2001). In addition, the timing of migration is critical; a delayed departure from the breeding grounds or stopover sites could result in an increase in competition between species and difficulty finding enough resources to complete the journey (Morris 1994). Blackpoll Warblers must store excess amounts of fat to reach their wintering grounds (Latta and Brown 1999).

Using fall-capture data from banding stations, we studied variation in age-specific Blackpoll Warbler fat reserves and timing of arrival at 3 New England fall-stopover locations (Hancock and York counties in Maine, and Plymouth County in Massachusetts), covering 2.65° latitude along the Gulf of Maine. We compared these results with eBird data recorded in the same counties to explore if the banding-station data (site-level) were concordant with the citizen-science–reported observational data covering a broader region (county level). We hypothesized that AHY Blackpoll Warblers would have greater fat reserves than HY Blackpoll Warblers, and that more AHY birds would be found in the most southern county of our study earlier in the migration season than HY birds.

Methods

From early September to late October (2011–2014, and 2016), we captured and banded Blackpoll Warblers at 3 coastal forests along the Gulf of Maine. The most northerly site (hereafter Northern; 44°14'N, 68°18'W), is on the Schoodic Peninsula, Hancock County, ME. We operated thirteen 12-m and six 6-m mist-nets to trap warblers at this location. The Central site was located in York County, ME (43º27’N, 70º24’W), 190 km southwest of Northern. Our banding site was ~800 m from the Saco River Estuary and ~2300 m from the Atlantic Ocean, where we operated 3 arrays of mist-nets, each with 5 interconnected, 12-m mist-nets. The southern-most site (Southern) is located on the coast of Cape Cod Bay (41°55’N, 70°32’W), Plymouth County, MA, 170 km south of Central. We operated fifty 12-m mist-nets at Southern.

Mist-nets were open from 0600 to 0930 every Monday and Wednesday from early September to late October each year. We determined fat content of individual Blackpoll Warblers by examining their tracheal pit. Fat, when present, had a yellow tint and was visible through the skin; 1 observer evaluated all birds at each site. We pooled all data for each site across all years because our sample size was insufficient to test for annual variation. The scaling system ranged from 0 (no fat present) to 5 (fat filling and bulging out of the pit) (Helms and Drury 1960). Fat in these deposits typically reflects the total-fat load in a bird’s body (Sutherland 2004). We determined age by plumage following Pyle (1997).

We also collected Blackpoll Warbler observational data from eBird (eBird 2017) for the counties where our 3 banding stations were located. These data include observations by citizen-scientists covering the same periods that the banding stations operated each year. Analogous to our banding data, we pooled weekly Blackpoll Warbler observations from eBird over the same periods as the banding data. Again, we pooled data across years; furthermore, we assumed little variation in observer effort across the sample period. We examined reports from September and October 2011–2014 and 2016, and found that 90 submitted checklists included Blackpoll Warbler sightings in Hancock County (Northern), 262 checklists included sightings in York County (Central), and 375 checklists included sightings in Plymouth County (Southern). We compared migration passage with both banding and eBird data but conducted age-specific analyses solely with banding data because eBird data consisted of all age-classes combined. We performed one-tailed *t*-tests to determine whether fat content differed between age classes.

Results

Timing of migration varied between locations and age classes. The majority of Blackpoll Warblers (80%) recorded in eBird in the Northern county occurred in a 24-d period (1–24 September) (Fig. 1). Blackpoll Warblers observed in the Central county showed a broader range of observation dates, with 80% arriving over a 28-d period (1–28 September). Birds arrived later and in a more protracted fashion in the Southern county, with 80% recorded over 40 d (1 September–10 October). Similar to the eBird temporal patterns, the majority of Blackpoll Warblers (80%) captured in the Northern, Central, and Southern sites occurred over 28 d (3 September–30 September), 33 d (3 September–5 October) and 41 d (3 September–13 October), respectively.

Both the Northern and Southern banding stations had a steadier and more extended range of capture dates, which juxtaposed the peaks found in the eBird observations (Fig.1). However, at the Central and Southern banding stations, Blackpoll Warblers arrived on similar dates as compared to the earlier arrival dates in the Northern county. Both the capture and eBird data illustrate that mean arrival was earlier in the Northern (mean ± SD = 28 September ± 9.1 d) as compared to the Central (2 October ± 5.7 d; $t_{61,62}$ = -2.47, P < 0.007) or the Southern sites (mean ± SD = 4 October ± 6.3 d). Mean arrival at the Central site was earlier than mean arrival at the Southern site ($t_{261,62}$ = 3.33, P = 0.0005).

