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Research Paper

Asynchronous movement patterns between breeding and stopover locations in a long-distance migratory songbird

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ABSTRACT. The species-specific migratory patterns and strategies of many songbirds remain unknown or understudied, as research in animal ecology is biased toward the breeding period, with the fewest studies on the migratory period across taxa. Identifying large-scale spatiotemporal migratory patterns is challenging, as individuals within a species may vary in their migratory behavior and strategies. The Yellow Warbler (*Setophaga petechia*) is a Nearctic-Neotropical migrant that is relatively well studied during the breeding season, but its species-wide migratory patterns remain understudied. Our aim in studying Yellow Warbler movement ecology was to characterize temporal migration patterns during fall migration. We sought to determine the temporal migration pattern among breeding locations, as determined by the hydrogen stable isotope values in feather samples collected at disjunct (~2000 km) stopover sites in the Gulf of Maine (n = 50) and the Gulf of Mexico (n = 150). We used a similarity matrix to group individuals into a geographic cluster by breeding location, which was then used as the response variable in a modeling analysis. Our results provide evidence that Yellow Warblers exhibit an asynchronous, type 1 temporal migration pattern with southern breeding populations initiating migration prior to northern populations. Using hydrogen isotopes, we identified the temporal migration patterns between geographic clusters, representing an individual's breeding location, and stopover sites along the Gulf of Maine and Gulf of Mexico, which fills a gap in understanding Yellow Warbler migration ecology.

Déplacements asynchrones entre les sites de nidification et les haltes migratoires chez un passereau migrateur de longue distance

RÉSUMÉ. Les tendances et les stratégies migratoires propres à chaque espèce de nombreux passereaux restent inconnues ou sous-étudiées, car la recherche en écologie animale est surtout axée sur la période de nidification et non sur la période migratoire. La détermination de tendances migratoires spatio-temporelles à grande échelle est un défi, car les individus d'une même espèce peuvent avoir des comportements et des stratégies migratoires différents. La Paruline jaune (*Setophaga petechia*) est un migrateur néarctique et néotropical relativement bien étudié pendant la saison de nidification, mais ses tendances migratoires à l'échelle de l'espèce restent peu étudiées. En étudiant l'écologie de déplacement de la Paruline jaune, notre objectif était de caractériser les tendances temporelles de migration pendant la migration d'automne. Nous avons cherché à déterminer la tendance temporelle de migration entre les sites de nidification à partir de valeurs d'isotopes stables de l'hydrogène dans les échantillons de plumes collectés dans des haltes migratoires disjointes (~2000 km), dans le golfe du Maine (n = 50) et le golfe du Mexique (n = 150). Nous avons utilisé une matrice de similarité pour assembler les individus en groupe géographique par lieu de nidification, qui a ensuite été utilisé comme variable explicative dans une analyse de modélisation. Nos résultats indiquent que les Parulines jaunes présentent une tendance temporelle de migration asynchrone de type 1, les populations nicheuses du sud entamant leur migration avant celles du nord. Au moyen d'isotopes d'hydrogène, nous avons déterminé les tendances temporelles de migration entre les groupes géographiques, représentant le lieu de nidification d'un individu, et des haltes migratoires le long du golfe du Maine et du golfe du Mexique, comblant ainsi une lacune dans la compréhension de l'écologie de la migration de la Paruline jaune.

Key Words: *autumn, spatiotemporal tracking, hydrogen stable isotope, Yellow Warbler (Setophaga petechia), Gulf of Mexico, Gulf of Maine, geographic assignments, migration synchrony*

INTRODUCTION

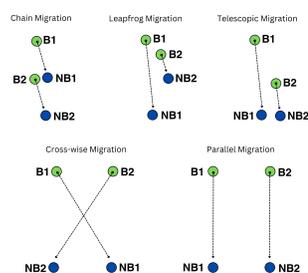
The majority of North American temperate bird species undergo annual migrations between breeding and non-breeding locations (Greenberg 1980, Rappole 1995). The species-specific migratory

patterns and strategies of many songbirds remain unknown or understudied, as research in animal ecology is biased toward the breeding period, with the fewest studies on the migratory period across multiple vertebrate orders (Marra et al. 2015). Moreover,

avian mortality rate is highest during the migratory period (Sillett and Holmes 2002, Paxton et al. 2017, Ward et al. 2018), and as human pressures (e.g., habitat fragmentation, climate change, artificial light at night) have contributed to declines in North American avifauna, migratory species have been particularly vulnerable (Rosenberg et al. 2019). Thus, strategies to reverse such declines can benefit from understanding the spatiotemporal patterns between periods of the annual cycle by identifying where migratory birds are throughout the year in order to enact targeted conservation and management actions.

