Individual timing consistency across purple martin (*Progne subis*) migrations

By

Colin Bridges

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Abstract

Migration timing in long-distance migratory birds plays an essential role in individual survival and fitness. Migration schedules determine when individual birds depart and arrive seasonally between their overwintering and breeding sites. Bird migration timing may be largely driven by internal routines with some plasticity to environmental conditions, but individual timing across migrations has been little explored. To investigate the consistency of individual timing across migrations, I examined the individual order of migration timing in purple martins (*Progne subis*), a neotropical migratory songbird that travels between breeding sites throughout eastern North America and winter sites in Brazil. Migration timing data were collected for 295 different individual purple martins spanning over nine years by using light-level geolocators deployed during the breeding season at sites across the range and collected at the same sites the following year. I used a linear mixed-effect model (LMM) to examine the influence of the rank order of departure dates in one season on the rank order of four subsequent migration events while controlling for the effects of breeding latitude, sex, and age. Overall, I found that the individual rank order of migration timing in purple martins was conserved across migrations. Rank order timing was consistent between fall departure date from the breeding site and spring arrival dates in the following year (0.28 ± 0.03, 95% CI 0.21-0.34), as well as the finer scale across fall migration departure and arrival dates (0.33 ± 0.05, 95% CI 0.23-0.42), over the wintering period (0.39 ± 0.04, 95% CI 0.30-0.48), and across spring migration (0.03 ± 0.001, 95% CI 0.026-0.033). These results demonstrate that purple martin exhibit consistency in individual migration timing throughout the annual cycle. Migration distance also played a significant role, as the consistency of rank order timing lessened with distance traveled. Understanding how individual birds time migrations and if individuals are consistent between events can provide insight into how shifts in the environment with climate change could lead to a mismatch if migratory birds are unable to adapt. Future studies should examine if purple martins are able to adjust their migration timing and how long these changes persist in response to environmental alterations.

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Introduction

Animal movement through dispersal or migration provides insight into how external environmental factors play a role in the behaviour and timing of such events and few are more prominent than the yearly migration of birds (Spiegel et al. 2017). As technology advances and we are able to track long distance migration more accurately, we can begin to look at the internal variation among individuals of a single breeding population who experience the same external stimuli and try to understand why there is a difference among their timings and if it is consistent across migrations (Spiegel et al. 2017, Bailey et al. 2021). These migratory traits that dictate individual differences in timing have been described as “micropersonalities” and may allow us to understand if they are relatively fixed or flexible when faced with environmental variation (Bailey et al. 2021). Many factors play an important role in influencing the behavioural timings of migratory songbirds such as environmental phenology correlated with latitude and photoperiod (Bani Assadi & Fraser. 2021, Neufeld et al. 2021). With the impacts of human activity, such as increasing light pollution and climate change, migratory birds who rely on very specific migration and nesting dates may be impacted negatively resulting in population declines (Both et al. 2006, Knudsen et al. 2011, Franklin et al. 2022). However, we still require further research on how environmental change impacts individual behavioural traits and timing in migratory birds, as how birds time their migration will impact responses to climate change (Fraser et al. 2019).

Purple martins (*Progne subis*) are a species of neotropical migratory swallow that breed in North America then migrate to Brazil and other parts of South America over the winter (Brown et al. 2021, Santos et al. 2021). They are considered synanthropic as they have grown to use human provided nesting sites over the years (Cook et al. 2021). They also exhibit natal philopatry where they often migrate back to the same locations they were born in or previously nested during the breeding season (de Greef et al. 2022). The tendency to return to a breeding site allows us to study individual birds over a period of multiple years and see if their timing of spring and fall migration are consistent and if they exhibit individual chronotypes differentiating their expression of behaviours as compared to other birds in the same population (Nilsson et al., 2014). Previous studies have observed that male purple martins tend to leave for migration earlier than females and older birds usually leave earlier than younger birds (Fraser et al. 2019, Neufeld et al. 2021, Bani Assadi et al. 2022). This may be due to older birds having more experience and leaving earlier to claim the best nesting sites, but the potential for individually consistent timing in purple martin timing requires further study (Neufeld et al. 2021, Bani Assadi et al. 2022).

The variability in timing observed in entire breeding populations of purple martins may be explained to some degree by phenotypic plasticity to environmental variation (Fraser et al. 2019). However, individual consistency in migration timing, particularly in spring (Fraser et al. 2019), could potentially indicate a role for individually consistent timing of migration. Individual variation in timing could be inherent and/or the result of generational change in new hatchlings based upon a mixture of inherited timing and environmental conditions experienced during development such as photoperiod (Fraser et al. 2019, Bani Assadi & Fraser. 2021, Franklin et al. 2022). Spring departure dates tend to be strongly correlated with spring arrival dates in purple martin (Neufeld et al. 2019) suggesting consistent schedules for individuals but whether there are distinct timing phenotypes within a population that are consistent across annual, long-distance migrations and across the annual cycle has not been fully explored.

The objective of this thesis was to investigate whether the migration timing in individual purple martins is consistent throughout the year across multiple migration events. I hoped to discover if purple martins who initiate migration to arrive early or later at their breeding and winter sites will also leave these sites in a similar order compared to others. Bar-tailed godwits (*Limosa lapponica*) exhibited individual schedules that were maintained across thousands of kilometres of migration (Conklin et al. 2010). Repeat-tracking of individual purple martins suggests a high degree of individual plasticity in migration timing around the calendar (Fraser et al. 2019), but whether individual chronotypes are maintained within this variation has not been explored. To achieve this objective, I used migration timing data collected by using light-level geolocators deployed at breeding sites across the range. I examined individual timing consistency at various sites across the breeding range and performed a linear mixed model (LMM) with the four yearly migration events to see which factors influence individual timing. I predict that, like godwits, purple martins will exhibit individual chronotypes that are maintained across their long-distance migrations. However, if conditions during migration disrupt individual schedules, I would expect these chronotypes to diminish as migration distance increases.

