

Circadian Patterns of Flight in a Long-Distance Migratory Songbird

by

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ABSTRACT

Migration is a common strategy in many different animal taxa, including birds. Most migratory songbirds migrate mainly at night (i.e., nocturnal migrants), with some species migrating primarily during daytime (i.e., diurnal migrants). Some birds can even combine nocturnal and diurnal flights, but these tend to be associated with barrier crossings (e.g., long overwater flights). Whether diurnally migrating songbirds also incorporate night flights into other periods of their spring migrations despite a lack of migration barriers has not been investigated. Further, we lack a precise understanding of the influence of specific environmental conditions on day or night flight behaviour. We investigated circadian patterns of flight in purple martins (*Progne subis*), a long-distance migratory songbird that journeys between nonbreeding areas in South America and breeding sites in eastern North America. We used direct-tracking (GPS loggers) of individual spring migrations to quantify the daily timing of flights, flight speed, flight distance, and altitude as well as whether these factors were associated with temperature. Birds were tagged with GPS loggers in Winnipeg, Canada, which collected location and altitude every two hours during spring migration. We used Movebank to align location data with average local temperature. We found that martins migrated mainly during daylight, but surprisingly, 15% of flights overland occurred during the night. The average speed for daytime and nighttime flights was similar. We found that neither temperature nor timing of flights influenced flight speed and distance travelled, but flights at higher altitudes were associated with longer flight distance and faster speeds. Our results suggest that a species classified as a diurnal migrant routinely makes night flights overland that are not associated with crossing known migratory barriers. Further studies could increase the

sample size of birds and the number of usable GPS fixes, which would allow us to track birds as close to their breeding grounds in temperate areas as possible.

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INTRODUCTION

Migration, where animals travel in groups or by themselves to follow seasonally variable resources and maximize daylight, is regulated by a circannual clock in combination with environmental stimuli (e.g., photoperiod) (Lack, 1968; Holberton and Able 1992; Safriel 1995; Ward and Raim 2011; Rose and Lyon 2013). Migration is common in many different animal classes around the world, including Mammalia (e.g., whales), Insecta (e.g., butterflies), and Aves (e.g., birds) (Wu et al. 2015; Andrews-Goff et al. 2018; Imlay et al. 2020). Due to how common migration is among different animal groups worldwide, we must learn the migratory movements of little-studied but declining populations, including birds, due to the high mortality rate during this annual phase (Sillet and Holmes 2002). Once we determine their migration routes, we can determine why migration has a high mortality risk and then focus conservation efforts on the factors most damaging to animal populations (Klaassen et al. 2014; Hewson et al. 2016).

Bird migration is classified into two categories depending on which hours of the day a bird flies during migration: nocturnal birds, who migrate at night, or diurnal birds, who tend to migrate during the day (Schmaljohann et al. 2007; Lavallée et al. 2021). These categories are not exclusive, especially when crossing barriers with few opportunities for refueling, such as deserts or seas (Moreau 1961; Schmaljohann et al. 2007), since many songbirds do not have the option of foraging during the crossing (Alerstam 2009). Without these barriers, there are some benefits to either single strategy (Alerstam 2009).

There are many inferred potential benefits of the nocturnal migration strategy. Some explanations for the evolution of this strategy include capitalizing on the available daylength to forage and refuel, then beginning migration when foraging opportunities become limited, such as near sunset (Lank 1989). Further benefits of nocturnal migration include the opportunity to

search for resource-rich areas during flight and foraging the day after landing (Lank 1989). Additionally, nocturnal migrants tend to fly at low altitudes (<2000m over sea level) and may benefit from more favourable winds, experience less evaporative water loss, and avoid more turbulent and high-velocity winds and heat during the day (Kerlinger and Moore 1989; La Sorte et al. 2015; Komal et al. 2017; Sjöberg et al. 2021).

Optimal times for diurnal migration may vary over the day. For example, diurnal migration during early morning at 0400 to 1200 and late afternoon between 1500 to 1800 at altitudes as high as >5000m above sea level is associated with less turbulent winds and lower temperatures (Kerlinger and Moore 1989; Ward and Raim 2011; Senner et al. 2018; Sjöberg et al. 2021). These conditions may, therefore, be favourable for a diurnal migration strategy, such as exhibited by those species that may be classified as fly-and-forage migrants (wherein a bird forages on the wing while airborne) (Ward and Raim 2011). Birds using this strategy can forage for resources that are not at constant locations while migrating and typically include migrants in the swallow family (Hirundinidae) and some raptors (Ward and Raim 2011).

Migrating birds can change their flight speed depending on the amount of refueling opportunities along their route (Alerstam and Hedenström 1998). When there are food-poor barriers, birds may rely on energy stores while flying quickly non-stop (Rubolini et al. 2002) at high altitudes as they travel over the barrier (Lathouwers et al. 2022). In contrast, when there are no barriers, birds can travel at slower speeds and at lower altitudes for shorter flight times as they use stopovers or fly-and-forage to refuel or a combination of the two, especially when crossing a resource-rich area, such as a lake for migrating piscivores (e.g., osprey (Linnaeus 1758)) (Alerstam and Hedenström 1998; Strandberg and Alerstam 2007; Bayly et al. 2018; Lathouwers et al. 2022). A fly-and-forage strategy may allow birds to arrive at their destination sooner since

there is a reduced need for stopover sites to refuel, which may otherwise cause birds to slightly deviate from their migration path to locate suitable stopovers and where they would take longer to refuel (Strandberg and Alerstam 2007; Imlay et al. 2020).

