

The Use of Nocturnal Flights for Barrier Crossing in a Diurnally Migrating Songbird: Implications for Our Understanding of Fly-and-Forage Migration Strategies

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Research

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Abstract

Background: The migration patterns of land birds can generally be divided into those species that migrate principally during the day and those that migrate during the night. Some species may show individual plasticity in the use of day or night flight, particularly when crossing large, open-water or desert barriers. However, individual plasticity in circadian patterns of migratory flights in diurnal songbirds that use a fly-and-forage migration strategy has never been investigated.

Methods: We used high precision GPS tracking of a diurnal, migratory swallow Purple martin, (*Progne subis*), to determine whether individuals were flexible in their spring migration strategies to include some night flight, particularly at barrier crossing.

Results: We found that individuals made large (sometimes >1000 km), open-water crossings of the Caribbean Sea and the Gulf of Mexico that included the use of night flight. Some birds-initiated barrier crossing flights at night, demonstrating that night flight is not only used to complete barrier crossings but may confer other advantages for diurnal birds. All birds also used some, shorter night flights when making overland flights not associated with barrier crossing. Birds were more likely to initiate water crossings with supportive northward winds, and preliminary data suggest that moonlight may influence nighttime migratory movements.

Conclusions: Overall, our results demonstrate an unexpected high degree of individual plasticity in migration strategies on a circadian scale in a 'diurnal' songbird and suggest that barrier crossing at night may complement fly-and-forage migration strategies.

Background

The migratory movements of animals can often be characterized by whether they occur primarily during daylight hours or during the night. Many diurnal land bird species that are usually active only during the day, migrate during the night can confer advantages of time and energy savings, and reduced predation [1, 2]. However, these 'nocturnal' migrants can also sometimes be observed moving in a migratory direction during the day [1], demonstrating some flexibility in circadian timing strategies. In many cases, these movements can be attributed to completing the crossing of a major ecological barrier, to re-orientate and correct movement errors, or to avoid poor weather [1,3,4,5]. For example, recent direct tracking data has shown that nocturnally migrating songbirds crossing the Sahara Desert during spring migration use some day flight in order to complete the crossing of this inhospitable barrier [2–4]. For other migratory land birds, day-night divides may be more impermeable barriers to migratory activity, or alternatively, flight pattern structure may be maintained despite changes in light regimes. For example, some nocturnal species, such as nightjars, may be restricted to nocturnal migration throughout their journeys [6,7] and some diurnal migrants moving north of the arctic circle may maintain the timing and duration of their diurnal flights, even when there are longer hours of daylight available [8].

Diurnally migrating birds need to both migrate and forage during the daytime and are thought to adopt a fly-and-forage strategy, where they both migrate and refuel during the day [9,10]. A fly-and-forage strategy may be supported by foraging opportunities that may occur during flight (such as for aerial insectivores), or at pauses during, or after, daily migratory flights [4,10]. It is predicted that diurnal migrants may incorporate nocturnal flights when they cannot benefit from energy deposition during a fly-and-forage strategy, such as when crossing ecological barriers or habitats with sub-optimal foraging [4]. Diurnal Eleonora's falcons (*Falco eleonora*) using a fly-and-forage migration strategy were found to be more flexible in their use of day or night flights during migration, particularly when crossing ecological barriers that did not provide insect rich areas for foraging [11]. However, whether diurnally migrating songbirds that use a fly-and-forage strategy of migration, such as swallows, use nocturnal flight during migration has been little investigated [12]. Recent investigations of swallow diurnal versus nocturnal movements confirmed only daytime movements [12]. However, direct tracking across migration of some diurnally-migrating species at large barrier crossings suggest some night flight may be incorporated, but has not been directly examined [13,14].

The diversity of migration timing strategies, especially in ecological barrier crossings, can also reflect species-specific, or intraspecific strategies [4,5]. For example, Whinchats (*Saxicola rubetra*) crossing the Sahara Desert had higher predicted speed and duration of flights as compared to when crossing the Mediterranean Sea, which is a considerably narrower barrier [15]. Investigations of the flexibility of diurnal or nocturnal migration over ecological barriers and across full migratory routes remain rare. New, high spatio-temporal precision in tracking technology that can be applied to studies of even small (< 100 g) migrants offers new opportunities to investigate migration timing strategies on a circadian scale.

As a trans-hemispheric long-distance migratory swallow, Purple martins (*Progne subis*) are thought to be exclusively diurnal birds that feed and migrate during the day using a fly-and-forage strategy [16]. They migrate up to 10,000 km seasonally between North

American breeding sites and South American overwintering sites choosing migratory routes that cross over the Gulf of Mexico or the Caribbean Sea, suggesting some night flight may be used to complete the crossing [13,14]. Our aim in this study was to apply high precision tracking using GPS units to determine whether this diurnal songbird uses both day and night flight to accomplish large ocean barrier crossings during spring migration, and/or whether they use nocturnal flights generally during their up to 10,000 km long journeys. Through this investigation, we tested the hypotheses that, 1) these diurnal migrants, that generally adopt a fly-and-forage strategy, may incorporate night flight at portions of their route where foraging opportunities are reduced or suboptimal, and 2) that night flights are associated with advantages of facilitating winds, or other time-savings that may be associated with the reduction of migration distance [4].

Methods

During the 2017 to 2019 breeding season we deployed a total of 98 GPS units (Pinpoint 10, Lotek Inc.) on adult Purple martins at four North American breeding locations (supplemental material, Table A). Purple martins were captured using drop-door traps at their nest boxes along with covering entrances with a painter's pole, and GPS units were mounted onto adults using a leg-loop backpack harness made of Teflon ribbon [17]. The mass of a tag (1.5 g) and harness was less than 3% of an adult Purple martin's body mass.