Understanding how individual birds time their migration and breeding over multiple years and if they express consistent individual timing is important for our perception of the ways climate change and human activity may impact these processes, and how this may contribute to long-term population declines in purple martins and other migratory songbirds (Rosenberg et al. 2019).

Methods

Data Collection

To achieve the objective of understanding individual migration timing consistency, data collected from light-level geolocators attached to individual purple martins were used to collect the migration timing data. Each individual bird was tagged during their breeding season as well as banded with a unique identification number (Figure 1), aged, and sexed based on their plumage (Pyle 1997). Migration timing data for 315 individual purple martins were available for my analysis across 11 different breeding sites (Table 1). The light-level geolocators were used to determine four key, yearly migration dates for each individual that were used for analysis. These were: date of fall departure from the breeding site; date of fall arrival at the over winter site in Brazil, date of spring departure from Brazil, and date of spring arrival back to the breeding site the following year.

Figure 1. An image of an after second year male purple martin held in the banders grip during processing which consisted of measuring its wing, tail, and tarsus length and applying the identification bands.

Table 1. Latitude and longitude of the 11 breeding sites tracked ranked by closest to furthest distance from the winter site in Brazil.

Breeding Sites	Latitude	Longitude
Florida	28.36	-81.59
South Carolina	33.87	-80.18
Texas	35.04	-101.93
Virginia	38.61	-77.26
New Jersey	40.38	-74.00
Pennsylvania	42.11	-80.14
Ontario	45.35	-75.82
South Dakota	45.59	-98.31
Minnesota	46.14	-93.72
Manitoba	49.73	-97.13
Alberta	52.39	-113.61

Light-level geolocators use sunrise and sunset to determine the coordinates of the tracker at a given time (Conklin et al., 2010). This method may pose issues when tracking bird species who spend prolonged periods of time in burrows or shade, however, purple martins are aerial foragers so their behaviour has little impact on light-data quality (Fraser et al., 2012). The light-level geolocators weighing 1.6 g were attached to the purple martins with a leg-loop harness made of Teflon ribbon that was applied after trapping them in their nests with a trap door. The same methods were used to recollect the geolocators when they returned the following year to retrieve the data. Data were downloaded using BASTrak software and analyzed using the FlightR package in R Studio (Fraser et al. 2012, R Core Team 2022. version 4.2.1, Rakhimberdiev et al. 2017).

Data Analysis

To determine whether migration timing was consistent in purple martins, I fit Linear Mixed Models (LMMs) on year-long migration timing data derived from tracking individuals across all sites from 2007 to 2016 (n=295) pooling all of the years to be ranked together. Individual birds with repeat tracking (n=20) over multiple years were removed so only one migration per year, per individual was used in analysis. I fitted four LMMs, one for each of four migration timing events around the annual cycle. The first was whether the ordering of individuals at their fall departure date from the breeding site on spring arrival date was consistent with the order of arrival dates in spring of the following year. Here I examined whether ‘rank spring arrival date’ (rank order of individuals) was influenced by the fixed effect of ‘rank fall departure date’, while controlling for the influence of other factors (see below). A significant effect would suggest individuals have consistent individual timing schedules that persist over multiple migration events. The other three models targeted migration timing at a finer, within-season scale. I examined whether the order of birds at their arrival after fall migration (‘rank fall arrival date’) was consistent with the order of their fall departures (‘rank fall departure date’ as a fixed effect). I also examined whether the order of arrival at the beginning of the wintering period (‘rank fall arrival date’) was consistent with the order of departure from the winter site (‘rank spring departure date’) as the fixed effect and whether the rank order of departure from the winter site on spring migration is consistent with the order of arrival at breeding sites (‘rank spring arrival date’).

In all models, I controlled for and investigated the influence of all other factors by assigning three additional fixed effects. The first of these was ‘Latitude’ to test if individuals belonging to lower latitude breeding sites expressed similar timing consistency when compared to those at higher latitude sites. If latitude significantly affects the timing consistency of individuals, there may be some role for environmental factors altering individual migration schedules as purple martins travel longer distances (i.e. birds breeding at higher latitudes travel the furthest from shared overwintering areas). I also included ‘Age’ as a fixed effect, as the individuals were classified as either SY or ASY and we may expect younger birds to have later timing generally (Morton & Derrickson. 1990). Lastly, we included ‘Sex’ as a fixed effect as we expected different selection pressures on male versus female timing across the annual cycle (Morton &

Derrickson. 1990). We also included two random effect variables: ‘Year’ and ‘Site’ in order to account for variable climate and environmental effects from site latitude and year which could influence migration timing (Fraser et al. 2019). All variables were fitted in LMMs using the lme4 R package (Bates et al., 2015) and a confidence interval of 95% was used for the fixed and response variable. The variance and standard deviation were calculated for the random effects. The models’ fit was tested through the MuMIn package (Grabman et al., 2019).

Single site rank order analyses were done for the four migration events at five different breeding sites (FL, VA, PA, MB, and AB) from the recorded data with the highest number of individuals in a single year. I scored each individual sequentially as to the order it arrived at the site as compared to other individuals from the same breeding population and year and performed a Rank Order analysis to determine whether individuals are consistently earlier or later within a breeding population (Supplemental Table 1).

Results

Using light-level geolocators, I tracked the four yearly migration dates of individual purple martins that disperse across the entire North American breeding range. I fit linear mixed models to see if the individual timings were influenced by the four fixed effects (previous associated migration event, latitude of the breeding site, age, and sex) and found that at both yearly and seasonal timescales, purple martin individual timing was generally consistent (Table 2).