Purple martins (*Progne subis*) (Linnaeus 1758) are mostly diurnal migratory birds in the swallow family that are thought to use a fly-and-forage migration strategy (Brown et al. 2021). They migrate hundreds of kilometres from the Amazon basin in South America, where they overwinter, to parts of the United States and southern Canada, where they breed (Fraser et al. 2012; Brown et al. 2021). When martins cross overwater barriers, they initiate crossing during the day and then continue migration into the night to complete the crossing, or they initiate crossing at night since they cannot forage effectively in this resource-poor area (Lavallée et al. 2021). Regardless of the time of initiation, martins covered more distance during diurnal flight than nocturnal flight. This pattern was seen as well for overland flight, where martins had long diurnal flights but short nocturnal flights, which likely occurred over food-poor areas when their fly-and-forage strategy was less efficient than in food-rich areas (Lavallée et al. 2021).

Martins consume insects from many different orders, including Hymenoptera, Diptera, Hemiptera, Coleoptera, Lepidoptera, Orthoptera, and Odonata (Beal 1918; Kelly et al. 2013; Oniki-Willis et al. 2022). They need to forage often since martins are estimated to consume about 9000-14000 insects per kilometre travelled during migration across their range in the US (Kelly et al. 2013). However, since unfavourable weather conditions (i.e., <6°C temperatures) can affect the availability of insects, they can likely also affect the foraging efficiency of martins during migration as martins likely use the fly-and-forage strategy (Lack 1968; Brown 1976; Gruebler et al. 2008; Hambäck 2021).

Daylight is very important for purple martins as they are diurnal birds that mostly use daylight hours for flights during migration. I hypothesized that purple martins employ a mostly diurnal, fly-and-forage strategy and that temperature will impact the timing, speed, and altitude of daytime migratory flights. I predicted that birds will avoid migratory flights at the temperature peaks of the day (i.e., midday), which would allow them to avoid the greatest temperatures and avoid turbulence. However, when birds do commence migration, I predicted that at high air temperatures near the ground, birds will fly at higher altitudes, which would be advantageous to the bird as it would avoid turbulence and thus maximize flight efficiency. Similar to altitude, I predicted that birds will have faster migration speeds at low temperatures (<6°C) as insect abundance would be lower and feeding opportunities would be limited.

METHODS

Field methods

In spring 2022, 25 adult purple martins were captured using drop-door traps installed on their nest boxes at FortWhyte Alive (49.82°, -97.22°) in Winnipeg, MB, Canada. An additional 10 purple martins were also captured using the same technique at a private residence (49.74°, -97.13°). After capture, birds were banded with a government-issued ID band and a field-readable ID-band. Each bird was measured (e.g., wing, tail, and tarsus length), weighed, aged, and sexed by plumage (Niles 1972; Pyle 1997).

Each bird was tagged with a GPS tag (Pinpoint 10, Lotek Inc.), using a leg-loop backpack harness made of Teflon ribbon, which weighed less than 3% of each bird's total weight (1.5g) (Rappole and Tipton 1991). Each tag was programmed using Lotek Pinpoint Host software (VHF-50). Tags were programmed to collect GPS fixes (i.e., longitude, latitude, and altitude) every two hours during spring migration from the Amazon basin to Canada. Since the battery life

of each tag would not support migration-long data collection, we programmed tags to activate ten days before the median crossing date of the Tropic of Cancer (23. 4°N) to capture the beginning of spring migration at tropical latitudes based upon previous tracking from this population (e.g., Neufeld et al. 2021).

In spring 2023, we recaptured seven tagged birds (four female and three males) using similar methods and migration data logged by each tag were downloaded using DLC PinPoint GPS interface. Although seven tagged birds were recaptured, data from three tags could not be used due to an inability to download the data from one non-functional tag (4212), one tag (4222) had only a single data point, and one tag (4227) logged movements in Brazil pre-migration. Due to the tag programming, all retrieved data from each tag were from the beginning of purple martin migration in South America to approximately the midway point in migration in Mexico (Neufeld et al. 2021; Fig. 1).

Analyses

Day versus night flights

For each two-hour flight for each individual, I determined distance in kilometres using Google Earth (<https://earth.google.com/web/>). I used an online publicly available data set from South and Central America called TimeandDay (<https://www.timeanddate.com/>). With these data, I used the nearest city (preferentially within 200km, but within 600km if closer cities/towns were unavailable) in South and Central America to categorize purple martin migration flights as either diurnal or nocturnal. Firstly, I converted the GMT of each position to local times using TimeandDay. Next, I categorized each time as to whether it occurred during local night (from after civil dusk to civil dawn), civil twilight (civil dawn and civil dusk), or daytime (from sunrise to sunset). Civil twilight was then ascribed to either daytime or nighttime flight depending on which time had more than one hour in the civil twilight block. Certain fixes were not used (e.g.,

tag 4215, fix number 14) since they did not provide any data, which may be due to a limited number of satellite fixes (i.e., <4). The single GPS fix made before these removed points were also removed to maintain similar travelling times between fixes (i.e., two hours instead of four hours between). I also removed any overwater flights and overland flights with distances less than 26 km as distances higher than this distance would indicate a migratory bout. I determined 26 km as the cut-off for migration flight since it was the longest logged distance by 4227 tag during pre-migration in Brazil. These flights were excluded since I focused on overland migration flights and non-migratory or overwater flights could bias my analysis. I quantified the distance of daytime and any nighttime flights and determined if there were any differences by creating a box plot in R version 4.3.2 (R Core Team 2023). I determined that my data was normally distributed and used a Generalized Linear Model (GLM) in R with ggplot2 (Wickham 2016), dplyr (Wickham et al. 2023), broom (Broom et al. 2023), and ggpubr (Kassambara 2023) in R.

