

Research Article

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Does wind speed and direction influence timing and route of a trans-hemispheric migratory songbird (purple martin) at a migration barrier?

<https://doi.org/10.1515/ami-2018-0005>

Received July 13, 2018; accepted October 26, 2018

Abstract: The influence of weather on the departure decisions and routes of migratory birds can now be further investigated with the use of direct tracking methods. We tested hypotheses for migration departure decisions and flight trajectories by determining the influence of wind speed and direction at the Yucatan peninsula in spring on departure date, migratory route, and longitude of arrival at the northern Gulf coast of a trans-hemispheric migratory songbird, purple martin (*Progne subis*). Birds were equipped with geolocators at their breeding colony and 36 were recaptured upon return after spring migration. While southerly tailwinds with low wind speeds prevailed at the Yucatan during the period of passage, we found that daily wind speed and direction were still important predictors of departure date. However, wind conditions at departure did not predict longitude of arrival at the US gulf coast after crossing the gulf. Birds appeared to favour the shortest distance across the Gulf of Mexico, aided by consistent tailwinds, but may have corrected for wind drift so as to land at a longitude near 88°, reflecting the shortest distance across from the Yucatan staging areas. Considering their use prior to departure, high quality roost sites at the Yucatan peninsula would be important conservation targets for this declining aerial insectivore.

Keywords: *Progne subis*; geocator; weather; NARR; Yucatan; Gulf of Mexico; GOM; trans gulf migration; spring migration; bird migration

1 Introduction:

Decades of research has been dedicated to understanding the innate mechanisms behind avian flight and orientation, as well as the influence of external conditions on migratory routes and timing (reviewed in Newton 2008). Strong evidence supports the existence of an endogenous spatiotemporal navigation system in migratory birds, with circannual rhythms cued by photoperiod triggering physiological processes that commence and regulate breeding, moulting, and migration (Gwinner 1996; Dawson et al. 2001). Despite these endogenous controls, there is still significant intra-individual variation within species' departure dates and trajectories suggesting some phenotypic plasticity at the individual level. A key question is the degree to which exogenous factors, such as weather, influence the migratory decisions of individuals from day to day, or year to year.

Departure decisions are influenced by a combination of factors. Wind may exert the strongest influence because it can affect flight energetics, direction of travel, and survival (Alerstam 1979). Optimal migration theory posits that migrants aim to achieve maximum flight efficiency while minimizing and balancing costs associated with time, energy, and predation risk (Alerstam and Lindstrom 1990). Wind has been shown to be an important factor in departure decisions as it affects the maximum fuel range for migrants (Alerstam 1979; Alerstam and Hedenstrom 1998). For example, the strongest predictors of whether Northern wheatears (*Oenanthe oenanthe*) would make a trans-oceanic flight or continental flight were the intersecting influences of sufficient fuel reserves and favourable wind direction (Schmaljohann and Naef Danzer 2011). Tree swallows (*Tachycineta bicolor*) migrating across the Gulf of Mexico departed on trans-gulf fall migrations only with favourable tailwinds, however, nearly all birds opted for circum-gulf routes during spring migration, ignoring favourable winds (Bradley 2014). Nightingales (*Luscinia megarhynchos*) may have been taking advantage

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of favourable winds on their spring migration detours as they were of the same duration but were longer distance, were not over areas with more suitable habitat availability, and had shorter stopovers than their autumn detours (Hahn et al. 2014).

The ways in which birds respond to favourable winds during their departure window may depend on their overall migration strategy. Bar tailed godwits (*Limosa lapponica*) make long, nonstop trans-Pacific endurance flight spanning 9 days (Gill et al. 2009), however, they consistently departed on days with seemingly neutral or unfavourable winds (Conklin and Battley 2011), and may instead respond to cues indicating long term favourable wind patterns (Gill et al. 2014). In contrast, great snipes (*Gallinago media*) fly non-stop across multiple ecological barriers, without much support from tailwinds (Klaassen et al. 2011). Their ground speeds of 54-97 km/hr, despite unfavourable winds, indicated their prioritization of time efficiency over minimizing energy costs (Klaassen et al. 2011) and may reflect a goal-oriented migration strategy (McLaren et al. 2014). However, snipe flights may not strongly reflect wind conditions because they are flying over land and therefore risks are lower.

Migration behaviour at geographical barriers provides an important opportunity to test hypotheses for departure decisions by migrants, since the risk for error is high. Many long-distance birds must choose whether to cross barriers like mountains, deserts, and oceans or to detour around them. Recently miniaturized tracking technology, such as light-level geolocators, has revolutionized the study of songbird migration (Stutchbury et al. 2009, McKinnon et al. 2013, McKinnon and Love 2018), and provides new opportunities to study the influence of wind conditions not only on stopover departure decisions but also on subsequent routes. Purple martins (*Progne subis*) are a model system for studying barrier crossing in songbirds – at commencement of spring migration, they depart from overwintering sites in the Amazon Basin, where the majority journey to the Yucatan peninsula where they embark on trans-gulf flights toward the US gulf coast (fig 1). We used purple martins originating from a breeding colony in northwestern Pennsylvania, where most birds (fig 1) make trans-gulf migrations in the spring (Fraser et al. 2013a). We investigated the effects of weather conditions at the northern Yucatan on the departure timing and route across the Gulf of Mexico. Wind speed and wind direction were expected to (1) influence the timing of migration across the Gulf of Mexico, and (2) the longitude of landfall upon arrival at the U.S coast. It was predicted that favourable southerly tailwinds at the Yucatan would increase the likelihood of departure, while northerly

headwinds would delay departure. Birds assisted by favourable winds were predicted to arrive at the US coast at a central longitude (i.e. shortest distance across); while those who departed on days with unfavourable winds would have more deviant routes.

