Circadian regulation of migratory flights in Purple Martins (*Progne subis*)

by

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Abstract

Long-distance migratory songbirds travel thousands of kilometers between their overwintering and breeding grounds. Abiotic factors, such as the amount of daylight available for flight and refueling, are expected to influence the initiation and duration of daily migratory flights. However, migratory behaviour at a circadian (24-hour) scale remains poorly understood in long-distance migrants because earlier tracking technologies, such as light-level geolocators, provided only 1-2 location fixes per day. This coarse temporal resolution prevented researchers from resolving the timing (initiation) and duration of individual flights within a day, limiting our understanding of how migratory behaviour responds to environmental conditions at fine temporal scales. This study investigated how daylength and time of day influence migratory behaviour during spring migration in purple martins (*Progne subis*), a long-distance aerial insectivore that uses a diurnal fly-and-forage migration strategy. Using high-resolution GPS tracking data from five individuals, I tested whether (1) daily migration distance increased with daylength, (2) movement varied across the day, and (3) nocturnal flights were associated with crossings of open-water barriers. Daily migration distance exhibited a positive correlation with daylength, with birds covering roughly 67 km more for each additional hour of daylight. Movement patterns were not uniform throughout the day; the most extensive distances were observed during midday and late afternoon, which contrasts with the prediction that peak movement would be in the morning when there tends to be less wind and air turbulence that can impede flight. Although, purple martins are primarily diurnal migrants, some individuals resorted to nocturnal flights, both during overwater crossings and overland, thereby indicating behavioural flexibility in initiation of circadian flight timing. Overall, these results highlight the significance of light availability in shaping migratory behaviour and indicates that purple martins

modify their daily activity patterns in response to environmental conditions. This study improves our understanding of migration strategies and may help predict how migratory species respond to changing environmental conditions.

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Introduction

Long distance migratory songbirds, travel thousands of kilometers each year between their temperate breeding ground in North America and overwintering areas in the tropics. The timing and duration of daily migratory flight behaviour is influenced by both intrinsic factors (like age, sex, individual timing phenotypes) and extrinsic factors including both abiotic variables (like daylength, temperature, wind, precipitation) and biotic variables (like competition and food availability) (Neufeld et al., 2021; Turcotte-van De Rydt et al., 2023). Despite extensive research on bird migration, relatively little is known about how environmental conditions influence the daily flight behaviour and movement patterns of migratory songbirds at fine temporal scales (McKinnon and Love, 2018).

Understanding environmental conditions on a 24-hour diel scale is particularly important for species that migrate primarily during the day. Strong winds and cold temperatures are examples of unfavourable weather conditions that might restrict flying time and decrease opportunities for feeding and refuelling (Shamoun-Baranes et al., 2017). For example, low temperatures can decrease insect activity (Winkler et al., 2013), which limits the amount of food available for flying insectivores, while strong headwinds raise the energetic cost of flight and may restrict migration speed (Packmor et al., 2020). Birds may therefore postpone their departure, shorten their flight duration, or take longer to refuel before continuing their migration.

Seasonal and latitudinal variation in daylength may also play an important role in shaping daily migratory behaviour. Since, diurnal migrations rely on daylight for both flight and foraging (refueling), longer daylength can increase the amount of time available for these activities each day. Increasing daylength at higher latitudes as birds travel north during spring migration may allow more time for flight and foraging, potentially increasing daily migration distances and migration speed. However, in tropical regions the relatively constant daylength (~12 hours) may

limit the time available for flight and foraging and therefore constrain migration speed (Alerstam, 2009; Turcotte-van De Rydt et al., 2023) .

Recent advances in tracking technology have improved our ability to study migration behaviour in small birds (<50g) (Bridge et al., 2011). Earlier tracking studies of songbirds used devices like light-level geolocators and early generation GPS units which, while useful for determining overall daily travel speeds and distances, they did not provide data on the timing and duration of flights within a day (McKinnon and Love, 2018). The data derived from these units typically recorded only 1-2 locations a day, which is not specific enough to determine the timing/duration of specific flights on a daily basis (McKinnon and Love, 2018). Newly developed high-resolution GPS tags that are small enough for <50 g birds can now provide more location fixes a day, thus permitting the migration speed and flight behaviour to be examined at much finer temporal scales (Hallworth and Marra, 2015; Lavallée et al., 2021).

Not all migratory birds separate flight from foraging; some species like purple martins (*Progne subis*) are thought to combine these two behaviours, using a fly-and-forage migration strategy (Alerstam, 2009; Alerstam and Hedenstrom, 1998; Hadjikyriakou et al., 2020), meaning they forage while flying. Since flying is energetically costly, this strategy may help offset the energetic demands of migration. This strategy is common among aerial insectivores, which capture flying insects while in flight. Some theoretical models suggest that a fly-and-forage strategy might help explain why some diurnal species maintain their daytime behaviour and also migrate during the day, as compared to the more common songbird strategy of seasonally switching to nocturnal migration, leaving the daytime for foraging to replenish fuel stores (Alerstam and Hedenstrom, 1998; Hadjikyriakou et al., 2020). Fly-and-forage migratory behaviour has been further supported by factual evidence, like satellite tracking studies

performed on osprey by Strandberg & Alerstam (2007), showing individuals stop at lakes along their migration routes to forage.

Longer daylengths at higher latitudes during spring migration may allow diurnal migrants, such as purple martins, to spend more time flying and foraging, potentially increasing migration rates as birds travel northward (Alerstam, 2009; Turcotte-van De Rydt et al., 2023). In contrast, tropical regions experience relatively constant daylength throughout the year, which may limit the maximum number of hours birds can spend flying each day during migration (Pokrovsky et al., 2021). Understanding how variation in light availability influences migratory behaviour may therefore help explain differences in daily movement patterns across latitudes.