I determined flight speed for daytime versus nighttime flights by dividing the distance between two points by the duration of travel between the two points (i.e., two hours). Next, I divided the quotient by two to find the distance travelled over one hour. To determine whether the time of day influenced the distance covered over 1 hour, I ran a GLM with distance in km as my response variable and altitude, temperature, and time of day as my independent variables. Data were first checked for normality (data were normally distributed except near the lowest and highest distance points) and all analyses were run in R. I next determined whether the average speed of daytime versus nighttime flights differed significantly. After separating times into daytime and nighttime, I averaged the flight speeds of each tag into day and night blocks, then averaged all daytime/nighttime blocks into a single final flight speed for daytime and nighttime

flights (Table 1). Lastly, I conducted a Welch two-sample t-test in R to determine if there are any differences in altitude between daytime and nighttime flights.

Environmental effects on flight speed

I uploaded all position points to Movebank (<https://www.movebank.org/>) and used their Environmental Data Automated Track Annotation System to align average temperature values 2m above the ground with each bird location point used in the distance analysis. All temperature points were interpolated from two surrounding values from the European Centre for Medium-Range Weather Forecasts dataset (Dodge et al., 2013). With these data, I used GLMs to determine if distance was significantly influenced by temperature, distance by time of day and temperature by time of day with gam (Hastie 2023). Finally, I also conducted GLMs to determine if temperature or altitude at the start of 2-hour flight segments had an impact on flight speed.

RESULTS

During spring 2023, we retrieved seven tags. Tags with data (i.e., six) collected a total of 299 GPS fixes, with each tag collecting a range of 1-75 fixes over 1-5 days in April and/or May. Some GPS fixes were removed if they were generated using a low number (<4) of satellites, which increases the possibility of location error, and fixes immediately after the fixes removed to standardize sampling interval (Hadjikyriakou et al. 2020). Additionally, fixes with distances less than 26km were removed since they were presumed to be foraging due to the low distance travelled. After these fixes were removed, a total of 72 GPS fixes remained with 3-35 fixes per tag. When tags were programmed to begin tracking migration (April 26, 2023), birds were on different parts of their migration. Purple martin migration can take two different migration routes, either over water (i.e., Caribbean Sea) or intermittent overwater and overland flights

across different countries in Central America (Fig. 1). However, some birds were still travelling across South America (Fig. 1).

Day versus night flights

Migratory night flights overland were uncommon, with 11 out of 72 individual flights (15%) occurring during dark hours (Fig. 2). Bird 4213 had 25 migratory flights, but 2 were during the night, and 23 were during the daytime, while 4215 had 3 daytime flights and no nighttime flights (Fig. 2). Bird 4234 had 10 migratory flights, and 3 were during nighttime while the other 7 were during daytime (Fig. 2). Bird 4241 had the greatest number of migratory flights (34), with 6 night flights, and 28 daytime flights (Fig. 2). I determined that distance travelled by birds did not differ significantly between daytime and nighttime flights ($F_{6,65}=1.15$, $P=0.34$, $n=72$; Fig. 2). Additionally, average daytime and nighttime migration speeds ($t=0.70$, $p=0.49$, $n=72$) and altitude ($t=-1.85$, $p=0.09$, $n=72$) did not differ significantly. Surprisingly, two birds (ID 4213 and 4241) had slightly greater average daytime speeds (16.79 ± 6.72 km/h and 13.58 ± 4.86 km/h) than nighttime speed (10.22 ± 2.35 km/h and 13.72 ± 5.16 km/h) (Table 1). Still, slightly higher daytime speeds did not appear to differ between sexes as these two birds were female and male, while 4234 (female) had greater average nocturnal flight speeds than daytime flight speeds (daytime: 15.41 ± 7.10 and nocturnal: 16.36 ± 4.78) (Table 1).

Based on the GLM results, temperature did not have a significant impact on the distance covered during 2-hour flight segments ($F_{1,70}=0.0058$, $p=0.94$, $n=72$; Fig. 3). Most migratory flights were diurnal below high temperatures ($>30^{\circ}\text{C}$), and they mainly travelled 26-75 km in each 2-hour flight time (Fig. 3). Although most birds migrated at similar distances and temperatures, two birds (ID 4234 and 4213) travelled the longest distances (<100 km) at the lower temperatures, near 25°C (Fig. 3). These flights occurred in daytime, and although one bird

(ID 4213) travelled over vegetation-rich grounds, the other bird (ID 4234) travelled in less vegetation-rich areas.

Although temperature varied significantly with the time of day ($F_{1,70}=20.64$, $p<0.002$; Fig. 5), I determined that distance did not change significantly with time of day ($F_{7,64}=0.95$, $p=0.48$; Fig. 4). Most migratory flights occurred within 0600-1600 hours during the greatest temperatures (Fig. 4; Fig. 5). Interestingly, the longest distance flights (i.e., >100km) occurred within early morning between 0600-1000 hours by after-second-year females (ID 4215 and 4234) before the temperatures peak at midday (Fig. 4; Fig. 5; Table 1).