Migration timing differed between HY and AHY Blackpoll Warblers. While AHY Blackpoll Warblers were more abundant in the Northern county earlier in the season, we captured more HY birds later in the fall, suggesting asynchronous timing between HY and AHY birds along the coast (Fig. 2). At the Southern county, in contrast, we caught 78% of HY birds prior to 6 October, while we caught only 48% of AHY prior to this date (Fig. 2).

At the Northern site, AHY Blackpoll Warblers had significantly greater fat scores than HY birds ($t_{61,24}$: -2.53, P = 0.007; Fig. 4). Similarly, AHY birds at the Central site had significantly greater fat scores than HY birds ($t_{19, 15}$ = -2.739, P = 0.005). At the Southern site, AHY and HY birds did not have statistically significant differences in fat scores ($t_{18, 62}$ = 1.426, P = 0.078; Fig. 3).

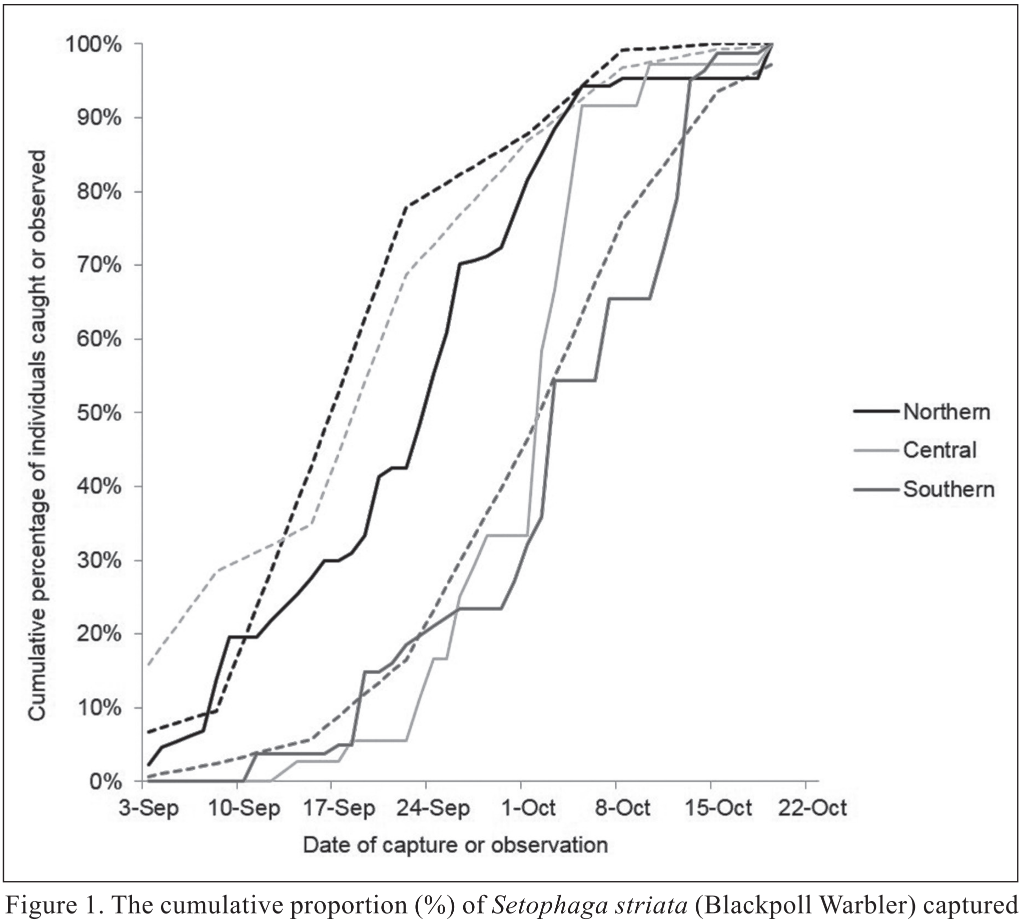

Figure 1. The cumulative proportion (%) of *Setophaga striata* (Blackpoll Warbler) captured and observed at Northern (Hancock, ME; 2013, 2015), Central (York, ME; 2011–2014, 2016), and Southern (Plymouth, MA; 2011–14, 2016) sites. Solid lines depict capture data from banding stations and dotted lines depict observational data from eBird.