Purple martins are long-distance migratory aerial insectivores that seasonally travel 7,000 – 12,000 km between breeding areas in central and eastern North America and overwintering areas in South America (Fraser et al., 2019; Turcotte-van De Rydt et al., 2023). They are considered primarily diurnal migrants that rely on fly-and-forage migration strategy (Lavallée et al. 2021), however earlier direct tracking using GPS tags revealed that these birds sometimes switch to nocturnal flights when they encounter and need to cross large open-water barriers like the Gulf of Mexico or the Caribbean Sea (Lavallée et al. 2021). In cases like these, nocturnal flights serve as an adaptive strategy to cross these open water barriers when there are limited foraging opportunities (Lavallée et al. 2021). Purple martins cross tropical and temperate latitudes during their spring migration, providing an opportunity to examine how they time their daily (circadian) flights in response to variation in abiotic factors (daylength and temperature) encountered while en route. Specifically, they migrate from tropical regions near the equator in South America (approximately −1° latitude), where daylength remains relatively constant at around 12 hours, to temperate breeding areas in North America (approximately 42°- 50°latitude), where daylength

during spring can exceed 14–15 hours. This represents an increase of roughly 3 hours of daylight, potentially allowing more time for flight and foraging each day (Alerstam, 2009).

In this study, I used previously collected high-resolution GPS tracking data from purple martins to examine how daylength influences their daily migratory behaviour during the spring migration from South America to North America. Specifically, I investigated how daily migration distance varies with light availability, how distances vary across different times of the day, and whether nighttime flights are associated with crossings of open-water barriers.

Hypothesis

Abiotic factors like daylength and time-of-day will shape the timing and duration of daily (circadian) migratory flight behaviours in diurnally migrating purple martins by restricting the time available for flight and/or altering the optimal environmental conditions under which flight occurs.

Predictions

Prediction 1: purple martins will have longer daily flight durations when daylengths are longer (therefore, spring flight durations will be longer in North America near breeding sites as compared to daily flights at tropical latitudes).

Prediction 2: most flight activity will occur during daytime hours, with greater movement distances occurring earlier in the day when the environmental conditions are more favourable for flight (like cooler temperatures and less wind turbulence during early morning than afternoon) (Kerlinger and Moore, 1989).

Prediction 3: Purple martins will primarily migrate during the day when travelling over land but will undertake nighttime flights when crossing large open-water barriers where foraging opportunities en route are limited.

Methods

Field data collection

This study used preexisting GPS datasets from 5 individual purple martins (*Progne subis*) that were tagged during the breeding season at 2 colonies in North America: 3 birds from Connecticut (41.784125 [latitude], -73.458608 [longitude]) and 2 birds from Wisconsin 44.167348 [latitude], -88.291502 [longitude]) in spring 2023. These birds were captured using drop-door traps that were installed on their nest boxes. Each bird was equipped with a leg-loop backpack harness made of Teflon ribbon and a GPS tag (1.5 g, Pathtrack) that weighed less than 5% of each bird's weight (Fair et al., 2010; Naef-Daenzer et al., 2001). Birds were recaptured in the following spring (2024) when they returned to their nest sites, and the archival tags retrieved. The identity (bird ID), relative age class and sex of the 3 individuals tagged in Connecticut were 58363 [After Second Year (ASY) and ♂], 58380 [ASY and ♀] and 58544 [ASY and ♂] and the 2 birds tagged in Wisconsin were 58572 [Second Year (SY) and ♂] and 58577 [SY and ♂].

During spring migration from southern to northern regions, tags were programmed to record GPS fixes (latitude, longitude, and altitude) every 4 hours. This allowed me to study purple martins' migration behaviour and strategy on a finer scale and helped me to look at the time of the day that flights were taken, which was not possible using earlier tracking technology (e.g., light-level geolocators) which only provided 1-2 locations per day (Fraser et al., 2017; Stutchbury et al., 2009). Tags were set to collect movement data across the full spring routes taken by these birds, thus spanning the tropical, subtropical and temperate regions they crossed during migration and provided important variation in latitude and daylength which enabled me to investigate the effect of daylength on daily flight initiation and daily distance covered by these individuals (Bridges et al., 2024; Fraser et al., 2013). During migration, martins must cross

numerous ecological barriers like the Gulf of Mexico and the Caribbean Sea, offering opportunities to understand the change in purple martins' flight pattern due to the lack of foraging and landing/rest opportunities (Lavallée et al., 2021).

Data analysis

Daylength versus daily distance travelled

To investigate whether local light availability affected the distance travelled by purple martins each day, I used GPS fix locations to calculate daily distance (km) travelled per individual bird during spring migration. To determine daylength at each fix location, I used the suncalc package in R studio to estimate sunrise, sunset, dawn and dusk times based on the GPS coordinates. To account for potential flights during low-light periods, twilight duration was also calculated. The total twilight hours were calculated as the sum of morning twilight period (dawn to sunrise) and the evening twilight period (sunset to dusk). The total daily light availability was calculated as the sum of daylength and twilight hours (Thieurmel and Elmarhraoui, 2019).

I filtered the GPS tracking data in 3 different ways before plotting it. The first was the removal of overwater flights since martins make continuous, non-stop flights when crossing these ecological barriers, because they cannot land and a combination of day and night flight is required to complete the crossing (Fraser et al., 2013; Lavallée et al., 2021). I therefore removed these overwater flights, because I was interested in focusing on whether martins make use of additional daylength as they travel further north during routine, overland migration. I determined the timing (start and end) of overwater flights for each tag by visual inspection of the flight paths using Google Earth. These points were then removed from the data.