Although I determined using GLMs that neither temperature nor time of day had a significant effect on flight distance, altitude increased significantly with distance covered ($F_{4,67}=3.44$, $p=0.01$) ($F_{1,70}=10.65$, $p=0.002$; Fig. 6). Similarly, flight speed was not significantly affected by temperature or time of day, while it was significantly affected by altitude ($F_{4,67}=3.44$, $p=0.01$). Purple martin flight altitudes ranged from 43-2435 m throughout all recorded migratory bouts with birds flying at 853.37 ± 598.73 m in daytime and 1275.5 ± 726.02 m at nighttime flights.

DISCUSSION

Fine-scale flight behaviours of small, migratory songbirds have been difficult to study until recently. Purple martins are considered to be primarily diurnal migrants who likely use available daylight to forage for food while migrating (Brown et al. 2021). However, using direct-tracking of migration with recently miniaturized and precise GPS tags, it has been discovered that they undertake some nocturnal flights. Still, these flights were assumed to be only to complete a journey across a resource-poor area (e.g., the Caribbean Sea) (Lavallée et al. 2021). Therefore, while some nocturnal flights were expected for purple martins, the extent of nocturnal

flights revealed in my even more detailed analysis of flight behaviour (i.e. every 2 hours), especially overland, was surprising (15% of total migration flights).

Further, I found that migratory flight speeds and distances were not associated with temperature or time of day, even though purple martins are mostly diurnal birds (Fig. 2, Table 1). These findings were surprising since nocturnal migrants typically have longer flights and fly at greater speeds than diurnal migrants (Liechti et al. 2018). These observations are typical due to the favourable environmental conditions that nocturnal migrants encounter, such as low temperatures (and subsequently low turbulence) and low winds (Kerlinger and Moore 1989; Eberhard 1996; Åkesson and Hedenström 2000). Additionally, martins must divide their time between migrating and foraging using a fly-and-forage strategy, which should further reduce their flight speed in daylight if they need to pause or slow their speed generally in order to catch aerial prey (Klaassen et al. 2008; Imlay et al. 2020). However, while not significant, I found that some birds (i.e., 4213, 4234, and 4241) did undertake their longest recorded flight distances (near 100 km) during early morning (0400-1200) and dropped off near midday (1200). Kerlinger and Moore (1989) estimated this time as optimal travel timing for diurnal migrants, both for favourable environmental conditions and to provide time for daytime foraging at the destination if flights terminate in advance of dusk.

Previous studies have demonstrated the ability of purple martins to travel overland at night, but these have all been associated with resource-poor areas, such as deserts or mountains (Moreau 1961; Lavallée et al. 2021). However, none of the nocturnal flights documented in this study occurred near known migratory barriers. For instance, besides the first ten GPS fixes, one bird (ID 4234) flew over vegetation-rich areas throughout all its recorded flights, even at night (Fig. 1). Additionally, one bird (ID 4213) had a nocturnal migratory flight point near the beginning of recorded migration near the middle of the State of Amazonas (Fig. 1). Each of the tagged birds that travelled in this open or

savannah habitat north of the Amazon (Venezuelan Llanos) flew during the dry season (Aug-Apr) which tend to have a lower insect abundance than during the rainy season (Apr-Nov) (Robinson 1986; Bertsch and Barreto 2008.). Most nocturnal flights occurred over this unsuitable habitat. Still, nocturnal flight was not exclusive to this area, either, as some flights occurred when birds flew over areas of wet forest, which would be expected to be good martin foraging habitat. These overland nocturnal flights over different areas suggest that they may be a previously unknown component of martin migration behaviour and less likely to be associated with unknown overland barriers.

Purple martins flew at various altitudes during their flights, ranging from <100 m to near 2500 m. While most altitude flights (<900 m) occurred during the presumed unsuitable habitat in Venezuela, there were some high-altitude flights in wet forests as well. Flights at high altitudes did not appear to be associated with crossing over high elevations (e.g., Andes mountains) either. Martins flew longer distances at high altitudes, which was expected for a diurnal migrant as they can exploit the favourable conditions associated with these altitudes (<900 m over sea level) (i.e., low turbulence and temperatures) (Senner et al. 2018; Sjöberg et al. 2021). However, contrary to our predictions, altitude did not vary with time of day or temperature, as reported for other migrating birds (e.g., black-tailed godwits) (Senner et al. 2018). This result is surprising since there were nocturnal flights, and during these times, it was predicted that they would fly at lower altitudes since they do not have to avoid high ground temperatures and turbulence as diurnal migrants would during the day (Senner et al. 2018; Sjöberg et al. 2021).

It was additionally surprising that temperature or time of day did not influence flight speed since it would seem that birds would change their speed depending on current environmental conditions and time to sunset or midday. Since these factors did not affect flight speed, we can assume that birds were flying at near constant speeds as they were not affected by the studied

environmental conditions. Birds continuing these migration speeds suggest that they are attempting to arrive at their breeding grounds early, regardless of environmental conditions. Arriving at breeding grounds early incurs several advantages as early arrivals can use high-quality habitats, which allow birds to produce a higher number of eggs and heavier fledglings due to the extra time and available resources at these habitats (Smith and Moore 2005).