Studying spatiotemporal patterns can shed light on the migration strategies by focusing on when and how birds from one region move relative to conspecifics from another region. Salomonsen (1955) describes five spatial migration patterns, briefly defined here, which can be exhibited by migratory birds (Fig. 1). Three of these spatial migration patterns are related to latitudinal distributions of birds between the breeding and non-breeding seasons: (1) chain migration, which occurs when southern and northern populations of a species exhibit the same spatial distribution in breeding and non-breeding areas; (2) leap-frog migration, which occurs when northern and southern breeding populations show the opposite spatial distribution in terms of latitude on the non-breeding grounds (i.e., northern breeding populations have non-breeding distributions farther south than southern breeding populations); and (3) telescopic migration, where breeding populations from different latitudes share non-breeding areas at similar latitudes (i.e., birds at the same non-breeding area exhibit different migration distances based on their breeding location; sensu Salomonsen 1955, Smith et al. 2003, Kelly 2006, Zenzal et al. 2018, Skinner et al. 2022). The other two spatial migration patterns are related to longitude and include (1) cross-wise migration, in which birds segregated into eastern and western breeding populations cross during migration and retain separation at the non-breeding area (i.e., individuals in the eastern part of the breeding range were found in the western part of the non-breeding range and vice-versa; sensu Salomonsen 1955, Witynski and Bonter 2018); and (2) parallel migration, in which birds segregated into eastern and western breeding populations retain the same longitudinal separation at the non-breeding area (i.e., individuals in the eastern part of the breeding range are also found in the eastern part of the non-breeding range and vice-versa; sensu Salomonsen 1955, Boulet et al. 2006).

Fig. 1. Conceptual illustrations of spatial migration patterns (sensu Salomonsen 1955). Breeding (B) and non-breeding (NB) locations are shown with numbers indicating the same population. See Introduction for a written description of each migration pattern.

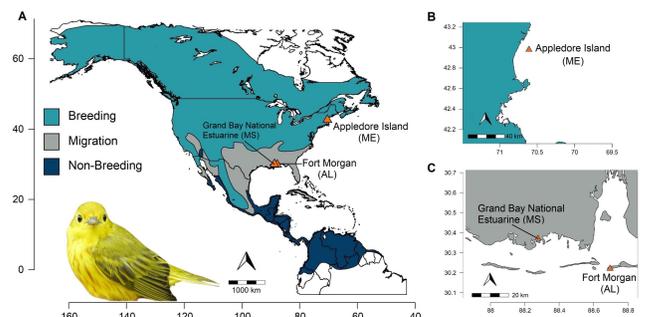


Smith and coauthors (2003) added to our understanding of migration patterns by defining two temporal migration patterns exhibited during autumn migration. The temporal migration patterns are: (1) type 1 migration, which occurs when southern breeding populations initiate migration prior to northern breeding populations; and (2) type 2 migration, which occurs when northern breeding populations begin to migrate before southern breeding populations (sensu Smith et al. 2003, Kelly 2006, Zenzal et al. 2018). Temporal, latitudinal, and longitudinal migration patterns likely occur in any combination, with combinations of temporal and latitudinal (mainly chain and leap-frog migration) being the best described (see Smith et al. 2003). Moreover, the timing of migration can be further nuanced by considering migratory synchrony, which describes a population's variation in migration over time (Bauer et al. 2016). Understanding the temporal migration pattern used by a species as well as the potential mechanism is crucial to developing regional and international conservation programs (e.g., Rosenberg et al. 2016, Cohen et al. 2017, Zenzal et al. 2019).

The Yellow Warbler (*Setophaga petechia*) is a Nearctic-Neotropical migrant with a broad breeding range that extends across much of North America (see Lowther et al. 2020 and references therein; Fig. 2). Given the broad range and commonness of the Yellow Warbler, it is not surprising that this species has been the focal species of extensive research using a variety of methods. For example, over the last few decades large-scale studies of Yellow Warblers have addressed morphology (e.g., Wiedenfeld 1991, Bay et al. 2021), migration (e.g., Kelly and Hutto 2005, Boulet et al. 2006, Kelly 2006, Witynski and Bonter 2018, Bay et al. 2021, Somveille et al. 2021), population distribution and change (Bay et al. 2018, 2021), as well as genetics (e.g., Klein and Brown 1994, Milot et al. 2000, Boulet et al. 2006, Bay et al. 2018). Despite this impressive breadth of research, there is little known about the temporal migration patterns of the species.

During autumn migration, the Yellow Warbler appears to be a relatively early migrant in the eastern portion of its range and a later migrant over a more protracted period in the western portion of its range (Bent 1953, Duncan and Weber 1985, Lowther et al. 2020).