I also removed non-migratory portions of the tracks, when birds were stopped at refueling sites (stopover days). This was done by calculating daily displacement for each bird by summing up all the displacement distances recorded within a day. Any day with a daily displacement

below 78 km was considered a likely a stopover, or non-migratory day. This cut-off was used based on roost site movement distances reported in previous studies of purple martins (Lalla et al., 2022), which distinguish local movements from longer distance travel (Fournier et al., 2019).

Further, I was interested in focusing on the impact of increasing daylight on daily flight distances. Any points recorded during dark hours (20:00– 3:59) were removed from the dataset to restrict the analysis to daylight movement periods, since they don't relate to the question. Times were first converted from GMT to local time where the tags were deployed using the lubridate package in R studio (Grolemund and Wickham, 2011), and then the points recorded during nighttime were removed.

I used a Linear Mixed-Effects Model (LLM) to test whether daily migration distance increased with greater light availability. Daily distance (km per day) was used as the response variable, with daylength and age as fixed effects. Bird ID and colony were included as random effects to account for repeated measurements from the same individuals and potential variation among colonies (Bates et al., 2015; Zuur et al., 2009).

Diel patterns in migratory movement

To examine how flight distances varied across the day and identify peak flight periods, I divided the GPS tracking data into six, 4-hour bins throughout the (24-hour) day. Before allocating flights to 4-hour bins, the total distance travelled per bird per day was calculated and days with a total displacement of less than 78 km were excluded from the dataset because, as noted above, these were assumed to be stopover or low-movement days rather than active migration (Lalla et al., 2022). The remaining GPS dataset was further divided into 6-time bins divided as follows: 0:00-3:59, 4:00-7:59, 8:00-11:59, 12:00-15:59, 16:00-19:59, 20:00-23:59. Each location fix was assigned to the time bin based on the local timestamp recorded by the tag.

Distances covered within each bin were calculated using the great-circle distances in R between sequential GPS fixes (Hijmans, 2023). These distances represent travel distance during the specific 4-hour periods of the day rather than overall daily distance for every individual bird on each migration day. To evaluate differences in flight distances within the 6 bins, I fit a LMM in R using lme4 and lmerTest packages (Bates et al., 2015; Kuznetsova et al., 2017). The total distance travelled within each time bin was the response variable, time bin and age were included as fixed effects, while bird ID and colony were used as random effects to account for repeated measurements. Model significance was assessed using analysis of variance (ANOVA) and the parameter estimates were obtained from the model summary (Zuur et al., 2009). Estimated marginal means and pairwise comparisons among time bins were calculated using the emmeans package with Tukey-adjusted tests (Lenth, 2022). This allowed me to assess whether flight distance varied across different times of the day while accounting for variation among individual birds and colonies.

Overland versus overwater night flights

To compare distances overland and water during nighttime, I first filtered the dataset to only include nighttime GPS points which were all the points recorded between 20:00-3:59 local time. This data subset was then used to further examine the location of purple martin nocturnal migration behaviour (Fraser et al., 2017; Lavallée et al., 2021). I further identified the overwater flight intervals by visually examining each bird's migration tracks in Google Earth and recorded the start and end times when birds crossed water bodies (Fraser et al., 2013). All the nighttime GPS points that fell within these intervals were classified as overwater flights, while the remaining points were classified as overland flights. Total distance travelled was calculated for each bird by summing the distances for overland and overwater flights which were further

grouped by bird ID and flight type. A paired t-test was used to compare total distances traveled overland versus overwater for the same individuals.

Results

GPS tags that provided high-resolution movement data (every 4 hours) throughout the spring 2024 migration were retrieved from five individuals from two study populations. These data were used to test whether daily migration distance increased with increasing daylight availability, whether migratory movement differed across different time bins and if these birds mostly resorted to night flights when crossing large open-water barriers. Accordingly, results are presented in three sections: (1) daily migration distance in relation to daylight availability, (2) distance travelled across different time bins of the day and (3) nighttime overland versus overwater flights.

Daylength versus daily distance travelled

During migration, the LMM conducted showed a significantly positive relationship between daylength and daily migration distance (β (model estimate) = 67.06 ± 13.65 SE (standard error), $t = 4.91$, $p = 1.31 \times 10^{-6}$) (Table 1). This result indicates that on an average, birds travelled ~67 km farther for each additional daylight hour. Age class had no detectable effect on daily distance travelled (β = 3.65 ± 36.81 SE, $p = 0.93$). Random effects indicated variation amongst individuals and colonies, however, most of the remaining variation in daily migration distance was unexplained by the predictors in my model. This suggests that additional environmental or behavioural factors may have influenced the daily distances recorded. Scatterplots of the raw data (Figures 2 and 3) show an overall increase in daily migration distance with increasing daylight availability, although there is a lot of variation. This pattern varies among individual birds (Figure 3). The lines in both figures are simple linear regression

fits to the raw data and are included for visualization only; the mixed-effects model provides a more reliable test of this relationship. When I combined daylength and twilight hours as total light availability, the model still showed a significantly positive relationship with daily distance travelled ($\beta = 60.14 \pm 12.00$ SE, $t = 5.01$, $p = 8.11 \times 10^{-7}$), indicating that birds travelled approximately 60 km farther per additional hour of available light (Table 1). Age class still remained non-significant ($p = 1.00$).