Tags were pre-programmed to collect positional fixes across spring migration at prescribed times that enabled the partitioning of day versus night flights. We programmed tags to align with breeding population-specific timing, previously identified through the use of light-level geolocators [13,14, Fraser et al. unpub. data], to capture the spring migration routes and timing we required for this investigation. Tags were therefore programmed to collect data points from early March (more southern breeding populations) to late April (more northern breeding populations). Tags were programmed to detect and save locations two or three times a day: 0600- and 1800-hours Central Daylight Time (CDT) (n = 8, Manitoba (MB) and Texas (TX) colonies); 0400- and 1600-hours Eastern Daylight Time (EDT) (n = 2, Pennsylvania (PA) and Florida (FL)); 0400, 1000 and 1600 hours (CDT) (n = 1, TX); 0000, 0600 and 1800 hours (CDT) (n = 1, TX). Detections at 0000 hours and at 1800 both reflected a portion of nocturnal flight [7], and therefore were combined to create a 12-hour night flight interval to make data comparable to those from other tags. Similarly, detections at 1000 hours were combined with detections at 0400 to make a 12-hour day flight interval for better comparison with other tags.

GPS units were retrieved in the year following deployment using the same methods of capture. Pinpoint software (Lotek Inc.) was used for data extraction. We defined flights between 1800 to 0600 and 1600 to 0400 hours as nocturnal flight and those between 0600 to 1800 and 0400 to 1600 as diurnal flight. Migration distances were measured as geodesic distances (km) between fixes using the R package *geosphere* [18].

Because the GPS tags collected locations on fixed schedules, the amount of daylight that occurred during the tracking periods varies as the season progresses and birds move substantial distances. We determined the amount of available daylight in each 12-hour track segment to address the possibility that some daylight occurring during the 'nighttime' flight time periods could account for some of the birds' movements during those periods. Daylight hours are defined as the time between sunrise and sunset (R package *suncalc*; [19]), and the amount of daylight per track was calculated according to the GPS locations and fix times at the beginning and end of a 12-hour track segment (i.e. time between sunrise or sunset at the bird's start location and sunset or sunrise at the bird's end location). Log-transformed 12-hour distances were regressed against amount of daylight in a linear mixed model (n = 190 day segments, 203 night segments).

To test the hypothesis that birds are more likely to cross large, open-water barriers. when the cost savings are the greatest, we compared the distances of water crossings to hypothetical circumnavigation around those water bodies by two methods. First, we measured the geodesic distances of simplistic, full, migration routes that birds could take if they flew only over land between their winter and breeding sites. We compared these routes to a second set of simplistic routes that connected, and included, the actual water crossings by the birds, which represent a combination of overland flight and water crossings. Then, we measured the distances of circumnavigational routes for each independent water crossing that each bird made, which represent the alternative that a bird would have when faced with a decision at the coast to launch a water crossing or reorient to remain over land. We also measured hypothetical water crossings to represent the alternative route when a bird had actually circumnavigated a water body. We fit a binomial regression with the decision to initiate a water crossing as the response variable, and the ratio of the distance across water to the distance around water as the predictor variable, with individual as a random effect. A ratio close to one indicates a low-cost savings by crossing the water, as the distances to follow a land or water route are similar.

We used the R package RNCEP [20] to retrieve surface-level U and V wind components from the NCEP/NCAR Reanalysis data provided by the NOAA/OAR/ESRL PSL, Boulder, CO, USA [21,22]. Wind variables for each GPS location were interpolated in time (from four daily measurements) and space (from global grids at varying spatial resolutions). We calculated wind direction and speed for each location, and classified wind direction into coarse northward flowing or southward flowing directions, between due west and due east, to test the influence of generally supportive or prohibiting winds in the preferred migratory direction (north during spring migration). We selected all GPS locations that occurred at coastal locations where birds could make a decision to initiate a water crossing or reorient to circumnavigate around the water body ($n = 31$), and based on their subsequent location, classified those coastal points into binary categories of 'launch' or 'did not launch' (i.e. 'reoriented'). We tested the likelihood of launching over a water body in a logistic regression, with wind speed, wind direction, and an interaction term including those variables, as fixed effects, and individual bird as a random effect.

We obtained moonlight data for each GPS location and time, using the R package suncalc [19] to test the influence of the fraction of moon face illuminated (MFI) on nighttime migratory movements. Binary occurrences ($n = 12$) of initiating a water crossing or reorienting to circumnavigate ('launch' or 'did not launch') were fit to a logistic regression model with MFI as a predictor variable and individual bird as a random effect. We also modeled the response of log-transformed distance to MFI (nighttime flights only) in a linear mixed model, which included an interaction between MFI and the binary classification of the flight occurring over water or over land, and individual bird as a random effect ($n = 203$).

Maps were created in ArcGIS 10.7 [23]. R version 3.6.1 [24] was used to create summary tables, and R version 4.0.3 for running the statistical analyses. We used the Bayesian package brms [25] to fit all linear models and validate models with posterior predictive checks. All model results reported here include 95% credible intervals. Wherever distance was included as a response variable, log-transformed distances produced better-fitting models than the original, non-log-transformed distances.

Results

During the breeding seasons of 2018–2020 we retrieved 12 GPS units ($n = 2$ FL, $n = 9$ TX, $n = 1$ MB). A tag retrieved in Texas recorded only 12 fixes and was excluded from our analysis. Among the remaining 11 tags, two began recording migration en route and two tags stopped recording data before birds reached their breeding sites (Fig. 1, 2). The number of useable points per individual ranged between 45–80 fixes per GPS unit (recorded over a sampling period up to ~ 40 days) with a total of 710 points from all 11 retrieved tags. After removing the points recorded outside of the migratory period (at breeding and wintering sites), a total of 461 points were used for further analysis of spring migration. Spring migration routes and timing fell within the range of what had been previously recorded when using light-level geolocator tags for these same breeding populations [13,14, Fraser et al. unpublished data]. Tag retrieval rates ($\sim 12\%$) were lower than previously reported in this species when using the same GPS units (tag retrieval at 17%, [26]), or when using tracking tags of similar weight and dimensions (retrieval rate of geolocators at 21–61%, [26,27]), and as compared to return rates for birds that were banded only (25–48%, [27]). Therefore, variation in survival rates between years and sites. could have contributed to the variation in tag retrieval within our study and the lower tag retrieval rate overall. Generally, tagged birds in this species tend to have similar return rates to birds that were banded only [27] and different tag types deployed in the same year at the same sites had comparable return rates [26]. However, since this study was not designed to test for factors contributing to tag retrieval rate, we cannot rule out a potential tag effect on survival. Further, sampling and re-sighting methods were not necessarily consistent across sites within this study or as compared to earlier studies; e.g. re-sighting, re-capture, and initial tagging occurred at varying times within the nesting cycle at different sites which could have contributed to variation in tag retrieval rates. A future study aimed specifically at investigating factors that may contribute to the retrieval rates of GPS units could better identify factors that influence retrieval rates.

