Breeding latitude is associated with the timing of nesting and migration around the annual calendar among Purple Martin (Progne subis) populations

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Abstract
Timing is critical for species that migrate seasonally, as timing mismatches can lead to reduced reproductive success and population declines. We investigated the effect of breeding latitude on the migration timing of a long-distance migratory songbird (Purple Martin, Progne subis subis) by using light-level geolocators deployed across breeding sites between 26° and 53° latitude (n = 329). We used nesting data (1st egg dates; n = 28,165) to explore latitudinal patterns in the timing of breeding. Using generalized linear mixed models (GLMMs) we found that breeding latitude was highly associated with timing around the calendar, explaining population-level timing across both spring and fall migration. Populations breeding at more northern latitudes migrated later in full (mean days/degree latitude = 2), in spring (mean days/degree latitude = 3), and nested later (days/degree latitude = 3) than populations breeding at more southern latitudes. Generalized additive mixed models (GAMMs) revealed significant non-linearity between breeding latitude and spring and fall migration timing, and the timing of nesting. In spring, the most northern breeders (> 40 degrees N) were more synchronous in their timing, departing their non-breeding sites and arriving earlier at their breeding sites relative to their breeding latitude. These most northern breeders also had similar nest timing and fall migration departure timing. Breeding latitude was also associated with seasonal partitioning of migratory and sedentary periods. The most northern breeders spent 10% more time on fall migration, 2% more at wintering grounds, 1% more on spring migration, and 13% less time at their breeding sites. Our results support the notion that selection for timing at breeding latitudes can have year round effects on the timing of seasonal events in long distance migratory songbirds. Future studies should examine whether these timing patterns associated with latitude limit phenotypic responses to climate change.

Keywords Songbird · Light-level geolocator · Migration tracking · Phenology

Zusammenfassung
Der Breitengrad des Brutgebietes steht im Zusammenhang mit Brut- und Zugzeitpunkt im Jahresverlauf bei Populationen der Purpurschwalbe (Progne subis).

Das Zeitmanagement ist für Arten, die saisonal ziehen, von entscheidender Bedeutung, da zeitliche Unstimmigkeiten zu vermindertem Reproduktionserfolg und Populationsrückgängen führen können. Wir untersuchten die Auswirkung des Breitengrades des Brutgebietes auf den Zugzeitpunkt bei einer langstreckenziehenden Singvogelart (Purpurschwalbe, Progne...

Introduction

The timing of migration can be critical for migratory birds – if the timing of arrival and departure are mismatched with optimal conditions for breeding, this could result in reduced fitness, and ultimately population declines (Both et al. 2006). Migratory songbirds breeding at more souther latitudes (shorter migration distances) may be selected to respond differently to seasonal changes compared to birds breeding at more northern latitudes (longer migration distances) (Alerstam and Högstedt 1980). For example, southern populations of Collared Flycatchers (Ficedula albicollis) departed from their wintering grounds and arrived at their breeding grounds earlier than northern populations (Briedis et al. 2016). Different breeding populations wintering in the same area may therefore respond differently to environmental cues to initiate migration, or timing may be driven mostly by endogenous, circannual routines (Gwinner 1996; Gwinner and Helm 2003). Populations that breed at more northern latitudes could have evolved to delay their departure from their wintering grounds to avoid risks involved in earlier or longer migration, including predation, weather extremes, and lack of food (Alerstam et al. 2003; McKinnon et al. 2014). Multi-year tracking studies that control for annual differences in environmental conditions would be ideal for comparing latitudinal variation in timing around the calendar. The Palearctic-Paleotropical study noted above (Briedis et al. 2016) demonstrates that breeding latitude may contribute importantly to timing outside of the breeding period, but studies investigating these patterns are rare, particularly in the Nearctic-Neotropical migration system (McKinnon and Love 2018; Gow et al. 2019).

Breeding latitude may also affect migration phenology within populations. Migration timing tends to differ between age classes – older individuals may migrate earlier than younger individuals, during both spring and fall migration (McKinnon et al. 2014; Wójcylanis-Jakubas et al. 2017). Older, more experienced individuals may be better at optimising their migration timing than younger, less experienced individuals (McKinnon et al. 2014). Between sexes, males tend to migrate earlier in spring than females (termed protracted migration) (Morrey and Ydenberg 2001; Kokko et al. 2006). In fall, males may depart for migration earlier than females, which may be explained by the hypothesis that higher reproductive investment for females results in later departure (Wójcylanis Jakubas et al. 2017). However, the opposite may be seen in which females depart earlier than males, particularly in younger age groups, supporting the hypothesis that males spend more days prospecting for potential nesting sites for the following year (Mills 2005; Lehikoinen et al. 2017). Furthermore, due to seasonal differences and constraints across latitudinal gradients individuals breeding further north may have relatively tighter migration schedules between sexes and/or age groups (Winkler et al. 2014). Further direct-tracking research would yield important additional insight into how sex and age class modulate migration timing within populations.

The migration of even small (<30 g) avian species can now be tracked in detail by using new biologging and biotelemetry technology, providing new opportunities to study migration phenology (Stutchbury et al. 2009; McKinnon et al. 2013; Taylor et al. 2017; McKinnon and Love 2018). Light-level geolocators are small devices that track changes in light intensity and can be used to obtain geographical information (Lisovski and Hahn 2012). Geolocators are
particularly useful for examining migration timing as they can provide daily spatio-temporal positions year-round (Stutchbury et al. 2009). In general, few studies to date have used direct tracking to examine how breeding latitude may affect migration timing of birds around the calendar (Conklin et al. 2010; Briedis et al. 2016; Loon et al. 2017; Gow et al. 2019; Åkesson et al. 2020). Furthermore, most evidence from these studies are from single species or populations (i.e. only one Palaearctic songbird or one shorebird species). Few studies have used multiple populations over a large latitudinal range for more than one year.