Diel patterns in migratory movement

Distance covered during each 24-hour period varied significantly across the six, 4-hour time bins (Figure 4). Results from the LMM indicated that birds travelled greater distances during daylight hours compared to the nighttime reference period (0:00-03:59) (Table 2). The longest distance covered was seen during 12:00-15:59 ($\beta = 69.97 \pm 8.26$ SE, $p < 0.001$), followed by 16:00–19:59 ($\beta = 58.27 \pm 8.26$ SE, $p < 0.001$), 20:00–23:59 ($\beta = 39.30 \pm 8.22$ SE, $p < 0.001$), and 08:00–11:59 ($\beta = 26.27 \pm 8.27$ SE, $p = 0.002$). Movement distances during 04:00–07:59 were lower but not significantly different from the reference period ($p = 0.159$). Estimated marginal means indicated that the predicted mean distances were highest during 12:00–15:59 (101.6 km) and lowest during 04:00–07:59 (20.0 km) (Table 3). Age class did not significantly affect distance covered ($\beta = 7.13 \pm 11.64$ SE, $p = 0.568$). Random effects indicated some variation among individuals (variance = 94.52) and relatively small variation among colonies (variance = 16.20), with most of the unexplained variation occurring within individuals across time bins (residual variance = 3883.67).

Overland versus overwater night flights

Purple martins generally travelled greater total distances during overland flights as compared to those taken overwater (Figure 5). The longest single distance travelled was

observed in bird 58363, which travelled much further overland at night (4094 km) than it did overwater (445 km). However, some individuals, such as 58572 and 58577, travelled similar distances at night whether over land or water. The difference between the total distance travelled overland and overwater was not statistically significant, according to a paired t-test ($t(4) = -2.11$, $p = 0.102$) (Table 4). With a 95% confidence interval between −3212.7 and 436.5 km, the mean difference between overland and overwater distances was −1388.1 km.

Discussion

This study looked at how daylength and time of day influence the migratory behaviour of purple martins during spring migration. My results show that daily distance travelled during migration increased with both longer daylengths and increased daylight availability, suggesting that increased light availability allowed these primarily diurnal migrants to travel further each day. Flight activity also varied throughout the day, where migration distances travelled were greatest at midday and late afternoon. Surprisingly, nocturnal flights were not significantly associated with open-water barrier crossings, with several individuals making long night flights overland.

Daylength versus daily distance travelled

I predicted that daily distance would increase with increasing daylength because it allows more time for diurnal migrants to fly and forage (refuel). The results aligned with my prediction, and I found that daily migration distance increased significantly with longer daylength. Birds travelled farther on the days with longer daylight (after accounting for daylength and twilight hours); this suggests that purple martins may extend their daily activity period and cover more distances during migration with increasing light availability. This relationship is consistent with migration theory that explains that diurnal migrants can benefit from longer daylight periods by

expanding their time window available for flight and foraging (Alerstam, 2009; Nilsson et al., 2013).

One possible explanation for this pattern, could be related to the fly-and-forage strategy used by purple martins. Since purple martins feed on aerial insects while flying (Brown, Airola and Tarof, 2021), longer daylight hours may allow them to maintain both foraging and migratory movement simultaneously. This has been demonstrated in migratory osprey, a species that paused on migration to capture fish (Strandberg and Alerstam, 2007), but my study is the first to demonstrate this pattern in a migratory songbird. Increased daylight therefore potentially allows for longer periods of daily flight by permitting birds to offset the additional energetic requirements involved. I found that the variation in daily distances was high across the migratory days, suggesting that other factors like wind conditions, insect availability, or individual behavioural decisions (like when to rest, stop or forage longer) may also influence daily migration routes and distances (Shamoun-Baranes et al., 2017).

Diel patterns in migratory movement

I predicted that most flight activity would be during the daylight hours, with greater movement distances observed early in the morning when the environmental conditions are more favourable for flight, such as cooler temperatures with less air turbulence in early morning as compared to the afternoon (Kerlinger and Moore, 1989). The results partly supported my prediction. Even though I observed most flight activity during daylight hours, the greatest movement (i.e. longest travel distances) were during midday and late afternoon hours (12-19:59) rather than early morning. These results suggest that even though purple martins are primarily diurnal migrants the timing of their peak movement depends on factors other than just temperature and wind turbulence alone. One possible explanation would the timing of aerial

insect availability. Insect activity usually increases with increased temperatures throughout the day (Deng et al., 2023; Taylor, 1963), resulting in greater prey availability during midday and afternoon periods. Alternatively, martins may use the early morning hours for refueling before they depart for long migratory flights, which could also explain this pattern. Further exploration of migratory and fueling movements using new technology such as accelerometers, may help to further explain these daily patterns of activity.

As a result, birds may extend their migratory movement later in the day to maximize foraging opportunities while continuing their northward migration. Furthermore, atmospheric conditions like wind patterns (e.g. tail winds) may become more favourable later in the day, potentially allowing martins to travel longer distances. The relatively low movement observed during early morning hours may reflect a period when individuals are resting, feeding locally or waiting for more favourable environmental conditions before undergoing long migratory flights.

Overland versus overwater night flights

I predicted that purple martins would be more likely to undertake nocturnal flights when crossing ecological barriers such as large bodies of water. Even though I observed several long-distance nocturnal flights in this species which is considered to be a primarily diurnal migrant, they were not associated only with overwater barrier crossings (e.g. Caribbean Sea or Gulf of Mexico). I also observed several long night flights when birds were overland. This indicates that purple martins may occasionally extend migration into the nighttime hours, rather than just using nocturnal flights exclusively as a strategy to cross large ecological barriers such as open water.