We found that 10 of 11 birds made large, open-water crossings during spring migration that included night flight (Table 1). These open water flights occurred when birds crossed the Caribbean Sea or the Gulf of Mexico. Total, straight line distances of these open-water crossings ranged from 96.9–1,107 km. The average total distance for night flights over water per individual was 357.11 ± 25.69 km compared to 559.79 ± 49.82 km for flights during the day. The average total spring migration distance for Texas birds was 6526.85 ± 660.98 km and for Florida birds was approximately 5530.53 ± 474.66 km. The total migration distance for the Manitoba bird was 7611.8 km (Table 2). All eight birds that made some crossing of the Caribbean Sea used night flight and all eight birds that crossed the Gulf of Mexico also used night flight. Six birds that crossed the Caribbean Sea or the Gulf of Mexico initiated these crossings during

dark hours, not only at the end to complete the crossings. Surprisingly, all 11 birds also made overland flights at night that were not associated with barrier crossing.

Table 1

Details of each individual purple martin from where they were overwintering and when they started and ended migration to their breeding colonies. A total for their day and night flight over water was calculated from the GPS detections every 12 hours.

Bird ID	Sex	Breeding ground	Wintering location	Migration start	Migration end	Number of day flight over water	Number of night flight over water
1598	M	Florida	-2.31, -54.12	26/01/2018	NA	1	2
1602	M	Florida	-1.15, -62.09	14/01/2018	5/02/2018	3	2
2810	F	Texas	-1.37, -61.70	08/03/2020	NA	1	2
48041	M	Texas	7.84,-69.95	12/03/2018	15/04/2018	2	2
48042	F	Texas	NA	12/01/2018	22/03/2018	1	1
48045	F	Texas	-3.78, -58.3	27/03/2018	17/04/2018	2	2
48046	M	Texas	-2.83, -60.51	30/03/2018	20/04/2018	3	3
48051	F	Texas	-6.84, -51.7	14/03/2018	16/04/2018	1	-
48052	M	Texas	-2.12, -55.56	17/03/2018	4/04/2018	3	2
48794	M	Texas	16.06,-89.12	12/03/2019	29/03/2019	1	1
2177	M	Manitoba	2.36, -65.23	18/04/2019	07/05/2019	3	2

Table 2

Total migration distance for 11 purple martins with the mean and standard errors calculated for the distance travelled over land and water during the day and night.

Bird ID	Breeding ground	Total distance (km)	Distance of land/day (km) (mean \pm SE)	Distance of land/night (km) (mean \pm SE)	Distance of water/day (km) (mean \pm SE)	Distance of water/night (km) (mean \pm SE)
1598	Florida	4859.26	258.77 \pm 34.75	43.71 \pm 14.38	592 \pm 0.00	362.50 \pm 16.62
1602	Florida	6201.80	151.81 \pm 28.96	44.90 \pm 10.98	452.63 \pm 145.31	432.5 \pm 119.85
2810	Texas	3907.73	240.28 \pm 25.16	45.39 \pm 13.08	630 \pm 0.00	419 \pm 74.95
48041	Texas	7138.05	163.29 \pm 26.59	13.30 \pm 3.75	353.5 \pm 141.77	302 \pm 61.51
48042	Texas	3620.68	206.49 \pm 37.89	68.50 \pm 28.43	635.69 \pm 0.00	235 \pm 0.00
48045	Texas	8079.28	275.04 \pm 45.72	34.12 \pm 7.03	672.5 \pm 109.95	275.5 \pm 59.74
48046	Texas	6784.23	209.21 \pm 36.37	22.05 \pm 4.37	428 \pm 104.19	368.66 \pm 52.39
48051	Texas	8397.53	200.92 \pm 21.80	37.35 \pm 7.69	497 \pm 0.00	0.00
48052	Texas	7515.37	235.98 \pm 57.95	50.63 \pm 19.13	666.33 \pm 159.49	440 \pm 173.05
48794	Texas	4152.84	187.07 \pm 43.88	24.17 \pm 5.27	154.00 \pm 0.00	417.00 \pm 0.00
2177	Manitoba	7611.80	207.98 \pm 33.37	53.23 \pm 14.42	787.67 \pm 8.03	377.50 \pm 65.40

Among the birds that migrated to Florida, Texas, and Manitoba the longest, straight line distance between points covered within 24 hours occurred while birds were migrating over the Caribbean Sea; these included a 1,222 km flight with 1,006 km occurring over water for a bird (ID 1602) originating at a FL colony, a 1,378 km flight with 852.56 km occurring over water (bird ID 48052, TX) and a 1,274 km flight with 1,107 km occurring over water (bird ID 2177, MB; Fig. 2). The average flight distance in 24-hours was approximately 295.03 \pm 17.9 km.

Migration rate over open water was highest over the Caribbean Sea at 79.58 km/h during the day (tag ID 48052) and 50.17 km/h at night (tag ID 1602). The highest migration speed during the day over land was 57.08 km/h (tag ID 48794) and 32.17 km/h at night (tag ID 1598; Table 3). The total average migration rate was 12.25 \pm 0.70 km/h.

Table 3

Average migration rate over land and water (km/h) during the day and night as well as highest migration rate over land and water during the day and night (km/h). C: over Caribbean Sea, G: over Gulf of Mexico.