We investigated latitudinal and individual patterns of spring and fall migration timing, as well as the timing of the nesting period using Purple Martins (Progne subis), a long-distance migratory songbird. The Eastern subspecies (P. s. subis) breeds across North America, east of the Rocky Mountains. Lattitudinally, their range extends as far north as central Alberta and southern Manitoba Canada, and as far south as southern Texas, Florida and the Gulf Coast U.S.A (Brown and Tarof 2020). All P. s. subis populations winter in South America, concentrating mostly in Brazil (Fraser et al. 2012, 2017). They have a strong tendency to return to the same nesting site every year (high site fidelity). Eastern Purple Martins nest almost exclusively in provisioned bird housing providing opportunities to deploy and retrieve migration tracking devices. Their aerial foraging in open country allows for high accuracy in light-level tracking from geolocators, due to more exposure to light (Lisovski and Hahn 2012). Purple Martins are one of many aerial insectivorous migrants that suffer from population declines that are generally greater in the northern part of their breeding range (Nebel et al. 2011; Smith et al. 2015; Michel et al. 2016). However, populations in the Southern and Gulf Coast states have also experienced declines during the last two decades (Tautin et al. 2009; Ray 2015; Sauer et al. 2017).

The main objective of our study was to investigate the sum effect of factors associated with breeding latitude on departure and arrival dates during spring and fall migration (the annual cycle), while also quantifying sex and age class differences. We hypothesized that strong selection on spring arrival at the breeding grounds tied to seasonality would shape spring migration timing and would have carry-over effects on subsequent life-history events, owing to relaxed selection on fall migration timing in this gregarious species that is non-territorial during the overwintering period. We therefore predicted that during spring migration, populations breeding at more southern latitudes should depart from their wintering grounds earlier, arrive earlier at their breeding sites, and nest earlier than populations breeding at more northern latitudes. We also hypothesized that if differing parental investment and other factors such as individual experiences contribute to sex and age differences within populations, then males should depart from wintering grounds and arrive at their breeding grounds earlier than females (Lehikoinen et al. 2017; Cadahia et al. 2017; Wojcizulanis-Jakubas et al. 2017). We also predicted that older (after second-year, ASY) individuals should depart from the wintering grounds and arrive at their breeding grounds earlier than younger (second-year, SY) individuals due to competition for nesting cavities (Morton and Derrikson 1990). Owing to post-breeding, bi-parental care in Purple Martins and their joining mixed flocks prior to, and during, fall migration (Brown and Tarof 2020), we predicted that there would be no differences in fall departure or arrival timing between sexes and age classes.

Methods

Data retrieval and preparation

Light-level geolocators (≤1.6 g; MK10s/12/12 s/14 s/20, British Antarctic Survey) were deployed on individual Purple Martins with Teflon leg-loop harnesses (Rappole and Tipton 1991; Stutchbury et al. 2009), and were retrieved the following year. Birds were trapped within their nest cavities via drop-door traps, and were sexed and aged by plumage (Pyle 1997). For geolocator retrieval the following spring (units are archival), birds were trapped using similar methods for deployment. Geolocation data were retrieved from several sites across North America, spanning 27 degrees of breeding latitude (Supplementary Table S1).

Although light-level geolocators provide fine-scale movement and timing data, they have some disadvantages. The precision of retrieved data can be compromised by external factors such as the amount of cloud cover, local topography (shorter day lengths in valleys), and shade from vegetation, as reduced light intensity can affect detection in sunrise and sunset times (Lisovski et al. 2012). However, shading may not be a major challenge in tracking open air foragers such as Purple Martins (e.g., latitudinal error from breeding grounds averages at 49–60 km, Fraser et al. 2012).

After retrieving tracking data from geolocators using BASTrak software (Fraser et al. 2012), we processed the data in R (version 3.6.3) using RStudio (version 1.1.463, R Core Team 2020). First, we used the BASTrag package (version 0.1.3, Wotherspoon et al. 2016) to calculate and edit sunrise and sunset times (twlight) using the threshold method, with a light threshold set at 32. Next, we used the GeoLight package (version 2.0.0, Lisovski and Hahn 2013) to get daily latitudinal and longitudinal coordinates, and residency periods. We then determined both spring and fall migration times (day of year). Lastly, we used the ggplot2 package (version 3.1.1, Wickham 2016) to explore the data and visualize our results.
Our three migration timing variables for both spring and fall migration were departure date, date of crossing at 23.4° N (Tropic of Cancer), and arrival date. Arrival at the breeding grounds was estimated at the twilight where there were fluctuations in light levels indicating the bird entering and exiting nesting cavities. All other dates were manually estimated by examining the location and timing files obtained using GeoLight. Departure date from breeding grounds was estimated when latitude began decreasing from the breeding location, and departure date from wintering grounds was estimated when longitude began decreasing from the last wintering site (which may be in a different location than when they arrive at the wintering area initially, as Purple Martins exhibit intratropical migration (Stutchbury et al. 2016)), because Purple Martins first migrate in a more westerly direction before taking more northerly movements (Fraser et al. 2013). The date of crossing the Tropic of Cancer, which provides an approximate half-way point for northern breeders was estimated at the first twilight below 23.4° N for fall, or above 23.4° N for spring. Arrival date at the wintering grounds was estimated when the bird reached a stationary period below 10° N where latitude and longitude ceased to change. Further analyses were performed in R, using R Studio.

To examine the effects of breeding latitude on timing during the nesting period, we used data from Project MartinWatch, a community citizen science project that began in 1995 in which individuals maintain housing and nests for Purple Martins. Citizen scientists monitor the nests regularly, and record data for submission online (Purple Martin Conservation Association 2017). These data include the date the first egg is laid, which is estimated by counting the number of eggs during a nest check, as instructed by nest check sheets provided by the Purple Martin Conservation Association (PMCA). Purple Martins lay one egg per day, so the first egg laying date can be inferred by counting backwards to the date when only one egg would have been in the nest (PMCA 2017). From the nesting data 28,165 nesting cavities were sampled from 38 breeding populations across Canada and the eastern United States between 1995 and 2014 (Figure, Supplementary Figure S1), and included parent ages (second year [SY] vs. after second year [ASY]), the date of the first egg laid, and the latitude and longitude in which data were recorded. Breeding latitude spanned between 25.5° N and 54.5° N.