Fig. 2. (A) Map of the breeding, migration, and non-breeding areas of the migratory Yellow Warbler (BirdLife International and Handbook of the Birds of the World 2021); (B) Location of the migration banding station at Appledore Island, Maine; (C) Locations of the migration banding stations that comprise the Gulf Coast sites, which were located in Fort Morgan, Alabama, and Grand Bay National Estuarine Research Reserve, Mississippi. Yellow Warbler photo credit: Emilie Ospina.



Across the range, Yellow Warblers have been found to exhibit leap-frog migration in terms of latitudinal distribution, but there are conflicting reports on longitudinal distribution (Boulet et al. 2006, Witynski and Bonter 2018, Bay et al. 2021, Somveille et al. 2021). Parallel migration was supported by a suite of tracking methods (banding records, stable isotopes, and genetic samples; Boulet et al. 2006), whereas cross-wise migration was found using light-level geolocators (Witynski and Bonter 2018). More recently, researchers have leveraged genetic information to connect breeding and non-breeding areas of Yellow Warblers, which illustrates that the spatial scale of the investigation may bias the spatial pattern observed (Bay et al. 2021, Somveille et al. 2021). Previous studies have suggested eastern and western populations appear to be distinct evolutionary units (Klein and Brown 1994, Milot et al. 2000, Kelly and Hutto 2005), so it is possible these populations exhibit different migratory strategies. However, none of these studies have investigated the temporal migration of Yellow Warblers to our knowledge.

Recent research has identified linkages between Yellow Warblers and climate-driven population changes (Mazerolle et al. 2005, Bay et al. 2018) as well as regional population declines across the breeding distribution (Fink et al. 2023), meaning that this currently widespread species may be at risk. Even with identified climate-driven declines and other challenges birds already face (e.g., habitat loss and degradation, human development, etc.), Yellow Warblers are still fairly common and may serve as a model for understanding migratory patterns. Therefore, we sought to examine the temporal migration patterns between the breeding locations of individuals captured at geographically distinct stopover locations over multiple years. We used two stopover locations ~2000 km apart to determine if patterns were similar across sites or if patterns changed in relation to distance from the non-breeding grounds. We modeled likely breeding area using stable isotope data from feather samples of Yellow Warblers collected during migration. Whereas many biotic (i.e., age) and abiotic factors can affect isotopic ratios in animal tissues (Haché et al. 2012), inert keratinous samples, such as feathers, integrate the naturally occurring gradients of hydrogen isotope ($\delta^2\text{H}$) values in precipitation during the molting period, which occurs on the breeding grounds for many species, including Yellow Warbler (Hobson and Wassenaar 1996, Bowen et al. 2005, Hobson et al. 2012, Lowther et al. 2020).

Our overall aim in studying Yellow Warbler movement ecology was to characterize temporal migration patterns and determine degree of synchrony. We examined the temporal migration pattern (degree of synchrony; type 1 vs type 2) among breeding locations, as determined by the $\delta^2\text{H}$ values in feather samples collected at stopover sites on Appledore Island, Maine, and along the northern Gulf of Mexico. In our analysis of temporal migration, we included fat score, age, and sex as covariates, which may help explain variation in arrival timing. We predict that birds from breeding areas closer to the stopover site will carry more fat stores because their energetic cost should be lower than individuals from further away. We expect all three covariates could interact with the phenology of Yellow Warblers through the stopover sites. If an interaction exists with fat score, we predict birds arriving earlier to be in better condition because of a greater abundance of resources earlier in the season. If an interaction exists with sex, we expect males to arrive earlier in the season, as found during their spring migration (Kammeraad 1964, Lowther et al. 2020). Finally, if there is an interaction with age, we

expect after-hatch year birds to arrive earlier given that they tend to be more efficient foragers (Wunderle 1991, Woodrey 2000), possibly allowing them to migrate faster (sensu Hake et al. 2003, Jakubas and Wojczulanis-Jakubas 2010).

METHODS

Feather sampling and processing

Young (hatch year) Yellow Warblers grow all their body and flight feathers while at their natal site (Lowther et al. 2020). Young birds then molt and replace only their body feathers prior to fall migration, whereas adult (after-hatch year) Yellow Warblers molt and replace all feathers (body and flight feathers) annually on their breeding grounds (Pyle 1997). Thus, the flight feathers of both adult and young birds, including rectrices, sampled prior to the next molt cycle incorporate the environmental isotope values of precipitation from the breeding ground locations (Hobson and Wassenaar 1996, Contina et al. 2022).