Spring Arrival at Breeding Site

The rank order of arrival of individual purple martins at their breeding sites in spring was significantly affected by the rank order of their fall departure from the breeding site in the previous year. It was also influenced by breeding latitude, and age, but not by sex. The rank order of fall departure from the breeding site had an effect of (estimate ± SE) 0.28 ± 0.03 (95% CI 0.21-0.34) ($p<0.001$) on the rank order of arrival back at the breeding site the following year. The latitude of the breeding site had an effect of (estimate ± SE) 7.49 ± 0.34 (95% CI 6.82-8.17) ($p<0.001$) on the rank order of arrival at the breeding site. The age of the purple martins (after second year) had an effect of (estimate ± SE) -17.28 ± 5.42 (95% CI -27.89--6.66) ($p<0.001$) on the rank order of spring arrival. The sex (male) of purple martins also had an effect (estimate ± SE) -7.05 ± 4.30 (95% CI -15.47-1.38) ($p=0.10$) on the spring rank order arrival, but it was not significant. The single site rank order analysis of fall breeding site departure and spring arrival also suggests a correlation between the two migration events for the Florida site as it was the only significant site (Supplemental Figure 1).

Fall Arrival Date at the Winter Site

The rank order of fall arrival at the winter site in the Amazon was significantly influenced by the rank order of fall departure from the breeding site and the latitude of the breeding site. The age and sex of the purple martins was estimated to have no significant impact on the migration timing consistency. The rank order of fall departure from the breeding site had an effect of (estimate ± SE) 0.33 ± 0.05 (95% CI 0.23-0.42) ($p<0.001$) on the following arrival at the winter site. The effect of the latitude of the breeding site on the fall arrival order (estimate ± SE) 6.00 ± 0.59 (95% CI 4.83-7.18) was also significant ($p<0.001$). Both the age (after second year) (estimate ± SE) -8.47 ± 6.93 (95% CI -22.05-5.10) ($p=0.222$) and sex (male) (estimate ± SE) -10.13 ± 5.53 (95% CI -20.96-0.70) ($p= 0.068$) of the purple martins had no significant impact on the rank order of arrival in purple martins migrating to the winter site. The single site rank order correlation between fall departure from the breeding site and fall arrival at the winter site also demonstrated a positive correlation between the two timings with the Florida site being significant (Supplemental Figure 2). A trend with longer migration distance decreasing the rank order correlation was also observed suggesting the breeding site latitude played a role in individual timing consistency following what was seen in the mixed model.

Spring Departure Date from Winter Site

Purple martins rank order of departure from the winter site in the spring was significantly affected by the rank order of arrival at the winter site in the fall, latitude, and the sex of the individual. Rank fall arrival at the winter site had an effect of (estimate ± SE) 0.39 ± 0.04 (95% CI 0.30-0.48) ($p<0.001$) on the rank of departure in the spring. The latitude of the breeding site was (estimate ± SE) 5.54 ± 0.47 (95% CI 4.62-6.46) ($p<0.001$) showing a significant impact on the spring departure order. The age of the individuals (after second year) was not significant (estimate ± SE) -8.08 ± 5.94 (95% CI -19.73-3.57) ($p=0.175$), but the sex (male) of the purple martins did significantly affect the winter site departure timing (estimate ± SE) -13.25 ± 4.69 (95% CI -22.44--4.06) ($p=0.005$). The single site analysis also suggested that there was some correlation between the arrival and departure from the breeding site, but it was only significant in the individuals belonging to the closest or lowest latitude site (Supplemental Figure 3).

Spring Arrival Date at the Breeding Site

Spring arrival at the breeding site was significantly affected by all measured fixed effects except sex. The rank order of spring departure from the winter site had a significant effect of (estimate ± SE) 0.03 ± 0.001 (95% CI 0.03-0.03) ($p<0.001$) on the rank order of arrival at the breeding sites in the spring. The latitude of the breeding site similarly had a significantly positive effect (estimate ± SE) 0.16 ± 0.02 (95% CI 0.12-0.20) ($p<0.001$) on the spring breeding site order of arrival. The age (after second year) of the individual also had a significant effect (estimate ± SE) -0.55 ± 0.17 (95% CI -0.89--0.21) ($p<0.001$). The sex (male) of the purple martins, however, had no significant effect (estimate ± SE) 0.05 ± 0.14 (95% CI -0.21-0.32) ($p=0.69$) on the rank order of spring arrival at the breeding site. This strong association between rank order of departure from the winter site and rank order of arrival at the breeding site during the spring was corroborated by the single site correlation analysis which was significant for all breeding sites across the range (Supplemental Figure 4).

Table 2. Summary of linear mixed model (LMM) testing for correlation in rank order of migration timing in purple martins created in R using the lme4 package with the marginal R^2 accounting for the variance of only the fixed effects in the model and the conditional R^2 accounting for both the fixed and random effects.