2 Materials and Methods:

2.1 Geolocator Deployment and Retrieval at Study Sites

Purple martin migration routes and timing were measured from several North American breeding sites from 2007 to 2013 by Fraser et al. (2013a) and a subset were utilized in this paper. Due to the observation that birds from colonies situated in the central portion of the breeding range were more likely to make trans-gulf migrations (Fraser et al. 2013a) than birds from east coast or western populations, only data from purple martins (n=36) breeding at the northwestern Pennsylvania colony (41°53'08"N, 80°07'46"W) and whom engaged in trans-gulf spring migrations were analysed. Breeding birds were banded and equipped with solar geolocators which were retrieved upon their return to the breeding colony the following spring. No difference was found between return rates of birds with and without geolocators (Fraser et al. 2012). To analyse the relationship between wind speed (m/s), wind direction (degrees), and departure date when crossing the Gulf of Mexico, we determined the date of each bird's last night at the Yucatan Peninsula (Mexico), departure date, longitude and latitude within the Yucatan, and longitude upon arrival at the U.S Gulf coast. As diurnal migrants, it was assumed that purple martins would make the decision to depart at dawn (approximately 0630 CST). After daylight saving time, on average, sunrise occurs around 0630 CST in Merida, Yucatan, Mexico; with the nearest time for available weather data at 0700 CST. Using observational counts and WSR 88D radar data, purple martin pre-migratory roost departures in South Carolina have been documented as taking place over an average of 68 min from the initial instance of departure at 40min before sunrise (Russell and Gauthreaux Jr. 1998, Russell and Gauthreaux Jr. 1999). Under the assumption that the initial spring migration departure would mirror pre-migratory roost departure behaviours, 0700 CST falls within the time range of purple martin departures if sunrise occurs at 0630 CST and thus serves as an appropriate time to analyze weather conditions. Sex was determined in the field from distinct plumage characteristics, and was used to test if there were differential effects of wind

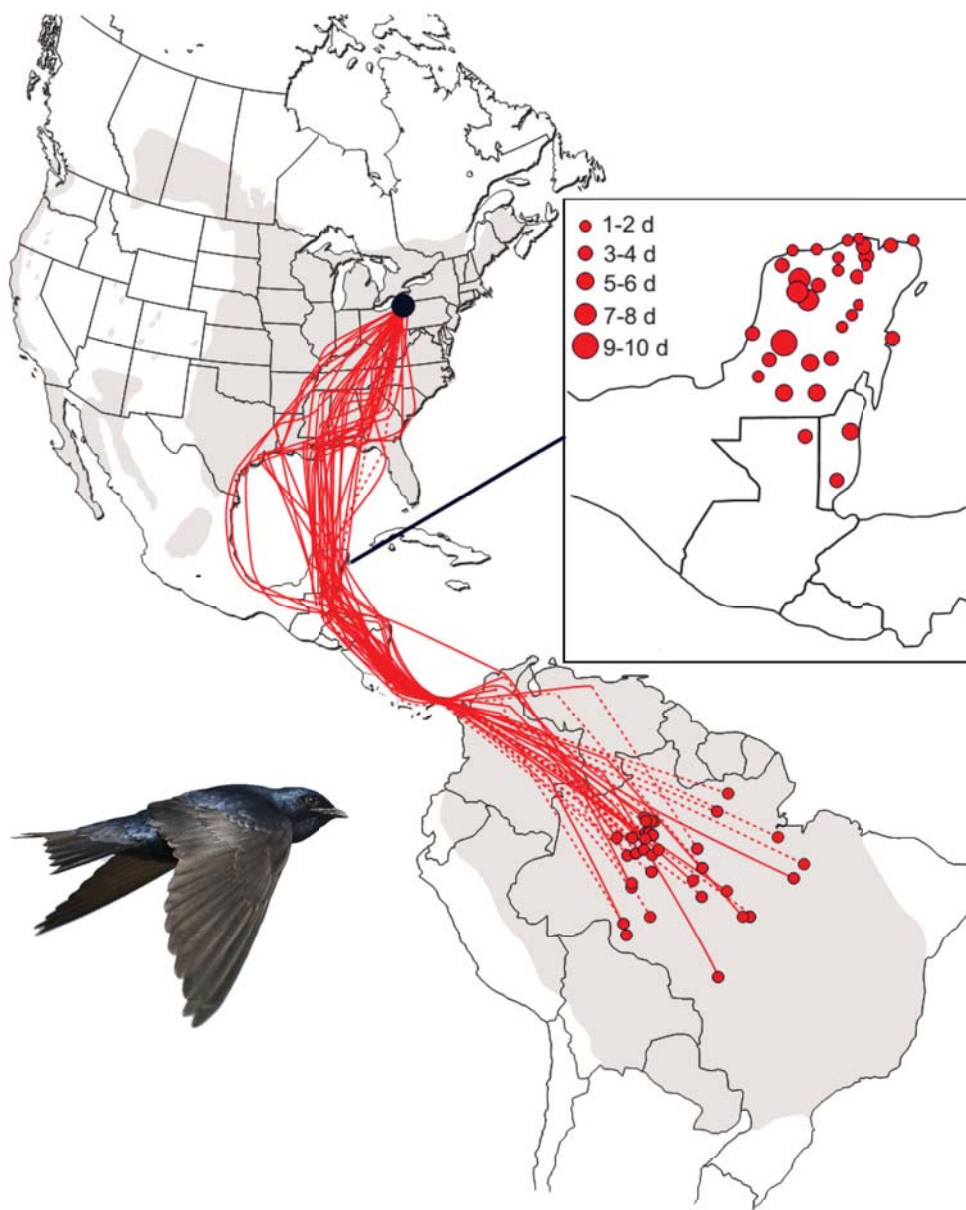


Figure 1. Spring migration routes and Yucatan stopover duration of purple martins ($n=41$; excluding 1 bird whose location fell over water at the Yucatan) originating from a northern Pennsylvania breeding colony. Dotted lines connect movements when latitude could not be determined due to the fall equinox. Solid lines represent movement from wintering grounds to Yucatan stopover, and departure from the Yucatan to the breeding site. The inset shows the duration of stopover days.

direction and speed on males and females who may differ in migration strategies.