Nocturnal movements may occur as a response to the short-term environmental conditions rather than the landscape features alone. For example, martins might extend their migration to nighttime hours when the wind conditions are favourable to maintain migration progress

(Liechti, 2006). Additionally, nocturnal flights may also be influenced by variation in food availability along the migratory route. Since, purple martins rely on aerial insects while migrating, areas with low prey abundance may limit opportunities for foraging during the day. In such situations, individuals may continue flying into the night in order to reach regions with higher prey availability or more areas with suitable foraging conditions. Indeed, exploring the overland habitat birds are crossing during dark hours may help us understand whether they perceive these areas as barriers. In my study, martins often resorted to nighttime flights over the Llanos of Colombia and Venezuela, a large open grassland region. Likewise, songbirds may use night flights to cross large land barriers encountered during migration, such as birds crossing the Sahara Desert when migrating from African overwintering sites to European breeding sites (Schmaljohann et al., 2007). All of these findings point to the possibility that purple martins' nighttime flights are not a regular strategy linked solely to overwater crossings, but rather flexible or opportunistic behaviour driven by other environmental factors (Schmaljohann et al., 2007).

While this study provides insight into how daylength and time of day influence migratory behaviour in purple martins, there were several limitations of this study. For example, the low sample size could have limited my ability to detect patterns in purple martin's migration behaviour, especially in relation to when they were taking the longest flights. Future studies with larger sample sizes and longer tracking periods could help determine whether the patterns observed here are consistent across individuals and migration seasons. Additionally, incorporating environmental variables such as wind speed, temperature, and insect abundance could provide a better understanding of how external conditions influence daily migration decisions. As purple martins rely heavily on aerial insects, looking at prey availability may

further explain the variation observed in daily migration and time of peak movement, particularly if the insect activity varies across the day. The relatively coarse temporal resolution of the GPS data (4-hour intervals) also limited the ability to distinguish between migratory and foraging movements. Newer tracking technologies with tags that collect points more frequently (for example, every 5 minutes), could help resolve these behaviours. In addition, my data didn't allow me to partition light and dark precisely, as some time bins likely include both conditions. Improved temporal resolution and more precise light classification would enhance our ability to resolve diel patterns in migratory behaviour.

Overall, this study highlights the importance of light availability and daily environmental conditions in shaping the migratory behaviour of purple martins during spring migration. Longer daily migration distances were associated with longer daylengths, suggesting that longer daylight hours enable birds to maintain their fly-and-forage strategy while extending their daily flight distance. Migration activity was observed to occur mostly during the daylight hours, with the greatest movements occurring during midday and late afternoon rather than early morning. Even though there were nocturnal flights, they were not only associated with open-water barrier crossings, likely indicating the presence of opportunistic nighttime migration in response to environmental conditions. These findings altogether contribute to a better understanding of factors influencing daily migratory behaviour and movement patterns in diurnal aerial insectivores.

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Table 1. Parameter estimates from linear mixed-effects models (LMMs) examining the effects of daylength and total light availability (daylength + twilight) on daily migration distance (km). Bird id and colony were included as random effects.

	Predictor	Estimate (β ± SE)	t value	p value
Model 1: Daylength	Intercept	−571.77 ± 175.88	−3.25	0.001
	Daylength	67.06 ± 13.65	4.91	<0.001
	Age (SY)	3.65 ± 36.81	0.10	0.93
Model 2: Total light availability	Intercept	−530.10 ± 164.10	−3.23	0.001
	Total light availability	60.14 ± 12.00	5.01	<0.001
	Age (SY)	3.72 ± 35.94	0.10	1.00

Table 2. LLM results comparing the distance travelled in six, 4-hour time bins by purple martins. Estimates (β ± SE), t-values, and p-values are shown relative to the reference period (00:00–03:59). Age class was included as a fixed effect, with bird ID and colony as random effects.

Predictor	Estimate (β) ± SE	t value	*p* value
Intercept (00:00–03:59)	28.10 ± 9.30	3.02	0.011
04:00–07:59	−11.66 ± 8.27	−1.41	0.159
08:00–11:59	26.27 ± 8.27	3.18	0.002
12:00–15:59	69.97 ± 8.26	8.47	<0.001
16:00–19:59	58.27 ± 8.26	7.05	<0.001
20:00–23:59	39.30 ± 8.22	4.78	<0.001
Age class	7.13 ± 11.64	0.61	0.568

Table 3. Estimated marginal means of total distance travelled (km) across 4-hour time bins extracted from LMM. Means are averaged across bird age classes (SY and ASY), letters indicate Tukey-adjusted pairwise comparisons where shared letters denote no significant difference ($\alpha = 0.05$).

Time bin	Estimated mean (km)	SE	95% CI	Significance group
04:00–07:59	20.0	7.90	3.36 – 36.6	a
00:00–03:59	31.7	7.92	15.0 – 48.3	a
08:00–11:59	57.9	7.89	41.3 – 74.6	b
20:00–23:59	71.0	7.85	54.4 – 87.5	b
16:00–19:59	89.9	7.88	73.3 – 106.5	c
12:00–15:59	101.6	7.87	85.0 – 118.2	c

Table 4. Results of a paired *t*-test comparing total nighttime migration distance travelled over land and over water (20:00–03:59 local time) across the five tracked birds.

Statistic	Value
t	-2.11
df	4
p-value	0.102
Mean difference (km)	-1388.11
95% CI	-3212.72 to 436.50 km