Model		**Estimate**	**95%CI (lower)**	**95%CI (upper)**	**mR^2/cR^2**
Rank order spring arrival date	**Fixed effects**				
	Rank order fall departure date	0.28	0.21	0.34	
	Latitude	7.49	6.82	8.17	0.79/0.83
	Age (ASY)	-17.28	-27.89	-6.66	
	Sex (M)	-7.05	-15.47	1.38	
	Random effects	**Variance**	**Std. dev.**		
	Year	270.38	16.44		
	Site	70.08	8.37		
Rank order fall arrival date	**Fixed effects**				
	Rank order fall departure date	0.33	0.23	0.42	
	Latitude	6.00	4.83	7.18	0.67/0.72
	Age (ASY)	-8.47	-22.05	5.10	
	Sex (M)	-10.13	-20.96	0.70	
	Random effects	**Variance**	**Std. dev.**		
	Year	89.96	9.49		
	Site	278.48	16.69		
Rank order spring departure date	**Fixed effects**				
	Rank order fall arrival date	0.39	0.30	0.48	
	Latitude	5.54	4.62	6.46	0.79/0.83
	Age (ASY)	-8.08	-19.73	3.57	
	Sex (M)	-13.25	-22.44	-4.06	
	Random effects	**Variance**	**Std. dev.**		
	Year	15.58	3.95		
	Site	103.82	10.19		
Rank order spring arrival date	**Fixed effects**				
	Rank order spring departure date	0.03	0.026	0.033	
	Latitude	0.16	0.12	0.20	0.90/0.92
	Age (ASY)	-0.55	-0.89	-0.21	
	Sex (M)	0.05	-0.21	0.32	
	Random effects	**Variance**	**Std. dev.**		
	Year	0.001	0.04		
	Site	0.35	0.59		

Discussion

In this thesis, I show that purple martins had consistent individual schedules that determined when an individual will arrive or depart in relation to other members of the population. These timings were consistent across the breeding range and the annual cycle, suggesting that individuals have set schedules which may leave them vulnerable to environmental disturbances and climate change if relatively fixed schedules align poorly with optimal conditions. The alteration of these specific timings and the environment may be contributing to the recent mass population declines observed in purple martins and other migratory songbirds (Rosenberg et al. 2019). I also found that for all four migration departure and arrival events (fall departure, fall arrival, spring departure, and spring arrival) there was a significant effect of latitude on migration timing order, suggesting that birds at lower latitudes migrate earlier. I also found that longer migration distances may weaken rank order consistency which was further supported by the single site analysis. An examination of rank order timing within single breeding sites also supports that the individual timings are correlated across the year and that, along with the significant effect of latitude on timing in the LMM, the distance migrated may have an impact on individual consistency. These fixed individual timings may also lead to a rapid loss in genetic diversity as they would be unable to adapt to shifts in environmental conditions.

Previous studies on individual bird migration timing consistency have suggested that in some species, such as the bar-tailed godwit, individual timing (rank order) is maintained across multiple migration events (Conklin et al., 2010). We tested to see if the rank order timing of individuals at a particular migration event were consistent with a future migration event in purple martins and found that these individual schedules are carried over the annual cycle. Our findings suggest there is consistent individual timing that can extend across roughly 8 months and thousands of kilometres of migration, where the order of fall departure from the breeding site significantly influenced the arrival order back at the same breeding site in the following year. Similar to previous studies done on the carry-over effects of bird migration during the breeding season, these findings suggest that inherent individual migration timings can be conserved across seasons (Conklin et al. 2010, Gow et al. 2019, Neufeld et al. 2019). In contrast, however, to the study done by Gow et al. (2019) on tree swallows (*Tachycineta bicolor*), we found that the influence of the individual purple martins migration timing did not break down for the non-breeding site events. This distinction between species may be a result of the purple martins all congregating together into the same area in Brazil during the winter while the tree swallows disperse over a large range throughout America and Mexico to winter. Alternatively, tree swallows also winter closer to their breeding range where they may receive climatic signals of spring phenology at distant breeding sites and may have evolved more flexible timing responses to seasonal or annual environmental variation compared to purple martins, diminishing the consistency of inherent individual schedules, allowing for more plasticity in departure date (Alerstam & Högstedt. 1980). My results suggest that the following three yearly migration events (fall departure-fall arrival, fall arrival-spring departure, and spring departure-spring arrival), similar to the breeding site to breeding site timings, were also significantly correlated suggesting that individual purple martin migration timing persisted throughout the entire year and carried over across all migrations. Of the four measured migration timings, the spring departure to spring arrival had the highest correlation between rank order of departure and rank order of arrival and took nearly half the time as fall migration did for higher latitude breeding sites. This may be explained as the birds must arrive at the breeding sites during optimal environmental conditions to maximize fitness and breeding success (Kokko. 1999, Gow et al. 2019). If this is the case, they may initiate migration due to a mix of inherent individual timing and environmental conditions signaling the optimal migration timing and complete the event as fast as possible conserving the order of timing across the spring migration (Spiegel et al. 2017). It is important to understand the nature of purple martin migration timing and if timing is consistent across multiple events as they may not be able to adjust to a shift in environmental conditions due to climate change if their individual migrations schedule is relatively fixed.

The latitude of the breeding site also played a significant role in the individual migration timing consistency of purple martins. When comparing migration events across sites in the individual analysis, I found birds belonging to breeding sites at higher latitudes showed lower correlation between the rank order of arrival or departure when compared to those located closer to the winter site. This may be due to the environmental conditions experienced over the course of migration and number of stopover sites required to refuel altering the migration order for the across year breeding site, fall, and spring migrations (Loon et al. 2017). Our results showed that the winter site fall arrival to spring departure was also affected by the breeding site latitude which may be due to individuals belonging to higher latitude sites further north breeding later in the season than those further south (Neufeld et al. 2021). Previous studies on the effect of latitude on tree swallow migration timing have also suggested that the migration departure date from winter site is predominantly driven by breeding latitude (Gow et al. 2019).