2.2 Geolocator Analysis

Clock drift of raw light data were adjusted using BASTRAK software (British Antarctic Survey). Transitions at sunrise and sunset were manually confirmed using TRANSEEDIT. Sections of data with shading or light peaks and nonlinear transitions before sunrise or after sunset were eliminated

from the dataset. Light level thresholds of 32 (MK16, MK10), or 5 (MK12, MK20) were used to determine sunrise and sunset transitions. The corresponding average sun elevation for these light levels was determined through live calibration data from birds at breeding sites before fall migration. Sun elevation was calculated separately for different geolocator models, as different models had different light sensitivities and were averaged across individuals within each year to better represent average conditions for migrating birds at unknown locations.

While the calibration period at breeding sites may not directly reflect conditions during the migratory period, calibration was conducted after breeding (to remove impacts of nestbox shading) and purple martins are generally open-country, aerial foragers across the annual cycle, thus seasonally-based shading of the light sensor is expected to have less of an impact than in other songbirds that use highly vegetated habitats and/or undergo seasonal habitat shifts. Latitude was not determined for 15 days before and after the spring equinox, when day length is similar everywhere, and during this time positions were based on longitude alone. LOCATOR software (British Antarctic Survey) was used to calculate latitude and longitude coordinates at midnight locations since purple martins are diurnal migrants. Anomalous locations (i.e., >1,000 km since previous fix 12 hours prior) were rejected. Our previous analyses of geolocator error at breeding sites indicate that our position estimates may be accurate to within 49–60 km in latitude (range: 0–210 km) and 38–48 km in longitude (0–196 km). For more details see Fraser et al. (2012).

2.3 Weather Data

Data for wind speed and wind direction were obtained from the North American Regional Reanalysis (NARR) dataset which is publicly accessible at Movebank (movebank.org) and provided by the National Oceanic and Atmospheric Administration (NOAA). NARR is produced by the NOAA's National Centre for Atmospheric Prediction (NCEP) and it is a high resolution, long term, regional dataset that integrates weather data collected from various sources (radiosondes, dropsondes, surface, satellites etc.) in 3hr cycles (UTC) resulting in 8 data outputs daily. As diurnal migrants, purple martins are assumed to depart early in the morning (or approximately around sunrise). Local wind speed and wind directions were calculated from the zonal (u ; m/s) and meridional (v ; m/s) wind components produced by NARR. Wind speed and wind direction (10m from ground level) were obtained from two days prior to departure across the Gulf to the day after. This allowed for comparisons of weather conditions before, on, and following departure across the Gulf, in order to test if birds time their departure for more favourable conditions. While purple martin migratory altitudes are unknown and it is possible they may migrate using a range of altitudes, we measured wind conditions at 10m as these would be relevant to departure decisions at the start of migration and purple martins have been observed migrating <10m over the ocean off the coast of Belize in spring (Fraser pers. obs). Favourable wind directions for northward migration

were defined as winds blowing from the SE to the SW.

2.4 Statistical Analysis

We compared the variance between mean wind speeds on dates two days prior to departure, the day before departure, departure day, and the day after departure using ANOVAs. We also compared the variance in deviation from mean arrival longitude between departure intervals from April to May. Linear regressions were used to test whether the absolute deviation from the mean longitude of arrival at the U.S Gulf coast could be predicted by wind speed, wind direction, and sex. In previous work, we did not find an influence of wing morphology on migration performance (Lam et al. 2015), thus we did not include wing length as a factor in our analysis. For the regression analysis using the U and V components of wind, we first conducted a principle components analysis to distill U and V wind into two metrics that were used in the model. Error diagnostics were performed on U and V components of wind direction and assumptions of normality and variance were met.

Since wind direction is a circular variable, we analyzed variance in wind direction on dates two days prior to departure, the day before departure, departure day, and the day after departure using a circular analysis of variance (Lund et al. 2017) with a high concentration F-test to determine if there was a difference in concentration in wind direction over the four days. In this analysis, we weighted wind direction by wind speed to examine these two factors simultaneously. To determine the relationship between wind direction and the deviation from the mean longitude of arrival at the US Gulf coast we used both Jammalamadaka-Sarma Correlation Coefficient and Fischer-Lee Correlation Coefficient circular tests (Pewsey et al. 2013). Wind selectivity at departure may have an influence on deviation from mean arrival longitude, such that those individuals crossing the gulf during low winds may be less likely to deviate from an arrival longitude reflecting the shortest distance across. Alternatively, if individuals incorporate drift to take full advantage of tailwinds, as in an energy-selected migration strategy, this may also lead to deviations from the shortest distance across.

While longitude is a circular variable, due to the minor variations between the absolute deviations from the mean arrival longitude, we treated it as a linear variable in our tests. This was done to complement the Jammalamadaka-Sarma Correlation Coefficient and the Fischer-Lee Correlation Coefficient circular tests, as well as to incorporate the effect of sex (which the circular tests cannot incorporate).