ID	Breeding ground	Migration rate land/day (mean \pm SE)	Migration rate land/night (mean \pm SE)	Migration rate water/day (mean \pm SE)	Migration rate water/night (mean \pm SE)	Highest migration rate land/day	Highest migration rate land/night	Highest migration rate water/day	Highest migration rate water/night
1598	Florida	21.56 \pm 4.88	3.64 \pm 3.98	49.33 \pm 0.00	30.21 \pm 1.38	36.58	32.17	49.33 C*	28.25 C
1602	Florida	12.65 \pm 2.48	3.82 \pm 0.96	37.72 \pm 12.10	36.04 \pm 9.98	44.67	20.75	53.42 G*	50.17 C
2810	Texas	20.78 \pm 2.06	3.78 \pm 1.09	52.50 \pm 0.00	34.92 \pm 6.24	30.58	14.33	52.50 C	43.75 C
48041	Texas	13.61 \pm 2.21	1.11 \pm 0.31	29.46 \pm 11.81	25.17 \pm 5.12	52.83	8.58	46.17 C	32.42 G
48042	Texas	17.21 \pm 3.15	5.71 \pm 2.36	52.97 \pm 0.00	19.58 \pm 0.00	42.25	26.25	52.97 G	19.58 G
48045	Texas	22.92 \pm 3.81	2.84 \pm 0.58	56.04 \pm 9.16	22.95 \pm 4.97	56.75	10.50	69 C	30 C
48046	Texas	17.43 \pm 3.03	1.83 \pm 0.36	35.66 \pm 8.68	30.72 \pm 4.36	42.17	6.75	56.92 G	41.42 C
48051	Texas	16.74 \pm 25.42	3.1 \pm 0.64	41.41 \pm 0.00	0.00	33.83	17.83	41.42 C	0.00
48052	Texas	19.67 \pm 4.82	4.22 \pm 1.49	55.52 \pm 13.29	36.66 \pm 1.00	56.75	28.08	79.58 C	38.08 G
48794	Texas	15.59 \pm 3.66	1.97 \pm 4.06	12.83 \pm 0.00	34.75 \pm 0.00	57.08	5.87	28.75 G	18.83 G
2177	Manitoba	17.33 \pm 2.78	4.44 \pm 1.20	65.64 \pm 0.66	31.45 \pm 5.45	42.92	17	67 C	39.17 C

Table 4

Distances of Purple Martin migratory routes including water crossings compared to routes constrained to land. Full migratory routes: distances are hypothetical shortest routes between winter sites and breeding sites that either include the actual water crossings of GPS-tracked birds, or follow strictly overland routes. Water crossings only: where birds made water crossings, hypothetical shortest distances of overland circumnavigations are compared. A ratio below one indicates a savings in distance travelled by using water crossings.

Full Migratory Routes			Water Crossings Only			
TagID	Distance Including Water Crossings (km)	Distance Over Land Only (km)	Water route:Land route distance ratio	Sum of Individual Water Crossings (km)	Sum of Circumnavigations (km)	Water crossing: Circumnavigation distance ratio
1602	5511	7380	0.75	2214	5540	0.40
1598	5712	8070	0.71	2422	5945	0.41
2177	6375	7395	0.86	3117	5520	0.56
2810	6161	6137	1.00	1247	2008	0.62
48041	5419	5482	0.99	1457	1751	0.83
48042	3323	3297	1.01	1120	1292	0.87
48045	7283	6905	1.05	1897	2414	0.79
48046	6466	6644	0.97	2388	3229	0.74
48051	7890	7744	1.02	498	625	0.80
48052	7089	7096	1.00	3416	4155	0.82
48794	2643	2703	0.98	417	493	0.85

During predominantly daytime flights, an increase in available daylight did not influence log distances (log km) traveled (slope 0.0024 [-0.0017, 0.0067]; Supplemental Fig S1a), but there was a statistically significant positive effect during predominantly nighttime flights (slope 0.013 [0.0065, 0.019]; Supplemental Fig S1b).

Hypothetical full-route distances between the winter sites and breeding sites are not always shorter when they include water crossings (Table 2). For eight of the 11 birds, an overland route was within 5% (longer or shorter) of routes that include water crossings. However, when birds are already at the coast and face a decision to cross a water body or circumnavigate it, crossing the water reduced the distance traveled (within those specific portions of the full route) to 40–87% of the alternative circumnavigation distance (Table 2). The probability of Purple Martins initiating a water crossing at the coast, rather than turning to circumnavigate over land, decreases as the potential savings in distance decrease (Supplemental Figure S2). That is, when the distances of a water crossing and the alternative circumnavigation were similar, birds were more likely to take the overland route than the overwater route.

The interaction between wind speed and direction was statistically significant (slope - 1.52 [-3.44, -0.13], with the effect of northward wind speeds being stronger than southward wind speeds (Fig. 3). The influence of MFI was weakly detected in both tests of moonlight influence (Fig. 4). Birds were more likely to initiate water crossings at night with higher levels of MFI (slope 18.52 [0.14, 80.30], although a small sample size ($n = 12$) resulted in wide credible intervals and our results should be interpreted cautiously. Log distances (log km) traveled during the night segments decreased as MFI increased (slope for overland flights was - 0.77 [-1.37, -0.18]; Fig. 4), but we did not detect a statistically significant difference in MFI effect between flights over land and flights over water (slope 0.70, [-1.49, 2.95].

Discussion

Our study provides the first direct-tracking evidence that swallows using a fly-and-forage strategy can also incorporate night flights into their migrations, particularly when crossing large, open-water barriers. The use of night flights in species usually characterized as diurnal, fly-and-forage migrants was predicted to occur at areas with reduced foraging opportunities, such as at barrier crossing [4]. This has recently been shown in falcons [11], but had not been demonstrated for diurnal songbirds such as swallows, that commonly cross ecological barriers [13,14] where some night flight was also predicted to be required to cross such great distances. Our direct tracking of adult purple martins using high precision GPS units support hypotheses for the use of nocturnal flights at barrier crossing

by otherwise diurnal migrants [4] and builds upon other recent direct-tracking evidence demonstrating the combination of day and night flights [e.g.28]. We also demonstrate how these flights are accomplished, wind conditions during night flights over water, and the rates travelled in comparison to daytime and overland flights.

Ten of the eleven purple martins that we tracked used night flight when crossing over water. In some ways this would be expected as birds migrating over open water would not have anywhere to stop for rest [29], and with a crossing of open water > 1000 km and flight speeds of 19–36 km/h, birds could not complete the cross during 12 hours of daylight. Barrier crossings may necessitate chiefly nocturnal or diurnal migrants to include flights during hours or light regimes where they do not typically migrate. This is because the distance required to cross these barriers, where landing and refueling is usually not possible, requires more than the available light or dark hours to complete. Despite a high prevalence of nocturnal flight in our study, the average migration distance over water was greater during the day as compared to the night. In part, this may be due to night flight being used primarily to finish off the crossing of the ecological barriers (13/19 open-water flights at night were to complete crossings). Similar to our findings for flights extending to cross day-night boundaries, several species of songbird incorporate some daytime flight into their otherwise nocturnal migrations in order to finish the crossing of the expansive migration barrier of the Sahara Desert [3,5,30].