The relative consistency of individual timings across fall and spring migrations differed, suggesting that although these two events could be seen as counterparts roughly covering the same distance (spring as compared to fall migration) and being between the same two sites (breeding and wintering), purple martins exhibit different seasonal behaviour. Fall departure from the breeding site to fall arrival at the winter site took between 20-60 days depending on the distance traveled. The rank order of departure and arrival in fall had higher correlation at lower latitudes and gradually decreased as the migration distance increased. This relationship was also supported by the single site analysis. This behaviour could be explained as weaker selection on fall timing, where purple martins take their time during the fall migration as compared to spring, often stopping to refuel at stopover sites to recover after the strenuous breeding season (Loon et al. 2017). There is likely weak selection pressure on winter site arrival timing, as without selection pressure on competing for mates and a nesting cavity in spring, purple martins roost colonially in Brazil during the winter with no anticipated time constraints to compete for resources (Loon et al. 2017, Santos et al. 2021). The spring migration, however, took only 20-30 days to complete even in individuals belonging to the northern-most sites. The LMM analysis revealed that there was very little standard error between the estimated effect of rank order of spring departure on the rank order of spring arrival at the breeding site. This result is further corroborated by the single site analysis where all sites regardless of latitude, as the birds may not spend long enough at stopover sites to be influenced by the environment, had significant correlation between the departure and arrival order. This behaviour suggests that purple martins initiate migration from the winter site when internal and the environmental signals indicate optimal breeding conditions and travel to the breeding site as fast as possible to not miss the short window (Gow et al. 2019). In addition to available food resources, the availability of human made nests could also be a significant selection pressure urging the purple martins to migrate rapidly during the spring (Cook et al. 2021).

It is important to understand the effect of latitude and location of the breeding site on purple martin migration as climate change disproportionately affects northern environments (Butler 2003). A shift in available food resources and optimal breeding conditions in the northern breeding sites would result in an offset between the birds perceived optimal time to migrate from Brazil and the actual optimal northern conditions ultimately leading to a reduction in fitness as the distance between the two sites increases.

The influence of individual purple martins age and sex on migration timing varied in effect throughout the year. We found that after second year birds were consistently earlier in migration dates than first year birds throughout the entire year which is consistent with the results of previous studies and could be due to their experience of earlier birds having higher success as they can access resources first (Fraser et al. 2019); however, the effect of age was only significant in the breeding site departure to breeding site arrival the following year and winter site departure to breeding site arrival. The influence of sex of the purple martins on timing consistency was similarly varied across seasons. Sex had a significant influence on the consistency of timing across the wintering period, being more consistent for females. Our results showed that female purple martins were earlier for all migration events except spring departure from the winter site to spring arrival at the breeding site where males initiated departure first. This result matches previous studies that focused on spring migration and found that males tended to initiate migration earlier than females (Morton & Derrickson. 1990, Neufeld et al. 2021).

Further research could be aimed at investigating environmental factors that may influence the relative consistency of purple martin migration timing by measuring the effects of temperature, daylength, and precipitation. Experimentally altering these conditions for one migration and recording the effects on future timings when compared to a control group may also allow us to see the plasticity in timings and if these altered timings persist over multiple events. Another factor that has been shown to affect post-breeding migration timing in individual purple martins is the natal nest hatch dates (Bani Assadi et al. 2022). Testing if individual schedules are determined by these natal nest timings and the environment during development would allow us to understand what determines the inherent individual timing in purple martins.

