The development and flexibility of timing to environmental variability in a migratory songbird

by

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Abstract

As spring phenology advances with climate change it may create a mismatch between the timing of critical resources and breeding, leading to population declines in some migratory species. To investigate whether long-distance migrants can adjust to their changing environment, I studied the flexibility within two parts of the annual cycle in the eastern subspecies of purple martin (*Progne subis subis*). First, I examined whether the period between the spring arrival date to the first egg-lay date, termed the 'arrival-breeding interval', was flexible to local environmental conditions or constrained by carry-over effects from migration. Direct tracking technologies paired with nest checks at breeding colonies across eastern North America were used to accomplish this first objective. Second, the period from hatch to fall departure was used to explore the influence of ontogenetic effects on the development of migration timing in juvenile birds. The second objective required an experimental manipulation of hatch date at wild purple martin colonies in southern Manitoba to delay the daylength, or photoperiod, experienced by the juveniles while in the nest. I found the arrival-breeding interval to be flexible to local environmental conditions at breeding sites, where shorter intervals were associated with higher temperatures while precipitation had a variable influence depending upon the geographic region. I found no evidence of carry-over effects on the duration of the interval and the interval did not influence fledging success. For my second objective, I found some support for the role of the ontogenetic effect on the development of migration timing in juveniles. Juveniles with experimentally delayed hatch dates did not advance their timing and migrated at a later date than controls. To conclude, my results demonstrate flexibility in timing to environmental conditions, where purple martins lay eggs earlier in warmer springs and that early-hatching juveniles may develop early migration schedules that may enable them to keep up with their changing environment. Future studies are needed to understand if longer arrival-breeding intervals are associated with more flexibility than shorter intervals and if the ontogenetic effects on timing in the nest set migratory timing around the annual cycle.

Keywords

Annual cycle, phenological mismatch, aerial insectivore, purple martin, direct tracking

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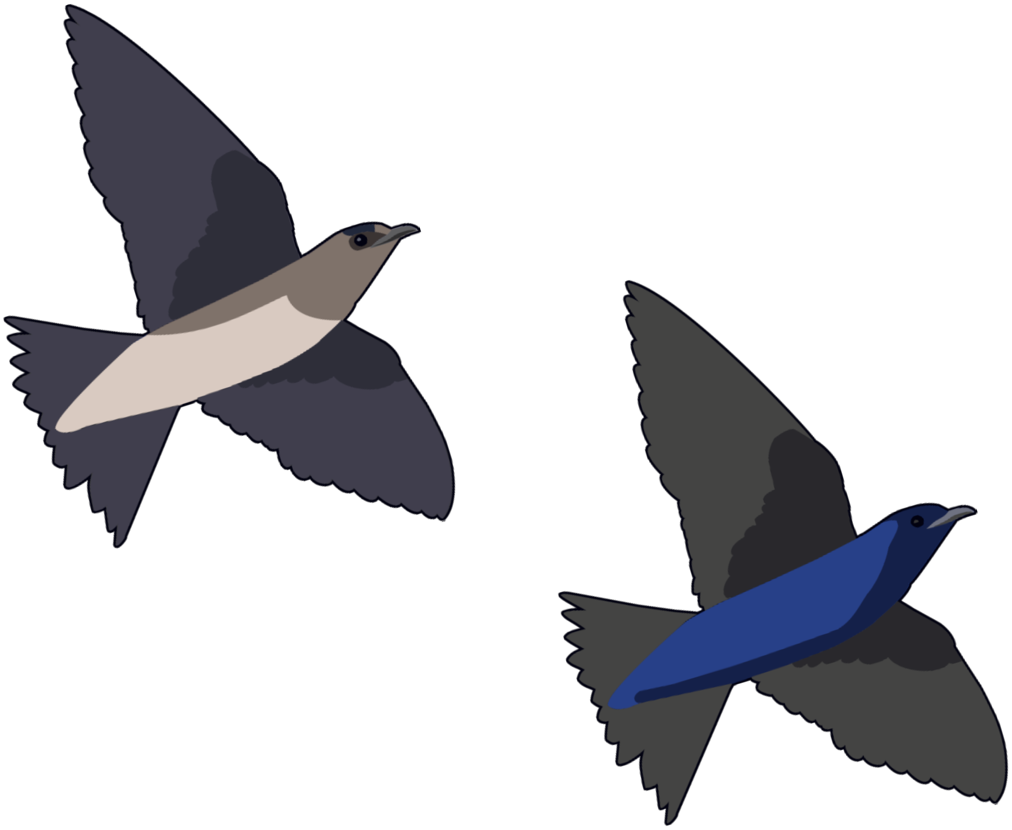

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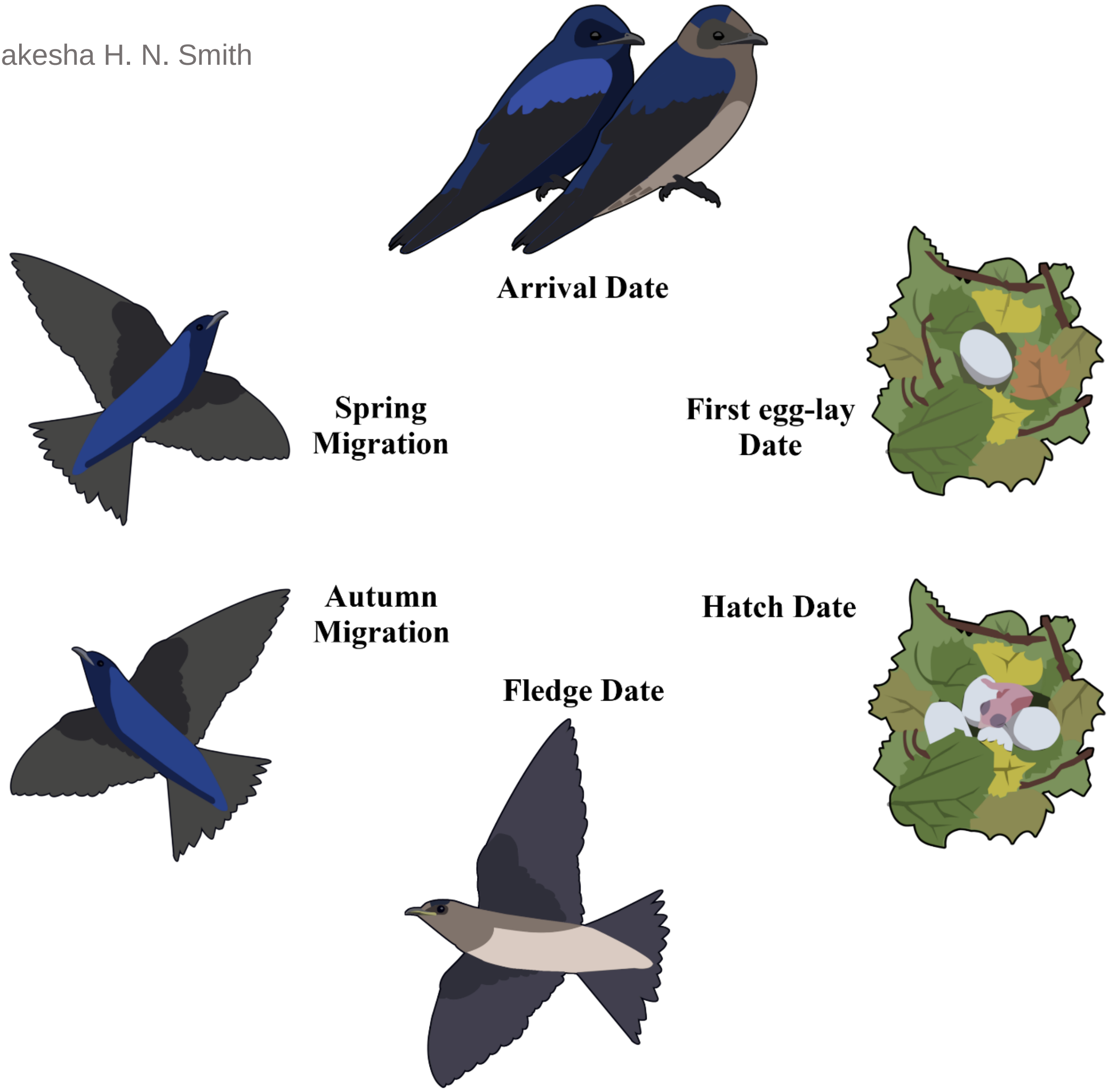
Chapter 1

General Introduction:
The importance of timing

Lakesha H. N. Smith



A general introduction

The avian world is a diverse, complex, and fascinating area of study; from the intricacies of courtship seen in male spotted bowerbirds (*Chlamydera maculata*) carefully spreading bones on the outskirts while placing glass close to the bower to attract females (Borgia, 1995), to the complex diversity of learned songs by the northern mockingbird (*Mimus polyglottos*) found in urban neighbourhoods throughout North and Central Americas and the superb lyrebird (*Menura novaehollandiae*) in the forests of southern Australia (Dalziell et al., 2022; Gammon, 2020). As a result, birds have long captured the attention of many ecologists, turning them into ornithologists, myself included. In particular, migration has been a long-time fascination of mine, defined simply by Berthold (1996) as 'any movement from one temporarily inhabited home area to another.' The migrations of greater than 80,000 km a year in arctic terns (*Sterna paradisaea*) (Egevang et al., 2010) and the fact that many passerine species as juveniles know when and where to migrate to without any guidance from other birds is simply astounding.

Migration in a changing environment

The evolution of migration is associated with several theories, one of which is based on the availability of seasonal resources and competition. Cox (1968) predicted the conditions needed for migratory movements to evolve were: (1) seasonally favourable habitats close to the current species range; (2) reduced intraspecific and interspecific competition in these habitats. In addition, for migratory behaviour to persist, the new areas would need to provide access to more food resources increasing survival and/or reproduction greater than the cost of migration. A comparison of bill morphology of North American migratory and Costa Rican resident species showed there to be less variation and smaller beak size in birds with a higher frequency of migration (Cox, 1968). Cox (1968) reasoned that species with more variable bill morphology would be able to exploit a variety of niches, while less variation in bill morphology would increase competition within a niche and thus increase the likelihood of becoming migratory. This evidence supports the hypothesis that migratory behaviour may evolve where there are high levels of competition near seasonally variable environments (Cox, 1968). Currently, there are approximately 9916 bird species on earth, of which only 1788 are long-distance migrants (Sekercioglu, 2007).

More recently, our changing environment caused by anthropogenic effects has raised questions about whether long-distance migrants will be able to shift their migration timing to keep up. Across North America and Europe, the climate is changing unevenly on spatial and temporal scales (Beck et al., 2018; Šeparović et al., 2013). Abiotic factors such as temperature, precipitation, and wind influence the phenology—the timing of cyclic life history events—of organisms (Lieth, 1974). The new environmental conditions have influenced the phenology of many plants, insects, mammals, and birds (Franks et al., 2007; Mayor et al., 2017; Parmesan & Yohe, 2003). To adjust to the changing climate, they need to either adapt via slow genetic change through generations or acclimate quickly via phenotypic plasticity to their environment (Knudsen et al., 2011). The ability to time critical life-history events such as migration and breeding timing is key to preventing a timing mismatch between breeding and when prey is most abundant. A phenological mismatch in timing can lead to reduced breeding success, which if unchanged may lead to dramatic population declines as seen in some populations of the pied flycatcher (*Ficedula hypoleuca*) (Both et al., 2006).

Genetics, photoperiod, and phenotypic plasticity in migration and breeding timing

A combination of genetics and endogenous rhythms are the main drivers of migratory timing in many passerine species (Berthold, 1993). In birds, the urge to migrate has some degree of heritability. This was demonstrated through an experiment that crossed Eurasian blackcaps (*Sylvia atricapilla*) from a migratory bird population with those from a non-migratory population, where 33% of the resulting offspring displayed migratory activity (Berthold, 1996). More recently, how the *CLOCK* (*Circadian Locomotor Output Cycles Kaput*) gene influences migration timing has been investigated. Specifically, when the poly-Q region of the *Clock* gene had a polymorphism with more glutamine residuals, nightingales (*Luscinia megarhynchos*) migrated later; however, the same effect was not seen in three other long-distance migrants (Saino et al., 2015). The reason the later migration was not seen in three of the four species may have been due to remaining levels of flexibility not within specific candidate genes but in broader regions of the genome that set endogenous rhythms which interact with photoperiod (Liedvogel et al., 2011).