To investigate how much time populations breeding at similar latitudes spend in each stage of their annual cycle, we performed k-means clustering to assign breeding colonies into groups based on latitude. We set the number of groups \( k = 5 \) through visualization to ensure populations were grouped on latitudinal bands (Fig. 3a; Pham et al. 2005). Prior to clustering we estimated the number of days each individual spent in four life cycle stages (breeding season, fall migration, wintering season, and spring migration) by calculating differences between migration departure and arrival dates (day of year). Since the wintering season overlaps the new year, fall arrival dates (as day of year) were subtracted from the full year (i.e., 365) before subtraction from spring departure dates. We calculated mean days spent in each stage and standard errors for each group, and then calculated percentages by dividing the means by the full year.

**Generalized linear mixed models**

For examining the effects of breeding latitude, sex and age class on spring departure date from the wintering grounds, we assigned ‘Spring Departure’ as the response variable. We assigned three variables as fixed effects: ‘Breeding Latitude’ has fixed values at each deployment site, and was used to examine whether differences in breeding latitude affect migration timing; ‘Sex’ to examine whether sex affects migration timing, and; ‘Age Class’ to examine whether age class (SY or ASY) affects migration timing. We assigned three variables as random effects: ‘Year of Deployment’ takes into account variation among years, such as environmental variation (e.g. seasonal temperatures or rainfall at either breeding or wintering sites); ‘Individual’ (band number) takes into account individual variability, as well as individuals that were tracked more than once, and; ‘Breeding Population’ takes into account variation among retrieval sites within each breeding population. Breeding population was defined by state or province, as many of the specific colonies within each state or province were in close proximity to each other (Supplementary Table S1). Breeding longitude was omitted from the models, as the northernmost birds were also at more western longitudes, therefore longitude was redundant for our study.

Similar assignments were applied to models examining effects on spring migration crossing at 23.4° N and spring arrival at breeding grounds, changing the response variable respectively. Models were also fitted on fall migration timing, examining the effect of the same fixed and random effects on fall departure from breeding grounds, fall migration crossing at 23.4° N, and fall arrival at wintering grounds.

For nesting data, our response variable was the date (as day of year) the first egg was laid at each nest. Our fixed effects were breeding latitude, the age class of the male parent (SY and ASY), and the age class of the female parent (SY and ASY), and our random effects were nesting year and the city or town (breeding colony) in which the breeding pair nested.

We fitted generalized linear mixed-effect models (GLMMs) for all variables involved using the ‘lme4’ package (version 1.1–19, Bates et al. 2015). Models were fit with
the gaussian error distribution and an identity link function. We calculated 95% confidence intervals for each relationship between fixed effects and the response variable using coefficients and standard errors. We manually calculated the percentage of variation explained by a random effect by dividing the variance of the effect by the total variance (including residual variance – Tables 1, 2, 3). To test how well the models fitted, we interred two K-squared values (K_GLMM; referred simply as $R^2$ in subsequent text) for each model using the ‘MuMln’ package (version 1.42.1, Barton 2019). The marginal $R^2$ value was the variance explained by the fixed effects, and the conditional $R^2$ was the variance explained by the whole model (Barton 2019). The higher these two values were, the better fit the model. We checked for assumptions of normality and equal variance in our residuals for each model (Zuur et al. 2010).

**Generalized additive mixed models**

We ran generalized additive mixed models (GAMMs) to account for non-linear patterns between breeding latitude and fall and spring migration timing, using the ‘gamm4’ package (version 0.2–6, Wood and Scheipl 2020). Our response variables were fall departure date from the breeding grounds, fall arrival date at the breeding grounds, spring departure date from the breeding grounds, spring arrival date at the breeding grounds. For all models, our smoothed term was breeding latitude (using cubic spline regression and number of knots $k = 10$), and our parametric fixed effects were sex and age class. Our random effects were year of deployment, and breeding population (state/province). All models, including the model for nesting data, were fit with the gaussian family and identity link, and were checked for normality and equal variance in residuals using the gam.check function from the ‘mgcv’ package (version 1.8–33, Wood 2017) (Zuur et al. 2010).

We also ran GAMMs on the nesting data, as there were non-linear patterns between breeding latitude and nesting timing. Our response variable was the day the first egg was laid (day of year). Our smoothed term was breeding latitude, using cubic spline regression (knots $k = 10$). Our parametric fixed effects were the age classes of the parents, and our random effects were nesting year and state or province in which the breeding pair nested.

**Migration rate analyses**

To explore whether migration rate varied by breeding latitude, we analyzed a subset of migration tracks ($n = 171$). To account for geogaphic outliers that might alter distance calculations, tags were processed using FLightR (version 0.5.0, Rakhimberdiev et al. 2017). Fall and spring departure and arrival dates from our GeoLight analyses were used to determine the start and stop dates to estimate mean migration distances, using the ‘sp’ package (version 1.4–4, Bivand et al. 2013). We then estimated fall and spring migration rate by dividing distance by the total number of days spent in migration. Generalized linear mixed models were used to fit these data. Our response variables were spring and fall migration rate (km/day), and our fixed effects were breeding latitude, sex, and age class. Random effects for fall migration rate were band number (individual), breeding population, and year of deployment. For spring migration rate, year of deployment was the only random effect, as band number and breeding population did not account for any variance in our model. We checked models for normality and equal variance in the residuals (Zuur et al. 2010); spring migration rate was log transformed to better fit parametric assumptions.

**Results**

Geolocators were retrieved from a total of 295 individual Purple Martins from 11 breeding populations at 27 breeding sites (Supplementary Table S1). Breeding latitude spanned 26.1° N and 53.0° N. Of the 295 individuals, 32 individuals were tracked more than once (repeat tracks), leading to a total of 329 annual tracks. Geolocation data spanned 11 years, from 2007 to 2018.