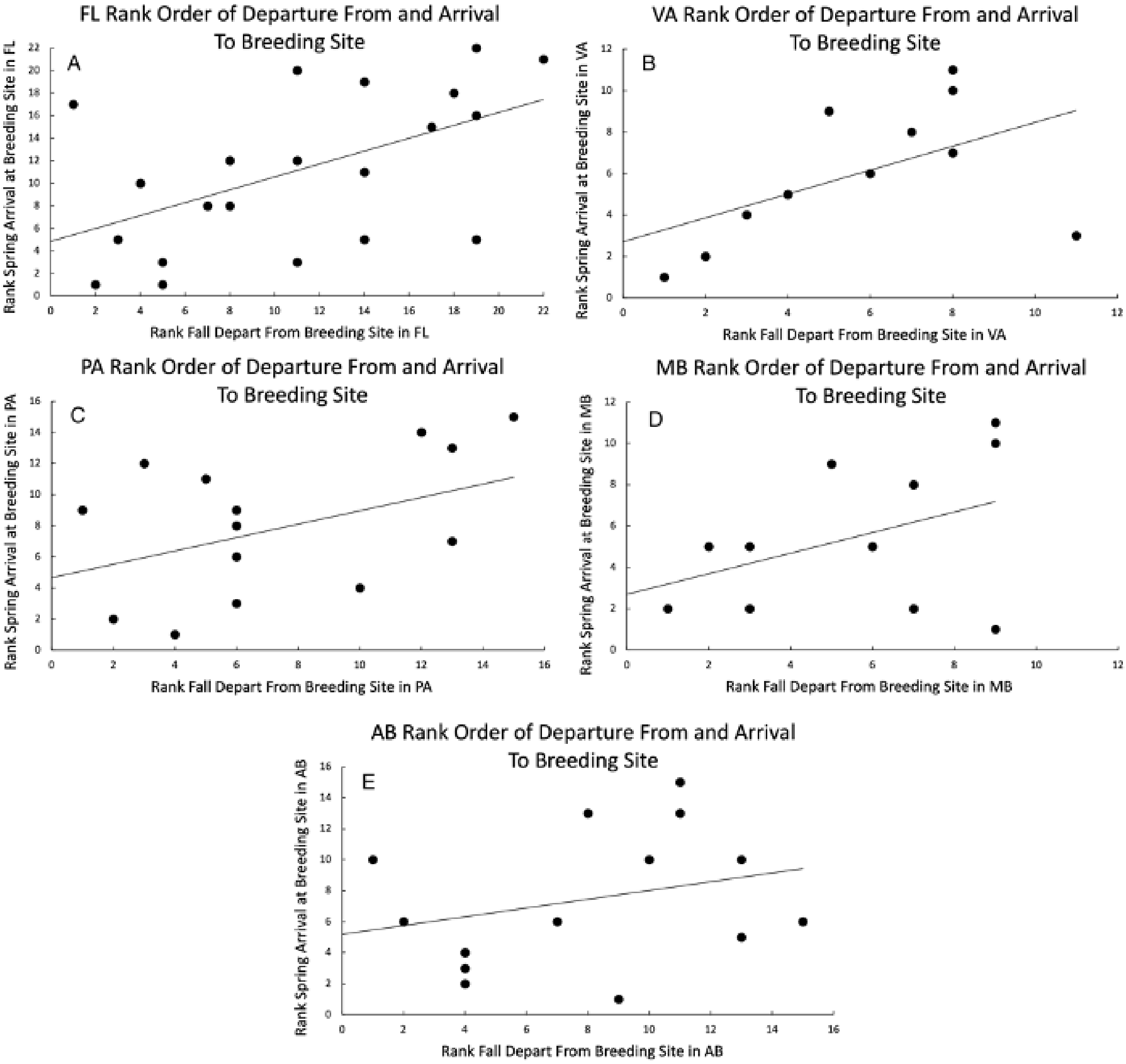
Conclusion

In conclusion, our results demonstrate that individual migration timing is consistent across the annual cycle in purple martins. We found that the rank order of migration departure or arrival is significantly consistent with the rank order of the subsequent migration event. This correlation even carries over across a full year, from fall breeding site departure to spring breeding site arrival in the next season. Latitude of the breeding site also played a significant role in the timing consistency of purple martins, possibly because individuals heading to breeding sites further north travel further and thus are exposed to more environmental variability over the course of migration which may alter individual departure to arrival order. This effect is exacerbated during the fall migration as purple martins spend roughly twice the amount of time as spring migration traveling to the winter site in Brazil and as a result spend more time at stopover sites, potentially diluting the consistency of individual schedules. Conversely, purple martins in the spring initiate migration when signaled for optimal environmental breeding conditions and tend to reach the breeding site as soon as possible to not miss the window. Understanding how individual purple martins time their migration and if it is consistent over multiple years is important as change and human activity may alter environmental conditions resulting in a mismatch in resources and arrival leading to the mass population declines long distance migratory birds have been facing.

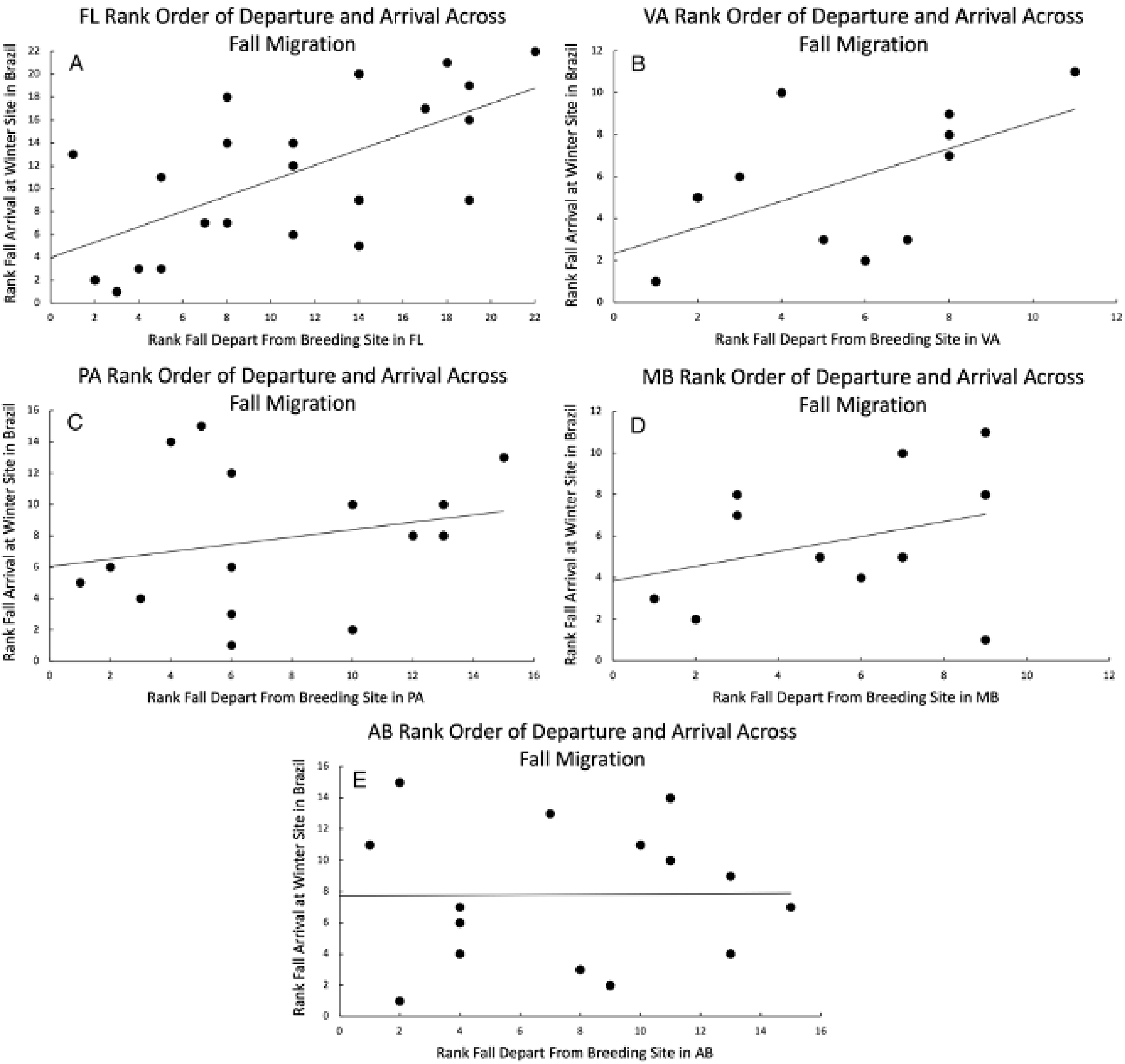
Supplemental Tables and Figures

Supplemental Table 1. Migration duration and distance traveled during the spring and fall migrations of tracked birds belonging to each of the 5 individual breeding sites reporting the mean and standard deviation.