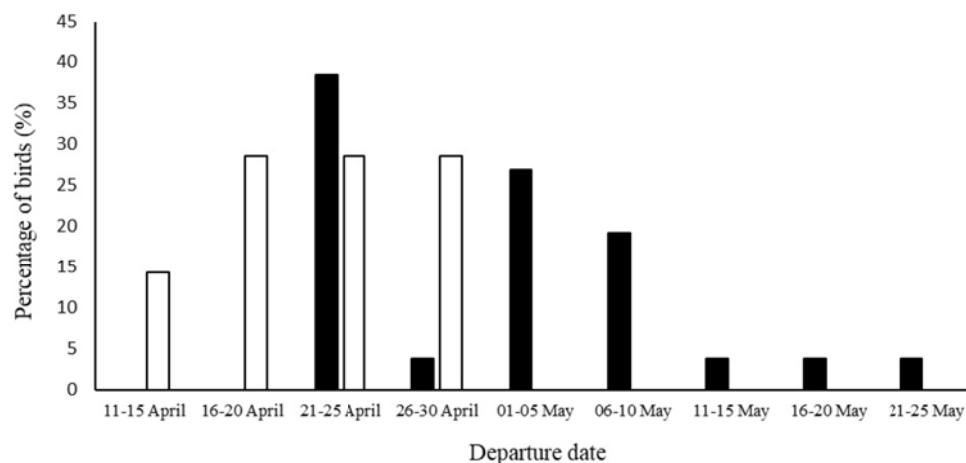


Figure 2. Departure dates from Yucatan stopover site of birds making trans-gulf journeys. Date of departure from the Yucatan for purple martins (males $n=7$; females $n=26$) on spring migration for the years 2007 to 2013. All birds had the same destination and bred at a colony in northwestern Pennsylvania. White and black bars refer to male and female birds respectively.

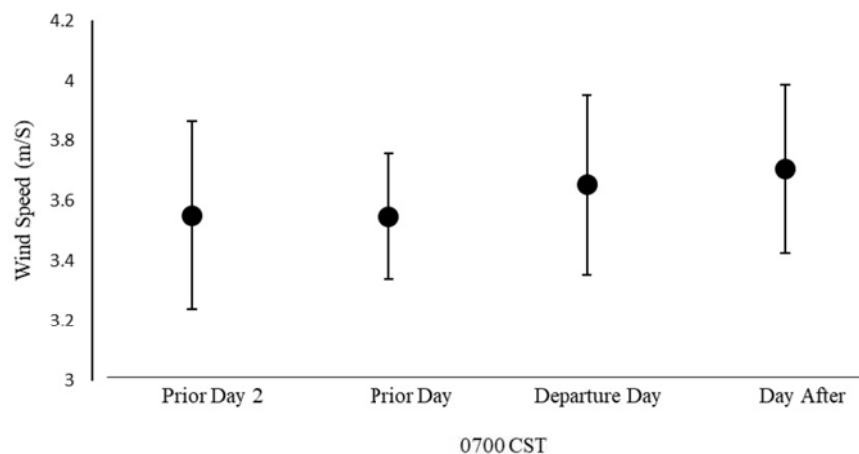


Figure 3. Relationship between wind speeds and departure from the Yucatan. Mean (\pm SE) wind speeds at 0700 CST at the Yucatan, Mexico relative to departure across the Gulf of Mexico migration of purple martins ($n=27$; excluding birds who stayed for only 1 night at the Yucatan; $F(3,104) = 0.80$, $p = 0.97$).

3 Results

Of 36 purple martins tracked from Pennsylvania, 33 (92%) made a northward trans-gulf migration (fig 1) during spring migration. Over all years, the timing of Gulf crossing among birds spanned over a month with two apparent peaks (fig 2). The interval in which most birds departed was from April 21-25 (36%; 10 females, 2 males) and from May 1-5 (21%; 7 females). All 7 male birds departed from the Yucatan by April 28 while more than half of female birds (57.7%) continued to depart on subsequent days up until May 21.

3.1 Wind Conditions at Departure

Only birds who spent a minimum of 2 nights ($n=27$) at the Yucatan were included in the subsequent analysis in figures 3 and 4. Wind speeds at 0700 CST were marginally higher on departure dates ($3.65 \text{ m/s} \pm 0.30\text{SE}$) and the day after departure ($3.71 \text{ m/s} \pm 0.28\text{SE}$) compared with prior to departure ($3.55 \text{ m/s} \pm 0.21\text{SE}$; fig 3). The variance between mean wind speeds two days prior to departure to one day after departure was not significant ($F(3,104) = 0.80$, $p = .97$). Over the four days, the majority of winds at 0700 CST blew from the ENE to SE (77.8%). In general, very few winds blew from the SSE to the ENE (22.2%) over the four

days at 0700 CST. The majority of winds two days prior to departure to the day before departure blew from the E and ESE (29.6%; 33.3% respectively; fig 4a, b). On the date of departure, the majority of winds blew equally from the E and SE (25.9% each; fig 4c). Lastly, on the day after departure, the majority of winds blew from the E (33.3%; fig 4d). When wind direction was weighted by wind speed in a single circular analysis, we found a significant main effect between days two days prior to one day after departure, ($F(3, 3927) = 19.22, p < .001$), suggesting individuals selected stronger winds from an E and SE direction at departure for crossing the gulf.