**Spring migration timing**

Considering confidence intervals, all three fixed effects (i.e. breeding latitude, sex, and age class) showed an effect on spring departure, spring crossing at 23.4° N, and spring arrival (Table 1). Overall, Purple Martins departed from their wintering grounds over 122 days, between January 10 and May 12. Martins arrived at their breeding grounds over 132 days, between January 28 and June 9. We found a positive trend between breeding latitude and spring departure date (Fig. 1a). Generally, for every 1 degree increase in breeding latitude, Purple Martins delayed spring departure from wintering sites by about 3 days, except at latitudes between 25 and 30° N where the trend leveled off (Supplementary Figure S2). This 3-day difference continued through the crossing at 23.4° N and arrival at breeding sites (Table 1). We also found differences in spring migration timing between sexes – males departed for spring migration about 4.6 days earlier than females. Males crossed 23.4° N and arrived at their breeding grounds about 3.7 and 3.2 days earlier than females, respectively (Table 1). There were differences in spring migration timing between age classes, with older (ASY) individuals departing their wintering grounds about 5 days later than adults.
Table 1  Summary of generalized linear mixed models (GLMMs) for spring migration timing in Purple Martins (*Progne subis*)

<table>
<thead>
<tr>
<th>Spring departure date</th>
<th>Estimate</th>
<th>Lower 95% confidence interval</th>
<th>Upper 95% confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fixed effects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breeding attitude</td>
<td>2.951</td>
<td>2.253</td>
<td>3.650</td>
</tr>
<tr>
<td>Sex*</td>
<td>-4.626</td>
<td>-7.133</td>
<td>-2.110</td>
</tr>
<tr>
<td>Age class**</td>
<td>5.215</td>
<td>2.372</td>
<td>8.059</td>
</tr>
<tr>
<td>Random effects</td>
<td>Variance</td>
<td>Standard deviation</td>
<td>% Variation</td>
</tr>
<tr>
<td>Year</td>
<td>13.46</td>
<td>3.669</td>
<td>5.325</td>
</tr>
<tr>
<td>Individual</td>
<td>73.22</td>
<td>8.557</td>
<td>28.966</td>
</tr>
<tr>
<td>Breeding population</td>
<td>128.56</td>
<td>11.338</td>
<td>50.858</td>
</tr>
<tr>
<td>Residual</td>
<td>37.54</td>
<td>6.127</td>
<td>14.851</td>
</tr>
<tr>
<td>Total variance</td>
<td>252.78</td>
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</tr>
<tr>
<td>GLMM $R^2$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marginal $R^2$</td>
<td>0.689</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conditional $R^2$</td>
<td>0.954</td>
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<td></td>
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Date of spring crossing 23.4° N

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>Estimate</th>
<th>Lower 95% confidence interval</th>
<th>Upper 95% confidence interval</th>
</tr>
</thead>
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<tr>
<td>Breeding latitude</td>
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<td>4.323</td>
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<tr>
<td>Sex*</td>
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<td>-6.414</td>
<td>-0.919</td>
</tr>
<tr>
<td>Age class**</td>
<td>4.904</td>
<td>1.926</td>
<td>7.800</td>
</tr>
<tr>
<td>Random effects</td>
<td>Variance</td>
<td>Standard deviation</td>
<td>% Variation</td>
</tr>
<tr>
<td>Year</td>
<td>14.64</td>
<td>3.827</td>
<td>5.179</td>
</tr>
<tr>
<td>Individual</td>
<td>84.40</td>
<td>9.187</td>
<td>29.855</td>
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<tr>
<td>Breeding population</td>
<td>137.63</td>
<td>12.535</td>
<td>33.762</td>
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<tr>
<td>Residual</td>
<td>26.02</td>
<td>5.101</td>
<td>9.204</td>
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<td>Total variance</td>
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<td>GLMM $R^2$</td>
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<tr>
<td>Marginal $R^2$</td>
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<tr>
<td>Conditional $R^2$</td>
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Spring arrival date

<table>
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<tr>
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<th>Estimate</th>
<th>Lower 95% confidence interval</th>
<th>Upper 95% confidence interval</th>
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</thead>
<tbody>
<tr>
<td>Breeding latitude</td>
<td>2.893</td>
<td>2.186</td>
<td>3.600</td>
</tr>
<tr>
<td>Sex*</td>
<td>-3.199</td>
<td>-5.761</td>
<td>-0.638</td>
</tr>
<tr>
<td>Age class**</td>
<td>6.747</td>
<td>3.989</td>
<td>9.505</td>
</tr>
<tr>
<td>Random effects</td>
<td>Variance</td>
<td>Standard deviation</td>
<td>% Variation</td>
</tr>
<tr>
<td>Year</td>
<td>20.72</td>
<td>4.552</td>
<td>7.789</td>
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<tr>
<td>Individual</td>
<td>88.02</td>
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<td>Breeding population</td>
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<tr>
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<tr>
<td>Conditional $R^2$</td>
<td>0.963</td>
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</tr>
</tbody>
</table>

*Male compared to reference group female

**SY individuals compared to reference group ASY individuals
Table 2  Summary of generalized linear mixed models (GLMMs) for fall migration timing in Purple Martins (*Progne subis*)

### Fall departure date

<table>
<thead>
<tr>
<th>Fixed effects</th>
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<th>Upper 95% confidence interval</th>
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<tr>
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<td>1.862</td>
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<td>Sex*</td>
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<td>−2.297</td>
<td>1.634</td>
</tr>
<tr>
<td>Age class**</td>
<td>3.368</td>
<td>1.044</td>
<td>5.692</td>
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<tr>
<td>Random effects</td>
<td></td>
<td>Variance</td>
<td>Standard deviation</td>
</tr>
<tr>
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<tr>
<td>Individual</td>
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<td>15.311</td>
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<td>Breeding population</td>
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<td>64.639</td>
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<td>18.296</td>
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<td>GLMM $R^2$</td>
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<td>Conditional $R^2$</td>
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Date of fall crossing 23.4° N