The right and left fifth rectrices of Yellow Warblers were sampled during fall migration on Appledore Island, Maine ($n = 50$; 42.9891° N , 70.6142° W), from 2016 to 2018 (August and September) and at two coastal sites along the northern Gulf of Mexico (September and October): Fort Morgan, Alabama (Bon Secour National Wildlife Refuge; $n = 134$; 30.2256° N , 88.0189° W) from 2005 to 2014, and Grand Bay National Estuarine Research Reserve, Mississippi ($n = 16$; 30.3713° N , 88.4311° W ; Table 1, Fig. 2), from 2006 and 2007. Samples from the Fort Morgan and Grand Bay National Estuarine Research Reserve sites (hereafter “Gulf Coast sites”) were combined for analysis because of similarities in habitat structure, function (sensu Mehlman et al. 2005), and proximity to each other (~44 km) as well as to the Gulf of Mexico (< 20 km). Additionally, each individual was banded with a U.S. Geological Survey aluminum leg band, visually assessed for fat score (Appledore Island: Cherry 1982, Morris et al. 1996; Gulf Coast sites: Helms and Drury 1960), measurements of unflattened wing length and mass were obtained, and, when possible, age and sex were determined (Pyle 1997). All banding and sampling were conducted under permits from the U. S. Geological Survey Bird Banding Laboratory (21221 and 22243), University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC; 11092210), and Canisius University IACUC (382).

Table 1. Sampling years and number of individuals sampled by stopover location for Yellow Warblers during fall migration. Appledore Island is located along the coast of the Gulf of Maine, whereas the other two sites, Fort Morgan and the Grand Bay National Estuarine Research Reserve, are located along the northern Gulf of Mexico coast and were combined for statistical analysis (Fig. 2).

Site	Years	Sample size
Appledore Island, ME	2016–2018	50
Fort Morgan, AL	2005–2014	134
Grand Bay National Estuarine Research Reserve, MS	2006–2007	16

One of the two sampled feathers from each individual was randomly selected for processing and was cleaned by using a two-step process (Paritte and Kelly 2009, Chew et al. 2019). First, feathers were soaked in a 2:1 chloroform:methanol solution for 30 s and dried overnight at room temperature. Feathers were then cleaned in a dilute detergent solution and rinsed of all detergent residue with distilled water (DI) before drying for a minimum of 24 h (1:30 Fisher Scientific Versa-Clean:DI water). Feather vane was cut starting at the distal end of the feather and weighed to $200 \pm 10 \mu\text{g}$ using a Mettler Toledo microbalance (model XS3DU) and packed into 3.5 mm x 5 mm silver capsules (Costech, 041066) for isotope ratio mass spectrometry analysis.

Isotopic determination

Samples and standards were allowed to equilibrate to local conditions for a minimum of three wk before analysis (Wassenaar and Hobson 2003). Hydrogen isotope measurements were made with a ThermoFinnigan Delta V isotope ratio mass spectrometer connected to a Thermal Conversion Elemental Analyzer (Thermo Scientific) at the Environmental Stable Isotope Lab at the University of Oklahoma. We adopted the delta notation ($\delta^2\text{H}$) of parts per mil (‰) from the standards ($\delta^2\text{H}_{\text{sample}} = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$) relative to the Vienna Standard Mean Ocean Water (VSMOW). To calibrate $\delta^2\text{H}$ values measured in feather samples, we used three standards that we report as mean: Caribou Hoof Standard (count N = 32; $\delta^2\text{H}$ CBS = -157.0‰), Kudu Horn Standard (count N = 34; $\delta^2\text{H}$ KHS = -35.3‰), plus an internal reference material Brown-headed Cowbird feathers (count N = 34; $\delta^2\text{H}$ BHCO = -42.7‰). Analytical precision is expressed as standard deviation (SD) of the reference material: CBS (count N = 32; SD = 1.3‰); KHS (count N = 34; SD = 1.2‰); and BHCO (count N = 34; SD = 2.2‰). Our laboratory protocol included the analysis of three reference standards every eight samples across all the mass spectrometer runs.

Geographic assignment of feather origin based on stable isotope analysis

We performed a Bayesian analysis to obtain the most likely breeding area of migratory warblers based on hydrogen isotope feather values ($\delta^2\text{H}_f$). To calibrate the growing season precipitation isotope values ($\delta^2\text{H}_p$; Bowen et al. 2005) to $\delta^2\text{H}_f$ values of Yellow Warblers of known origin (N = 32; Hobson et al. 2012), we used the *calRaster* function of the ‘assignR’ package (Ma et al. 2020) in the R statistical language (version 4.1.0; R Core Team 2022). Then we generated individual-based posterior probability density maps restricted to the breeding distribution range (BirdLife International and Handbook of the Birds of the World 2021) using the *pdRaster* function in ‘assignR.’ We used the R package ‘isocat’ (Isotope Origin Clustering and Assignment Tools) to cluster migrants into groups of common breeding locations (Campbell et al. 2020) based on a similarity matrix of the probability surfaces obtained from ‘assignR.’ First, we computed the pairwise comparisons of Schoener’s D-metric between all posterior probability raster layers. Then we calculated the mean aggregated probability surfaces for each cluster in the package ‘isocat.’ We adopted a hierarchical approach through the *cutree* function in the R package ‘dendextend’ (Galili 2015) and determined the number of clusters by setting the bracketing height threshold = 0.25. These clusters were used in the next step of analysis (see below).