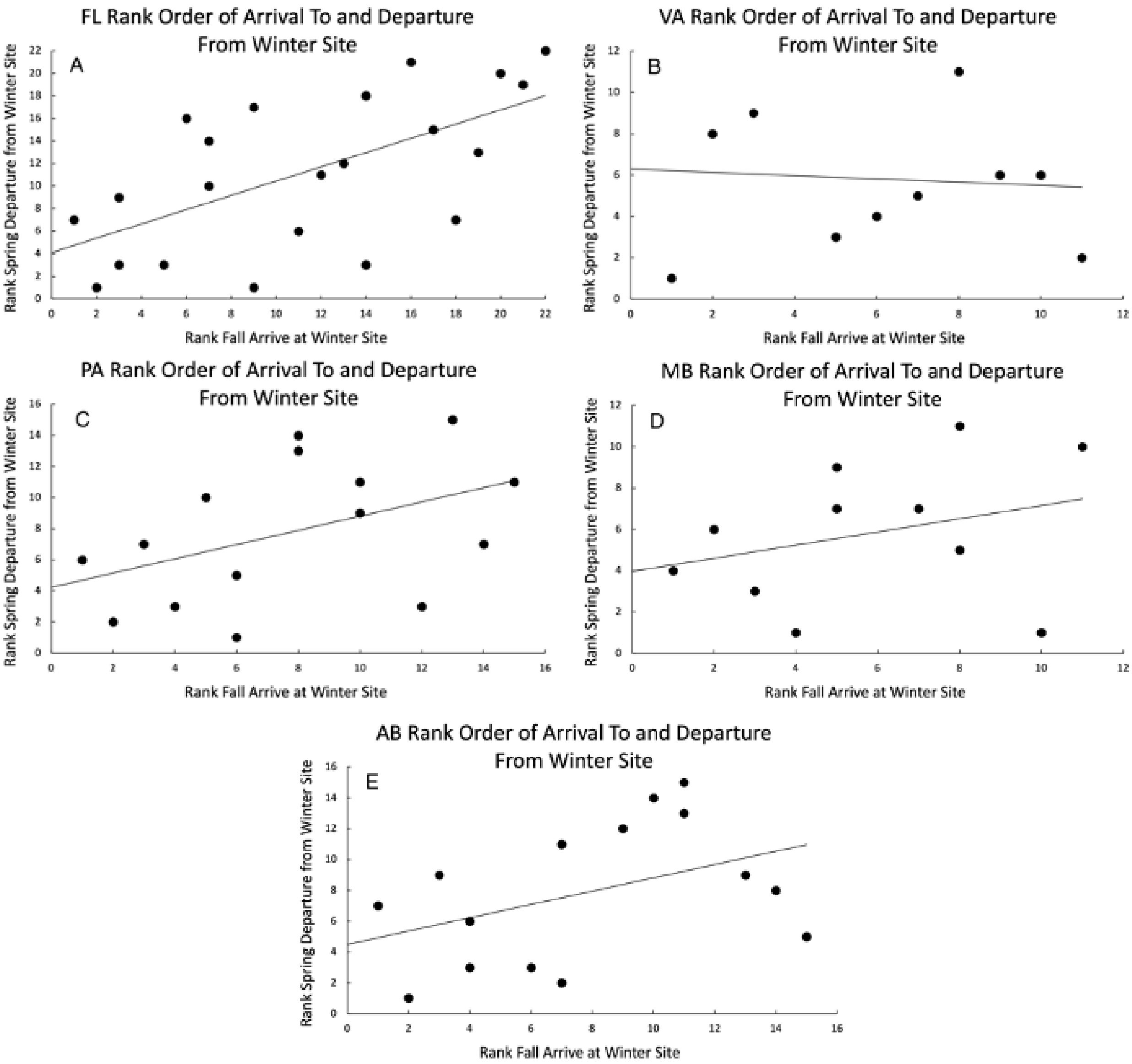
Location	Spring Migration Duration (Days)	Spring Migration Distance (Km)	Fall Migration Duration (Days)	Fall Migration Distance (Km)
FL	18.9 ± 5.2	5381 ± 613	20.2 ± 7.8	5466 ± 698
VA	18.8 ± 3.9	7187 ± 1222	41.5 ± 10.9	6626 ± 799
PA	22.8 ± 6.5	7566 ± 902	44 ± 7.5	6823 ± 916
MB	23.5 ± 6	8026 ± 840	52.7 ± 11.9	8572 ± 643
AB	26.3 ± 5.8	9164 ± 748	63.8 ± 12.5	9412 ± 1013