<table>
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<th>Fixed effects</th>
<th>Estimate</th>
<th>Lower 95% confidence interval</th>
<th>Upper 95% confidence interval</th>
</tr>
</thead>
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<td>Breeding latitude</td>
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<td>0.922</td>
<td>2.151</td>
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<td>−1.041</td>
<td>5.660</td>
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<tr>
<td>Random effects</td>
<td></td>
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<td>Standard deviation</td>
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<tr>
<td>Year</td>
<td>7.761</td>
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<td>4.456</td>
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<td>44.287</td>
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<td>Breeding population</td>
<td>96.362</td>
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<td>33.708</td>
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<tr>
<td>Residual</td>
<td>24.649</td>
<td>4.965</td>
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<td>Total variance</td>
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<tr>
<td>GLMM $R^2$</td>
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<tr>
<td>Marginal $R^2$</td>
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<tr>
<td>Conditional $R^2$</td>
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### Fall arrival date

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</thead>
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<td>1.932</td>
<td>3.497</td>
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<tr>
<td>Sex*</td>
<td>−2.934</td>
<td>−5.765</td>
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<td>Age class**</td>
<td>5.005</td>
<td>1.719</td>
<td>8.291</td>
</tr>
<tr>
<td>Random effects</td>
<td></td>
<td>Variance</td>
<td>Standard deviation</td>
</tr>
<tr>
<td>Year</td>
<td>14.25</td>
<td>3.775</td>
<td>4.538</td>
</tr>
<tr>
<td>Individual</td>
<td>75.11</td>
<td>8.666</td>
<td>23.920</td>
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<td>Breeding population</td>
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<td>66.96</td>
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<td>GLMM $R^2$</td>
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<td></td>
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<tr>
<td>Marginal $R^2$</td>
<td>0.599</td>
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<td></td>
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<tr>
<td>Conditional $R^2$</td>
<td>0.915</td>
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<td></td>
</tr>
</tbody>
</table>

*Male compared to reference group female

**SY individuals compared to reference group ASY individuals
Table 3  Summary of generalized linear mixed model (GLMM) for the timing of the first egg laying date in Purple Martins (Progne subis)

<table>
<thead>
<tr>
<th>First egg date</th>
<th>Estimate</th>
<th>Lower 95% confidence interval</th>
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</thead>
<tbody>
<tr>
<td>Fixed effects</td>
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<td></td>
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<tr>
<td>Breeding latitude</td>
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<td>2.682</td>
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<td>Male parent age class**</td>
<td>7.630</td>
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<td>5.354</td>
<td>5.032</td>
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</tr>
<tr>
<td>Variance</td>
<td>10.050</td>
<td>3.171</td>
<td>7.135</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>6.816</td>
<td>32.978</td>
<td></td>
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<tr>
<td>% Variation</td>
<td>84.350</td>
<td>9.184</td>
<td>59.886</td>
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<tr>
<td>Total variance</td>
<td>140.850</td>
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</tr>
</tbody>
</table>

**SY individuals compared to reference group ASY individuals

Among the random effects, breeding population accounted for most of the variation explained by the model, ranging between 48.0% and 55.8%. Individuals accounted for approximately 29.0% to 33.1% of variation. Year accounted for the least amount of variation through spring migration, ranging between 5.2% and 7.8%. Residual variation ranged between 9.2% and 14.9% (Table 1). We also found that, when determining R² values for the models, marginal R² ranged from 0.67 to 0.71, while conditional R² ranged from 0.95 to 0.97 (Table 1) (Fig. 2).

All three of our GAMM models showed a significant non-linear relationship between breeding latitude and spring departure date, the date of spring crossing at 23.4° N, and spring arrival date, with positive trends between degrees latitude and migration timing dates similar to our GLMM results (Supplementary Figure S2). The effective degrees of freedom (edf; the amount of non-linearity in the smoothed line) for spring departure was 4.40, and about 81.4% of the deviance is explained by the departure model. For the crossing model, edf was 3.41, and about 83.4% of the deviance was explained by the model. For the arrival model, edf was 3.38, and about 78.5% of the deviance was explained by the model (more detailed summaries of each model are in Supplementary Table S2).

**Fall migration timing**

Purple Martins departed from their breeding grounds over 94 days, between June 15 and September 17. Purple Martins arrived at their wintering grounds over 137 days, between July 4 and November 18. We found a positive trend in fall migration between breeding latitude and migration timing (Fig. 1b). Generally, for every 1 degree increase in latitude Purple Martins had fall departure dates that were about 1.2 days later. The difference increased to 1.5 days at the 23.4° N fall crossing, and increased up to 2.7 days at arrival at the wintering grounds (Table 2).

![Fig. 1](image1.png) Raw data showing the relationship between breeding latitude and migration timing for (a) spring migration and; (b) fall migration. Lines were plotted using LOESS smoothing.

![Fig. 2](image2.png) Raw data showing the relationship between breeding latitude and the timing of the first egg laid. The line of fit was plotted using LOESS smoothing.
At the individual level, males departed for fall migration about 0.3 days earlier than females, males crossed at 23.4° N about 0.4 days earlier than females, and males arrived at the wintering grounds about 3 days earlier than females. However, based on confidence intervals only sex had a significant effect on fall arrival timing (Table 2). There was also a difference in timing between age classes, as older (ASY) individuals departed for fall migration about 3.4 days earlier than younger (SY) individuals. At the fall crossing at 23.4° N SY individuals crossed about 2 days later than ASY individuals, and arrived at their wintering grounds in South America about 5 days later than ASY individuals. Based on confidence intervals, age class had a significant effect on fall departure and arrival, but not the fall crossing (Table 2).