Photoperiod, or daylength, acts as a synchronizer of circadian (daily) and circannual (yearly) rhythms, which program key stages within the annual life cycle of birds. The role for photoperiod in synchronizing circadian rhythms was shown in an experiment by McMillan (1970). White-throated sparrows (*Zonotrichia albicollis*), a nocturnal migrant, experimentally exposed to 24 hour dim light exhibited a switch of migratory restlessness from nocturnal to diurnal activity (McMillan et al., 1970). When exposed again to natural photoperiod, migratory restlessness became synchronized again and the sparrows showed migratory restlessness at night. Circannual rhythms initiate key stages such as the timing of moult (growing in new feathers), gonadal maturation (breeding condition), and migratory restlessness (migration) in nocturnal migratory birds (Gwinner, 1989, 2003). Circannual rhythms are also synchronized by photoperiod, which was shown in an experiment where photoperiod was held constant (12 hours of light 12, hours of dark) for 10 years of an African stonechat's (*Saxicola torquatus*) life

(Gwinner, 2003). Over the years the timing of gonadal maturation and moult occurred earlier each year without the shortening or lengthening of the daylight experienced in the wild (Gwinner, 2003). Together circadian and circannual rhythms are critical timing mechanisms which cue birds to begin key stages of their life cycle, such as spring and fall migration.

Phenotypic plasticity has been shown to provide more fine-scale tuning in migratory timing, which may respond to environmental conditions (Knudsen et al., 2011). Temperature, precipitation, food availability, habitat suitability, and more can affect a bird's body condition influencing migratory and breeding timing (Both et al., 2004, 2010; Gienapp et al., 2007; González et al., 2020; Shave et al., 2019; Sockman & Courter, 2018). Species with low phenotypic plasticity may be unable to respond to changing environmental conditions and the evolution of earlier timing may be too slow to match the pace of climate change. In contrast, species with high levels of phenotypic plasticity such as the purple martin (*Progne subis*) may be able to acclimate more quickly to new conditions (Fraser et al., 2019). Understanding how much phenotypic plasticity avian species have and factors that may constrain plasticity will allow us to gain further insight into how birds may adjust to climate change.

Purple martins and people

The Eastern subspecies of purple martin (*P. subis subis*) originally were secondary cavity nesters, using old cavities from woodpeckers, snags, or crevices under boulders for their nest sites up until around the 1940s, when they transitioned to using only human-made housing for nesting (Allen & Nice, 1952). Alexander Wilson wrote in 1812 that nest boxes were set up by humans for purple martins by Indigenous people of Chactaw and Chichasaw communities in the form of hollowed-out gourds or calabash which they would hang on trees (Allen & Nice, 1952). Around the same time, Alexander Wilson noted that African American slaves also placed calabash on the ends of long canes close to living quarters to attract purple martins (Allen & Nice, 1952). White settlers also offered a place for purple martins to stay as early as the early 1710s as written by Catesby (Allen & Nice, 1952). Although it is unknown if the settlers observed this behaviour from the Indigenous peoples, or vice versa, and took it up as their own since oral knowledge may have been lost while written knowledge has persisted. In any case, the mutualistic relationship between humans and purple martins is relatively old. Humans would put up houses in exchange for purple martins chasing away cats, dogs, crows, hawks, eagles, and vultures which may prey on deer hides, meat, and poultry (Allen & Nice, 1952). In addition, humans would be able to admire their beautiful plumage and lively song (Allen & Nice, 1952). Today, the eastern subspecies of purple martins rely solely on human-made houses and are very rarely seen nesting on natural substrates due to human-caused destruction of their natural nest sites in flooded forest. Due to their reliance on purple martin houses, we can monitor them throughout the breeding season making them a great study species for research on long-distance migrants.

The eastern subspecies of purple martins are long-distance migrants breeding in eastern North America and then migrating to South America in winter, travelling between 7,000-14,000 km during migration (Fraser et al., 2019). The timing of spring departure and spring arrival in purple martins shows large within-individual variation, indicating there is phenotypic plasticity within migration timing (Fraser et al., 2019). As diurnal migrants, they are one of the few passerine species which migrate during the day and may use a fly-and-forage strategy (Lavallée et al., 2021). The prey of purple martins is variable depending on the location, although is typically composed of flies (Diptera) and dragonflies (Odonata) (Forsman et al., 2022), which they capture in flight since they are aerial insectivores. During the breeding season, purple martins construct nests made of small sticks, grass, and leaves in which they lay one clutch containing on average 3-6 eggs (Allen & Nice, 1952; Brown et al., 2021).

Purple martins are aerial insectivores which are one of the taxonomic groups of birds experiencing the steepest population declines since the 1970s (Rosenberg et al., 2019; Smith et al., 2015; Spiller & Dettmers, 2019). Habitat loss, decreased insect availability, environmental contaminants, and phenological mismatches have been proposed to be working together in causing the declines (Spiller & Dettmers, 2019). More research is needed specifically regarding phenological mismatches caused by climate change to determine if aerial insectivores can keep up with advancing springs.

Thesis outline

To provide a greater understanding of mechanisms long-distance migrants may use to respond to their changing environment, we require more knowledge on the flexibility in breeding timing and to learn more about how migration timing is set. I explored timing within different stages of the avian annual cycle in a long-distance migrant, the purple martin (*P. subis subis*) (Figure 1.1).

In **Chapter 2**, to investigate whether birds can flexibly adjust their nest initiation dates, I explored factors influencing the period from when a bird arrives at their breeding grounds until it lays its first egg, called the ‘arrival-breeding interval’ (Low et al., 2019). I tested how local environmental conditions and carry-over effects from migration influence the length of the arrival-breeding interval to gain insight into the plasticity of nest timing and its potential constraints. I show that nest timing was flexible to local environmental conditions, but that these effects differed across regions. By combining data from across a large geographic range, I was able to investigate the complexity of what influences the arrival-breeding interval

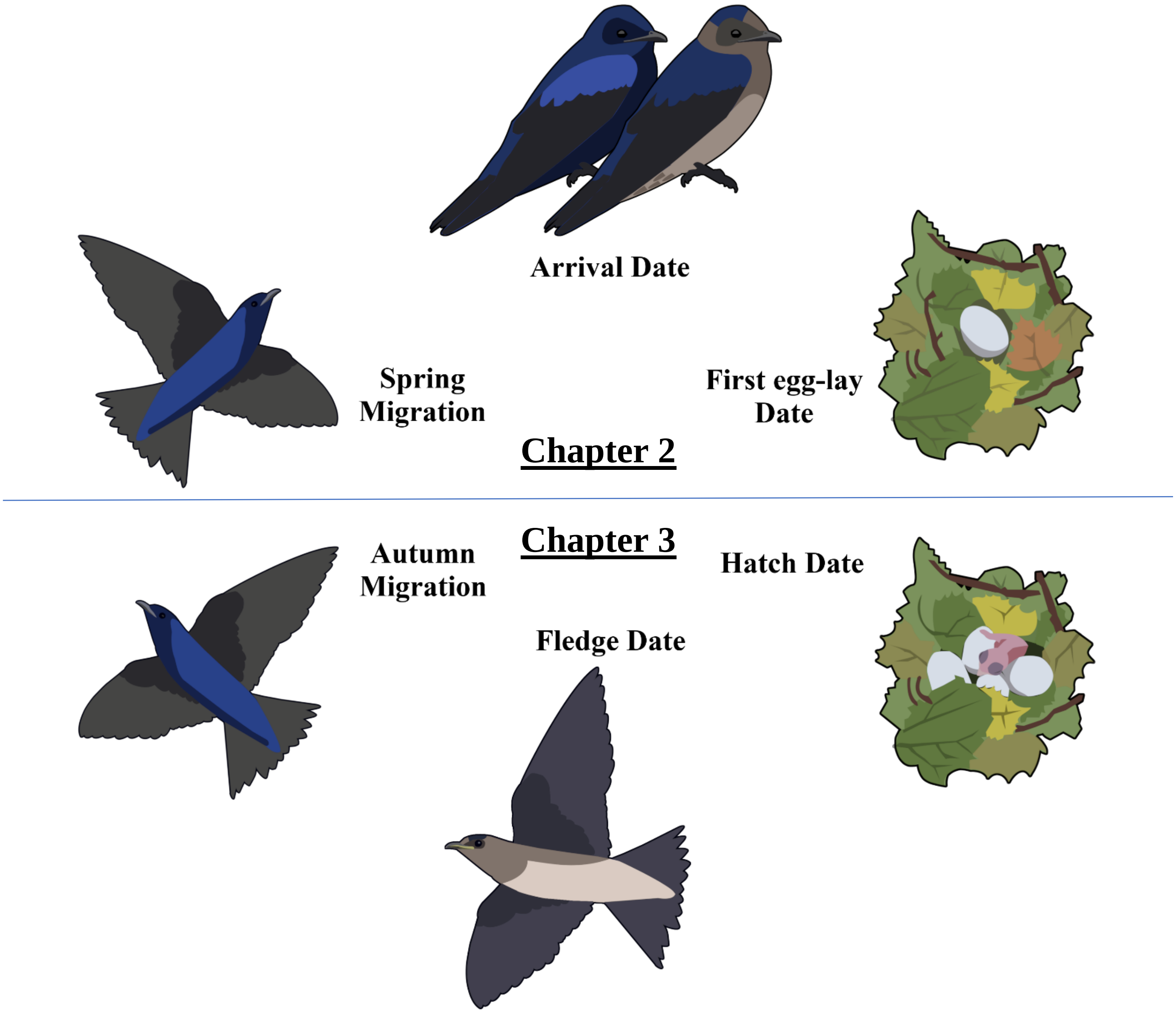


Figure 1.1. Shows the different stages within the annual cycle of a purple martin. In Chapter 2 (above the line) I focus on the period from spring migration to the first egg-lay date looking at the flexibility of the arrival-breeding interval. Then in Chapter 3 (below the line), I focus on the hatch date to the departure date of fall migration and how it influences the timing of migration in juveniles.

duration which may provide further insight into whether long-distance migrants can advance their egg-lay date in response to advancing springs with climate change.

In **Chapter 3,** I turned my focus to the second half of the annual cycle to investigate how migratory timing may be shaped in young birds through an ontogenetic effect of photoperiod, where daylength during development may set migration timing. Such a mechanism may provide a swifter adjustment to advancing springs, if earlier nesting results in birds with earlier timing. In a manipulative field experiment, I delayed the hatch date of a cohort of nestlings to determine whether this flexibly altered their subsequent fledge and departure timing as compared to controls. I found support for an ontogenetic effect of hatch date, where delayed juveniles departed on their fall migration later than controls. I discuss the implications of this ontogenetic effect for responses to climate change.

Finally in **Chapter 4**, using the knowledge gained from prior chapters, I summarise the ability of purple martins to adjust their breeding timing, via the arrival-breeding interval, and how migration timing is set, via the ontogenetic effect. I describe how they connect to advance breeding and migration timing within the annual life cycle of a long-distance migrant. I also highlight a few knowledge gaps to be addressed in future studies.

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Chapter 2

Arrival-breeding interval is flexible in a songbird and is not constrained by migration carry-over effects

Lakesha H. N. Smith, Kevin C. Fraser

Abstract

As spring phenology advances with climate change, so too must the timing of animal phenology to keep up with the new environmental conditions. Long-distance migratory birds may be particularly restricted in their ability to adequately adjust their arrival time at the breeding grounds, since they overwinter far from environmental signals indicating the timing of spring conditions. However, the period between arrival at the breeding ground and the first egg lay date, termed ‘arrival-breeding interval’, may provide an opportunity for birds to flexibly adjust the timing of their nest to match local conditions. To investigate the flexibility of the arrival-breeding interval in a long-distance migrant, the purple martin (*Progne subis*), we hypothesized: 1) if there is phenotypic plasticity in egg-lay date to local conditions upon arrival, interval duration will vary with local environmental conditions; 2) if the interval is constrained by factors during migration, then carry-over effects from migration will influence the interval duration; and 3) if longer intervals are beneficial, then these will be associated with higher fledging success. To address these questions, we used a migration tracking and breeding dataset (n = 133) collected over 9 years in 8 states/provinces throughout the entire eastern North American breeding range of the species. We found that the duration of the arrival-breeding interval was flexible to local environmental conditions. Warmer spring temperatures resulted in shorter arrival-breeding intervals across the range. More precipitation resulted in longer intervals in the southern and coastal regions, but shorter intervals in northern region. Carry-over effects of migration rate and stopover duration did not influence the length of the arrival-breeding interval in any region. Longer intervals corresponded to earlier arrival dates at breeding sites but were not associated with higher fledging success. Overall, the plasticity of the arrival-breeding interval may provide purple martins with the flexibility required to time their breeding to optimal conditions at breeding sites. Understanding if the arrival-breeding interval is flexible or constrained sheds light on species that are unable to react to their changing environment and may require additional conservation efforts.