However, we also found that 60% of individuals that used night flight for open water crossings also initiated these crossings at night. Night flights were therefore not only used to complete crossings initiated during daytime as could be predicted based on behavior of diurnal migrants crossing ecological barriers [9,16]. Our results support optimal timing hypotheses for fly-and-forage migrants, where it was predicted that daily travel schedules may shift toward night flights in areas that do not offer good foraging opportunities [4]. Ocean crossing during dark hours may support an otherwise diurnal, fly-and-forage migratory strategy in songbirds. In fly-and-forage, migrants can both migrate and refuel during daylight hours. Aerial insectivores such as purple martins and other swallows may be able to catch insect prey while heading in a general migratory direction or make short stops or detours to accomplish this task while maintaining their migration [9], or migratory flights may be undertaken in the morning daylight hours, leaving the afternoon for foraging and refueling [4]. Indeed, such a strategy may be evident in Bank swallows (*Riparia riparia*), where during fall migration travel speeds were slower suggesting they were actively refueling while migrating [31].

During open-ocean or other barrier crossing, the advantages of being able to forage while migrating may be reduced or eliminated, as aerial insect availability may be limited or absent over open ocean or desert [4]. In this case, selection may favor night flights for barrier crossing in fly-and-forage migrants in the same way that it does in other species that are diurnal foragers, but that migrate at night. This may serve as an advantage particularly over ecological barriers such as the Sahara Desert where birds are at higher risk of evaporative water loss during the day [32,33]. Purple martins may also select barrier crossing flights at night to confer other advantages, such as cooler temperatures, lighter winds, or other environmental factors such as reduced predation that may facilitate open-water crossing at night [34]. The migration speeds we measured for purple martins support this, where rates were highest when they were making open water crossings over the Caribbean Sea (e.g. up to 80 km/h).

Birds that engage in ocean crossing and incorporate night flights may reflect a time minimization strategy [22], where barrier crossing at the Caribbean Sea or Gulf of Mexico may greatly reduce overall distances travelled, and thus minimize the overall time and energy required to complete spring migration [35,36]. Indeed, the ocean crossings we documented reflect significant 'short cuts', as compared to an overland route throughout the same regions (i.e. Tag ID 48042: Gulf of Mexico crossing of 871 km versus around the Gulf route of 937 km). In some species, constraints of day-night light regimes for migration may preclude barrier crossing, as recently demonstrated in a nocturnally migrating nightjar that took the longer-route around the Gulf of Mexico, rather than crossing, which would have saved time and energy but required some daytime flight [7]. Our results show, at least for purple martins, that nocturnal flight does not pose a restriction to large barrier crossing, as it may do for nightjars. It would be valuable for future work to compare and contrast how the constraints of diurnal, fly-and-forage migrants may differ from nocturnal-restricted species that must migrate and forage within dark hours.

In addition to large, open-water flights at night, we observed shorter night over land. However, like night flights over water where we anticipate foraging opportunities to be low, these flights too may also be over areas that offer fewer foraging opportunities [4]. We found that night flights over land were much shorter than over water, suggesting night flights over land are a less used strategy in purple martins. There is also the potential that some of the flights we documented as 'night' flights, occurred around sunrise or sunset and therefore could have been completed in the twilight hours. Indeed, this was observed through automated radio tracking [37] of four swallow species that utilize a fly-and-forage strategy [12]. Our GPS tags were programmed to collect positions around 4am or 6am and 4 pm or 6 pm local time, which across spring migration effectively divides flights between daylight and dark hours. However, flights

occurring close to these times could be miscategorized. A positive relationship between 'nighttime' flight distances and amount of daylight available during each 12-hour track segment (Supplemental Figure S1b) indicates that some of the flight attributed to nighttime—especially in the shortest overland tracks—likely took place during daylight hours. However, the relatively small amounts of daylight available in each track could not reasonably account for long migratory flights. Further fine-scale tracking with higher sampling frequencies would enable confirmation of whether overland flights during strictly dark hours are used by martins or other swallows.

Incorporating water crossings into migrations between winter sites and breeding sites does not necessarily mean that purple martins were choosing the shortest routes (Table 2). If birds were to select the shortest routes, then those returning to breeding sites north or east of the Gulf of Mexico would benefit from taking shortcuts over the Caribbean Sea, Gulf of Honduras, and Gulf of Mexico, but Texas-breeding birds may actually add distance to their routes by navigating across those water bodies. Other factors may explain the broad-scale tendency to use coastal areas, hence putting the birds in positions that do make water crossings viable (Table 2). Overland routes through Central America contain a considerable amount of high-elevation terrain, so they may choose to avoid flight over mountain passes. For fly-and-forage migrants, low-lying coastal regions may also contain more resources for foraging. If purple martin migratory routes at a broad spatial scale generally favour coastal regions, then water crossings may be used as a tactic to save time and distance (Table 2), although may be avoided when those benefits are limited (Supplemental Fig. S2). When the birds are at the coast, facing a decision to cross the water or circumnavigate, supportive northward winds, combined with anticipated distance savings, may then play an important role in the departure decision. On the other hand, if atmospheric conditions over large water bodies are favourable for long migratory flights, birds may select routes that include water crossings, even if the total migration distance is longer as a result.

Our data indicate that the probability that purple martins will initiate water crossings during northbound spring migration increases with stronger winds flowing in a northward direction (Fig. 3). To a lesser degree, strong southward winds were likely to inhibit water crossings. While we did not have sufficient data to include a day/night distinction in the model, we do not suspect that wind has a varying effect on decision to initiate water crossings during day or night (see annotations of Fig. 3). However, regardless of wind factors, almost all instances of a bird reorienting to circumnavigate occurred during nighttime segments, and most water crossings were initiated during the day, suggesting that initiating water crossing at night is not generally favoured. Recent investigation has revealed that seascapes may provide energetic advantages through a combination of uplift and/or wind conditions ("energy seascape", [34,37]). While these advantages would apply the most to birds using soaring flight, our results suggest that birds may make crossing decisions based upon the energetics of the seascape. Further investigation of conditions at-sea during day and night would be a valuable area of future investigation.