Statistical analysis

We used an information theoretic approach to identify the temporal migration pattern between breeding clusters and stopover locations and to identify potential covariates that may explain variation in arrival timing. Given that our response variable (breeding region) was categorical, we compared multinomial logistic regression models for the Appledore Island and Gulf Coast sites through Akaike’s information criterion corrected for small sample sizes (AIC_c). For both stopover sites, our non-correlated predictor variables ($|\text{Spearman’s } \rho| < 0.35$) included Day of Year and Fat Score. We assumed birds arrived the day of initial capture and converted the calendar date to ordinal day (Day of Year). Because of differences in methodology with assessing fat score between the Appledore Island and Gulf Coast sites, we standardized fat score between the two locations based on the written descriptions (Helms and Drury 1960, Cherry 1982, Morris et al. 1996) in order to interpret our results on the same scale. For the Gulf Coast sites analysis, we had sufficient samples to include age and sex in the analysis. Data from Appledore Island had too few individuals of known sex (n = 28) or of adult age class (n = 3) to include models with age or sex. However, we did analyze the subset of data with known sex for Appledore and did not find sex to be included in the top models, confirming our decision to exclude sex, which allowed us to include individuals of known or unknown sex in our final analyses. The final analysis resulted in 5 and 34 models for the Appledore Island and Gulf Coast sites, respectively. Analyses were performed by using the ‘mnet’ (Venables and Ripley 2002) and ‘AICcmodavg’ (Mazerolle 2020) packages in the R statistical language (R Core Team 2022).

RESULTS

Breeding distributions

Based on the stable isotope similarity matrix, five breeding clusters were defined, which were numbered in order of decreasing latitude within the Yellow Warbler breeding range (Fig. 3). For individuals sampled at Appledore Island, breeding regions tended to be more southern and eastern than birds sampled at the Gulf Coast sites, as few birds (n = 4) were assigned to each of the two northernmost clusters. The remaining three clusters of Appledore Island birds had an increasing number of individuals progressing southward, ranging from 10 to 18 (Appendix 1 Table S1). At the Gulf Coast sites, the number of individuals migrating from each of the five clusters ranged between 21 and 40 (Appendix 1 Table S1). The largest group was from the northernmost cluster.

Temporal migration

The timing of arrival at the stopover sites also varied among geographic breeding clusters. Arrival at Appledore Island was earlier than at the Gulf of Mexico, such that individuals within a geographic cluster arrived at Appledore ~10 days earlier than individuals from those same clusters appeared on the northern Gulf of Mexico coast. Additionally, even within a geographic breeding cluster, there was variability in Day of Year, contributing to weak synchrony within a cluster (Fig. 4).

For Appledore Island, the top five models had a cumulative weight of 1.0; three of the five models included Day of Year; however, the second ranked model was the Null model (Table 2). The most

Fig. 3. Mean aggregated probability surface for each of five geographic clusters based on stable hydrogen isotope analysis. Warmer colors indicate a higher probability of breeding location, and cooler colors signify a lower probability (A - E). The number of individuals with membership within each cluster that were captured at either the Appledore Island or Gulf Coast sites during fall migration (F).