Keywords

Purple Martin, phenotypic plasticity, arrival-breeding interval, local conditions, carry-over effects

1 | Introduction

Phenotypic plasticity is crucial for avian species to keep up with the year-to-year variation in climate, by adjusting various stages within the annual cycle (Conklin et al., 2021; Fraser et al., 2019; Vedder et al., 2013). Earlier variable spring weather has resulted in earlier plant growth (Cleland et al., 2007) and insect emergence (Buckley et al., 2017; Thackeray et al., 2016). Migratory animals which winter far from their breeding grounds may not receive the meteorological signals of an earlier spring, which is a particular problem in the case of long-distance migratory birds (Gordo et al., 2005). Birds arriving too late to their breeding grounds may result in a mismatch between the timing of peak prey abundance and the timing of nesting which can lead to low breeding success and population declines (Both et al., 2006, 2009, 2010; Saino et al., 2011). By adjusting the timing of critical stages within the annual cycle to new environmental conditions, such as the timing of arrival and breeding, long-distance migrants may be able to avoid a phenological mismatch with key resources.

Arrival at the breeding grounds is a key stage within the annual cycle since individuals arriving earlier can claim prime territories, pair with fit mates (Kokko, 1999), and maximize clutch size and fledging success (Tomotani et al., 2018; Winkler et al., 2014), thereby increasing fitness. However, avian migration timing (e.g. spring departure dates and arrival dates) is fairly constrained in many species by endogenous timing (Berthold, 1996; Coppack & Both, 2002). For instance, in the long-distance migrant the pied flycatcher (*Ficedula hypoleuca*) spring arrival dates remained similar over 20 years while the timing of egg-laying advanced (Both & Visser, 2001). Unchanging arrival dates suggest that migratory schedules may be more rigid, whereas the timing of breeding may exhibit a higher degree of phenotypic plasticity to local conditions encountered upon arrival.

An adjustment to local environmental conditions via phenotypic plasticity may provide enough flexibly for birds to lay eggs at optimal times. However, the first egg-lay date may be constrained by the timing of arrival at breeding sites, leaving insufficient time for birds to adjust their lay dates in response to local conditions once at their breeding sites (Both & Visser, 2001). Carry-over effects from migration may constrain the timing of egg laying, but has not been studied extensively (Harrison et al., 2011). Faster migration rates and shorter stopover durations during spring migration can incur high energetic costs that carry-over to impact breeding activities. This is due to the increased energy expenditure from higher rates of travel, requiring more time to recover after arrival at breeding sites and to gain resources to support egg laying (Hedenström & Alerstam, 1997). The majority of long-distance migratory songbirds are income breeders, acquiring food resources used for reproduction after arrival (Langin et al., 2006; Nooker et al., 2005; Stephens et al., 2009), and may limit the speed at which females can lay their first egg. Therefore, carry-over effects from migration may set the lower limit of how short the arrival-breeding interval can become and, thus, may cause a mismatch in timing. Our understanding of how local conditions and migration together influence the period from arrival at breeding grounds to laying the first egg, i.e. the ‘arrival-breeding interval’ (Low et al., 2019), requires further study.

Egg-lay timing may exhibit phenotypic plasticity to local environmental conditions encountered once on the breeding grounds, potentially reducing phenological mismatch. The advancement of earlier egg laying to warmer temperatures in early springs has been widely documented in many avian species (Hoover & Schelsky, 2020; Shave et al., 2019; Tomotani et al., 2018; Tøttrup et al., 2010; Visser et al., 2009). In the case of northern wheatear (*Oenanthe oenanthe*), earlier arriving birds were able to flexibly alter their breeding timing based on local conditions encountered after arrival; however the same could not be said for the late arrivers (Low et al., 2019). Warmer temperatures may act as a direct cue to lay eggs (Visser et al., 2009), or indirectly by increasing food abundance, or by reducing energetic costs (Dunn, 2004). Precipitation also influences the timing of egg-laying, with increased rainfall leading to later lay dates particularly in aerial insectivores (Sockman & Courter, 2018). Delayed breeding in this case may be caused by decreased foraging ability in heavy rain as flying insects are grounded during this time (Cox et al., 2019). Therefore, if there remains plasticity within the arrival-breeding interval to local conditions at the breeding grounds, then birds may be able to breed at the optimum time.

Throughout Europe and North America the weather varies widely, and the climate is changing at different rates across the continent (Beck et al., 2018; Šeparović et al., 2013). In Europe, the effect of temperature on laying date varied between populations of pied flycatchers. Specifically, there were stronger advancements of the first egg-lay date located in populations with higher spring temperatures (Both et al., 2004). Further support for how differing temperature influences egg-lay date across a large geographic region comes from purple martins (*Progne subis*) breeding throughout eastern North America. Selection favoured early egg-laying in warmer years and was strongest at northern latitudes (Shave et al., 2019). This evidence demonstrates that local conditions will likely differ across a species' entire breeding range and, therefore, the response of arrival-breeding interval length to local conditions likely vary as well. A deeper understanding of the phenotypic plasticity to environmental variability in the arrival-breeding interval throughout a wide range would provide more insight into which populations are most vulnerable. If plasticity allows for subtle adjustments to be made to the arrival-breeding interval, then this may be a mechanism that may allow for some birds to reduce the mismatch between peak prey and peak breeding and maximize fledging success.

To increase our understanding of how carry-over effects from migration and local conditions influence the arrival-breeding interval across a large geographic range we studied the eastern subspecies of purple martin (*Progne subis subis*). Using a dataset of light-level geolocators collected across 10 years throughout eastern North America combined with associated nest timing data, we were able to address our three hypotheses. First, we hypothesized that if there is phenotypic plasticity in the arrival-breeding interval then nest timing will vary in response to local environmental conditions and the interval length will vary by region. We predicted that warmer temperatures would result in shorter intervals and high levels of rainfall would lengthen the interval. We predicted local conditions would have a greater effect at more northern latitudes, where temperature variation is larger. Second, we hypothesized that if the arrival-breeding interval is constrained by factors during migration, then carry-over effects from migration will influence interval length. We expected these effects would vary by region, owing to the large variation in migration routes and stopover durations among populations (Neufeld et al., 2021; Turcotte-van de Rydt, 2022). We predicted that faster migration rates and shorter stopovers during migration would lead to longer arrival-breeding intervals. For regional differences, we expect northern breeders to have longer intervals due to their longer, more energetically costly migrations. Lastly, if longer arrival-breeding intervals are related to early arrival, then longer intervals would increase overall fledging success as they would have first choice of high-quality nest sites, mates, more time for females to acquire resources for egg laying, and more time to construct a nest.

2 | Materials and methods

2.1 | Study species and study sites

Purple martins are long-distance diurnal migrants (Lavallée et al., 2021). In spring, they can migrate anywhere between 7,000-14,000 km from South America to North America (Fraser et al., 2019). As aerial insectivores, they feed on flying insects year round (Brown et al., 2021). The eastern subspecies breeds east of the Rocky Mountains, primarily nesting in human-made houses (Brown et al., 2021). Purple martins are colonial nesters and typically lay a single clutch of 3-6 eggs per year (Brown et al., 2021).

Study sites were located throughout eastern North America in Florida (26.1°N, 81.7°W; 28.4°N, 81.6°W), Virginia (38.6°N, 77.3°W), New Jersey (40.4°N, 74.0°W), Pennsylvania (42.1°N, 80.1°W), South Dakota (45.6°N, 98.3°W), Minnesota (46.1°N, 93.7°W; 46.4°N, 94.2°W), Manitoba (49.7°N, 97.1°W; 49.8°N, 97.0°W; 50.2°N, 97.1°W), and Alberta (52.4°N, 113.6°W). Due to the large area that our sites covered and the different nest timing and migration timing that purple martins have been previously shown to have throughout eastern North America (Neufeld et al., 2021; Shave et al., 2019), the study sites were grouped using a k-means clustering algorithm. K-means clustering groups data based on similarity (Pham et al., 2005) and we used latitude and average temperature to form groups. To choose the number of groups, we tested k=3 and k=4 and found 4 groups to be the most parsimonious, with all individuals in one state or province being grouped into the same cluster, or region (Pham et al., 2005). The northern region contained purple martins from Alberta and Manitoba breeding colonies (n = 54), the central region contained purple martins from Minnesota and South Dakota colonies (n = 18), the coastal region contained purple martins from New Jersey, Pennsylvania, and Virginia colonies (n = 39), and lastly, the southern region contained purple martins from Florida colonies (n = 21; Figure 2.1).

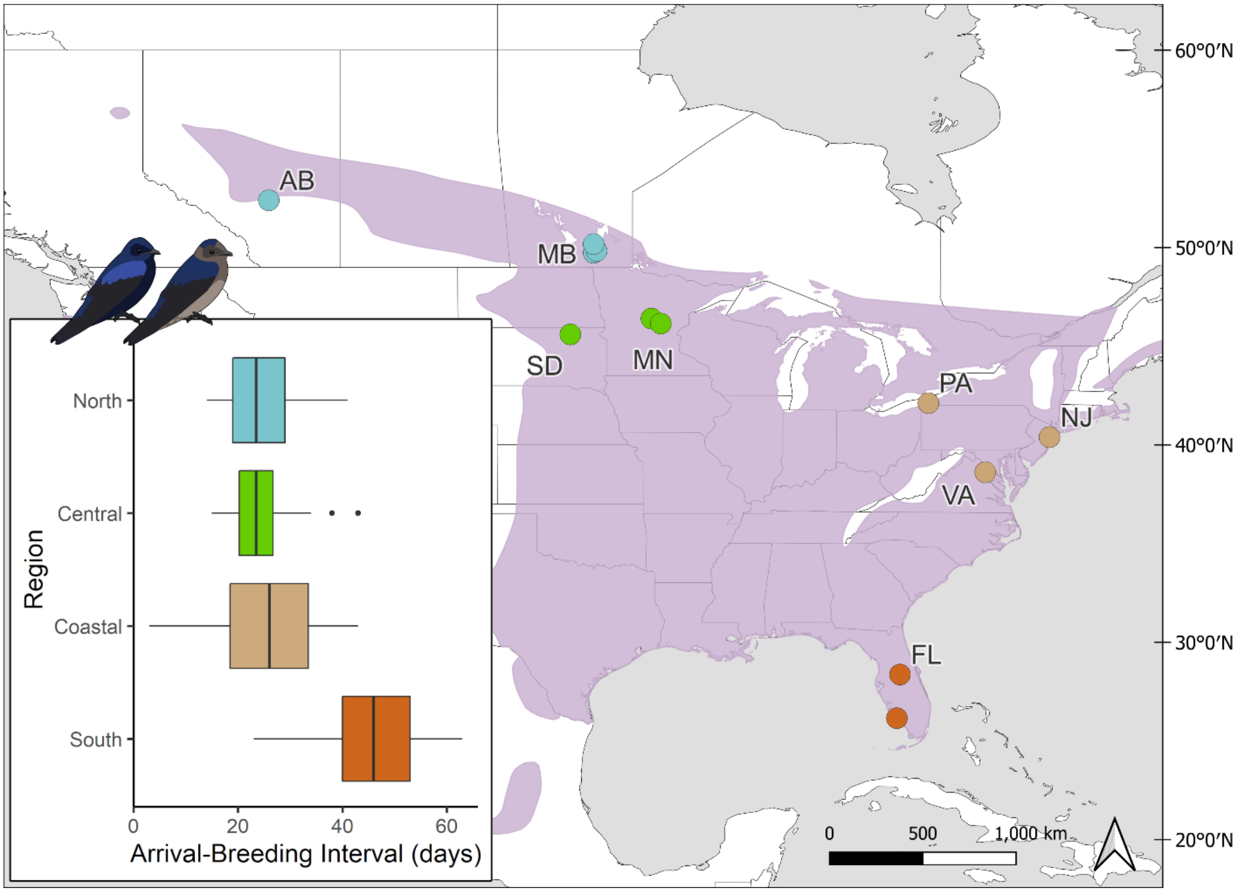

Figure 2.1. Displays purple martin breeding colony locations used in the study (indicated by the points) and their associated regions. The breeding distribution is shown in purple. The northern region is blue (n = 54), the central region is green (n = 18), the coastal region is beige (n = 39), and the southern region is red (n = 21). The box plot shows the variation within the arrival-breeding interval length of each region. Purple martin distribution by BirdLife International and the Handbook of the Bird of the World (2022).

2.2 | Data collection

We used a dataset containing both arrival dates and laying dates in order to calculate each purple martin's arrival-breeding interval. Altogether, 132 individuals had accurate arrival-breeding intervals and were collected from 2008, 2010-2017. Data from the northern region was collected between 2013-2017, the central region was collected between 2012-2014, the coastal region was collected from 2008, 2010-2013, and the southern region was collected in 2014. Ten birds were tracked over more than one year.