3.2 Wind Conditions and Longitude of Arrival

The mean longitude of landfall upon arrival at the U.S Gulf coast was $88^\circ \pm 0.47\text{SE}$. There was a wide range in arrival location along the U.S coast from 83° to 94° and up to ca. 1000 km apart. There was no relationship between wind speed at departure and deviation from mean longitude

of arrival ($R^2 = .013, F(1, 31) = .41, p = .53 > .05$; fig 5); the relationship remained nonsignificant when sex was considered ($R^2 = .069, F(2, 30) = 1.12, p = .34 > .05$; fig 5). There was no evidence that deviation from mean arrival longitude and wind direction at departure were correlated using either the Jammalamadaka-Sarma Correlation Coefficient ($n=33, r/S = -.044, p = .84 > .05$) or the Fischer-Lee Correlation Coefficient ($r_{FL} = -.005, p = .84 > .05$) (fig 6a, b).

In the multiple regression used to test factors influencing arrival longitude, the three predictors (PC1 wind, PC2 wind, and sex) explained 24% of the variance ($R^2 = .24, F(3, 29) = 3.13, p = .04 < .05$). The PC1 and PC2 representing variation of U and V wind did not significantly predict deviation in arrival longitude (PC1, $b = .06, p > .05$; PC2, $b = .19, p > .05$, however sex was a significant factor ($b = -.45, p = 0.01, < .05$), potentially reflecting differences in timing between the sexes (fig 2). The birds with the 2 highest deviations of 6.8° and 4.6° were both females experiencing winds from the E and SE respectively (fig 6a,b). In addition, they were among the

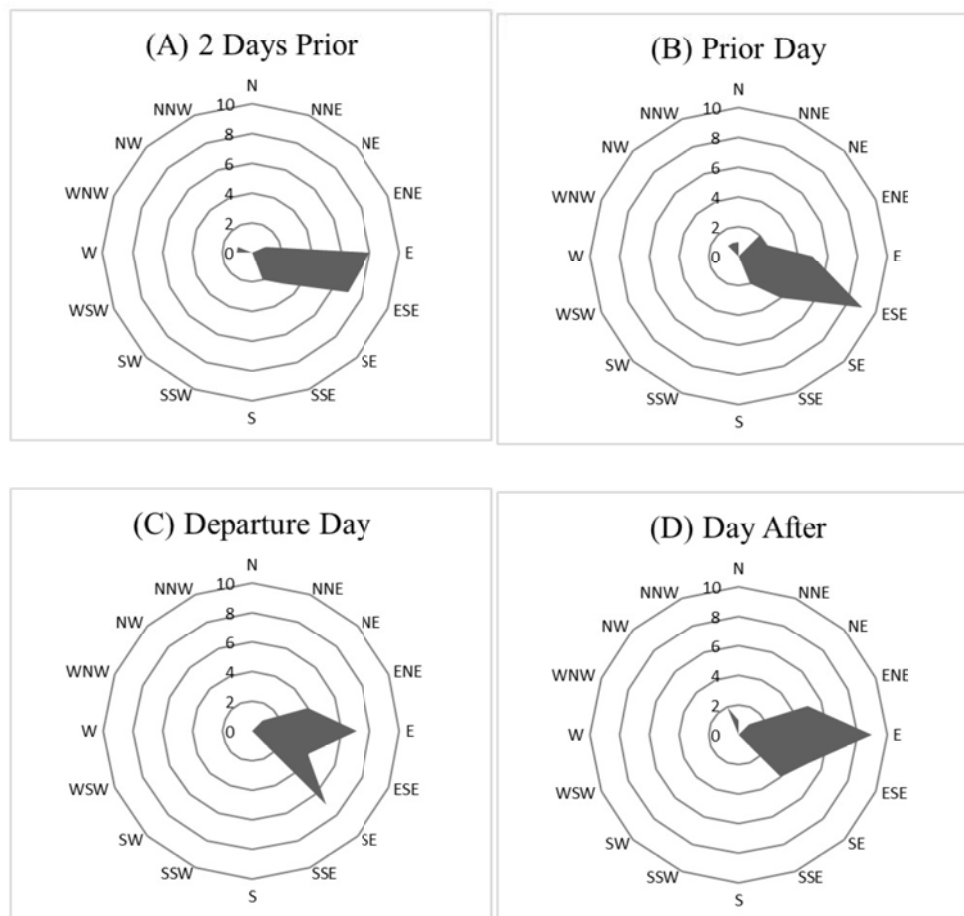


Figure 4. Relationship between wind direction and departure from the Yucatan. Wind direction at 0700 CST at the Yucatan, Mexico from two days prior to spring departure date to the day after ($n=27$; excluding birds who stayed for only 1 night at the Yucatan). Wind direction weighted by wind speed was significantly concentrated by day ($F(3, 104) = 19.22, p < .0001$). Winds are blowing from the indicated directions.

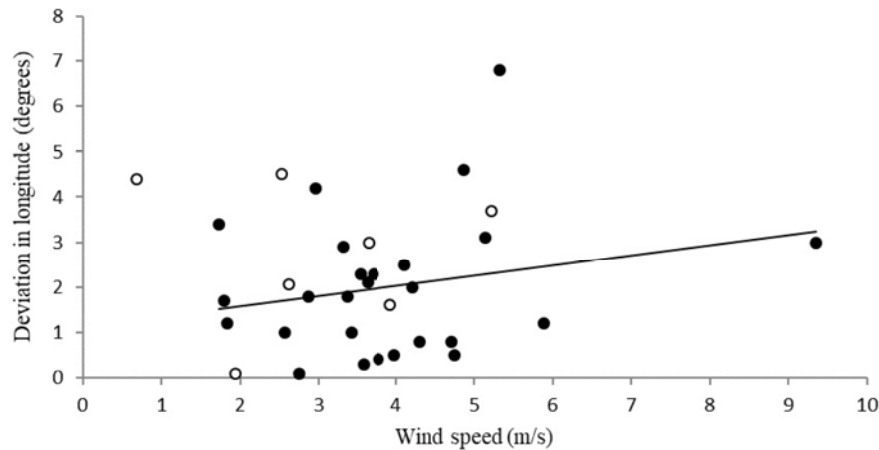


Figure 5. Effects of wind speed upon departure on the longitude of arrival at the U.S. gulf coast. Relationship between wind speed at departure at 0700 CST at the Yucatan, Mexico and the absolute deviation from the mean longitude (88°) at landfall of purple martins ($R^2 = .013$, $F(1, 31) = .41$, $p = .53 > .05$) upon their arrival at the U.S Gulf coast. White and black circles refer to male and female birds respectively.