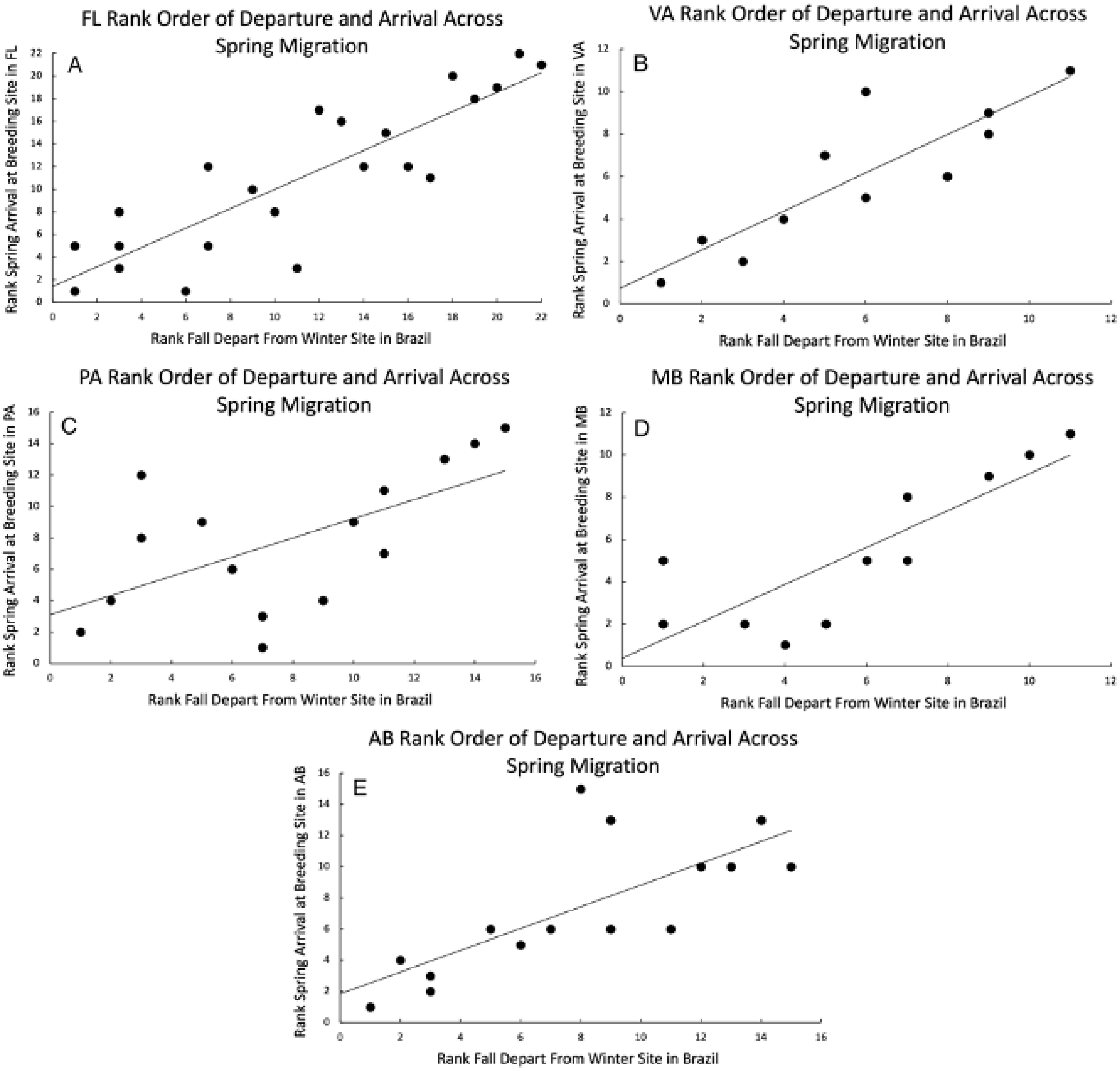
Supplemental Figure 1. Purple martin **breeding site** migration timing comparing the departure in fall (x-axis) to the arrival the following spring (y-axis) in the individuals of the five tracked sites; (**A**) Florida (r_s=0.54, n=22, p-value=0.01), (**B**) Virginia (r_s=0.52, n=11, p-value=0.09), (**C**) Pennsylvania (r_s=0.42, n=15, p-value=0.12), (**D**) Manitoba (r_s=0.42, n=11, p-value=0.2), and (**E**) Alberta (r_s=0.3, n=15, p-value=0.27).



Supplemental Figure 2. Purple martin **Fall migration** timing comparing the departure from breeding site in fall (x-axis) to the arrival in the winter site in fall (y-axis) in the individuals of the five tracked sites; (**A**) Florida (r_s=0.64, n=22, p-value=0.001), (**B**) Virginia (r_s=0.56, n=11, p-value=0.07), (**C**) Pennsylvania (r_s=0.23, n=15, p-value=0.4), (**D**) Manitoba (r_s=0.32, n=11, p-value=0.33), and (**E**) Alberta (r_s=0.01, n=15, p-value=0.97).



Supplemental Figure 3. Purple martin **winter site** migration timing comparing the arrival in fall (x-axis) to the following departure in spring (y-axis) in the individuals belonging to the five tracked sites; (**A**) Florida (r_s=0.61, n=22, p-value=0.002), (**B**) Virginia (r_s=-0.08, n=11, p-value=0.8), (**C**) Pennsylvania (r_s=0.45, n=15, p-value=0.09), (**D**) Manitoba (r_s=0.3, n=11, p-value=0.36), and (**E**) Alberta (r_s=0.43, n=15, p-value=0.11).



Supplemental Figure 4. Purple martin **Spring migration** timing comparing the departure from winter site in spring (x-axis) to the arrival in the breeding site in spring (y-axis) in the individuals of the five tracked sites; (**A**) Florida (r_s=0.86, n=22, p-value=2.7055E-07), (**B**) Virginia (r_s=0.87, n=11, p-value=0.0005), (**C**) Pennsylvania (r_s=0.61, n=15, p-value=0.016), (**D**) Manitoba (r_s=0.83, n=11, p-value=0.001), and (**E**) Alberta (r_s=0.74, n=15, p-value=0.001).

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