2.2.1 | Migration Data Analysis

Light-level geolocator tags (≤ 1.6 g; MK10s/12/12 s/14 s/20, British Antarctic Survey), attached via a Teflon leg-loop harness (Rappole & Tipton, 1991), were deployed on adult purple martins. Adult purple martins have high site fidelity and return to the same colony each year, thereby allowing retrieval of the device. In addition, each individual was aged at capture as either in its second year of life (SY) or after its second year of life (ASY), and sexed using plumage characteristics (Pyle, 1997). However, since we used the spring migration tracks in the following year, the age of the birds analyzed correspond to their third year of life (TY) or after their third year of life (ATY).

To determine spring arrival dates, the migration data were processed in R (version 3.6.1) using RStudio (version 1.2.5001, R Core Team 2019). To define and correct twilight events, i.e. sunrise and sunset, 'BAStag' with the light threshold of 32 was used (Neufeld et al., 2021). 'BAStag' is a package used to import and plot light graphs to detect and edit twilight events from British Antarctic Survey archival tags (version 0.1.3, Wotherspoon et al., 2016). Next, 'GeoLight' (version 2.0.0, Lisovski & Hahn, 2012) was used to create latitudinal and longitudinal coordinates, which were used to determine arrival dates (Neufeld et al., 2021).

To create the spring migration tracks used to calculate the migration rate and stopover duration the package 'FLightR' was used. 'FLightR' (version 0.5.2, Rakhimberdiev et al., 2017) uses a hidden Markov chain model which provides a better estimation of migration routes than previous packages since it also takes into account the twilight before and after the twilight in question. In addition, the template fit observational model in 'FlightR' also takes into account the change in the brightness of the light with the angle of the sun and accounts for some shading (Rakhimberdiev et al., 2017). To create our tracks we ran the particle filter with 1 million particles, with known.last set as equal to true and check.outliers to true.

Next, to calculate the stopover timing and durations the function 'stationary.migration.summary' was used with a probability cut-off of 0.1 and a minimum stay of 3 twilights. The stopover duration is the amount of time during the spring migration an individual is stopped for 3 or more twilights with a probability of movement less than 0.1. Three twilights, the equivalent of 36 hours, were chosen since purple martins typically migrate during the day (Lavallée et al., 2021). So, if a purple martin stayed in a spot for 36 hours it would encompass two days and one night and is more representative of a bird not using an opportunity to fly during the day. The 50% quartiles were used to calculate the duration of each stopover during migration. When birds were stationary at their breeding or wintering sites, we excluded them as stopovers since they were not actively migrating.

Once all the migration tracks were created, the total migration distance was calculated using the package 'sp' (version 1.4.6, Bivand et al., 2013) using code that was adapted from Hill et al. (2019). Then spring migration rate and stopover duration for each individual were calculated. The total migration rate (km/day) was calculated as the total distance of migration divided by the number of days an individual was migrating, found by subtracting the arrival date from the departure date. The stopover duration was the proportion of spring migration time spent on stopovers and was calculated by dividing the total duration of stopovers (in days) by the total days of migration. Stopover periods were inspected and biologically implausible migration rates were corrected manually. For example, purple martins can fly >1000 km a day to cross the Gulf of Mexico (Lavallée et al., 2021), yet it is unlikely for a martin to fly at speeds of >1000 km/day during the entire migration. So, we corrected the stopover durations (which influences migration rate) by designating a stopover as a bird remaining in a similar longitude and latitude (varying by ~ 0.2°) for 3 or more twilights. Individuals with biologically unrealistic migration rates of over 1000 km/day after correcting for stopover durations were excluded from the dataset.

2.2.2 | Nest Data

Nesting data for each individual was collected following guidelines by "Project Martinwatch" which provided data on the first egg-lay date and the number of young that fledged (Purple Martin Conservation Association, 2017). Researchers and citizen scientists would check purple martin nests every 5 to 7 days throughout the breeding season following Purple Martin Conservation Association (PMCA) guidelines. The first egg-lay date was estimated by counting the number of eggs in the nest. Since female purple martins lay one egg a day consecutively, the current date could be subtracted by the number of eggs in the nest to determine when the first egg was laid (PMCA, 2017). For males, the first egg-lay date was the day the female he was paired with laid the first egg in the nest. Although extrapair young are common in purple martins, they have been primarily observed in the nests of second-year birds, where males had about 29% paternity in their nests, as compared to birds three or older which had about 96% paternity (Morton et al., 1990). Since our study had 3-year-old birds and after 3-year-old birds the majority of the offspring in the nest likely belong to the male. Purple martins start incubation when the penultimate, second to last, egg is laid and typically incubate for 15-18 days (Brown et al., 2021). Upon hatching, the nestling's age (days old) is determined based on size and plumage development, allowing the accurate estimation of the hatch date. To determine how many juveniles successfully fledged the number of juveniles in a nest that were a minimum of 26 days old were counted as successfully fledged (PMCA, 2017).

2.2.3. | Weather Data

Average daily temperature (°C) and total daily precipitation (mm) in Canada and the United States were collected using the package 'weathercan' and 'GSODR' respectively, in R version 4.1.2. The package 'weathercan' extracts historical weather data from Environment and Climate Change Canada (version 0.6.2, Lazerte & Albers, 2018). While 'GSODR' (Global Surface Summary of the Day - GSOD) extracts average daily weather data from USA National Centers for Environmental Information (Sparks et al., 2017). The closest weather station to the colony that contained complete data for both temperature and precipitation was chosen. The distances from the weather stations to the colony ranged from 3 km to 42 km (Supplemental Table 2.1).

The average temperature during each bird's arrival-breeding interval included the migration arrival dates obtained by using light-level geolocators and the first egg-lay dates collected by nest monitoring, as explained above. The mean temperature during the arrival-breeding interval was calculated including the day of arrival to the day the first egg was laid. The mean of the total daily precipitation during the interval was also calculated for each bird.

2.3 | Statistical analyses

All statistical analyses were done using the package 'glmmTMB' (version 1.1.3, Brooks et al., 2017) in R (version 4.1.3) using RStudio (version 2021.09.2, R Core Team 2022). We used LMMs to incorporate random effects into the model and LMs when random effects were not included. Colony, individual, and year were chosen as random effects. However, due to the categorical variable of region, most of the variation in location is already removed from the model and therefore colony was excluded from all models. The random effect of individual was also removed from the model since it accounted for little of the variation within the data. In addition, age and sex were considered in the analysis as covariates, yet after testing if there is an interaction between variables there was no interaction found between them and sex so it was excluded from all models.

We examined the effect of local conditions, temperature and precipitation, on the arrival-breeding interval in different regions. To determine the varying influence of temperature on the dependent variable, the arrival-breeding interval, we made a model which included an interactions between fixed effects of temperature: region. A similar model was created on the influence of precipitation on the arrival-breeding interval across regions, it included a precipitation: region interaction. For both models in addition to the interaction, additional variables which may explain part of the variation such as age and the random effect of year were included.

Next, the effect of carry-over effects from migration (migration rate and stopover duration) on the arrival-breeding interval in different regions, was modelled. To determine if the migration rate influences the dependent variable, the arrival-breeding interval, differently across regions we included interactions between the fixed effects migration rate: region. The other variable included in the migration rate model was age; year was excluded from this model due to convergence problems, therefore we used an LM. The effects of stopover duration on arrival-breeding interval across regions had an interaction of stopover duration: region. The stopover duration model had additional variables which may explain part of the variation such as age, and the random effect of year were included.

Finally, we investigated whether the number of successfully fledged young was influenced by the length of the arrival-breeding interval in any region. We fit a model with the number of fledged juveniles as the dependent variable, an interaction between arrival-breeding interval: region, and additional variables of first egg-lay date, age, and the random effect of year.

The first egg-lay date was included as earlier egg-lay dates have been shown in previous studies to influence the number of fledged young (Tomotani et al., 2018). In addition, to determine if birds with longer arrival-breeding intervals tend to be birds that arrive earlier, we fit a model with arrival-breeding interval as the dependent variable which included the interaction arrival date: region as well as age. The random effect of year was excluded from this model due to inability to converge.

3 | Results

3.1 | Variation within the arrival-breeding interval

The length of the arrival-breeding interval generally increased from north to south. The mean interval length in the northern region was 24.1 ± 6.20 days (n = 54), in the central region was 25.0 ± 7.41 days (n = 18), in the coastal region was 26.1 ± 8.82 days (n = 39), and in the southern region was 45.7 ± 10.10 days (n = 21). The shortest interval length of 3 days was seen in a three-year-old male in the coastal region, while the longest was 63 days in a male older than 3 years in the southern region. In regards to sex, the mean interval length of males on average was 29.4 ± 12.1 days (n = 64) while females had interval lengths on average of 27.0 ± 9.71 days (n = 68). Of the 132 birds with arrival-breeding intervals across 10 years, accurate spring migration tracks were collected for 126, and fledging success was collected for 110 individuals.

3.2 | Effect of local effects on arrival-breeding interval

We found an effect of local conditions on the length of the arrival-breeding interval (Table 2.1). First, the local effect of temperature had a negative relationship with the duration of the arrival-breeding interval from North to South (model coefficients for each region: north = -2.22 ± 0.75, CI = -3.69 to -0.74; central = 1.02 ± 0.96, CI = -0.86 to 2.89; coastal = -0.09 ± 0.95, CI = -1.96 to 1.78; south = -2.24 ± 1.66, CI = -5.51 to 1.02). For example, birds encountering a 1˚C increase in temperature in the northern region had an interval length that was 2.22 days shorter (Table 2.1a, Figure 2.2a). There was no difference found between the northern region and the other three regions, meaning that there was a similar negative effect of temperature from North to South.

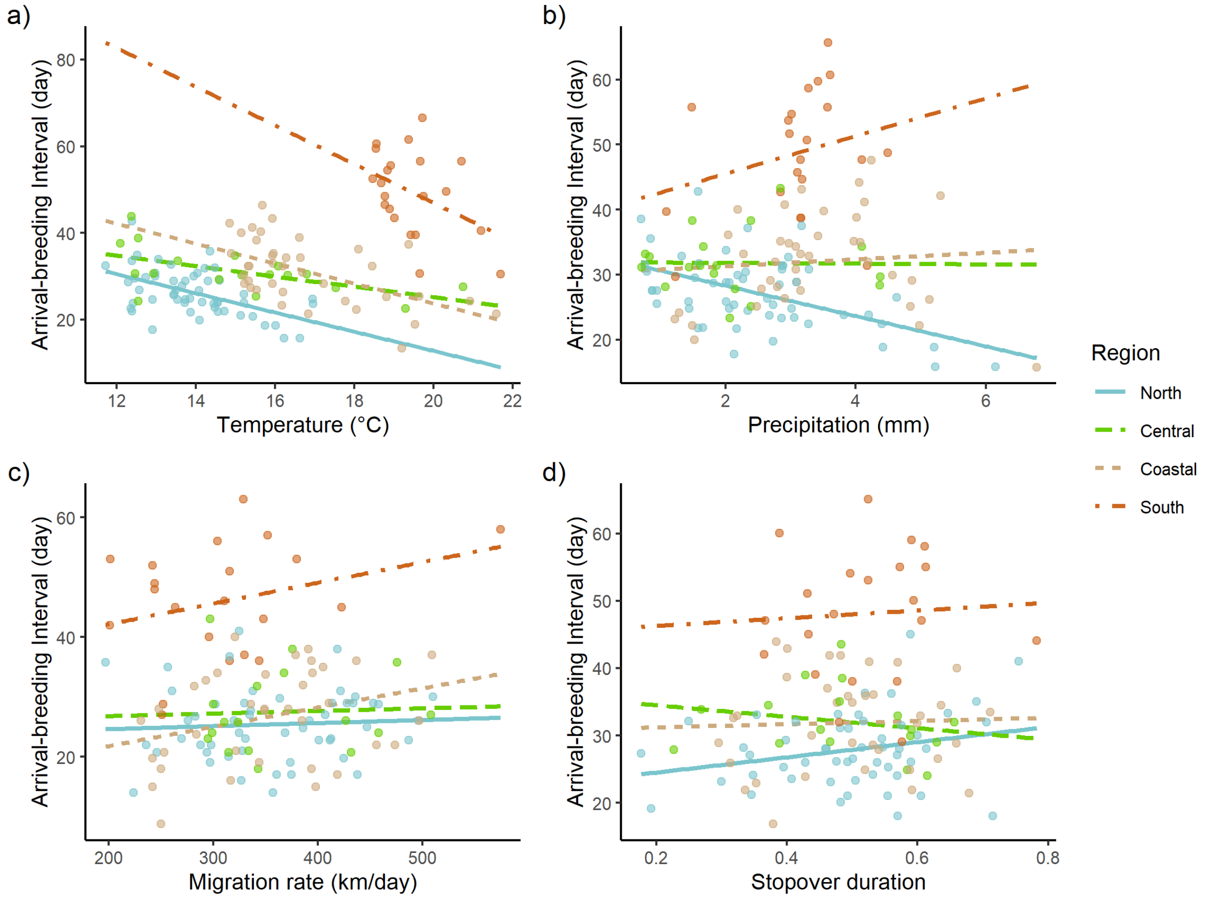

Figure 2.2. Displays the estimates of (a) average temperature (˚C) during the arrival-breeding interval (n = 132), (b) average total precipitation (mm) during the interval (n = 132), (c) average migration rate (km/day) over the entire spring migration (n = 126), (d) stopover duration is the proportion of time spent on stopovers during migration (n = 126), on length of interval in 4 regions. The north region is represented by blue, the central region by green, the coastal region by beige, and the south region by red.