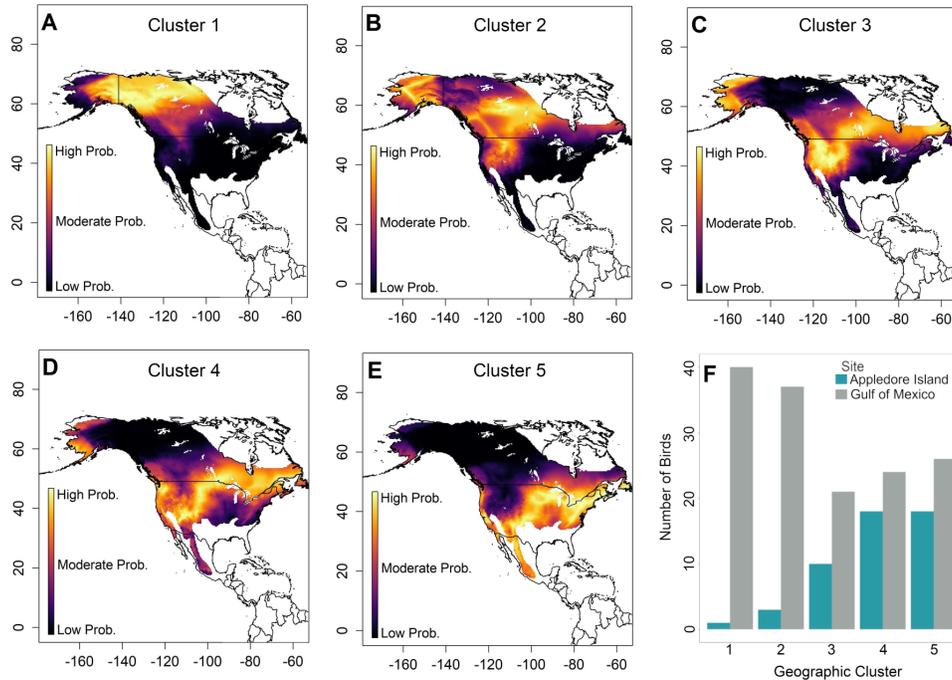
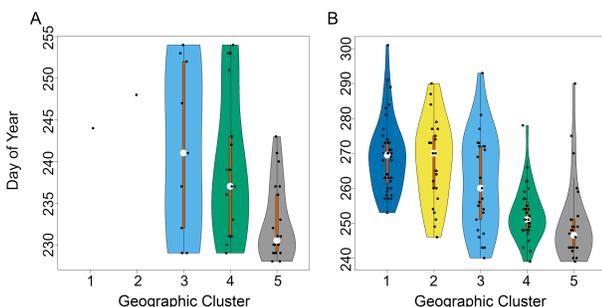


Fig. 4. The relationship between capture day and geographic cluster, based on stable hydrogen isotope analysis, at the Appledore Island, Maine (A), and Gulf Coast sites (B). The shape of the violin indicates the probability of individuals being in a particular area of the distribution with thick areas indicating higher probability and thin areas indicating lower probability. The black dots indicate individual data points, the white dot indicates the median, the orange rectangle indicates the interquartile range, and the black line illustrates the rest of the range barring any outliers (indicated as black dots outside the range).



supported model for Appledore Island was the model with only Day of Year as a model variable, but both this model and the Null model had a $\Delta AIC_c < 2$ (Table 2). Average passage date for the

most southern geographic cluster (cluster 5) was much earlier (~8 days) than clusters 3 and 4, representing more northern breeding regions (Fig. 4A).

At the Gulf of Mexico sites, all of the top five models included Day of Year with a cumulative AIC_c weight of 1.0 (Table 3). The top model had only Day of Year as a model variable. The second-best model, also with a $\Delta AIC_c < 2$, was the additive model of Day of Year and Age (Table 3). Passage date (Day of Year) was earlier for the geographic clusters of more southern birds (clusters 4 and 5), whereas clusters representing more northern birds had later passage dates (Fig. 4B). In terms of age, there were more samples from hatch year birds ($n = 111$) compared to after-hatch year birds ($n = 39$) overall. Most after-hatch year birds originated from cluster 1 ($n = 11$) and the fewest originated from cluster 2 ($n = 4$), whereas the most hatch year birds originated from cluster 2 ($n = 34$), followed closely by cluster 1 ($n = 29$), and the fewest originated from cluster 3 ($n = 13$; Appendix 2 Fig. S1). We found no effect of fat score at either site (Appendix 2 Fig. S2).

DISCUSSION

Our results from two disjunct (~2000 km) stopover sites provide evidence that Yellow Warblers exhibit a type 1 temporal migration pattern that is asynchronous between breeding and stopover locations. At both the Appledore Island and Gulf Coast sites, temporal synchrony differed across geographic clusters such that birds coming from the most southerly breeding locations migrated earlier relative to those from more northern breeding areas. Despite previous work on the spatial patterns of Yellow Warblers,

Table 2. Akaike Information Criterion (AIC_c) model selection on assigned breeding cluster based on feather hydrogen isotope ratios (see Methods) for 50 Yellow Warblers passing through Appledore Island, Maine, during fall migration. Candidate models included combinations of the following variables: Day of Year and Fat Score. The top five candidate models, which encompass all the models we tested, are provided in addition to the AIC_c weights (w_i), log-likelihood, delta AIC_c (ΔAIC_c), and number of model parameters (K).

Candidate model	w _i	Log-likelihood	ΔAIC _c [†]	K
Day of Year	0.68	-59.16	0	8
Null	0.32	-65.23	1.51	4
Fat Score	<0.01	-60.28	31.22	16
Day of Year + Fat Score	<0.01	-52.73	36.61	20
Day of Year * Fat Score	<0.01	-48.08	146.57	32

[†] Lowest AIC_c score: 137.83.