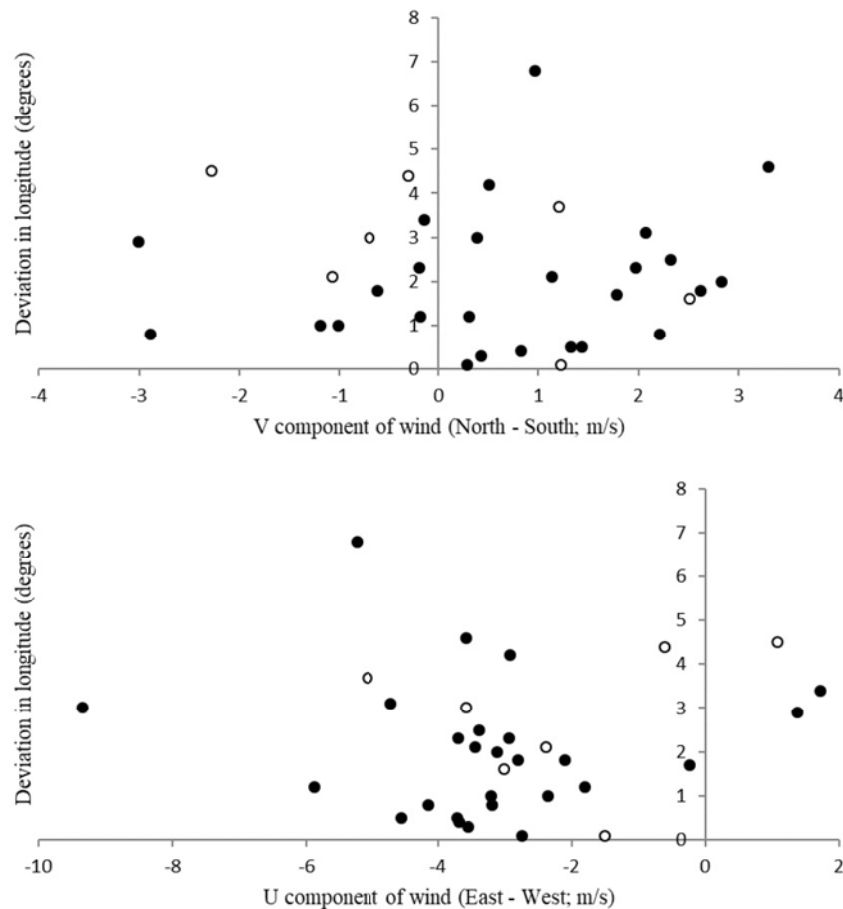


Figure 6. Effects of wind conditions upon departure on the longitude of arrival at the U.S. gulf coast. Relationship between the U and V components of wind direction at departure at 0700 CST at the Yucatan, Mexico and the absolute deviation from the mean longitude ($88^\circ \pm 0.47SE$) at landfall of purple martins upon their arrival at the U.S Gulf coast. U and V wind direction did not have a significant influence on deviation in longitude of arrival. A) (Top figure) Negative V values represent winds blowing from the north and positive V values represents winds blowing from the south. B) (Bottom figure) Negative U values represent winds blowing from the east and positive U values represents winds blowing from the west. White and black circles refer to male and female birds respectively.

last 3 birds that flew across the Gulf of Mexico. However, the variance in mean absolute deviation between departure intervals (fig 2) was nonsignificant ($F(8, 9) = 3.23, p = .20$). The bird with the highest deviation of 6.8° had a stopover duration of 1 day and travelled the longest distance of any individual from the Panama border (with Colombia) to the breeding site (5900 km). The bird with the second highest deviation of 4.6° had the longest stopover duration of 10 days.

Although purple martins rarely detoured around the Gulf (3/36), this route is expected to increase migration distance and duration. The average distance to the breeding site (Pennsylvania) from a common starting point (Panama border with Colombia) for circum-gulf flights was $5689 \text{ km} \pm 106\text{SE}$, and for trans gulf flights was $5042 \text{ km} \pm 65\text{SE}$. Circum-gulf flights took on average $17 \text{ days} \pm 2\text{SE}$, and were 3 days longer than trans gulf flights which took $14 \text{ days} \pm 1\text{SE}$. Thus circum-gulf routes increased distance by 12.8% and migration duration by 21%. Sample sizes of circum-gulf migrants are too small for statistical comparison.

4 Discussion

We found that wind speed and direction at the Yucatan were significant predictors of departure timing for crossing an open-water barrier (Gulf of Mexico). Our results show weather conditions around the time of spring crossing may generally support trans-gulf flights, with the majority of winds blowing from the E to the SE. Indeed, the majority of birds (66%) departed with winds blowing from these directions (fig 4c). While most winds were favourable and there was no significant difference in wind direction two days before departure date to the day after departure (fig 4a-d), we found that a combination of wind direction and wind speed shows that birds tended to select stronger winds from an easterly and south-easterly direction at the time of their departure.