Discussion

From north to south, we caught >50% of Blackpoll Warblers at each respective site over ~18 d, covering 2.65° latitude. These data concur with Cooke's (1904) and Murray's (1965) work indicating that this species travels SSW down the northern Atlantic Coast, although individual birds may not follow a coastal-specific migratory path (Smetzer et al. 2017). Blackpoll Warbler abundance peaked earlier at the most northern latitude and later at the most southern latitude. Banding data followed similar latitudinal trends, but peaks were not as sharp as in eBird data. At the banding stations, we captured the majority of Blackpoll Warblers later in the season when compared to the observational eBird data, particularly in the Northern and Central counties. The discrepancies between the 2 sources could arise from varying sample sizes because eBird sample sizes (*n* = 230, *n* = 1225, *n* = 1476) were considerably larger than banding sample sizes (*n* = 87, *n* = 42, *n* = 82) throughout all 3 counties (samples organized from north to south, respectively). Incongruities could reflect differing collection periods in the eBird and banding data. While eBird observations consisted of all Blackpoll Warblers seen or heard in particular counties throughout the months of September and October, the banding effort only included the birds caught 2 days each week between 0630 and 0930 in September

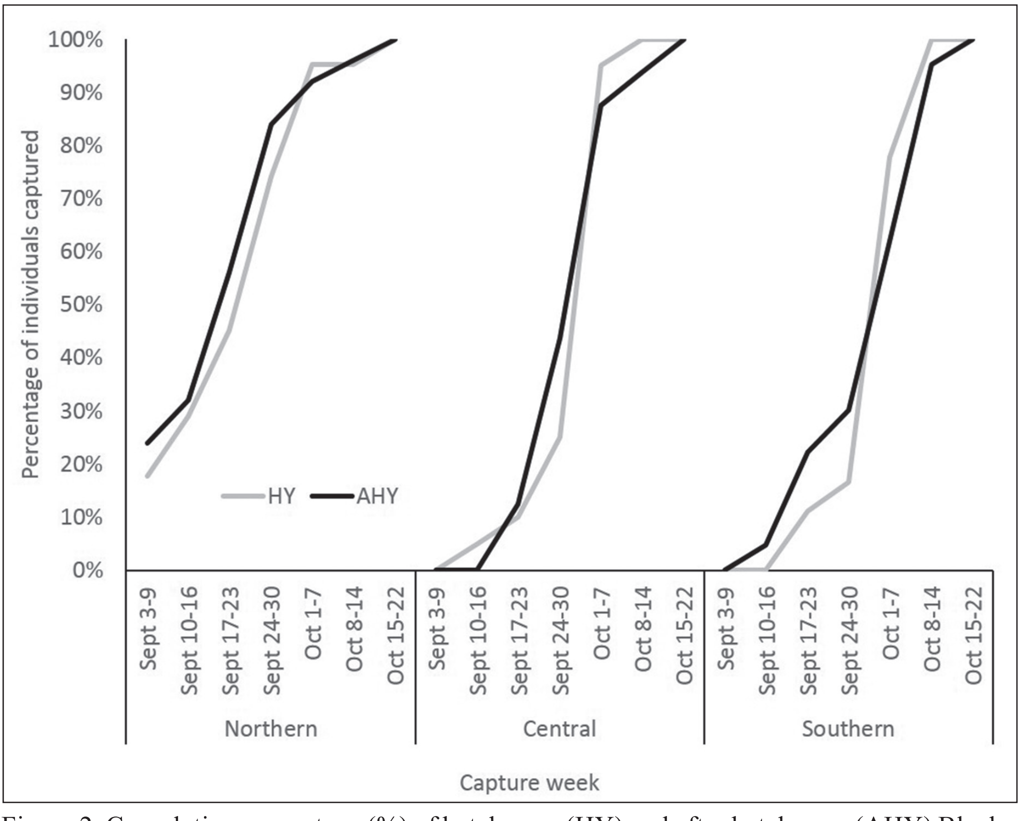

Figure 2. Cumulative percentage (%) of hatch-year (HY) and after hatch-year (AHY) Blackpoll Warblers captured during fall migration at 3 banding sites along the Gulf of Maine.

and October. Finally, differences between banding and eBird data could reflect birds congregating at coastal and inland sites at different latitudes (e.g., Smetzer et al. 2017). Regardless of differences in peak arrival between the 2 datasets, our results were consistent with our hypothesis that peak Blackpoll Warbler passage would occur earlier at higher latitudes. In the 1970s, Blackpoll Warblers migrated through New England and New Jersey from early September through the first week of October (Murray 1979), which is consistent with both data sets, as the majority of Blackpoll Warblers were observed between 15 September and 8 October.