Table 3. AIC_c model selection on assigned breeding cluster based on feather hydrogen isotope ratios (see Methods) for 150 Yellow Warblers passing through sites on the northern coast of the Gulf of Mexico during fall migration. Candidate models included combinations of the following variables: Day of Year, Age, Sex, and Fat Score. The top five candidate models are provided in addition to the AIC_c weights (w_i), log-likelihood, delta AIC_c (ΔAIC_c), and number of model parameters (K).

Candidate model	w _i	Log-likelihood	ΔAIC _c [†]	K
Day of Year	0.65	-207.75	0	8
Day of Year + Age	0.28	-203.96	1.67	12
Day of Year + Sex	0.05	-205.77	5.29	12
Day of Year * Age	0.01	-202.21	7.99	16
Day of Year + Sex + Age	0.01	-202.40	8.37	16

[†] Lowest AIC_c score: 432.52.

temporal migration patterns and, more specifically, patterns between breeding and stopover sites had yet to be investigated. The pattern observed here is consistent with a type I migration pattern, and the degree of variation within and among geographic breeding clusters suggests asynchronous migration. Type I migration patterns have also been found between natal origin and stopover sites during fall migration in Orange-crowned Warblers (*Leiothlypis celata*), Common Yellowthroats (*Geothlypis trichas*), Sharp-shinned Hawks (*Accipiter striatus*), and Ruby-throated Hummingbirds (*Archilochus colubris*; Smith et al. 2003, Kelly 2006, Zenzal et al. 2018). These results provide the first information on the temporal migration patterns of Yellow Warblers between breeding and stopover locations.

Age was also associated with geographic cluster at the Gulf Coast sites, which suggests differences in abundances of hatching year and after-hatching year birds across clusters. We found age to be included in the second-best model at the Gulf Coast sites with hatch year birds making up over twice as many samples as after-hatching year birds. The disparity in age classes is also evident at Appledore Island, as all but a few samples at this site originated from hatch year birds. Age-dependent migration at coastal stopover sites during autumn is not uncommon, as numerous

studies have documented higher numbers of hatch year birds during autumn migration along coast lines (i.e., the coastal effect; sensu Ralph 1971, 1978, 1981), including at our sites (e.g., Morris et al. 1994, 1996; Woodrey and Moore 1997, Morris and Glasgow 2001, Zenzal and Moore 2016). Our Gulf Coast site results illustrate age-dependent differences in stopover site use from individuals departing the same breeding area. There are two potential interpretations for these results: hatch year and after-hatch year Yellow Warblers from the same population use different migratory pathways, similar to other species (e.g., Hake et al. 2003, Trierweiler et al. 2014, Vega et al. 2016), or it is possible that both age classes use the same pathways, but after-hatch year birds try to avoid typically resource-poor coastal sites (sensu Mehlman et al. 2005, Schaub et al. 2008). One possible direct approach to support or refute these hypotheses would require a substantial miniaturization in tracking devices, such as GPS tags, suitable for attaching to small warblers.

Our study shows that stopover sites along the northern Gulf of Mexico support birds from throughout the Yellow Warbler breeding range during fall migration. In contrast, few birds from breeding clusters 1 and 2 passed through the Maine stopover site (Appledore Island), which is likely due to the low probability of birds from geographic clusters 1 and 2 migrating from those northwestern breeding areas to the northeastern Atlantic coast. The expansive breeding range of the Yellow Warbler could make enacting breeding population-specific conservation during the stationary breeding and non-breeding phases of the annual cycle more challenging. However, our results indicate that en route conservation efforts may benefit this species across its range. Specifically, our coastal stopover sites supported bird populations from across the breeding range, illustrating the conservation value of stopover sites along large ecological features (e.g., oceans). We have identified similar temporal migration patterns at two disparate stopover sites, which increases our understanding of migration strategies in Yellow Warblers. A future study could integrate abundance or genetic data with our cluster analysis to further refine cluster assignments for Yellow Warbler. Because migration tends to have the highest rate of mortality across the annual cycle (e.g., Sillett and Holmes 2002, Newton 2007, Paxton et al. 2017, Ward et al. 2018), future efforts that provide information for targeted management during stopover can help improve the probability of an individual having a successful migration.