My results suggest that purple martin migratory flight distances, altitudes or speed was not significantly affected by daytime or nighttime, despite purple martins generally being considered diurnal migrants. Additionally, since they are aerial insectivores, it was thought that flight behaviour would change depending on insect availability, such as temperature (Brown 1976). Even though temperature was correlated with time of day, purple martin's flight behaviour (i.e., distance, altitude or speed) was not correlated with temperature. Further studies could investigate purple martin flight in temperate areas, where temperatures are more variable and cooler, since my study was limited to the tropics (i.e., South America and Southern Mexico) (Ghalambor et al. 2006). This increased scope could examine the temperature effects for hourly flights across all of a purple martin's migration to understand how climate change could impact flight behaviours, especially since migration timing can have devastating consequences for a bird's fitness, directly or indirectly. Therefore, we must understand the conditions that birds, especially declining bird populations, encounter during migration. Then, we could determine how these conditions change over time because of human activity, such as climate change, and if there are ways in which they could be rectified for future bird populations.

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TABLE 1. Data retrieved from after-second-year purple martin (*Progne subis*) tags over spring 2023 migration.

Bird ID	Sex	No. GPS Fixes	Migration track start-end	Location(s) travelled	Daytime migration speed (km/h) (mean±SD)	Nighttime migration speed (km/h) (mean±SD)
4219	F	N/A	N/A	N/A	N/A	N/A
4222	M	1	N/A	N/A	N/A	N/A
4227	M	64	April 26-May 1, 2023	Brazil	N/A	N/A
4234	F	22	April 26-April 27, 2023	Venezuela	15.41±7.10	16.36±4.78
4213	F	65	April 26-May 1, 2023	Brazil, Colombia, Venezuela	16.79±6.72	10.22±2.35
4241	M	75	April 26-May 2, 2023	Venezuela, Colombia, Panama, Caribbean Sea, Costa Rica, Nicaragua, Honduras	13.58±4.86	13.72±5.16
4215	F	72	April 26-May 1, 2023	Caribbean Sea, Belize, Mexico	11.21±4.57	N/A

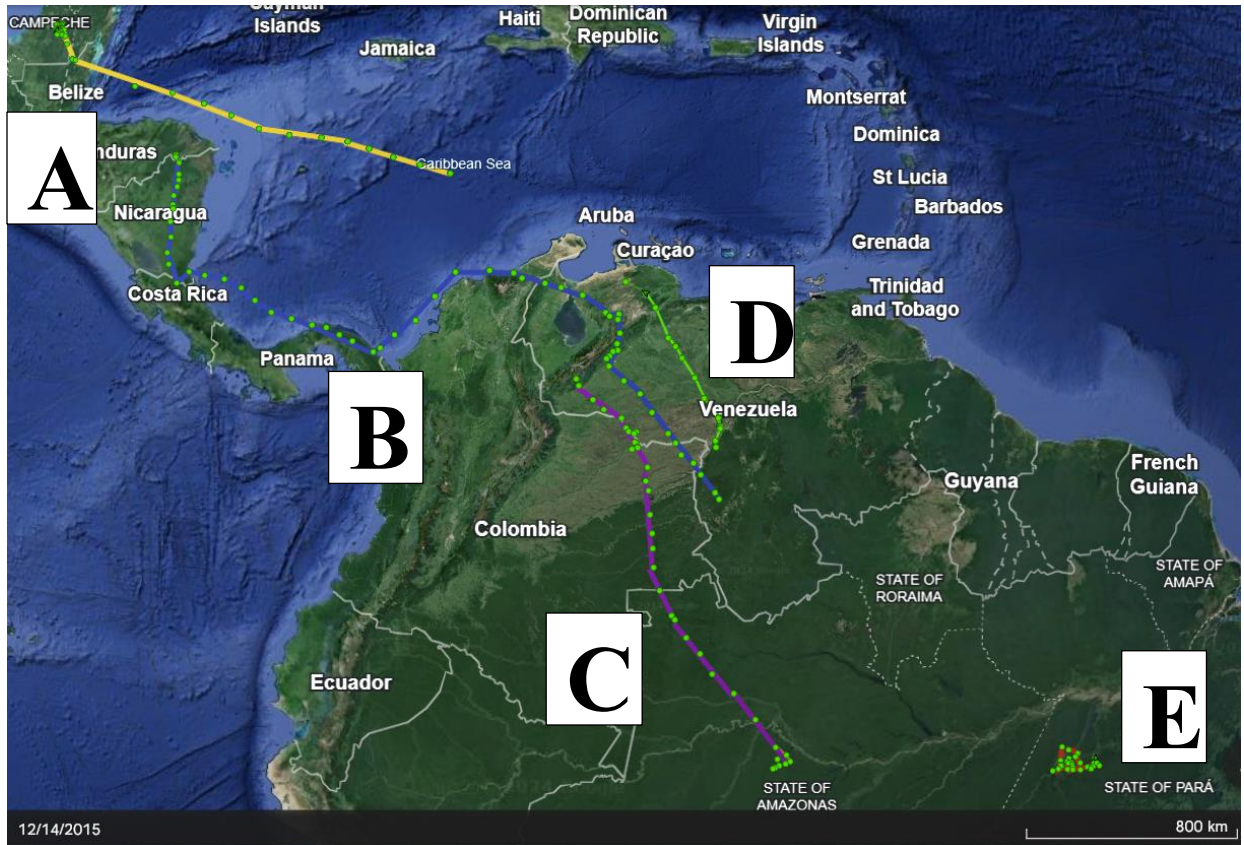


FIGURE 1. Five purple martin (*Progne subis*) migration tracks collected from GPS tags over spring 2023 migration with tag numbers (number of GPS fixes). **A)** 4215 (72); **B)** 4241 (75); **C)** 4213 (65), **D)** 4234 (22), and **E)** 4227 (64).