We found a statistically significant effect of increased moonlight on the probability that martins will initiate water crossings at night (Fig. 4), but we interpret these results with caution, due to a small sample size. Additionally, although the difference in MFI effect between flights over land and flights over water was not statistically significant, we also had a comparatively small sample of water crossings (Fig. 4). Moonlight illuminating the night sky may have contrasting effects when birds fly over land or over water. Over land, a brightly lit sky may put a migrating songbird at risk of being more visible to predators, and a species that normally migrates during daylight hours may be at a distinct disadvantage. Conversely, predation risk may be lower over open water, thus minimizing the risk that bright moonlight would impose. We suggest that further investigation into the influence of moonlight on night flights in typically diurnally-migrating songbirds could clarify a possible relationship.

If purple martins migrate near the coast because of foraging opportunities, then they are in a position to take local shortcuts via water crossings. However, there is a possibility that water crossings play their own role in full, broad-scale route selection. For example, 1) supportive northward winds over water may save birds energy, and make longer routes worthwhile, 2) they can incorporate night flight into the long water crossings where they would not have the opportunity to forage, and 3) water crossings may help to avoid predation, which may be suggested by our preliminary results in relation to moonlight.

Conclusion

This is the first study of a swallow that uses a fly-and-forage strategy to examine circadian patterns of flight across migration to see how selection has potentially shaped day-night circadian migratory behaviors in these species. Our study demonstrates that a diurnal bird that uses a fly-and-forage migration strategy incorporates the use of nocturnal flights, mostly at barrier crossing, to both complete the crossing and possibly to confer additional advantages of optimal timing in a fly-and-forage strategy and the benefits offered by

night flights more generally. Future research could target further within-day patterns of movement, to test hypotheses for how diel foraging and refueling patterns may support the combination of night and day flights and open-water crossing in fly-and-forage migrants.

Declarations

Ethics approval and consent to participate: This research was conducted with approval from Animal Care Committees.

Consent for publication: All authors consent to publication

Availability of data and materials: Data will be made publicly available.

Competing interests: No competing interests to declare

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Author's contributions: CDL, SBA, and KCF conceived the project and designed the study, all authors conducted fieldwork, CDL, SBA, and AMK analyzed the data, CDL and KCF drafted the manuscript, all authors contributed to editing the manuscript.

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Figures

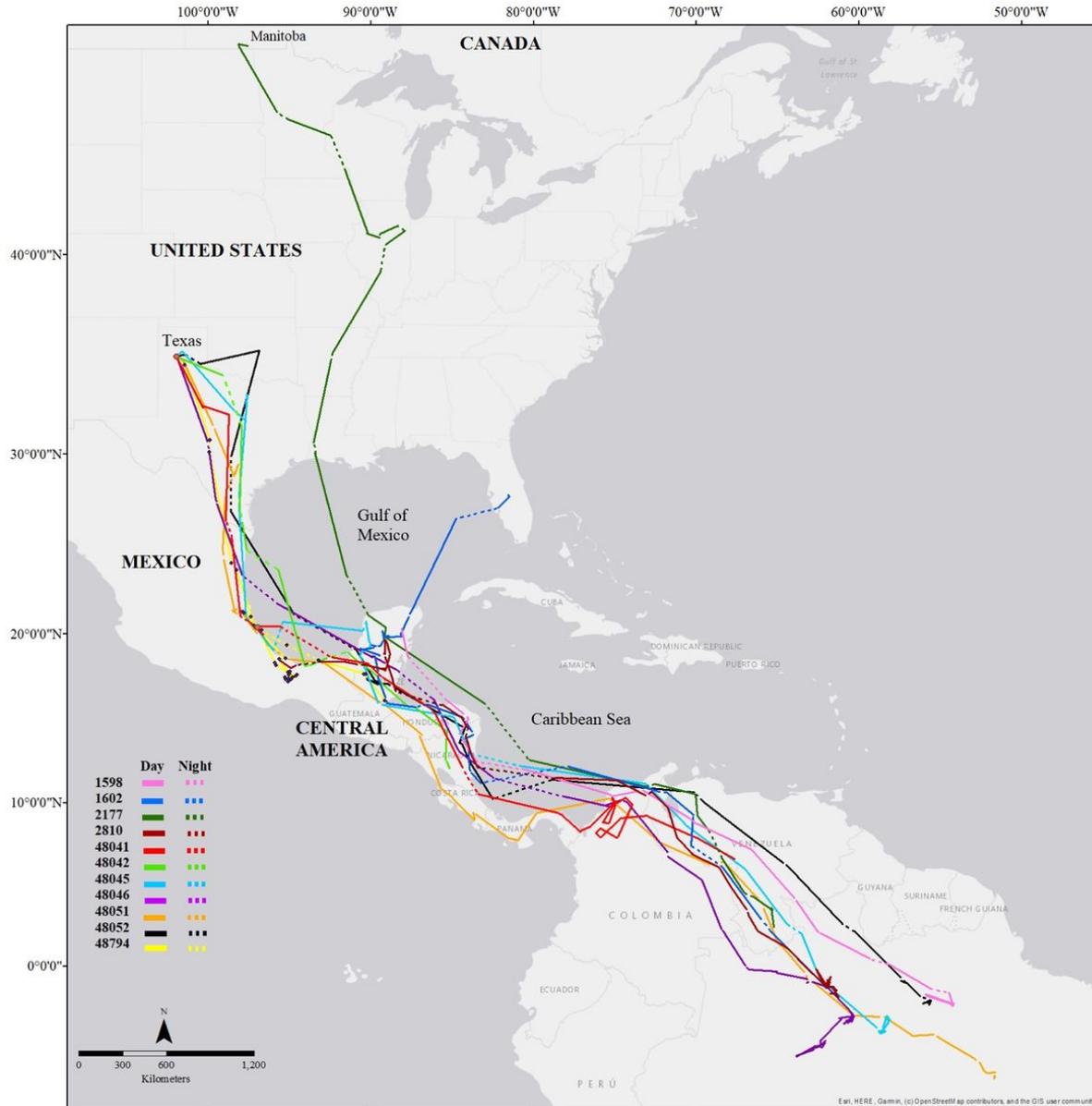


Figure 1

Global Positioning System locations of eleven spring migration tracks of purple martins from 2018-2020 going to three breeding locations, Texas and Florida, USA and Manitoba, Canada from their South American overwintering grounds. Straight lines do not necessarily reflect exact migratory paths. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