Second, we found the effect of precipitation on the arrival-breeding interval to vary by region (Table 2.1b, Figure 2.2b). The local effect of precipitation had a positive relationship with the length of the arrival to breeding interval for coastal and southern regions, indicating that birds experiencing more precipitation had longer arrival-breeding intervals. The positive relationship between precipitation and interval length was found to be strongest in the southern region with a 1 mm increase in precipitation leading to an increase in interval length by 5.23 ± 1.88 days. In the central region, precipitation had less of an influence on the length of the arrival-breeding interval which lengthened by 2.85 ± 1.25 days. In sharp contrast, a 1 mm increase in precipitation in the northern region led to a 2.33 ± 0.87 day decrease in the length of the interval. The influence of precipitation in the Central region was not different from that of the northern region, perhaps due to its low sample size (n = 18).

Table 2.1. Summary of the influence of local effects of temperature and precipitation on the arrival-breeding interval. (a) Parameter estimates from a linear mixed model of temperatures effect on the interval length (n = 132). (b) Parameter estimates from a LMM of precipitations effect on the interval (n = 132). Regions include North, Central, Coastal, and South and Age includes Third year or After third year.

Fixed effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**
a. Temperature: Region + Age + (1|Year)				
Temperature	-2.22	0.75	-3.69	-0.74
Third year	-4.07	1.34	-6.69	-1.45
Temperature: Central	1.02	0.96	-0.86	2.89
Temperature: Coastal	-0.09	0.95	-1.96	1.78
Temperature: South	-2.24	1.66	-5.51	1.02
Random effects	Variance		R^2	
Year	9.44		marginal	0.65
Residual	35.27		conditional	0.72

b. Precipitation: Region + Age + (1|Year)				
Precipitation	-2.33	0.87	-4.03	-0.63
Third year	-5.64	1.42	-8.42	-2.87
Precipitation: Central	2.28	1.73	-1.11	5.66
Precipitation: Coastal	2.85	1.25	0.40	5.30
Precipitation: South	5.23	1.88	1.55	8.91
Random effects	Variance		R^2	
Year	8.17		marginal	0.59
Residual	42.36		conditional	0.65

In both local condition models, there was an influence of age on the length of the arrival-breeding interval. Third year purple martins had a shorter arrival-breeding interval than older birds, likely due to their known late arrival in spring (Morton & Derrickson, 1990). The temperature model explained a large amount of variation within the arrival-breeding interval with a marginal $R^2 = 0.65$ and including the random effect of year the conditional $R^2 = 0.72$. Our precipitation model also explained a good amount of the variation within the data with a marginal $R^2 = 0.59$ and year explaining part of the variation with a conditional $R^2 = 0.65$.

3.3 | Effect of migration carry-over effects on arrival-breeding interval

We found there to be no influence of carry-over effects from migration (*i.e.* migration rate and stopover duration) and their interactions between regions on the length of the arrival-breeding interval (Figure 2.2, Table 2.2). Therefore, carry-over effects were not found to influence the length of the arrival-breeding interval within or among different regions. The lack of relationship may be due to the long arrival-breeding interval purple martins across all regions which on average was 28.2 ± 11.0 days (n = 132). Age again was seen to have an influence on the length of the interval with third year birds having shorter arrival-breeding intervals than older birds.

Table 2.2. Summary of the influence of carry-over effects including Migration rate model and Stopover duration model on the Arrival-breeding Interval. (a) Parameter estimates from a linear model describing the interaction between Migration Rate: Region (n = 126) and (b) parameter estimates from a linear mixed model describing the interaction between Stopover Duration: Region on Arrival-breeding interval (n = 126). Both models contain Age as a covariate, with random effect of Year.

Fixed effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**
a. Migration rate model				
Migration rate	0.005	0.013	-0.021	0.031
Third year	-5.757	1.551	-8.798	-2.717
Migration rate: Central	-0.001	0.029	-0.057	0.055
Migration rate: Coastal	0.027	0.021	-0.014	0.068
Migration rate: South	0.029	0.023	-0.016	0.075
			R^2	
			marginal	0.599
b. Stopover duration model				
Stopover	11.30	8.61	-5.57	28.16
Third year	-6.95	1.50	-9.90	-4.00
Stopover: Central	-19.86	16.35	-51.90	12.18
Stopover: Coastal	-8.92	13.67	-35.70	17.87
Stopover: South	-5.60	17.19	-39.29	28.08
Random effects	Variance		R^2	
Year	9.41		marginal	0.55
Residual	44.63		conditional	0.63

3.4 | Effect of arrival-breeding interval on fledging success

Overall, longer arrival-breeding intervals did not increase the number of juveniles that successfully fledged in any region (0.03 ± 0.04 young, CI = -0.11 to 0.06, see Table 2.3). However, we did find longer arrival-breeding intervals were related to earlier arrival, with a one-day earlier arrival corresponding to a 0.43 day increase in interval length (Supplemental Table 2.2), it did not result in higher fledging success. Instead, the weak negative relationship between fledge success and first egg-lay date had a stronger influence (-0.05 ± 0.02 young, CI = -0.10 to -0.01). For example, birds that laid 20 days later in the season had approximately 1 less offspring fledge than those who laid earlier. Third year purple martins did not differ from older adults in the number of young fledged which may have been due to the unequal sample size between third year (n = 33) and after third year birds (n = 99).

Table 2.3. Fledge success model parameter estimates from a linear mixed model describing the interaction between Arrival-breeding Interval: Region (North, Central, Coastal, South), First Egg-lay Date, Age (Third year, After third year), and random effect of Year on Fledging Success (n = 104).

Fixed effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**
Fledge success model				
Interval	-0.03	0.04	-0.11	0.06
Central	-2.01	1.80	-5.55	1.52
Coastal	-1.97	1.45	-4.81	0.86
South	-5.34	2.61	-10.45	-0.23
Third year	0.20	0.38	-0.53	0.94
First egg-lay date	-0.05	0.02	-0.10	-0.01
Interval: Central	0.07	0.07	-0.06	0.20
Interval: Coastal	0.02	0.05	-0.08	0.12
Interval: South	0.03	0.06	-0.09	0.15
Random effects	Variance		R^2	
Year	0.30		marginal	0.09
Residual	2.21		conditional	0.20

4 | Discussion

To learn if long-distance migrants can adjust their arrival-breeding interval to local environmental conditions by laying eggs earlier or determine if the interval is constrained by migration, we studied purple martins across their breeding range. If there is phenotypic plasticity within the arrival-breeding interval it may allow migrants to keep up with year-to-year fluctuations in environmental conditions. Our study confirmed that higher temperatures shortened the arrival-breeding interval similarly in all regions. Precipitation had variable results, with more rain in the North appearing to be beneficial and advancing the timing of nesting, while in the South more rain may have been detrimental, delaying nesting and resulting in longer intervals. Egg-laying dates did not appear to be constrained by carry-over effects of migration rate or stopover duration on the arrival-breeding interval. Longer arrival-breeding interval lengths corresponded with an earlier arrival, yet did not result in higher fledging success. Altogether our findings align with previous studies demonstrating the interval is more influenced by local conditions (Low et al., 2019; Tomotani et al., 2018) and contradicts previous studies suggesting breeding timing is constrained by arrival to breeding grounds (Both & Visser, 2001). Furthermore, we found fledging success was not affected by the length of the interval. This may indicate that the long arrival-breeding interval purple martins have may currently contain enough phenotypic plasticity to remain matched with advancing spring phenology.

We found higher temperatures shortened the arrival-breeding interval, thus resulting in an earlier lay date (Figure 2.2). Our findings contribute to recent evidence that lay dates of migratory songbirds can be flexible to local environmental conditions (Hoover & Schelsky, 2020; Low et al., 2019; Tomotani et al., 2018). For instance, northern wheatears were found to have shorter interval lengths in early springs, when they arrived later and had prior experience (*i.e.* subadults vs adults) (Low et al., 2019). In addition, purple martins experiencing warmer springs tend to lay eggs earlier and produce more juveniles (Shave et al., 2019). Conversely, low temperatures can delay egg laying by decreasing prey availability (Shipley et al., 2020), leading to a decline in body condition (Brown & Brown, 2000). We found, surprisingly, that the influence of temperature was similar in all regions. We had predicted a greater impact of temperatures in the North, where cooler temperatures were more prevalent and variability was higher. This suggests that birds across latitudes may time their nests flexibly to local temperatures, even where there is lower variability in temperature. In addition, our study took a new approach compared to previous studies by using the mean temperature during each individual's arrival-breeding interval instead of relying on a set period of one month (Both & Visser, 2001; Hoover & Schelsky, 2020), or using the sliding window approach (Smith et al., 2020; Tomotani et al., 2018). Our findings further provide support for warmer spring temperatures resulting in shorter interval lengths throughout the purple martin's eastern breeding range.

We found marked variation in the influence of precipitation on interval length between regions. Our prediction was that increased rainfall would decrease foraging opportunities leading to a longer arrival-breeding interval. However, increased precipitation led to shorter interval lengths in the northern region but had the opposite effect, leading to longer intervals, in the coastal and southern regions (Table 2.1b). This raised the question of what changed the influence of precipitation between the North and South. One explanation for why more rain in the South reduced breeding conditions while the opposite effect was seen in the North may be due to the time of day in which precipitation typically occurs. In the Southern United States, most rainfall occurred during the day, in the afternoon, in the spring and summer (Prat & Nelson, 2014). Rain during the day would be detrimental to aerial insectivores because insects are not actively flying during periods of cold or wet weather and reducing the time available for foraging (Brown & Brown, 2000). This may be a reason precipitation in the South led to a longer arrival-breeding interval. In contrast, in the North (in the Canadian prairies) rainfall primarily occurs overnight and into the early morning (Chakravarti & Archibold, 1993). Since purple martins are primarily diurnal (Brown et al., 2021; Lavallée et al., 2021), martins in the North may have more time to forage for insects during the day than purple martins in the South. Additionally, in all regions increased rain during the breeding season may increase insect abundance, due to an increased number of water bodies in which larval stages of their prey (for instance, dragonfly nymphs) can grow. This concept has yet to be formally studied and future studies could look at the timing of rainfall throughout the day and insect availability and its impact on aerial insectivores.

Carry-over effects of migration rate and stopover duration were not found to influence the length of the interval, which may be partly due to the long arrival-breeding interval purple martins have. For example, northern wheatears can arrive and breed in approximately 15 days on average (Low et al., 2019), and pied flycatchers have an average arrival-breeding interval of 11 days (Tomotani et al., 2018), compared to an average of approximately 28 days in purple martins. Long arrival-breeding intervals may allow martins plenty of time to replenish depleted energy stores from migration before breeding, therefore the interval length is not yet constrained by carry-over effects from migration.

The long interval length in purple martins may be caused by intraspecific competition between males to arrive at their breeding grounds earlier since there are limited quality cavity sites. Cavities higher in the house have been found to have decreased predation from ground-dwelling predators increasing the likelihood of nestling survival (Morton & Derrickson, 1990). More competition may generate a ‘cascading’ competition for an earlier arrival, so birds are arriving earlier than what is needed for the onset of breeding (Kokko, 1999). Another reason may be due to the interspecific competition between purple martins and other cavity-nesting species, which are typically introduced house sparrows (*Passer domesticus*) and European starlings

(*Sturnus vulgaris*) (Brown et al., 2021; Turcotte-van de Rydt, 2022). Establishing and defending a cavity early in the season may allow purple martins to reserve their cavity so they can wait for more favourable breeding conditions to breed. Therefore, purple martins may have longer arrival-breeding intervals compared to other long-distance migrants thus allowing them to flexibility react to their local conditions. However, the same might not be true for species with shorter arrival-breeding intervals which may be constrained by carry-over effects from migration, and possibly the time it takes to find a mate, build a nest, and develop sexual organs. Also, as the temperatures continue to rise the arrival-breeding interval of purple martins may continue to shorten until the first egg-lay date may be constrained by carry-over effects.