Fat content was significantly lower in HY than AHY Blackpoll Warblers in the Northern and Central counties. Likewise, a similar difference in fat levels has been documented in several other species (Jakubas 2010, Woodrey and Moore 1997). Both Jakubas (2010) and Woodrey and Moore (1997) attributed this difference in fat to HY birds having a lower social status and not being able to compete for food resources with AHY birds. They also postulated that HY birds were more vulnerable to predation due to inexperience, which required them to expend more energy trying to escape from predators during migration.

Fat content values in the Southern county were inconsistent with the Northern and Central site. The fat content of HY and AHY Blackpoll Warbler fat content did not differ significantly at the Southern site as it did at the Central site. Previous studies of Blackpoll Warblers at coastal stopover sites during fall migration

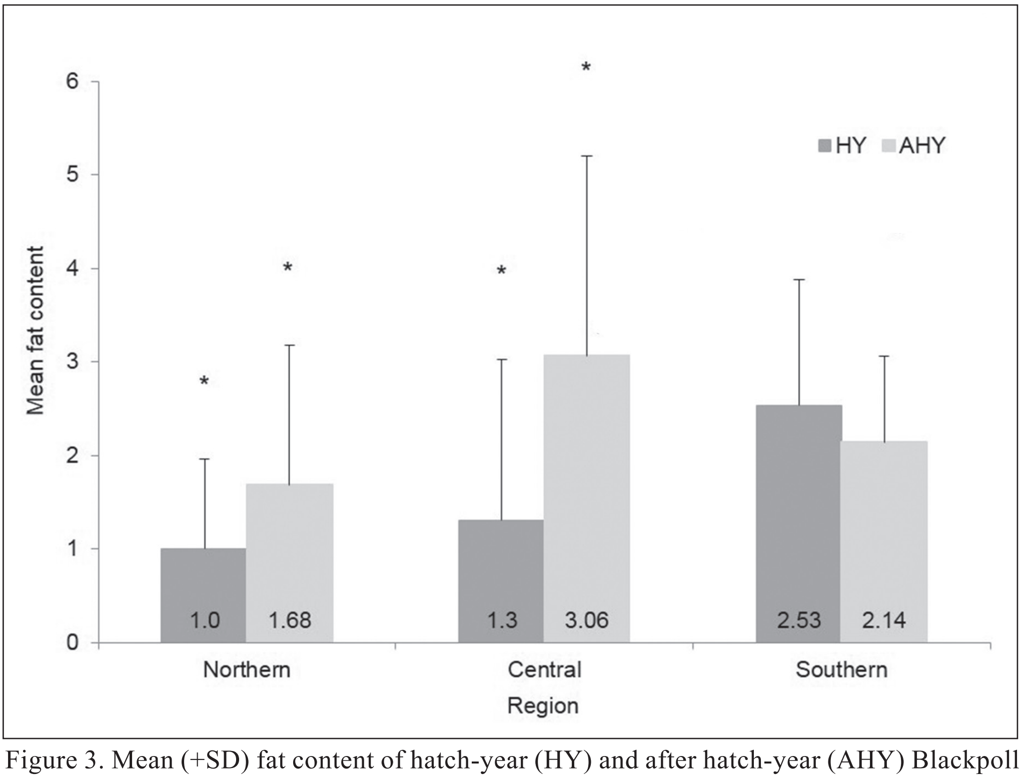

Figure 3. Mean (+SD) fat content of hatch-year (HY) and after hatch-year (AHY) Blackpoll Warblers banded at 3 coastal sites along the Gulf of Maine. Significant results are marked with an asterisk (*), where HY and AHY birds differed significantly within a given site.

reported fewer individuals with extensive fat stores than might be expected (Morris 1994). However, we had a small sample size to detect differences at this site (AHY: $n = 63$; HY: $n = 19$).

Relative differences between HY and AHY Blackpoll Warbler body condition and migration timing was apparent in this study. While we do not know the fitness consequences of our observations, apparent survival of HY birds can be equal to or lower than AHY birds in both long- and short-distance migrants (e.g., Perlut and Strong 2016). Although it is more advantageous to have high fat content at the time of departure, it is possible that warblers that had a fat score of 0 could slowly locate and retain enough resources to complete their journey while at all stopover locations. In 2013, we recaptured 2 Blackpoll Warblers within-season at the Central site. One had a fat content of 3 on 30 September and a fat content of five 2 days later when recaptured on 2 October; the second had a fat content of 4 on 30 September and a fat content of five 14 days later when recaptured on 14 October. If these warblers choose to stay at the stopover location for an extended amount of time, it is apparent that they can build up their fat reserves for their transatlantic flight to their wintering grounds. Hatch-year birds may simply need more time at stopover sites to build up fat reserves prior to large-distance flights (Moore and Kerlinger 1987).

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