Among random effects, again breeding population accounted for most of the variation explained by the model, ranging between 50.2% and 64.6%. Individuals accounted for variation ranging between 15.3% and 25.6%. Year accounted for the lowest variation, ranging between 2.0% and 4.5%. Residual variation was between 14.2% and 21.3% (Table 2). We also found that, when determining $R^2$ values for the models, marginal $R^2$ ranged from 0.32 to 0.60, while conditional $R^2$ ranged from 0.88 to 0.92 (Table 2).

Exceptions to these trends arose from our GAMM results, where the trend became negative between 25 and 30° N, and at about 46° N and northward during fall departure (Supplementary Figure S3a-b). Our GAMM results for fall departure date, the date of fall crossing at 23.4 N and fall arrival date also showed a significant non-linear relationship between breeding latitude and our response variables (Supplementary Figure S3). For the fall departure model, edf was 4.25, and the model explained about 61.1% of the deviance. For the crossing model, edf was 3.88, and about 66.9% of the deviance was explained by the model. For the arrival model, edf was 1.00, and about 65.1% of the deviance was explained by the model (more detailed summaries of each model are in Supplementary Table S3).

First egg laying date

Purple Martin first egg dates occurred over 136 days, between March 10 and July 24. Breeding latitude had a significant effect on the timing of the first egg laid, as a 1 degree increase in latitude led to an approximate 3-day delay in egg laying (Table 3), though the trend leveled off at about 44° N (Supplementary Figure S4). Age class of both parents also affected egg laying timing. Nests with an ASY male parent had first egg dates about 8 days earlier than nests with an SY male parent. Nests with an ASY female parent had first egg dates about 5 days earlier than nests with an SY female parent (Table 3). Breeding population accounted for about 53% of the variation explained by the model, year accounted for about 7% of the variation, and residual variation was about 60%. The marginal $R^2$ was 0.636 and the conditional $R^2$ was 0.782.

Our GAMM results showed a significant, non-linear relationship between breeding latitude and the first egg laying date (Supplementary Figure S4). The edf was 3.95, and about 72% of the deviance was explained by the model (details of the model results are in Supplementary Table S4).

Testing for differences in migration rate

A total of 171 tracks were used in analysing differences in spring and fall migration rate. Across all populations, rates during spring migration ranged between 115 and 681 km/day, and rates during fall migration ranged between 49 and 446 km/day.

For spring migration, breeding latitude had an effect on migration rate, with rate increasing by about 0.004 log km/day for every 1 degree increase in latitude. There were no differences in migration rate between sex or age classes. Among random effects, year accounted for about 7% of the variation (Table 4). The marginal $R^2$ value was 0.070, and the conditional $R^2$ value was 0.145. Also, spring departure date was positively correlated with spring arrival date (Supplementary Figure S5).

For fall migration, breeding latitude had an effect on migration rate. For every 1 degree increase in latitude, rate decreased by about 4 km/day. There were no differences in migration rate between sex or age classes. Among random effects, breeding population accounted for about 6% of the variation, year accounted for about 2% of the variation, and individuals accounted for about 1% of the variation (Table 4). The marginal $R^2$ value was 0.241, and the conditional $R^2$ value was 0.312.

Time spent in annual cycle

From the k-means clustering, Group 1 consisted of populations from Florida and southern Texas, USA, ranging between 26 and 28° N; Group 2 consisted of populations from Alberta and Manitoba, Canada, ranging between 49 and 53° N; Group 3 consisted of populations from Virginia and New Jersey, USA, ranging between 38 and 40° N; Group 4 consisted of populations from northern Texas and South Carolina, USA, ranging between 3 and 35° N; Group 5 consisted of populations from Pennsylvania, South Dakota, and Minnesota, USA, and Ontario, Canada, ranging between 42 and 46° N (Fig. 3a). Across all 5 groups, populations spent between 25.6–38.8% of their annual cycle in the breeding season. During fall and spring migrations, populations spent between 6.2–16.2% in fall, and between 5.7–7.3% in spring. Populations spent
Table 4  Summary of generalized linear model (GLMM) testing for differences in spring and fall migration rate in Purple Martins (Progne subis)

<table>
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<th>Upper 95% confidence interval</th>
</tr>
</thead>
<tbody>
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</tr>
<tr>
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</tr>
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<td>Standard deviation</td>
<td>% Variation</td>
</tr>
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</tr>
<tr>
<td>Individual</td>
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<td>1.08</td>
</tr>
<tr>
<td>Breeding population</td>
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</tr>
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</table>

<table>
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<th>Spring migration (log transformed)</th>
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<td>Total variance</td>
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</table>

*Male compared to reference group female
**SY individuals compared to reference group ASY individuals

between 48.9 and 51.1% of the annual cycle in the wintering season (Fig. 3a). On average across all 5 groups, populations spent about 93–142 days in the breeding season, about 23–59 days in fall migration, about 179–187 days in the wintering season, and about 21–27 days in spring migration (Fig. 3b).

Discussion

We demonstrate how factors associated with breeding latitude have an important impact on timing, not only during the breeding season, but around the calendar (the annual cycle) in a long-distance migratory songbird. We found that populations that breed at more southern latitudes migrated and nested earlier than populations that breed at more northern latitudes. Since individuals from widely distributed breeding populations share the same overwintering areas (Fraser et al. 2012, 2017) yet depart for spring migration at very different times, our results suggest a strong role for population-specific, circannual schedules in timing. We also found differences across the annual cycle by sex and age class. Sex had an effect on spring migration timing, with males migrating earlier than females. However, during fall migration sex did not affect migration timing at departure from the breeding grounds and the Tropic of Cancer crossing. Age class affected spring and fall migration timing, with older individuals migrating earlier than younger individuals, but the effect was relatively weaker during fall migration. Age class also affected the first egg laying date, with older parents laying earlier than younger parents.