We found age to influence the length of the arrival to breeding interval with three-year-old birds having shorter intervals than older, more experienced, purple martins. Our finding aligns with a previous paper which found three-year-old purple martins arrived on average 11 days later than adults (four years old or more) (Morton & Derrickson, 1990). Therefore, they may arrive when spring has progressed further and be able to lay earlier, resulting in a shorter arrival-breeding interval, if they can find a suitable cavity and mate. Also, individuals arriving later in the season still managed to lay their eggs around the same time as the majority of other birds are laying (Morton & Derrickson, 1990). In our analysis, we had a small sample size of three-year-old birds which restricted us from determining if the younger birds had reduced fledging success as a result of the shorter arrival-breeding interval length and would be an avenue for further studies.

There appeared to be no difference in the length of the arrival-breeding interval between the sexes. Male purple martins have been shown to typically arrive earlier than females by approximately six days, therefore we expected the length of their interval to be longer (Fraser et al., 2019; Neufeld et al., 2021). However, the lengths of the arrival-breeding interval are similar between males and females, which may be due to having different ages of purple martins within the sample. A study on purple martins showed that only males ages 3, 5, and 7 had noticeably earlier arrival than females while, ages 4 and 6 were roughly equal (Morton & Derrickson, 1990). Therefore, the influence of earlier arrival may have been diminished once the ages were pooled together. Yet, there may also be an advantage for females to arrive earlier as well to get the best nesting sites and partner since they are also limited. There have been sightings of female purple martins defending cavities and competing with other females for nest cavities (Smith personal observations). Therefore, there could be competition between females that advances the arrival dates of females to be closer to the arrival dates of males. It is important to note that on average males had a two-day longer arrival-breeding interval than females though this difference was not significant.

We discovered longer arrival-breeding intervals are related to earlier arrival dates but did not influence the fledging success of juveniles (Table 2.3). This differs from our prediction of a longer arrival-breeding interval resulting in higher fledging success. If earlier arrival resulted in higher quality nest cavities and mates then we expected that more time would result in higher fledging success, but this was not the case. One reason may have been due to cold snaps decreasing the body condition of early arriving adults leading to a reduced body condition (Shipley et al., 2020), prolonging the arrival-breeding interval. A second reason may be that early-arriving martins do not start building their nest immediately upon arrival. Instead, they take their time to choose a cavity (Allen & Nice, 1952; Morton & Derrickson, 1990) which may result in later-arriving third-year birds, which begin building closer to arrival dates, to have roughly similar amounts of time to build their nest as compared to early arrivals. Therefore, earlier arrival may result in a favourable cavity location but may not translate into a higher quality nest since they could spend similar amounts of time constructing their nests. A third reason that may influence martins in northern populations, birds arrive before the buds containing leaves have begun growing on the trees, leaves which they use to line the inside of the cup in their nest (Brown et al., 2021). Several hypothesis exist for the benefits of fresh leaves in nests: they increase egg hatching success by controlling the loss of moisture; they contain defensive chemicals used to inhibit bacteria growth in the nest; and to prevent the hatching of parasites that feed on young (Clark & Mason, 1985). So, the emergence of leaves may constrain the earlier arriving purple martins since they need to wait for green leaves before finishing their nest and laying eggs. The availability of fresh leaves may constrain the ability of early arrivers to lay eggs earlier and may be why purple martins lay eggs around the same time regardless of arrival date, however, future studies are required.

In conclusion, the arrival-breeding interval in purple martins is influenced by local conditions of temperature and precipitation has differing influences across their breeding range. Carry-over effects from migration were not yet constrained by the length of the interval and fledge success did not increase with longer intervals, indicating that purple martins may still be able to prevent the mismatch between peak prey and peak breeding. Our study demonstrates that there may be sufficient phenotypic plasticity within the long arrival-breeding interval purple martins currently have, but follow-up studies on the individual plasticity of egg-lay dates are required. Long-distance migrants with longer arrival-breeding intervals may have more flexibility within their interval length allowing them to adjust their timing with local conditions encountered on breeding grounds allowing them the flexibility to acclimate to warmer springs. However, long-distance migrants with shorter arrival-breeding intervals may not contain plasticity and may be constrained by carry-over effects from migration leading to a phenological mismatch between breeding and peak prey availability. Future studies could compare avian species with short and long arrival-breeding intervals to determine if longer arrival-breeding intervals are flexible to local conditions and shorter intervals are constrained by migration. Increasing our understanding of the flexibility or inflexibility within arrival-breeding intervals may allow more targeted conservation efforts aimed at species that are unable to react flexibly to their changing environment.

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Supplementary Material

Supplemental Table 2.1. A summary of the weather stations located closest to purple martin colonies with adequate daily temperature and precipitation data.

Weather Station	Colony	Latitude	Longitude	Distance from Colony (km)
Lacombe CDA 2 Alberta	Alberta	52.45	-113.76	12
Winnipeg A CS Manitoba	Manitoba (Howden) Manitoba (RV)	49.92	-97.25	22 22
Stoney Mountain Manitoba	Manitoba (OHM)	50.12	-97.17	6
Brainerd Lakes Regional Airport	Minnesota (Brainerd) Minnesota (Mille lake)	46.41	-94.13	5 42
Aberdeen Regional Airport	South Dakota	45.44	-98.41	19
Erie INTL/T. Ridge Field Airport	Pennsylvania	42.08	-80.18	5
Newark Liberty International Airport	New Jersey	40.68	-74.17	36
Washington Dulles International Airport	Virginia	38.94	-77.45	39
Orlando International Airport	Florida (Disney)	28.43	-81.33	27
Naples Municipal Airport	Florida (Naples)	26.12	-81.78	3

Supplemental Table 2.2. Relationship between Arrival-breeding Interval and Arrival Date Fledge using a linear model describing the interaction between Arrival Date: Region (North, Central, Coastal, South), and Age (Third year, After third year) on length of the interval (n = 132).

Fixed effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**
Arrival date	-0.43	0.10	-0.62	-0.24
Central	-2.54	23.40	-48.40	43.33
Coastal	-4.84	15.71	-35.63	25.94
South	-11.52	14.31	-39.57	16.53
Third year	-2.93	1.22	-5.32	-0.53
Arrival date: Central	-0.02	0.18	-0.37	0.34
Arrival date: Coastal	-0.02	0.12	-0.26	0.21
Arrival date: South	-0.19	0.15	-0.48	0.10
			R^2	
			marginal	0.73

Chapter 3

Experimental delay in hatch date modulates departure timing in wild, juvenile long-distance migrants

Lakesha H. N. Smith, Kevin C. Fraser

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Abstract

The climate is changing at a rapid pace and advancing spring phenology, creating and increasing mismatches across trophic levels. Long-distance migrants may be limited in their ability to advance their timing to match new conditions, since their timing is largely controlled by endogenous rhythms. However, migratory timing may be flexible to the photoperiod experienced by juveniles when they hatch through an ontogenetic effect, which may provide a mechanism for a more rapid advancement in timing. To determine whether photoperiod influences migration timing for juvenile birds, we experimentally delayed the hatch date of wild purple martins (*Progne subis*) in southern Manitoba, Canada and then tracked them using automated radio-telemetry to determine their fall departure timing. We predicted that if there was an ontogenetic effect of hatch date, then experimentally delayed birds would depart later than controls that hatched 4 days earlier. We found some support for the ontogenetic effect of hatch date as delayed juveniles departed their colony about 4 days later than controls, at photoperiods that were 0.22 hours shorter. However, post-fledging parental care may also constrain the flexibility of departure date. Future studies are required to investigate if the ontogenetic effect of hatch date carries to future life stages and to explore if the adjustment of post-fledging period is masked by parental care.

Keywords

Ontogenetic effect, long-distance migrant, purple martin, climate change, migratory timing

1 | Introduction

A fundamental question in the study of avian long-distance migration is which exogenous and/or endogenous factors trigger the start of migratory movements. Exogenous cues such as temperature (Burnside et al., 2021; Klinner & Schmaljohann, 2020; Tøttrup et al., 2010; Van Doren & Horton, 2018), wind (Eikenaar & Schmaljohann, 2015; Liechti, 2006), and precipitation (Haest et al., 2019) have been shown to fine-tune migration departure timing. Other external cues which may influence timing include food availability (Studds & Marra, 2011), indirectly influenced by temperature and precipitation, and the social environment (Deakin et al., 2021). Yet in long-distance migrants, migratory timing is primarily influenced by internal rhythms. Endogenous rhythms are timed using a biological clock mechanism composed of daily (circadian), or yearly (circannual) rhythms that are synchronized by photoperiod (Berthold, 1996; Gwinner, 2003). Migration timing is largely heritable (Pulido et al., 2001), but can also be influenced by the timing of breeding (Mitchell et al., 2012). Most studies on endogenous timing have been conducted in laboratory settings on nocturnal migrants who exhibit migratory restlessness (or German: *Zugunruhe*) (Berthold, 1996; Gwinner, 1989). Additional studies are required to determine how diurnal long-distance migrants use their endogenous clock, synced via photoperiod, to time their migration in the wild.

Understanding what influences migration timing is critical in determining if migratory species can adjust to climate change. Earlier phenology of many plants and insect emergence across North America and Europe (Both et al., 2009; Parmesan & Yohe, 2003; Renner & Zohner, 2018; Thackeray et al., 2016) can negatively impact late arriving long-distance migrants leading to phenological mismatch and reduced breeding success (Both et al., 2006; Mayor et al., 2017). Factors influencing the timing of spring migration have been extensively studied due to the impact they have on breeding success. Early arrival is linked to earlier egg-laying and increased clutch size (Winkler et al., 2014), matching peak prey abundance to breeding timing (Both et al., 2006), and increased probability of juvenile recruitment (Tomotani et al., 2018). Fall migration timing is also important since mortality during fall migration has a considerable influence on the demographics of a population (Hewson et al., 2016). Birds hatched later in the season that have later fall migration timing may undergo a rapid moult producing shorter lower quality feathers possibly decreasing both flight and foraging abilities (Hall & Fransson, 2000). Additionally, later departure may increase risk of cold snaps occurring which has in the past resulted in the deaths of hundreds of thousands of swallows and martins in Europe (Newton, 2007). Therefore, it is crucial for migration timing to be flexible to maintain high levels of breeding success and survival.

While timing adjustments to climate change may require microevolution through many generations (Charmantier & Gienapp, 2014), phenotypic plasticity in some species may allow for a rapid adjustment of migratory timing. Phenotypic plasticity may exist within the ontogenetic effect proposed by Both (2010) where the photoperiod, or daylength, a nestling bird is exposed to while in the nest sets the timing of migration into adulthood. Both (2010) had observed that pied flycatchers (*Ficedula hypoleuca*) breeding further north and hatching later in the breeding season experienced shorter photoperiods (*i.e.* hatched after the summer solstice). The shorter photoperiods the later hatched birds were exposed to may have led to their earlier migration through northern Africa the following spring as compared to birds which hatched earlier or at more southern breeding sites (Both, 2010). Additional support for ontogenetic adjustments in response to photoperiod comes from laboratory experiments. Eurasian blackcap (*Sylvia atricapilla*) juveniles were exposed to a photoperiod 6 weeks earlier than the local photoperiod

(Coppack et al., 2001). Under the simulated photoperiod, juveniles displayed migratory restlessness at an older age but approximately one month earlier than controls exposed to a natural photoperiod (Coppack et al., 2001). This laboratory study suggested earlier hatch dates are associated with an earlier photoperiod result in earlier onset of migration timing. These studies demonstrate that migratory birds may be able to rapidly adjust their timing of migration using the environmental cue of photoperiod.