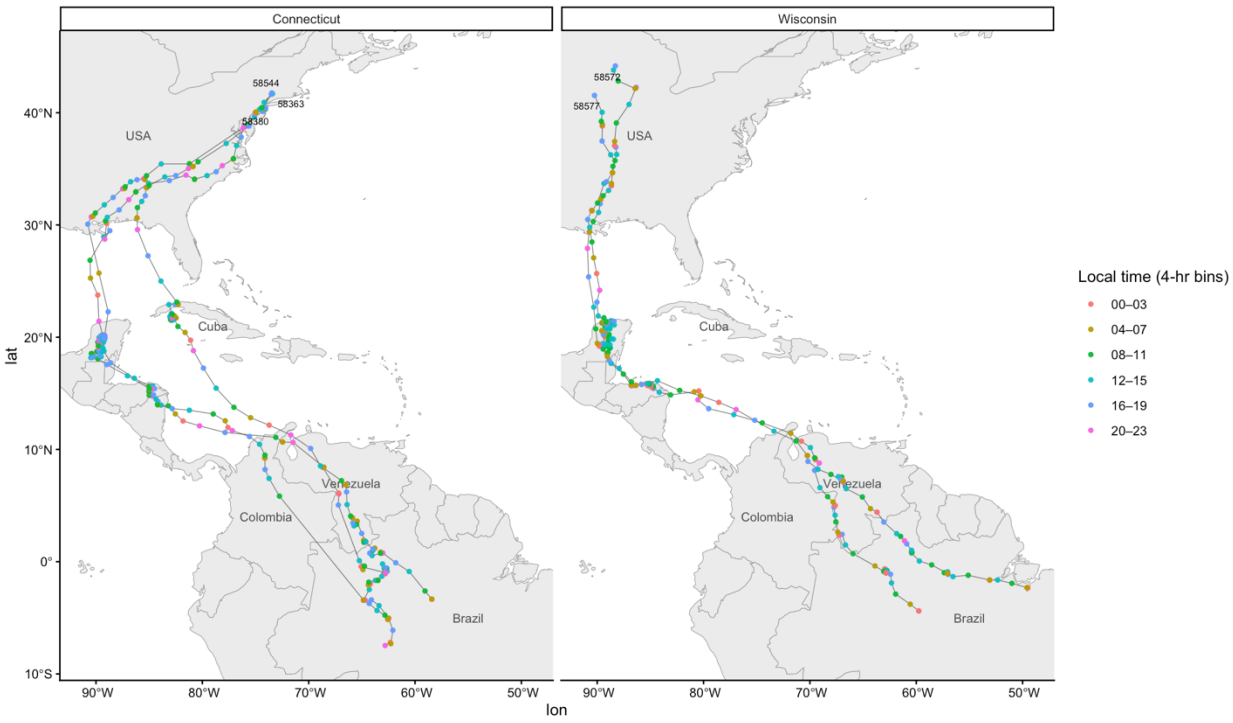

Figure 1. Spring migration tracks of birds tagged in Connecticut and Wisconsin showing their flights from overwintering sites in South America to breeding sites in North America. Each point represents a recorded location during migration, and the colours represent the local time divided into six 4-hour bins.

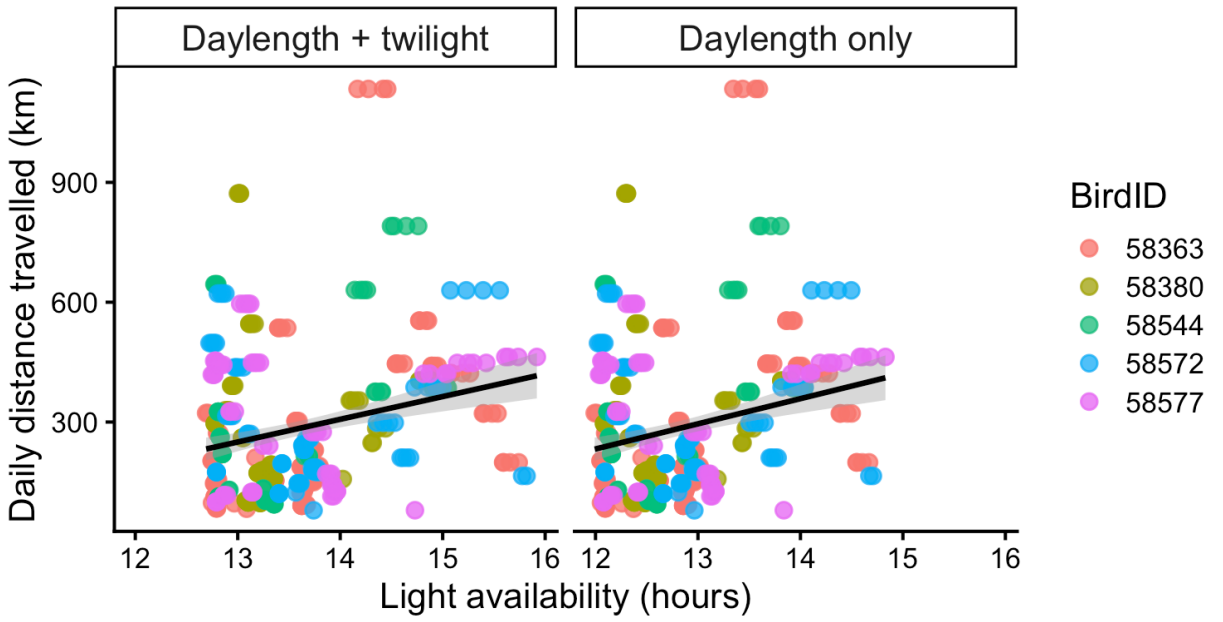

Figure 2. Relationship between light availability (hours) and daily distance travelled (km) during spring migration. Light availability was calculated as either daylength plus twilight (left) or daylength only (right). Each point represents the daily movement for each individual bird and is coloured by bird ID. The black line shows the fitted linear regression with the shaded area representing the 95% confidence interval.