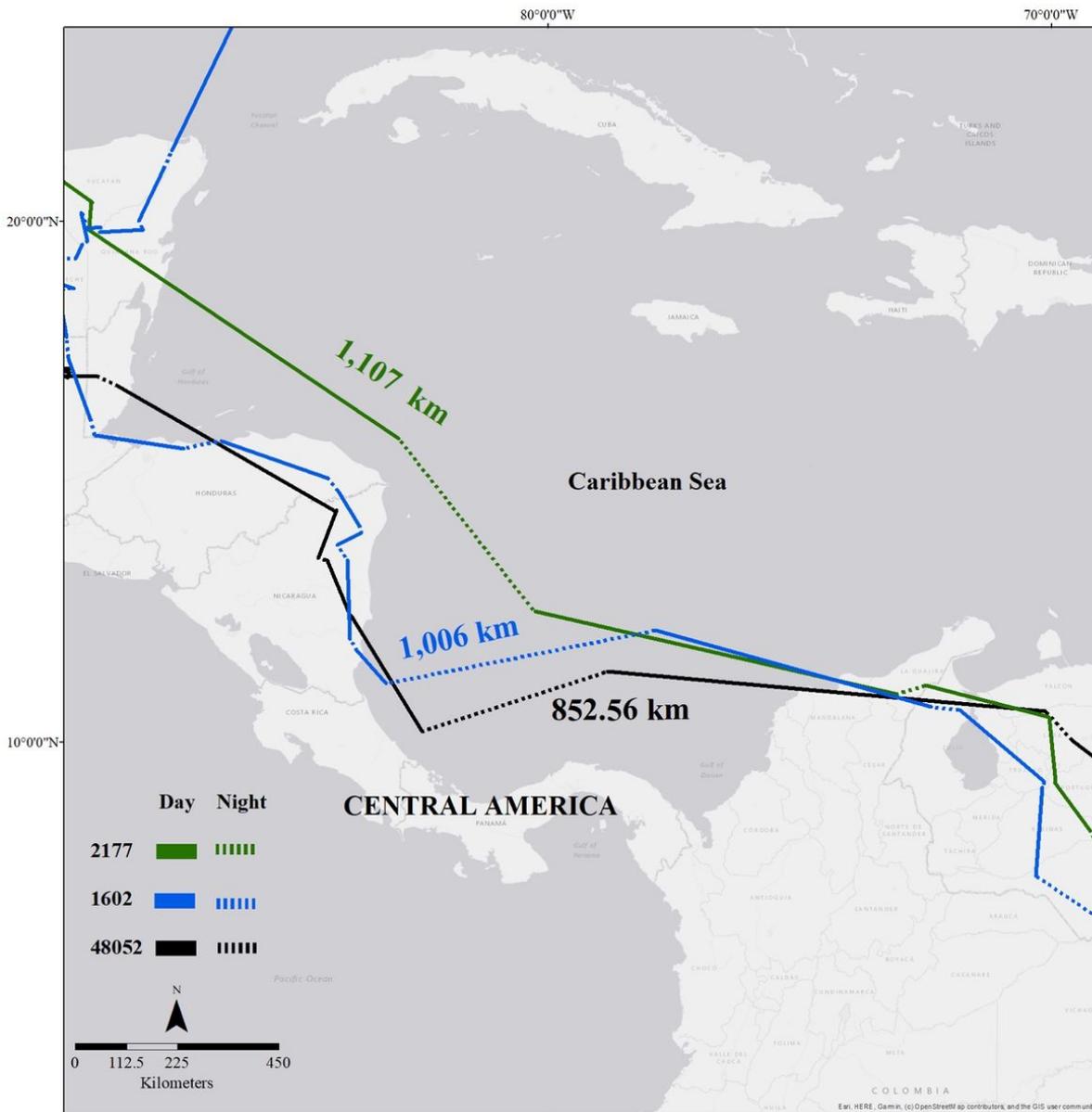


Figure 2

Longest migration distances over a 24-hour span crossing the Caribbean Sea for three purple martins returning to their breeding grounds in Manitoba, Canada (2177), Florida (1602) and Texas, USA (48052). Distances represent straight line flight over water and do not necessarily reflect exact flight path. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