Recent field experiments have been aimed at studying these effects in wild populations and have found varying support for the ontogenetic effect of hatch date on subsequent timing. In a hatch date delay experiment using a wild population of pied flycatchers, later hatching juveniles arrived later to breeding sites the next spring, but only in the first year, suggesting little support for an ontogenetic effect of hatch date on long-term adult timing (Ouwehand et al., 2017). Instead, the authors suggested carry-over effects from hatching later may have led to later arrival for experimentally delayed birds and that variation in timing may be more driven by inherited timing schedules, *i.e.* genetics. Meaning, early birds will lay eggs early and their offspring will have early migratory schedules, while the reverse is true for late birds (Pulido et al., 2001). An experiment on purple martins (*Progne subis*) in North America investigated the influence of ontogenetic effects by using programmable lighting in nest boxes to experimentally hold the photoperiod to the duration at the summer solstice (Bani Assadi & Fraser, 2021). Juveniles exposed to the consistently long photoperiod fledged approximately one day later and departed the colony roughly 2 days later as compared to juveniles exposed to natural photoperiods (Bani Assadi & Fraser, 2021). Further research is required to investigate the potential for an ontogenetic effect of hatch date, to determine if there is potential for phenotypic adjustment to climate change.

Here, we further investigate the autumn departure timing of a long-distance migrant, the eastern subspecies of purple martin (*Progne subis subis*) using an experimental manipulation of wild juveniles. Nest timing in this species may be flexible to local temperatures at breeding sites (see Chapter 2; Shave et al. 2019) and variation in hatch dates may expose birds to different photoperiods that could influence their subsequent timing through an ontogenetic effect. To investigate the ontogenetic effect of hatch date on migration timing, we experimentally delayed the hatch date of juveniles by four days as compared to controls. This manipulation was within natural variation in hatch dates within our study colonies. Fledging and colony departure dates were collected using automated radio-telemetry (Motus Wildlife Tracking System; Taylor et al., 2017). We expected that the post-fledge to colony departure period, previously reported for this species to be about 0-12 days (Bani Assadi et al., 2022; Brown, 1978), would provide a period of time with which juvenile birds could advance or delay their timing in response to the experimental manipulation. We predicted that if there was an ontogenetic effect of hatch date on subsequent timing, then experimentally delayed birds would have similar durations at the colony post-fledge as compared to controls and have later colony departure dates (*i.e.* do not compensate by departing earlier). We also predicted that if there was an effect of inherited timing on subsequent timing, that experimentally delayed birds would have shorter durations at the colony post-fledge than controls and have similar departure dates to ‘catch up’ to the controls.

2 | Materials and methods

We used three breeding colonies of purple martins located near wetlands: Oak Hammock Marsh a ~ 36 km^2 situated in the prairie north of Winnipeg in southern Manitoba, Canada (50.17°N, 97.13°W); FortWhyte Alive a ~ 2.7 km^2 situated within the city of Winnipeg (49.82°N, 97.23°W); a private residence in Howden with a ~ 0.2 km^2 backyard situated south of Winnipeg

(49.73°N, 97.13°W). Purple martins at our colonies migrate approximately 8400 km in spring from their wintering grounds in the Amazon Basin in Brazil typically arriving in Southern Manitoba at the end of April to the end of May (Turcotte-van de Rydt *unpublished*). In the spring and summer of 2021, Oak Hammock Marsh had two housing units with 14 nest cavities and 4 gourds per house for a total of 36 cavities, FortWhyte Alive had two housing units also with 14 gourds for a total of 28 cavities, and the private residence in Howden had 3 housing units each with 4 gourds, making for a total of 54 cavities. The houses had winch systems which allow lowering of the houses to allow for nest checks which were conducted every day from nest initiation to the end of egg laying and every 2-3 days from the hatch date until fledging. Nest initiation was the date we first spotted several pieces of nest material—for example, coarse grass, twigs, or dead leaves (Brown et al., 2021)—used by purple martins inside the cavity. The ease of monitoring cavities during the breeding season made purple martins an excellent species for our photoperiod, *i.e.* egg delay, experiment.

To delay the hatch date, and thereby the photoperiod that juvenile purple martins are exposed to while in the nest, we delayed the start of incubation following methods used by Ouwehand et al. (2017). Cavities were randomly assigned in each colony to two treatment types: either control (two-day delay in hatch date) or delayed (six-day delay in hatch date). Since purple martins usually lay one egg a day consecutively (Brown et al., 2021), we would remove both control and delayed eggs from the nest each day they were laid and replace them with fake non-toxic replica eggs (Dummy Eggs, 24 × 20mm, Lakeland, Florida, United States). The removal of the egg every day was to reduce the chance of the adult commencing incubation before we removed them from the nest since once incubation is halted the eggs may not hatch. Martins will lay on average between 3-6 eggs in one clutch per year (Brown et al., 2021). In our population during the study, clutch sizes ranged from 2-7 eggs. The real eggs from the same cavity were placed into containers lined with 100% natural wool (Organic Cotton Plus, Ridgefield, Connecticut, United States) or 100% natural cotton (The Warm Company, Lynnwood, Washington, United States) batting, and stored in the ground close to the house to keep eggs cool and reducing the handling time to decrease chances of egg damage. Nests were checked the day after the clutch was completed, meaning no new egg was laid the next day. Since martins may occasionally skip one day of laying (Smith L. pers. obs.), we waited an extra day (delaying controls by 2 days) to confirm the clutch was complete before returning the control eggs back into the nest. Refer to Appendix I for nest manipulation procedure. For the delayed nests we waited an extra four days, so six days altogether, before removing the fake eggs and returning the real eggs to the nest. In total we manipulated 35 nests: at Oak Hammock Marsh we had 4 controls and 3 delayed, at FortWhyte Alive we had 9 controls and 9 delayed, and at Howden we had 5 controls and 5 delayed. All work was approved by the University of Manitoba's Animal Care Committee Protocol number F18-016/1/2 (AC11349).

Of the 35 experimental nests, 27 had juveniles which successfully hatched with no abnormalities observed. Control nests had 75.0% of their eggs successfully hatch which was slightly higher than eggs in untouched nests of 69.8%, however, delayed nests only had 24.2% of eggs hatch (Supplemental Table 3.1). Cool storage was used to prevent the development of young prior to incubation, however, it can also affect hatch success and subsequent juvenile development (Wiggins & Gustafsson, 1998). In our experiment the hatch success for delayed juveniles was much lower than expected, which may have been due to storing the eggs in the ground. The temperature fluctuations in Southern Manitoba are large, and likely caused condensation to form on the eggshell reducing the gas exchange that led to decreased egg viability. Instead, storing the eggs onsite at a constant temperature below physiological zero, the temperature below which egg development is halted (Williams & DeLeon, 2020), may increase the hatch success of future egg delay experiments. A study on nest attentiveness in purple martins showed that nest attentiveness decreases more sharply after the ambient temperature rises above 24˚C (Williams & DeLeon, 2020). So the physiological zero of purple martins may be below 24˚C, and storing eggs below this temperature, for example at a constant 18˚C, may prevent the egg from developing and also prevent condensation from forming on the egg. However, to our knowledge this method has not been tested and requires further literature review combined with future studies to determine if it will increase the survival of juveniles with delayed hatching.

The actual hatch date was collected from nest checks every 2-3 days paired with aging sheets provided by project Martinwatch as part of Purple Martin Conservation Association (2017) allowed us to get accurate ages. Once the juveniles were ~20 days old all were weighed and then banded with a federal and field readable colour band so they could be resighted the following spring. To obtain departure dates, one randomly chosen juvenile per nest was fitted with a radio-telemetry tag except in two delayed nests where 2 juveniles were tagged. Altogether there were 28 juveniles, 14 controls and 14 delayed. The radio-telemetry tags (NanoTag model NTQB2-4-2S, Lotek Inc., Newmarket, Ontario, Canada), part of the Motus Wildlife Tracking System (www.motus.org; Taylor et al., 2017), were attached via a leg-loop harness (Rappole & Tipton, 1991), using polypropylene thread which with the tag weighed ~1.1 g (12 × 8 × 8 mm, length, width, and height). The average weight of our tagged nestlings was 57.3 ± 4.6 g, but juveniles lose weight before fledging to weigh approximately 50 g (Allen & Nice, 1952). Therefore, the ~1.1 g tag added only 3% more to a juvenile’s total body weight. The tags emit a radio signal every 30.7 s, which are picked up by a radio-telemetry receiver located onsite at each colony. Tags were expected to emit signals for 756 days. All receivers had an omnidirectional antenna (detection range ~ 500 m), and two nine-element Yagi antennas (detection range ~ 15 km).

To determine the departure date (time zone UTC), we first filtered out false and ambiguous tag detections using the ‘motus’ package (version 3.0.0, Brzustowski & LePage, 2019) in R (version 3.6.1) using Rstudio (version 1.2.5001, R Core Team 2019). After data cleaning we compared the pattern of signal strengths from the first few days with the radio tag and looked for when this pattern started fluctuating irregularly. The day of the first fluctuation (indicating first flight) was called fledge date (Supplemental Figure 3.1) (Bani Assadi et al., 2022). To confirm fledge date we compared the fledge dates from our radio tags with fledging dates determined from nesting monitoring. All fledge dates aligned with the nesting data confirming our fledge dates determined via tag signals were accurate. Departure date from the colony was considered as the last day a signal was picked up by the receiver, indicating that the juvenile had departed the colony (Bani Assadi & Fraser, 2021). One control tag stopped being detected while in the nest so neither fledge or departure dates were collected. One control and one delayed tag were detected into September, indicating the tags fell off or juvenile mortality, so their departure dates where not used in analysis. In addition, the receiver at Oak Hammock Marsh did not function for two days after a storm, so departure dates for two delayed juveniles were missed. We then converted the departure date to photoperiod length, the time between dawn and dusk, during the day the juvenile was last detected (time zone CDT). In the spring of 2022, the radio receivers were reinstalled at each breeding colony before birds arrived in spring. Resighting for returning banded and tagged birds was done at each colony every other day from

May until the end of June to obtain arrival dates and first egg-lay dates of returning juveniles. Unfortunately, no arrival dates or first egg-lay dates were collected due to high levels of juvenile dispersal or mortality.

To determine if there is a difference between control and delay juveniles in the time they spend during their nestling and post-fledging periods we used a linear model (LM). We analyzed the data using R version 4.1.3, in Rstudio (version 2021.09.2, R Core Team 2022) using the package 'glmmTMB' (version 1.1.3, Brooks et al., 2017). First, to investigate whether nestling periods were the same in both groups, we made a model with the dependent variable as nestling period with fixed effects of treatment, control or delayed. Second, to determine if there was a difference between post-fledging periods between controls and delayed juveniles, our model included the dependent variable post-fledging period with fixed effect of treatment and nest initiation date as a covariate. Nest initiation date was included because we initially saw a trend that even within the same colony different purple martin houses had slightly different nesting, egg-laying, and departure timing which we wanted to account for in our model. In addition, nest initiation date was only used in the post-fledge period and departure photoperiod (meaning the daylength the bird experienced on the day of departure) models since we predicted control juveniles would have a longer post-fledge period and depart at earlier photoperiods than delayed juveniles. The nestling period model did not include nest initiation date as a covariate since we did not predict a difference in nestling period between earlier and later hatched juveniles. Lastly, to answer our question of whether migration timing is primarily set by an ontogenetic effect of photoperiod in the nest, we used departure photoperiod as the dependent variable with the fixed effect of treatment and nest initiation date as a covariate. Nest ID was considered as a random effect since there was one delayed nest in which two juveniles were tagged in the same nest.

However, since there was only one pair from the same nest in our departure photoperiod model, we decided to include both juveniles in our analysis.

3 | Results

All purple martins in our study started building nests between 2 May and 8 June (mean ± SD 27 May ± 6.86 days), and began laying eggs (*i.e.* 1st egg dates) between 6 June and 20 June (11 June ± 3.58 days). Eggs hatched between 28 June and 11 July (5 July ± 3.81 days) and juveniles fledged between 24 July and 14 August (3 August ± 4.45 days). Of our 14 control birds and 14 delayed birds that were tagged, we got accurate fledging dates for 13 controls and 14 delays. Fall departure dates from the colony varied from 25 July and 21 August (8 August ± 5.65 days). We obtained fall departure dates for 12 control and 11 delay birds.

To determine if the nestling period is similar between treatments and if the ontogenetic effect was influencing the duration of the post-fledging period, we compared both periods by treatment type. The nestling period—the time from hatch to fledge where juveniles remain in the cavity—did not vary by treatment (95% CI -1.82 to 2.64, Table 3.1a) and ranged between 25 to 42 days, with controls remaining in the nest on average for 28.2 ± 1.24 days and delayed nests averaging 28.6 ± 4.09 days. The post-fledge period—the time from fledging to departure from the colony—for controls and delayed birds was similar among treatments (95% CI -1.54 to 3.04, Table 3.1b). The mean and standard deviation of the post-fledging period for controls and delayed birds were 4.25 ± 2.93 days and 5.00 ± 2.93 days, respectively, and ranged between 1-10 days. One delayed juvenile had a longer nestling and post-fledging period than the rest causing a slightly longer post-fledge duration in the delayed treatment. Our results showed that control and delayed juveniles spend similar amounts of time as a nestling and during their post-fledging period (Table 3.1, Figure 3.1). Therefore, providing support for the ontogenetic effect of delayed and control birds spending similar durations at the colony post-fledge.