Our study is one of the first to examine the effect of breeding latitude on migration timing across the annual cycle in a Neotropical songbird using direct tracking methods. Moreover, our study spanned a wide latitudinal
range (about 25 degrees latitude), enabling a broad test of the impacts of breeding latitude for a widely distributed species. Our findings support the patterns observed in other migratory birds through direct tracking, such as in Bar-tailed Godwits (*Limosa lapponica*) breeding at 59–71° N, Collared Flycatchers breeding at 49–57° N, Tree Swallows (*Tachycineta bicolor*) breeding between 35–65° N, and Common Swifts (*Apus apus*) breeding at 37–67° N. For most of these
species, populations breeding at more southern latitudes generally had earlier spring migration (Conklin et al. 2010; Briedis et al. 2016) and arrived earlier than the populations breeding at more northern latitudes (Conklin et al. 2010; Briedis et al. 2016; Gow et al. 2019; Åkesson et al. 2020). However, as in the case of Bar-tailed Godwits and Collared Flycatchers, these patterns continued past the breeding period, where populations breeding at more southern latitudes had earlier departure and arrival dates across the annual cycle (i.e. including fall migration) as compared to the more northern breeding populations (Conklin et al. 2010; Briedis et al. 2016). In contrast, for Tree Swallows, breeding latitude driven timing patterns broke down as birds reached the wintering grounds where winter arrival and spring departure dates were not strongly affected by breeding latitude (Gow et al. 2019). Wintering closer to breeding sites may enable Tree Swallows to receive cues as to conditions at their breeding sites, which may promote more variable spring departure times in relation to annual conditions, as compared to Purple Martins which must cue their migrations to breeding sites from much further away.

Unlike godwits in which birds from more northern populations departed later and had longer spring migrations than more southern populations (Conklin et al. 2010), spring migration timing in Purple Martins remained relatively constant (see estimates in Table 1). For example, birds breeding in Manitoba, Canada depart from their wintering grounds, cross at the Tropic of Cancer, and arrive at their breeding grounds about 60 days later than birds breeding in Florida, U.S.A. Purple Martins across all populations spend about 6–7% of the annual cycle in spring migration, which is less variable compared to the percentages spent in the other annual cycle stages such as the breeding season (26–39%) and fall migration (6–15%) (Fig. 3a).

Our GAMM results showed that during spring migration the line describing the relationship between spring departure and arrival timing and breeding latitude began to flatten at about 45° N (Supplementary Figure S2), indicating that more northern breeding Purple Martins departed and arrived at their breeding sites earlier relative to their breeding latitude. These results show that breeding latitude patterns break down > 45° N, with birds breeding between approximately 47° and 53° latitude sharing spring migration timing from start to finish (Supplementary Figure S2). Since this pattern is similar across spring migration and years, it seems most likely that these patterns are driven by selection for timing at the breeding grounds, and not based on within-winter environmental influences. The most northern breeders do fall into a similar climate zone (such as defined by the Köppen-Geiger Climate Classification (KGCC) where regions are based on annual temperature and precipitation data, Peel et al. 2007; Shave et al. 2019) which may have selected for similar timing for birds breeding across these latitudes.

Our migration rate analyses show an increase in spring migration rate for more northern breeders. Generally, there may be several reasons for why later, more northern birds could have higher migration rates. Purple Martins are diurnal migrants (Brown and Tarof 2020) and therefore must fly and forage throughout the day. As days are getting longer north of the equator through the spring migratory period, the more northern populations departing later from the wintering grounds will therefore experience a longer day length, which may provide additional daylight for migration and foraging, potentially resulting in a higher migration rate. More northern breeders with later passage times in spring may also encounter spring phenology that is further advanced, which could provide higher food abundance (i.e., aerial insects) and with warmer spring temperatures would lower the costs of thermoregulation; which can be high at stopover in spring (Wikelski et al. 2003). A third reason for higher migration rates among more northern breeders could be because birds departing later are time-selected to fly faster in the season (Alerstam 2011; Briedis et al. 2018). Future studies could examine factors that may contribute to variation in migration rate, like stopover duration (Schmaljohann 2018), to further investigate the potential for latitude-based differences in spring migration timing.

More northern breeding populations overwintering in the same areas as southern breeders likely depart for spring migration later to avoid the risks of early and/or longer migration (Alerstam et al. 2003). For Purple Martins that breed in northern temperate regions, adverse weather conditions such as unexpected cold spells can result in food scarcity and increased energetic costs for flight and thermoregulation, leading to higher mortality risk (Brown and Brown 1999; Newton 2007). Therefore, selection would be strong to avoid arriving too early in spring (Milnes et al. 2017). Our results demonstrate that it is migration departure timing that is delayed for more northern breeders, possibly to avoid the increased risk that would be incurred by earlier departure but longer migration (Nilsson et al. 2013), considering that the lowest survival rates are generally expected during the migratory period for songbirds (Sillett and Holmes 2002).

The patterns we show of later arrival for birds at higher latitudes may be generally predicted for spring migration, where the effect of latitude on spring phenology and strong selection for spring arrival may drive these latitudinal trends (Conklin et al. 2010). However, it is more surprising that these patterns carry around the calendar year. While we may generally expect more relaxed selection on fall timing in this gregarious bird that joins roosting flocks post-breeding and is non-territorial in winter (Brown and Tarof 2020), seasonal gradients in temperature and resources across latitudes or seasonal patterns of fall weather (e.g., storm activity in the
gulf region during fall) may be predicted to introduce further effects on timing. Thus, our findings support the general inference that the effects of breeding latitude on migration timing are stronger than other seasonal effects such as extreme weather conditions (Heckscher 2018), as southern populations migrated earlier than northern populations regardless of any annual variation (accounted for by year).