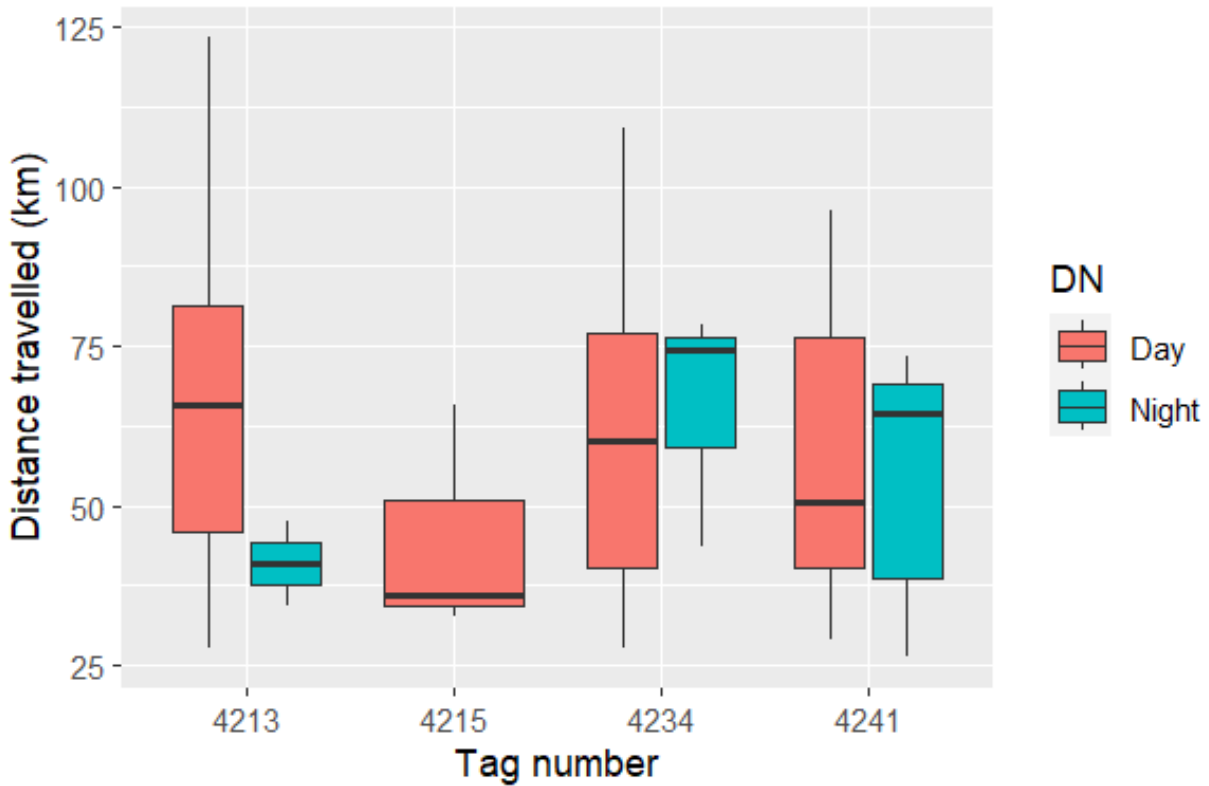


FIGURE 2. Boxplot comparisons of day vs. night distances at a 2-hour scale for tagged purple martins 4213 ('Day,' n=23; 'Night,' n=2), 4215 ('Day,' n=3), 4234 ('Day,' n=7; 'Night,' n=3), 4241 ('Day,' n=28; 'Night,' n=6) during spring 2023 migration. Whiskers represent 1.5 times the Interquartile Range (box) and black horizontal lines represent medians. In a GLM test, distance travelled was not a significant predictor of Day or Night flight ($F_{1,71}=0.37$, $p=0.55$).