We could not have measured energetic condition at departure from the Yucatan, but this may pose an additional influence on the departure decisions of migrants, as was found for blackpoll warblers (*Setophaga striata*) (Covino et al. 2015). Similarly, a multi-species study of migratory routes using automated telemetry (Deppe et al. 2015) revealed that humidity levels of 62% or lower were indicative of favourable wind conditions, and predicted individual departure for trans-gulf migrations in some species, but only when these conditions coincided with optimal fat stores. These results illustrate the potential for important interactions between energetic condition

and local weather conditions in determining departure decisions; such interactions could be investigated as important additional factors influencing departure decisions in the purple martin system.

Gauthreaux et al. (2006) generated atmospheric migration trajectories for trans-gulf flights of several groups of birds using weather data and hypothesized that a) wind direction over the gulf would be responsible for variance in arrival longitude, b) prevailing winds would result in a common arrival longitude, or c) regardless of wind variability, birds would arrive at an optimal longitude after crossing. At all altitudes studied (500m, 1500m, and 2500m) and wind directions, the trajectories of migrants converged at 95° suggesting that birds may be targeting optimal arrival longitudes reflecting the shortest distance across. Thus, while birds may be taking advantage of tailwinds upon departure, these may not determine their final longitude of landing at the coast, if they are targeting an arrival point that reflects the shortest distance across the barrier. For purple martins, we found that wind direction at departure was not a predictor of deviation from the mean arrival longitude of 88° at the U.S Gulf coast (fig 6a, b). Thus, purple martin routes across the gulf may reflect the shortest distance and they may not fully utilize the prevailing winds which otherwise would favour 93° . Similarly, radar tracking revealed that long-distance migratory passerines flying between Europe and Africa did not select for favourable wind conditions upon departure and flight trajectories were independent of the presence of headwinds or crosswinds, compromising their flight speeds (Alerstam et al. 2011).

We did not find a relationship between deviation from the mean arrival longitude and departure date. Spring migration rate in purple martins is far more rapid than fall (Stutchbury et al. 2009), potentially due to the dual selective pressures of seasonal differences in environmental conditions en route and competition at breeding sites, where earlier arrival in spring may confer advantages in terms of mate and nest site selection. Furthermore, spring stopovers at the Yucatan Peninsula are shorter in duration and last for 1 to 4 days (fig 1), whereas fall stopovers last 2 to 3 weeks. This suggests that spring migration may be more time-selected, and birds may depart even if conditions are not optimal.

Our multi-year study shows that individuals crossed an ecological barrier in spring under relatively favourable (tail) wind conditions, suggesting potential selection for gulf crossing under optimal conditions for this population. We reveal that even under these favourable conditions, birds may make more fine-scale departure decisions based upon wind strength and direction. Future research

using new, detailed archival (GPS) or real-time movement tracking could be aimed at determining factors during gulf crossing that may impact the speed and direction of barrier crossing. These techniques would also enable researchers to determine the consequences and mortality risk of varying departure timing and migratory routes. Lastly, the identification of precise roost locations used prior to crossing the Gulf would allow researchers to focus conservation action at critical stopover locations during spring migration.

Acknowledgements: We thank the many dedicated volunteers who assisted with geolocator deployment and retrieval, permits, and the availability of colonies for research. This work was funded by the Natural Sciences and Engineering Research Council of Canada, National Geographic Society, proceeds from the book *Silence of the Songbirds* (Stutchbury 2007), the University of Manitoba, and the Purple Martin Conservation Association. Special thanks to B. J. M. Stutchbury for her comments on the manuscript.