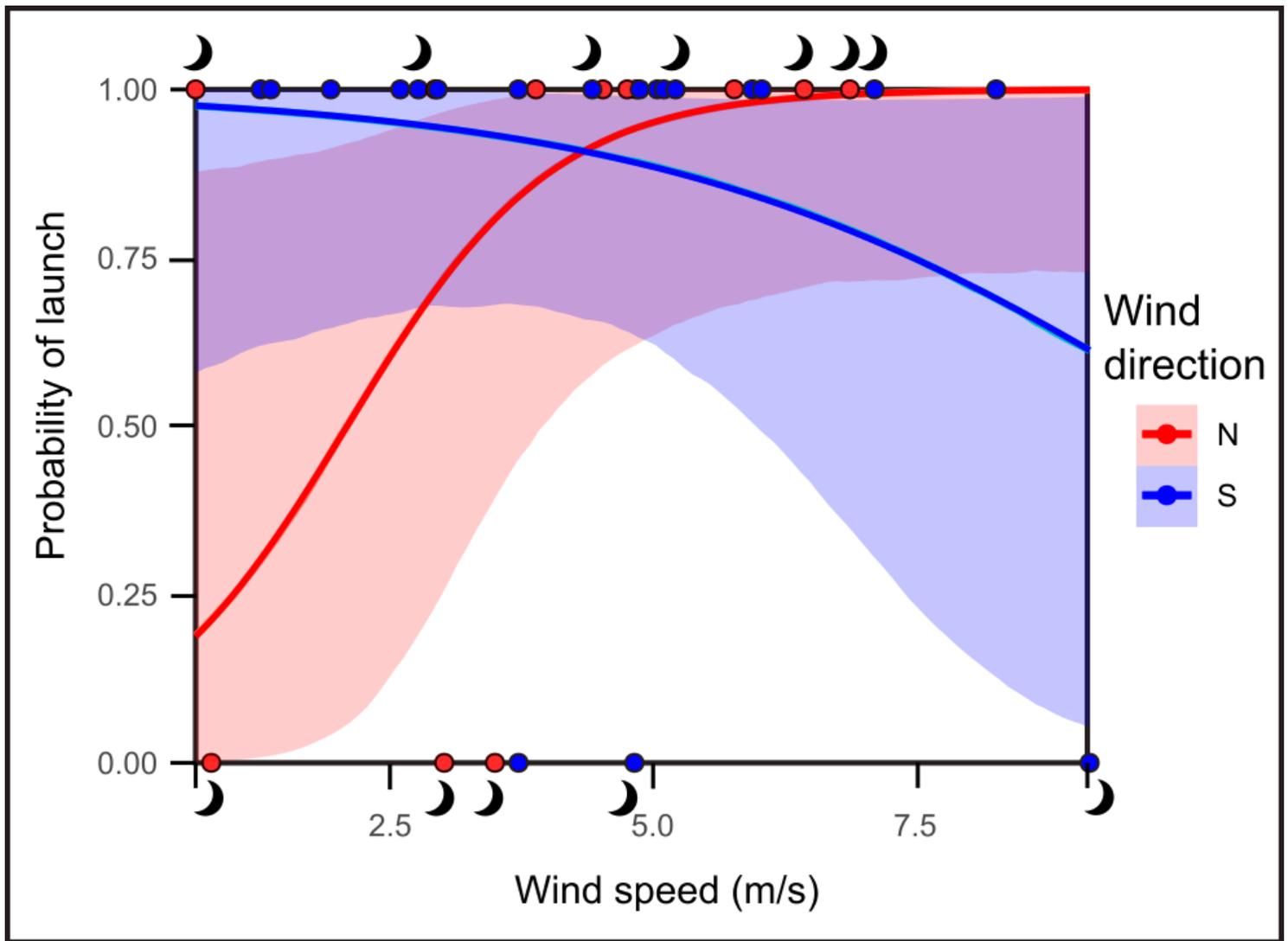


Figure 3

Probability that a Purple Martin initiates a water crossing, compared to altering course to circumnavigate, as a function of wind speed and direction. Individuals are more likely to initiate a water crossing in strong northward winds, and less likely to launch in strong southward winds, during northbound spring migrations. Actual data points are plotted for reference. Black crescents indicate coastal launches or turns that occurred during the 12hr segments representing nighttime flights.

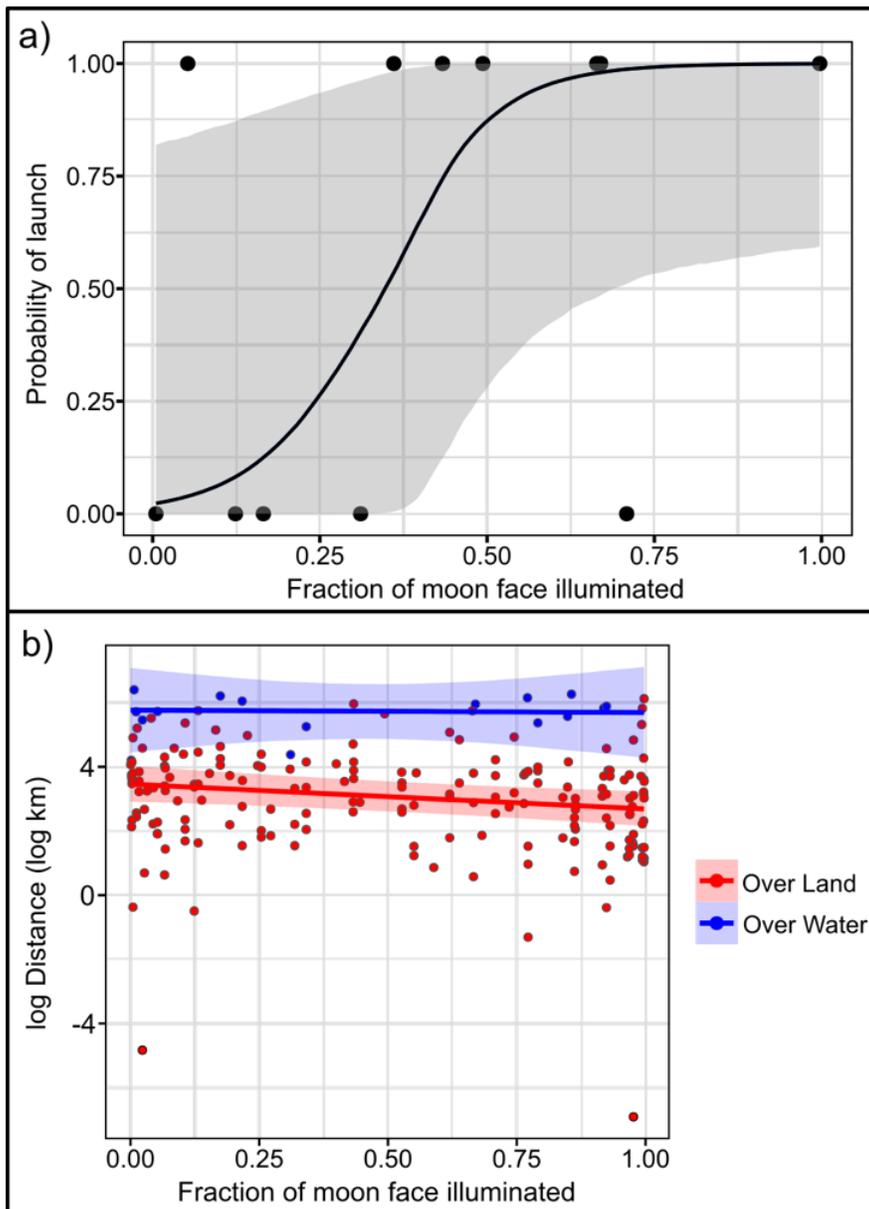


Figure 4

Influence of increasing moon face illumination (fractions of 0 and 1 represent new moon and full moon periods, respectively) on purple martin movements during spring migration. a) An increase in moon illumination weakly increases the probability that individuals will launch water crossings at night, rather than reorient to circumnavigate over land. b) An increase in moon illumination is associated with shorter distances travelled during night flights when travel occurs over land, but not over water. Actual data points are plotted for reference.

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