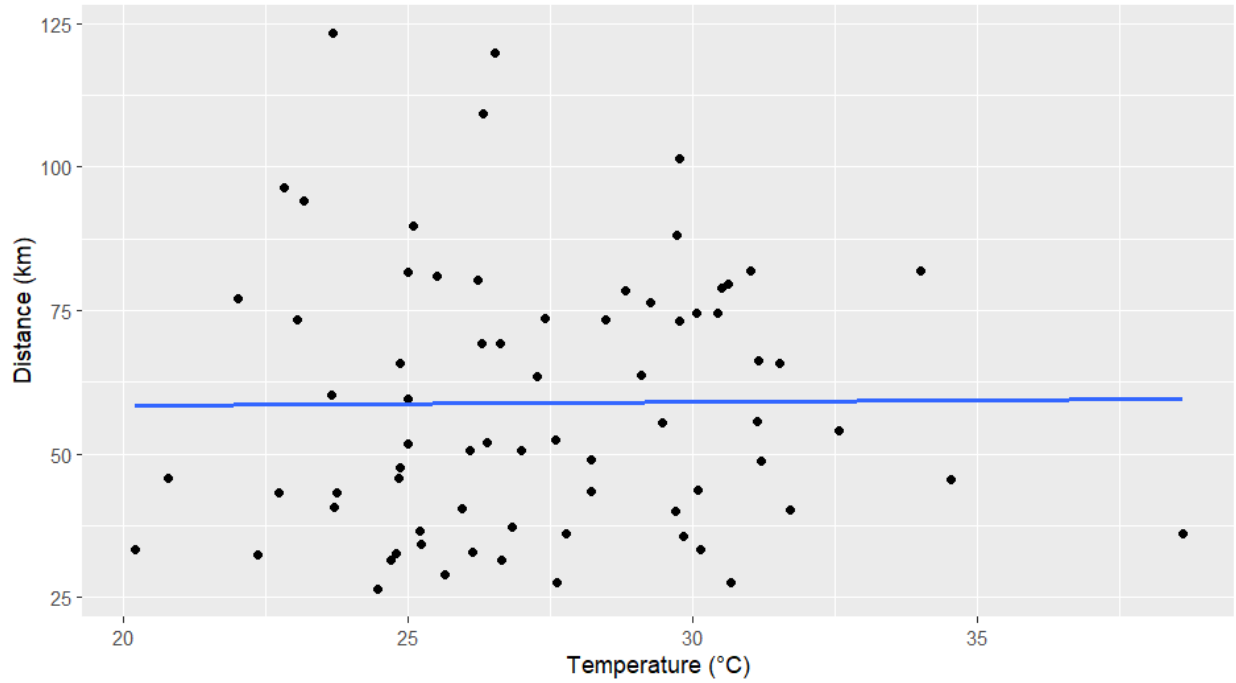


FIGURE 3. Plot of the distance travelled (km) over average temperature (°C) for individual migration points every two hours from April 26-May 2, 2023, of four purple martins (*Progne subis*) (i.e., 4213, 4215, 4234, and 4241) with line of best fit. In a GLM test, temperature was not significantly correlated with distance ($F_{1,70}=0.0058$, $p=0.94$).

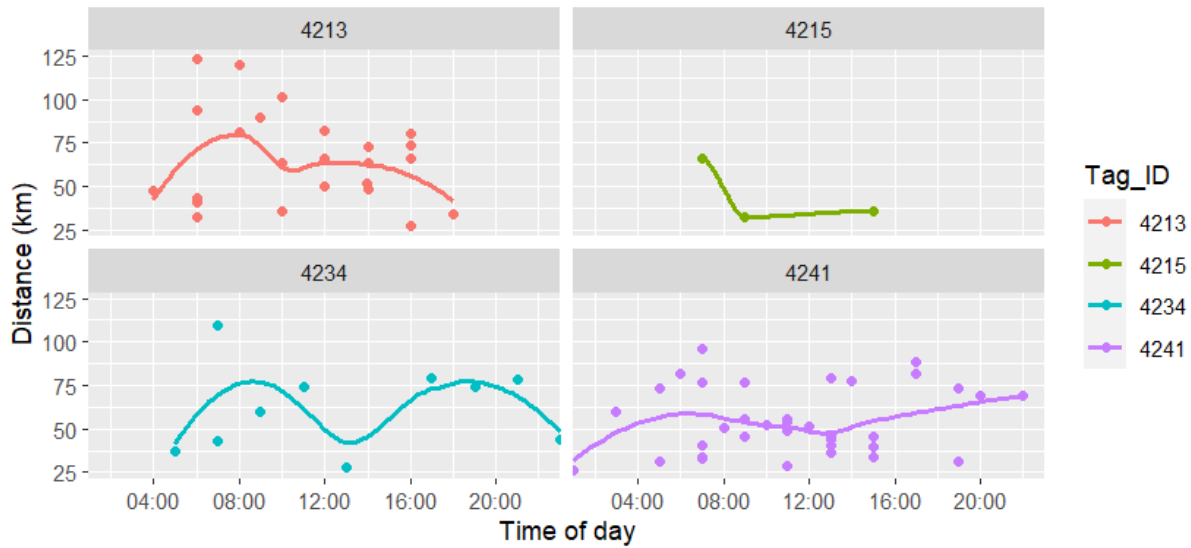


FIGURE 4. Plot of the distance travelled (km) over time of day every two hours from April 26-May 2, 2023, of four purple martins (*Progne subis*) (i.e., 4213, 4215, 4234, and 4241) with lines of best fit. In GLMs, time of day was not significantly correlated with distance ($F_{7,64}=0.95$, $p=0.48$).