Author Contributions:

T.J.Z., A.C., H.B.V.Z., and K.M.C. formulated the questions; T.J.Z. and K.M.C. collected data, supervised field work, and provided feather samples; A.C., K.M.C., and D.A. supervised lab work; L.K.K. performed lab work; A.C. processed the stable isotope data and performed the cluster analyses; T.J.Z. statistically analyzed the data; L.K.K., H.B.V.Z., and T.J.Z. wrote the first draft of the introduction; L.K.K., T.J.Z., and A.C. wrote the first draft of the methods; K.M.C. and H.B.V.Z. wrote the first draft of the results; T.J.Z. wrote the first draft of the discussion; T.J.Z. and K.M.C. prepared tables; T.J.Z. and A.C. created figures; T.J.Z., K.M.C., D.A., A.C., and H.B.V.Z. provided substantial edits on the manuscript.

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**Asynchronous movement patterns between breeding and stopover locations in
a long-distance migratory songbird**

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Appendix 1: Supplemental Table

Table S1. Number of Yellow Warblers that belong to each geographic cluster based on capture location.

Geographic Cluster	Appledore Island, ME	Fort Morgan, AL	Grand Bay, MS	Total
1	1	36	4	41
2	3	34	4	41
3	10	21	0	31
4	18	22	3	43
5	18	21	5	44

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Appendix 2: Supplemental Figures

Figure S1: The distribution of age classes by geographic cluster from birds captured at the Gulf of Mexico sites. Hatch Year (HY) birds are on their first migration, while After Hatch Year (AHY) birds have completed at least one spring migration prior to this season.

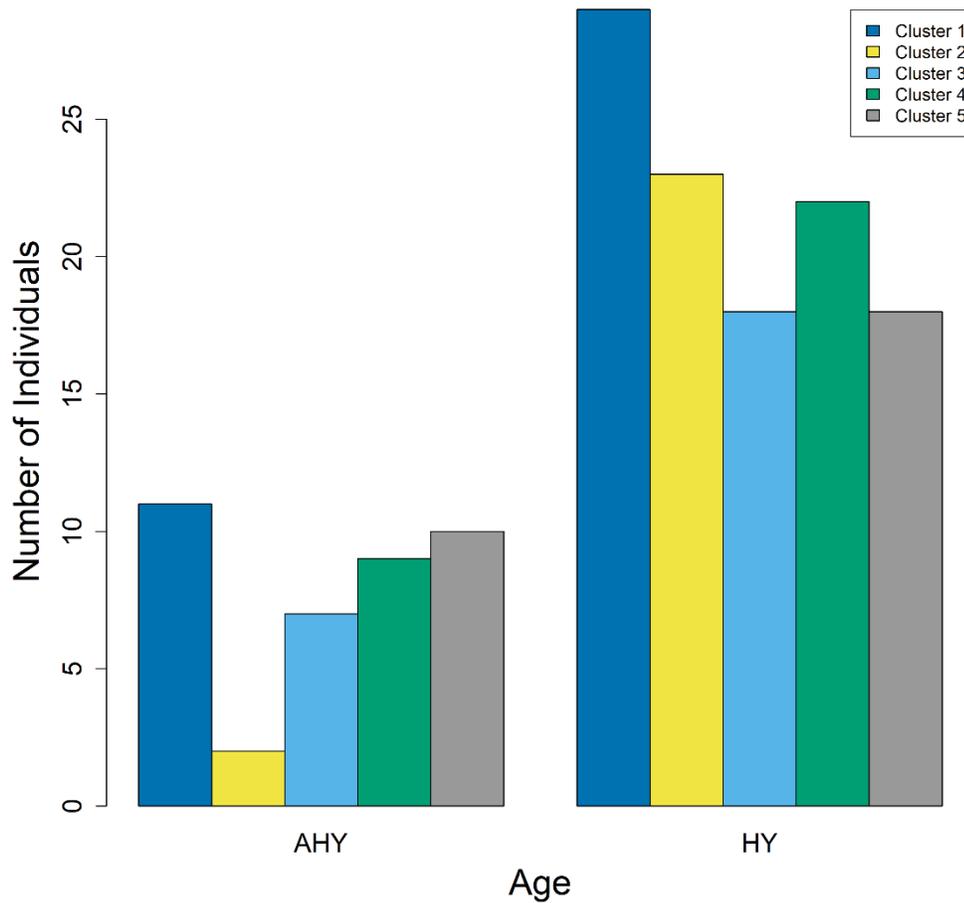


Figure S2: The relationship between fat score and geographic cluster, based on stable hydrogen isotope analysis, at the Appledore Island, ME (**A**) and Gulf Coast Sites (**B**). The shape of the violin indicates the probability of individuals being in a particular area of the distribution with thick areas indicating higher probability and thin areas indicating lower probability. The black dots indicate individual data points, the white dot indicates the median, the orange rectangle indicates the interquartile range, and the black line illustrates the rest of the range barring any outliers (indicated as black dots outside the range).