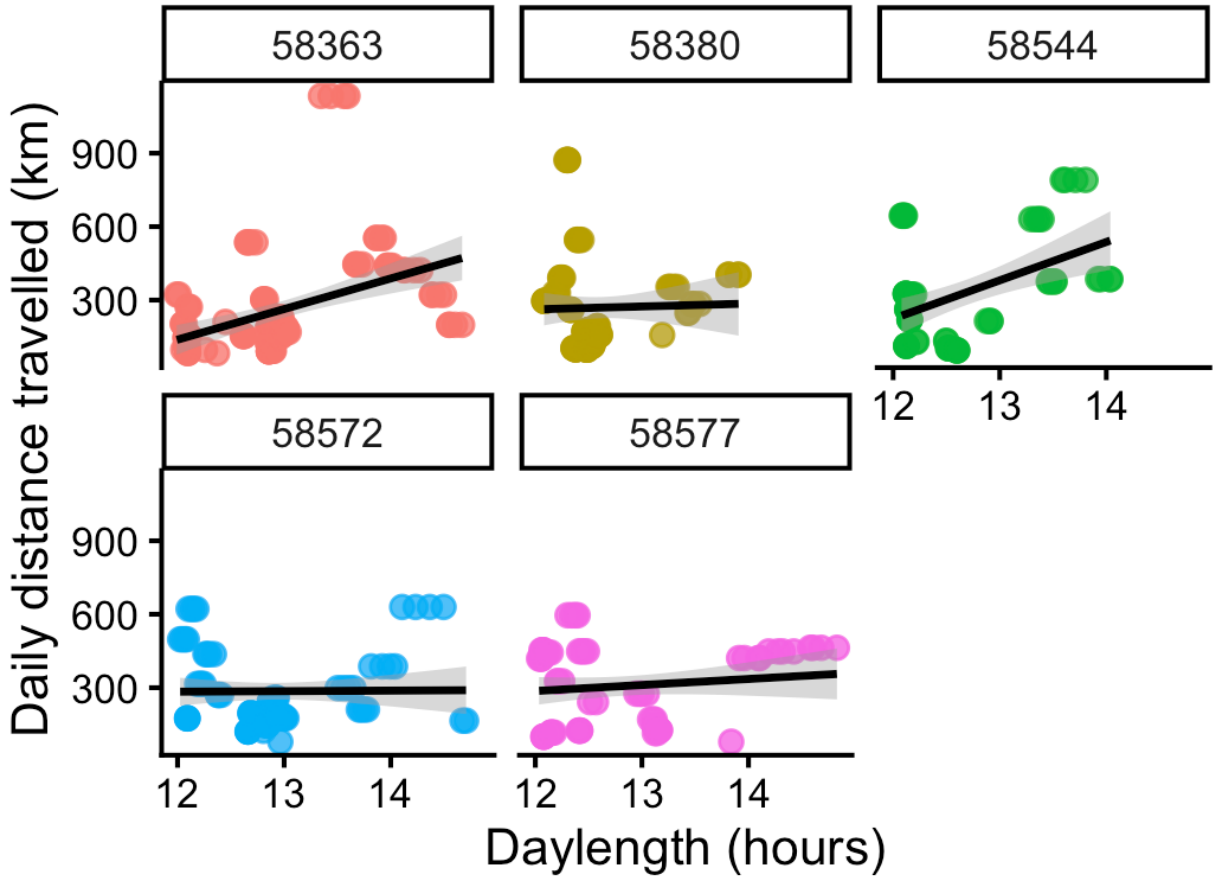

Figure 3. Relationship between daylength (hours) and daily distance travelled (km) for individual birds during spring migration. Each panel represents a different bird ID, and points show daily movement distances. The black line represents the fitted linear regression for each individual, with the shaded area indicating the 95% confidence interval.

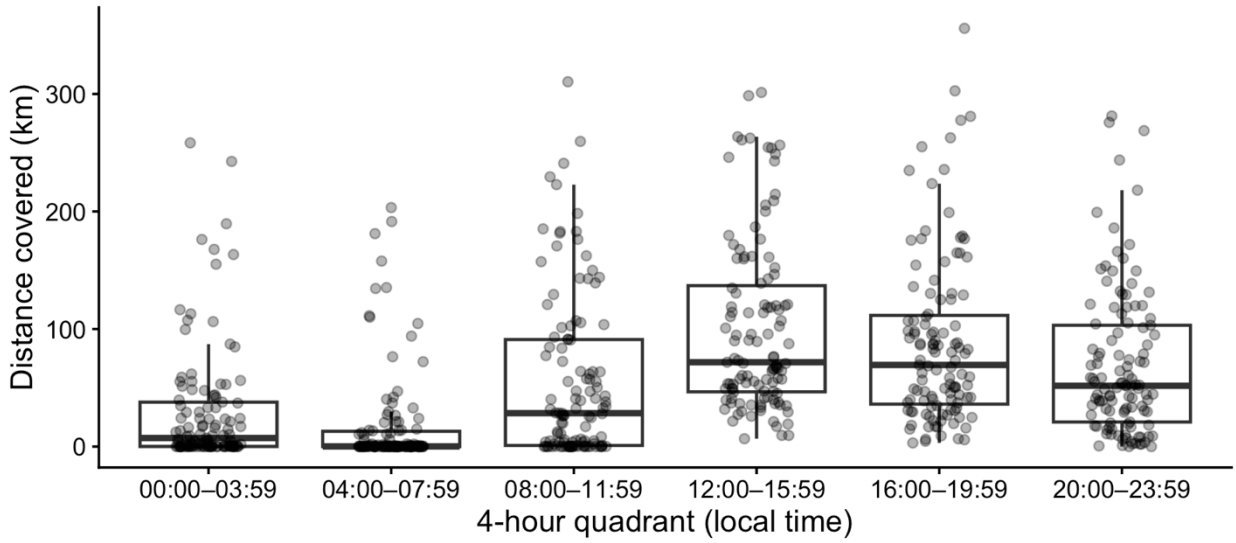

Figure 4. Distance covered (km) across six 4-hour local time intervals during spring migration. Boxplots show the distribution of distances travelled within each time bin, with the median, interquartile range, and whiskers representing variability in movement distances. Points represent individual movement observations.