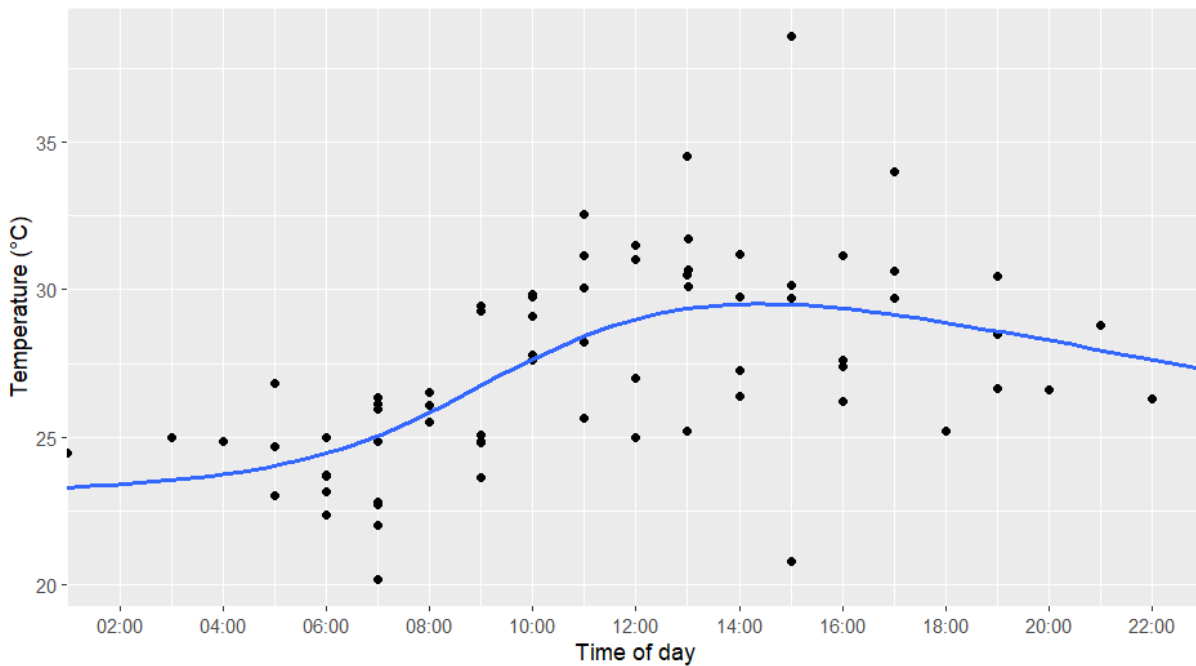


FIGURE 5. Plot of the average temperature (°C) over time of day for individual migration points with a line of best fit. Every point is a single GPS fix every two hours from April 26-May 2, 2023, of purple martins (*Progne subis*). In GLMs, time of day was significantly correlated with temperature ($F_{1,70}=20.64$, $p<0.001$).

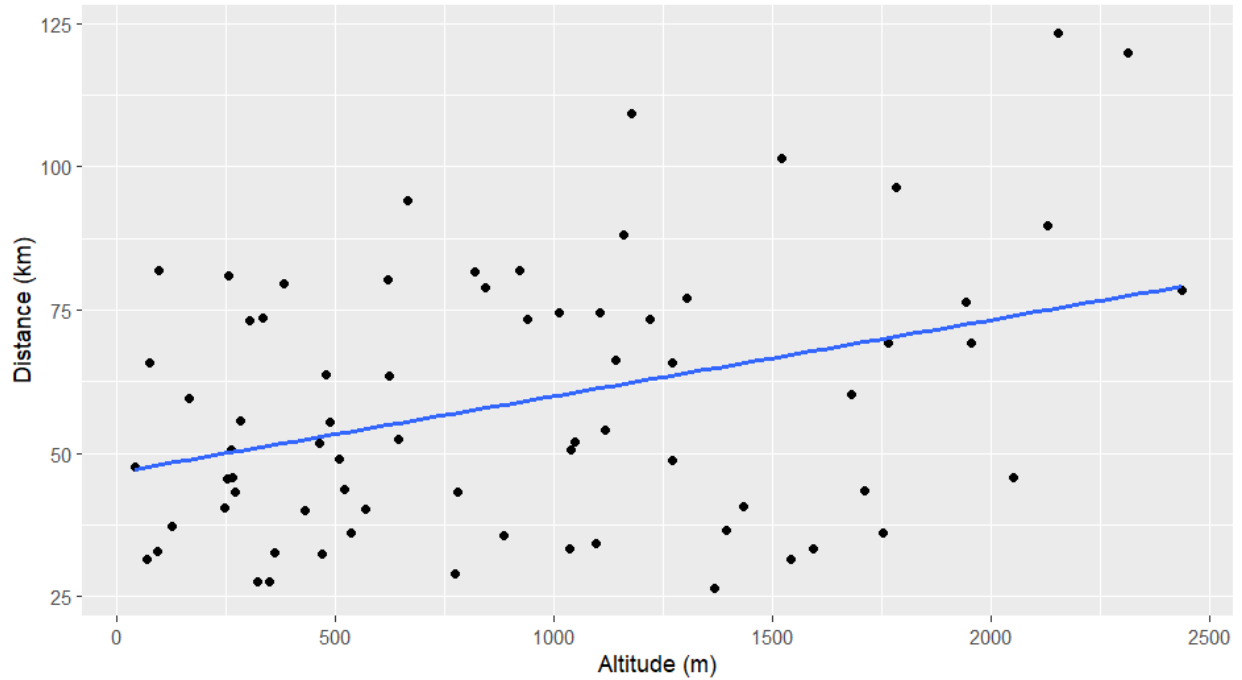


FIGURE 6. Plot of the distance (km) over altitude (m) for individual migration points with a line of best fit. Every point is a single GPS fix every two hours from April 26-May 2, 2023, of purple martins (*Progne subis*). In a GLM test, altitude was significantly correlated with distance ($F_{1,70}=10.65$, $p=0.002$).