In spring, birds must time their migration to get the most out of the breeding season, gaining access to peak food resources to successfully breed and fledge offspring (Alerstam et al. 2003). During the fall, however, selection pressure on the timing of migration south may be more relaxed. In this season, migration may be more energy-selected, with birds spending more time at stopovers or reducing flight speed (Nilsson et al. 2013; Schmaljohann 2018). Some populations breeding further north may even depart for fall migration earlier than populations south of them, as they experience harsher seasonal constraints, and may depart from their breeding grounds in response to colder fall temperatures (Newton 2009). This was a pattern we observed for Purple Martins, where birds breeding north of ~46°N departed earlier on their fall migration than birds breeding at slightly more southern latitudes (Fig. 1 and Supplementary Figure S3a). Although timing tied to breeding latitude may affect fall migration through carry-over or domino effects (Gow et al. 2019), individual carry-over effects such as breeding condition prior to fall migration may be at play, resulting in more variable fall migration timing within populations (Stutchbury et al. 2011). We found that overall, more northern breeders had a slower fall migration rate and arrived later at their overwintering sites as compared to southern breeders. This is due to the prolonged stopovers (which could also be considered alternative residency periods) for more northern breeders that tend to occur mid-fall migration in the Yucatan region (Van Loon et al. 2017). During the nonbreeding season Purple Martins are not territorial and roost together in large groups (Brown and Tarof 2020) so we would expect low selection pressure on winter arrival dates, as compared to other insectivorous migratory songbird species that are territorial in winter, such as the Wood Thrush (Hylocichla mustelina) (Rappole et al. 1989; Stanley et al. 2015) where arrival timing was more consistent for birds originating from different breeding latitudes (Stutchbury et al. 2011; Stanley et al. 2012). Hence breeding latitude, while having an effect on fall migration timing, was not as strong an association as compared to spring migration.

During spring migration, males migrated earlier than females as predicted, indicating protandrous migration in Purple Martins. This pattern of migration is consistent with both theoretical models of differential timing of spring migration (i.e., protandry and earlier arrival by older individuals) and generally with empirical evidence for differential timing in passerines (Kokko 1999; Morbey and Ydenberg 2001; Kokko et al. 2006). Male Purple Martins defend, and may fight intensely, over nest cavities (Brown and Tarof 2020). Early arrival by older male Purple Martins may serve to maximize fitness in this system where extra-pair young are common (Morton et al. 1990; Brown and Tarof 2020). Sex had little to no effect on timing during the fall migration, as also predicted by empirical evidence for migratory land birds (e.g., Mills 2005). Purple Martins form mixed-sex flocks during the fall migration, and are non-territorial in the winter (Brown and Tarof 2020), thus selection for protandrous migration would likely be more relaxed. Timing and patterns of fall migration across breeding latitude may therefore be more strongly tied to seasonality at breeding sites and migratory conditions along fall routes. A decline in favourable environmental conditions at the end of the breeding season may drive the initiation of fall migration, whereas environmental and social conditions (e.g., roosts) encountered en route may determine rate and stopover patterns.

As predicted overall, older (ASY) individuals migrated earlier than younger (SY) individuals during spring migration. Younger birds, having undergone only their first year of migration, have less experience with migration routes as compared to older birds that have completed fall and spring migration more than once. Generally, the migration of younger birds may be less optimal (e.g., fewer resources leading to longer refueling times), resulting in delays to their destinations (e.g., Hockey et al. 2007). Indeed, younger individuals are likely stopping more frequently to refuel (McKinnon et al. 2014). Age class affected fall migration timing as well, as our results showed an increasing delay in timing for SY individuals as compared to ASY individuals, again potentially relating to reduced efficiency in younger birds (McKinnon et al. 2014). However, for the delay in fall departure from the breeding grounds, SY individuals could be prospecting areas for potential nesting sites for use in the following year (Doligez et al. 2004). The Rank Advantage Hypothesis may help explain age-related differences in migration timing, particularly during spring, as older males arriving at the breeding sites early defend their territories against other males, including younger individuals which would be less competitive (Kokko et al. 2006). Due to competition for nesting cavities and mates, as well as the risks to arriving early at the breeding grounds, younger birds may be selected to arrive later than older birds, therefore endogenous cues could also play a role in timing differences between age classes (Morton and Derrickson 1990) alongside individual experiences.

As expected, we found that breeding latitude was associated with the timing of breeding. However, the confidence bands were narrower compared to the migration models, our level of certainty in the model ($R^2$) was lower (Table 3). This discrepancy could be due to the weaker connection between
migration arrival date and the timing of nest initiation, where more southern populations have a longer interval between spring arrival date and first egg date than more northern breeding populations (Shave et al. 2019). Further, individual Purple Martins may show flexibility in the timing of nesting in relation to local environmental conditions (Shave et al. 2019), thus weakening the connection between breeding latitude and timing of nest initiation. Our results support the hypothesis that migration timing for long-distance migrants may be more endogenously cued and constrained than the timing of breeding. Such constraints can impact adaptive responses to climate change (Both et al. 2006) and should be further investigated in Purple Martins in light of our results.

**Conclusion**

We show that breeding latitude is highly associated with migration timing around the calendar for widely distributed populations (26°–53° latitude) of a declining, long-distance migratory songbird. To better understand latitudinal patterns, future studies should focus on whether latitude affects other parts of the annual cycle, such as migration routes and stopovers. Timing is critical for many migratory species, as mismatches in timing can negatively impact populations, especially those that breed further north (Both et al. 2005). Many migratory birds in particular are currently declining (Barkham 2018), and learning more about how populations may be partitioned across time and space will provide insight into the causes of decline and provide the knowledge needed for prioritizing conservation efforts.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s10336-021-01894-w.

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**Authors’ contributions** LKN and KCF developed the ideas and designed the study. LKN, SM, and KCF designed and KCF conducted statistical analyses. LKN wrote the paper. All authors conducted fieldwork and assisted with editing the manuscript.

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**Data availability** Tracking data will be made publicly available on Movebank (https://www.movebank.org/cms/movebank-main).

**Code availability** Analysis code will be made publicly available on Movebank.

**Declarations**

**Conflicts of interest** None to declare.

**Ethics approval** This research was approved by the University of Manitoba’s Animal Care Committee.

**Consent to participate** All authors have consented to participate.

**Consent for publication** All authors have consented for publication.

**References**


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