References

- Akesson S., Hedenstrom A., Wind selectivity of migratory flight departures in birds, *Behav Ecol Sociobiol.*, 2000, 47, 140-144
- Akesson S., Walinder G., Karlsson L., Ehnbohm S., Nocturnal migratory flight initiation in reed warblers *acrophalus scirpaceus*: effect of wind on orientation and timing of migration. *J Avian Biol.*, 2002, 33, 349-357
- Alerstam T., Wind as selective agent in bird migration, *Ornis Scand.*, 1979, 10, 76-93
- Alerstam T., Hedenstrom A., The development of bird migration theory, *J Avian Biol.*, 1998, 29, 343-369
- Alerstam T., Lindstrom A., Optimal bird migration: the relative importance of time, energy, and safety, In: Gwinner E. (Eds), *Bird migration: physiology and ecophysiology*, Springer-Verlag, New York, 1990
- Alerstam T., Chapman J., Backman J., Smith A., Karlsson H., Nilsson C., *et al.*, Convergent patterns of long distance nocturnal migration in noctuid moths and passerine birds, *Proc. R. Soc. B.*, 278, 2011, 3074-3080
- Bradley W. D., Clark R. G., Dunn P. O., Laughlin A. J., Taylor C. M., Vleck C., *et al.*, Trans gulf of Mexico loop migration of tree swallows revealed by solar geolocation, *Curr Zool.*, 2014, 60, 653-659
- Buler J. J., Moore F. R., Migrant-habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications, *J. Ornithol.*, 2011, 152, S101-S112
- Bulyuk V. N., Tsvey A., Timing of nocturnal autumn migratory departures in juvenile European robins (*Erithacus rubecula*) and endogenous and external factors, *J Ornithol.*, 2006, 147, 298-309
- Butler R. W., Williams T. D., Warnock N., Bishop M. A., Wind assistance: A requirement for migration of Shorebirds?, *Auk.*, 1997, 114, 456-466
- Conklin J. R., Battley P. F., Impacts of wind on individual migration schedules of New Zealand bar-tailed godwits, *Behav. Ecol.*, 2011, 22, 854-861
- Covino K. M., Holberton R. L., Morris S. R., Factors influencing migratory decisions made by songbirds on spring stopover, *J. Avian Biol.*, 2015, 46, 73-80
- Dawson A., Verdun K. M., Bentley G. E., Gregory B. F., Photoperiodic control of seasonality in birds, *J Biol. Rhythms.*, 2001, 16, 365-380
- Deppe J., Ward M., Bolus R., Diehl R., Celis-Murillo A., Zenzal Jr T., *et al.*, Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico, *Proc. Natl. Acad. Sci. USA.*, 2015, 112, E6331-E6338
- Eikenaar C., Schmaljohann H., Wind conditions experienced during the day predict nocturnal restlessness in a migratory songbird, *Ibis.*, 2015, 157, 125-132
- Fraser K. C., Stutchbury B. J. M., Silverio C., Kramer P. M., Barrow J., Newstead D., *et al.*, Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore, *Proc. R. Soc. B.*, 2012, 279, 4901-4906
- Fraser K. C., Stutchbury B. J. M., Kramer P., Silverio C., Barrow J., Newstead D., *et al.*, Consistent range-wide pattern in fall migration strategy of Purple Martin (*Progne subis*), despite different migration routes at the Gulf of Mexico, *Auk.*, 2013a, 130, 291-296
- Fraser K. C., Silverio C., Kramer P., Mickle N., Aeppli R., Stutchbury B. J. M., A trans hemispheric migratory songbird does not advance spring schedules or increase migration rate in response to record-setting temperatures at breeding sites. *PLOS ONE.*, 2013b, 8, e64587.
- Gauthreaux Jr. S. A., Belser C. G., Welch C. M., Atmospheric trajectories and spring bird migration across the Gulf of Mexico, *J. Ornithol.*, 2006, 147, 317-325
- Gill Jr. R. E., Douglas D. C., Handel C. M., Tibbitts T. L., Hufford G., Piersma T., Hemispheric-scale wind selection facilitates bar-tailed godwit circum-migration of the Pacific, *Anim. Behav.*, 2014, 90, 117-130
- Gill Jr. R. E., Tibbitts T. L., Douglas D. C., Handel C. M., Mulcahy D. M., Gottschalck J. C., *et al.*, Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier?, *Proc. R. Soc. B.*, 2009, 276, 447-457
- Gwinner E., Circadian and circannual programmes in avian migration, *J. Exp. Biol.*, 1996, 199, 39-49
- Hahn S., Emmenegger T., Lisovski S., Amrhein V., Zehtindjiev P., Liechti F., Variable detours in long distance migration across ecological barriers and their relation to habitat availability at ground, *Ecol. Evol.*, 2014, 4, 4150-4160
- Helms IV. J., Godfrey A., Ames T., Bridge E., Are invasive fire ants kept in check by native aerial insectivores?, *Biol. Lett.*, 2016, 12, 20160059
- Klaassen R. H. G., Alerstam T., Carlsson P., Fox J. W., Lindstrom A., Great flights by great snipes: long and fast non-stop migration over benign habitats, *Biol. Lett.*, 2011, 7, 833-835
- Lam L., McKinnon E. A., Ray J. D., Pearman M., Hvenegaard G. T., Mejeur J., *et al.*, The influence of morphological variation

- on migration performance in a trans-hemispheric migratory songbird, *Animal Migration*, 2015, 2, 86-95
- Lund U., Agostinelli C., Package: "Circular" in R., 2017, <https://cran.r-project.org/web/packages/circular/circular.pdf>
- McKinnon E., Fraser K. C., Stutchbury B. J. M., New discoveries in landbird migration using geolocators and a flight plan for the future, *Auk*, 2013, 130, 211-222
- McKinnon E., Love, O.P., Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging, *Auk*, 2018, 135, 834-856
- McLaren J. D., Shamoun-Baranes J., Dokter A. M., Klaassen R. H. G., Bouten W., Optimal orientation in flows: providing a benchmark for animal movement, *J. R. Soc. Interface*, 2014, 11, 20140588
- Newton I., *The Migration Ecology of Birds*, 1st ed., Academic Press, London, 2008
- Pewsey A., Neuhauser M., and Ruxton G., *Circular statistics in R*, 1st ed., Oxford University Press, New York, 2013.
- R Core Team., *R: A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Austria., 2017, URL <https://www.R-project.org/>
- Russell K., Gauthreaux Jr. S., Use of weather radar to characterize movements of roosting purple martins, *Wildl. Soc. Bull.*, 1998, 26, 5-16
- Russell K., Gauthreaux Jr. S., Spatial and temporal dynamics of a purple martin pre-migratory roost, *Wilson Bull.*, 1999, 111, 354-362
- Saino N., Rubolini D., Hardenberg J. V., Ambrosini R., Provenzale A., Romano M., *et al.*, Spring migration decisions in relation to weather are predicted by wing morphology among trans-Mediterranean migratory birds, *Funct. Ecol.*, 2010, 24, 658-669
- Schmaljohann H., Naef-Danzer B., Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird, *J. Anim. Ecol.*, 2011, 80, 1115-1122
- Schmaljohann H., Fox J. W., Bairlein F., Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world, *Anim. Behav.*, 2010, 84, 623-640
- Stutchbury B. J. M., Tarof S. A., Done T., Gow E., Kramer P. M., Tautin J., *et al.*, Tracking long distance songbird migration by using geolocators, *Science*, 2009, 323, 896
- Weber T., Hedenstrom A., Optimal stopover decisions under wind influence, *J. Theor. Biol.*, 2000, 205, 95-104
- Weber T. P., Alerstam T., Hedenstrom A., Stopover decisions under wind influence, *J. Avian Biol.*, 1998, 29, 552-560