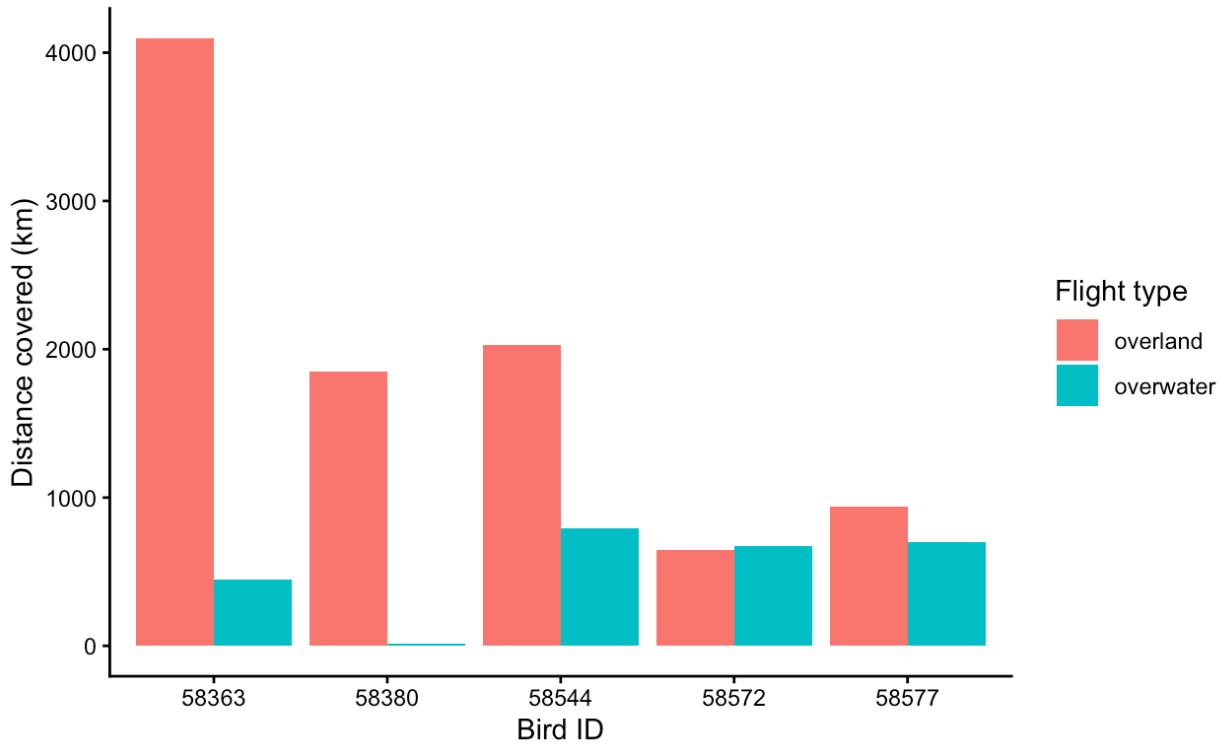

Figure 5. Total distance covered (km) by each bird during nighttime migration (20:00–03:59), separated by flight type. Bars show the distance travelled overland and overwater for each bird id.

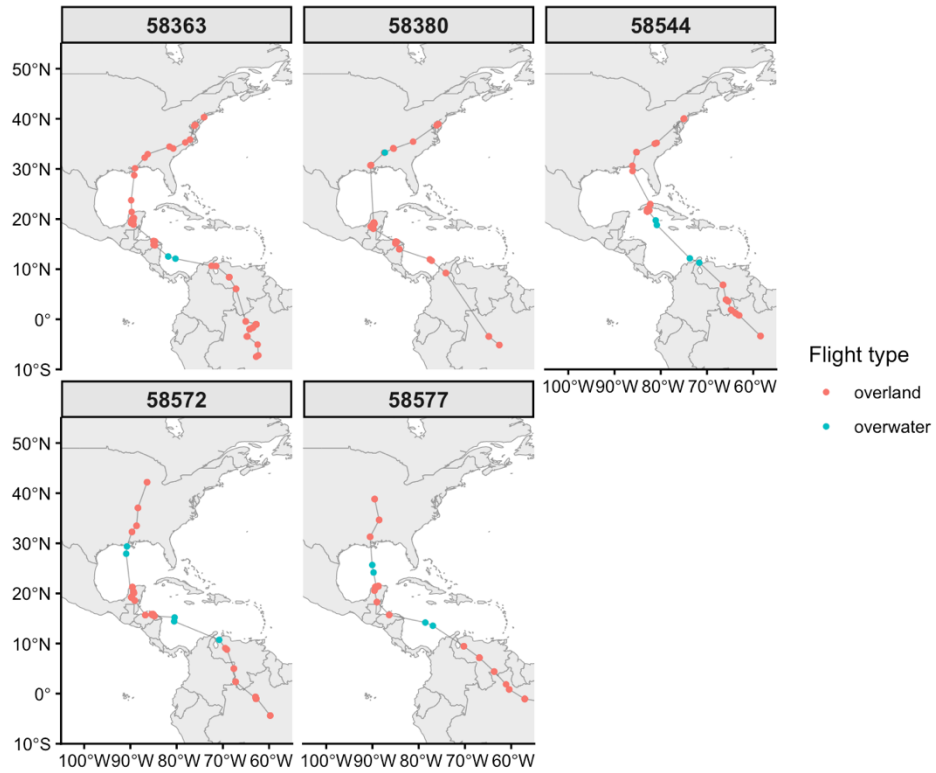

Figure 6. Nighttime GPS locations (20:00–03:59 local time) for each bird during spring migration. Each panel shows an individual bird ID, with points coloured by flight type (overland or overwater).