Table 3.1. Parameter estimates of linear models to determine if (a) nestling period ($n_{control}$ = 13, n_{delay}= 14) and (b) post-departure period ($n_{control}$ = 12, n_{delay}= 11) are influenced by treatment type.

Fixed effects	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
a. Nestling model				
Treatment: Delay	0.41	1.14	-1.82	2.64
			R^2 = 0.5	
b. Post-departure model				
Treatment: Delay	0.75	1.17	-1.54	3.04
Nest Initiation date	0.02	0.08	-0.14	0.18
			R^2 = 2.0	

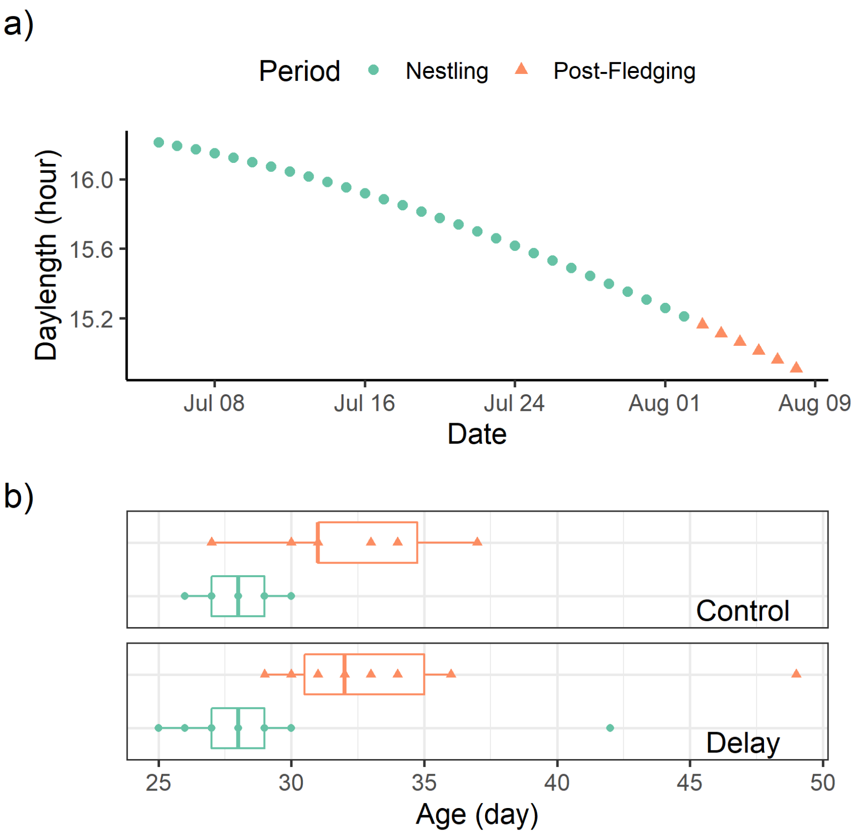

Figure 3.1. (a) Shows how daylength shortens throughout the breeding season from average hatch date to first fledge (the 'nestling period', shown in green) and first fledge to average departure date (the 'post-fledging period', shown in orange) of all juveniles in the experiment. (b) A boxplot showing the age of control and delay juveniles for the period of time spent as a nestling (green circle) or post-fledging (orange triangle).

Due to our small sample size, we were unable to include temperature in our model, as a change in temperature has been shown to induce migratory behaviour in laboratory settings (Klinner & Schmaljohann, 2020). Yet, when we compared the temperature change between the minimum and maximum temperatures on the day before departure to the day of departure there did not appear to be a difference (Supplemental Figure 3.2). Therefore, temperature likely did not have a large influence on the departure decisions of wild juvenile purple martins.

Control juveniles, encountering longer photoperiods while in the nest, departed the colony earlier than delayed birds (Figure 3.2). At our colonies the daylength begins to decrease after the summer solstice on 20 June, therefore, longer days are earlier in the season. Our delayed birds departed at photoperiods that were 0.223 hours shorter and accounted for 27% of the variance (95% CI -0.416 to -0.030, Table 3.2). The nest initiation date had a small effect with one-day later nest initiation resulting in a departure photoperiod delayed by 0.011 hours (95% CI -0.025 to -0.002). To obtain an approximate number of days that delayed juveniles left after control juveniles we ran a model with departure date as the dependent variable with treatment and nest initiation date as fixed effects. Our date model showed that delayed juveniles departed 4.35 days later than control juveniles (95% CI 0.49 to 8.22, Table 3.2). Although our departure date estimate is not exactly equivalent to the photoperiod estimate it provides us with a rough approximation that the delayed juveniles may have departed ~ 4 days later than control juveniles.

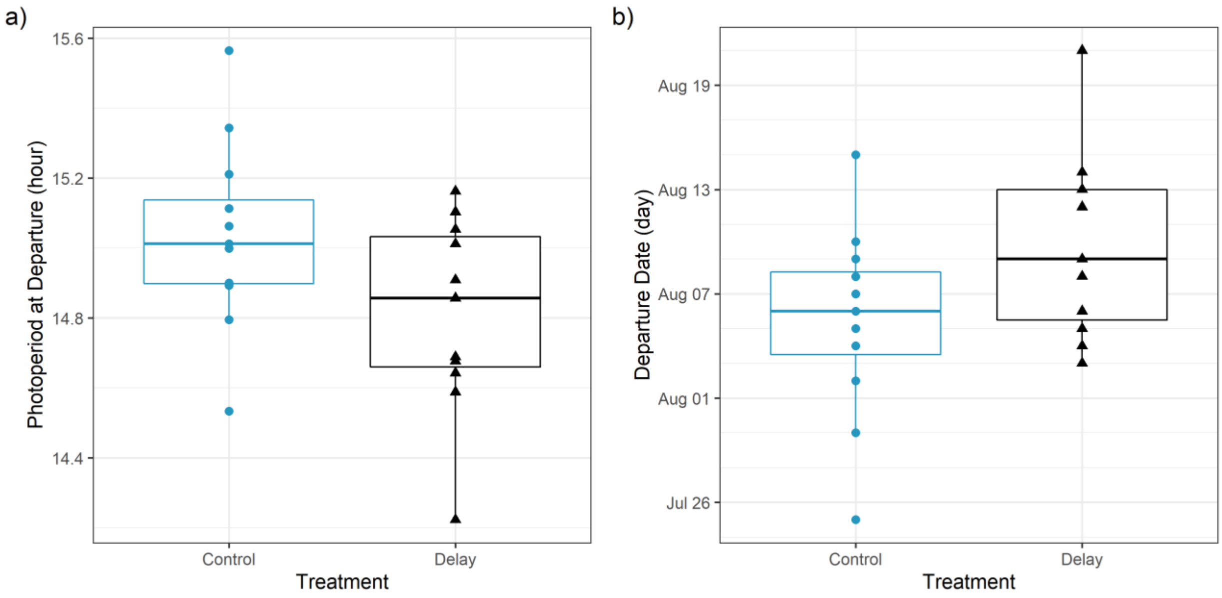

Figure 3.2. Shows the raw data showing the (a) the photoperiod at departure and (b) the date of departure by treatment, control (2-day delay) or delay (6-day delay) hatch date. Control birds (n = 12) departed earlier, at longer photoperiods, while delayed birds (n = 11) departed later, at shorter photoperiods

Table 3.2. Parameter estimates from two linear model determining the influence of treatment type, control or delay, and accounting for the variation in nest initiation date on departure timing in juvenile purple martins ($n_{control} = 12$, $n_{delay} = 11$, $R^2 = 0.27$). CI stands for confidence interval and SE stands for standard error.

Fixed effects	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Photoperiod model				
Treatment: Delay	-0.223	0.098	-0.416	-0.030
Nest Initiation date	-0.011	0.007	-0.025	-0.002
Date model				
Treatment: Delay	4.35	1.97	0.49	8.22
Nest Initiation date	0.22	0.14	-0.04	0.49

4 | Discussion

The hatch date for nestling birds can expose them to variable photoperiods that may influence their subsequent short- or long-term movement timing which could provide a mechanism for a more rapid response to climate change (Both 2010). We experimentally delayed the hatch date of purple martins while controlling for nest initiation date (a proxy for inherited timing), to explore the role of ontogenetic effects on migration timing. We found that delayed juveniles spent similar durations at the nesting colony post-fledge and departed the colony later than control birds. Our results provide some evidence to support the ontogenetic effect of hatch date, and conversely a lack of support for the effect of inherent timing, on the timing of juvenile post-fledge movements.

As predicted for an ontogenetic effect of hatch date, delayed birds spent similar durations of time in the nest as a nestling and during their post-fledge periods resulting in later departure dates as compared to controls (Figure 3.1b). This study therefore contributes to growing evidence that photoperiod in the nest can subsequently influence post-fledge movement timing (Ouwehand et al. 2017, Bani Assadi et al. 2021). The delayed nestlings experienced photoperiods at departure that were 0.22 hours shorter than controls, which corresponded to departures that were around 4 days later than controls and therefore matched the duration of our experimental delay (Table 3.1). Our results align with a previous laboratory experiment where Eurasian blackcaps were exposed to photoperiods that corresponded to calendar dates that were 6-weeks earlier than the natural photoperiod. Juveniles exposed to earlier photoperiods exhibited migratory restlessness about 4-weeks earlier than they would have in the wild (Coppack et al., 2001). Our experiment, therefore complements earlier laboratory studies and adds to previous inferences (Both, 2010) and field experiments (Bani Assadi & Fraser, 2021) suggesting an influence of photoperiod in the nest on timing.

We did not find support for inherent migration timing advancing the fledge to departure timing of experimentally delayed birds. An experiment examining the heritability of fall migration timing in blackcaps showed additive genetic variation resulted in over a one-week delay in migration when selecting for later onset of migratory behaviour (Pulido et al., 2001). Delayed juveniles in our experiment were expected to have similar inherent timing to the control juveniles (*i.e.* their natural nest initiation dates were similar). If their earlier, inherent timing was to play a role in their fall departure timing, we would have expected a shorter fledge to departure interval for delayed birds, but this was not the case.

However, the 1-10 day fledge to departure period we found in this study may not have provided a duration sufficient for delayed birds to shorten their post-fledging duration as compared to controls. In this case, inherent timing could have been masked by the time required for post-fledge parental care or the time needed for the development of skills juveniles require before their departure. Therefore, the influence of post-fledge parental care also needs to be considered, as post-fledge periods likely overlap with periods of parental provisioning. Previous work on purple martins found that juveniles can be provisioned by parents up to 5 to 7 days post-fledge (Brown et al., 2021). Since juveniles in our experiment departed the colony on average 4 days post-fledge for controls and 5 days post-fledge for delays, they may have been constrained by their foraging ability.

We intended our experimental manipulation of 4 days to fall within natural variation in nest timing. This builds on previous studies, where larger difference in photoperiod were made to create a more pronounced effect. For example, a laboratory experiment determining if photoperiod influences the timing of moult and fall migration timing (measured via migratory restlessness) on Eurasian blackcaps compared nestlings hatched in May to those hatched in August (Berthold, 1993). However, large manipulations of photoperiod, by delaying the hatch date of eggs, are difficult in wild populations since it may lead to decreased hatch success (see Supplemental Table 3.1; Ouwehand et al., 2017; Wiggins & Gustafsson, 1998) or nest abandonment by the parents (Goutte et al., 2011). Further, large manipulations would not reflect variation in the natural world. For instance, for the northern wheatear (*Oenanthe oenanthe*) mean arrival and egg-lay dates only advanced around 5-6 days over 24 years (Low et al., 2019), and cerulean warbler's (*Setophaga cerulea*) have advanced their dates by less than 4 days over 38 years (Connare & Islam, 2022). With the 4-day delay in hatch date in our experiment, the difference in photoperiod was much smaller between our treatment groups, but reflects the range of natural variation in nest dates in the purple martin system, which may have a higher relevance for our understanding of ontogenetic responses to photoperiod.

To conclude, we found support for an ontogenetic effect of hatch date on the post-fledge movement timing of juvenile songbirds, where juveniles with experimentally delayed hatch dates had similar fledge to depart durations as earlier hatching birds (controls), and thus departed the colony ~ 4 days later. The next step would be to determine if the post-fledge period and parental care influences departure timing and whether ontogenetic effects on timing become 'fixed' and carry-over into the next year. If ontogenetic effects influence timing into adulthood, this would be key for our understanding of how long-distance migrants may respond to ongoing climate change.

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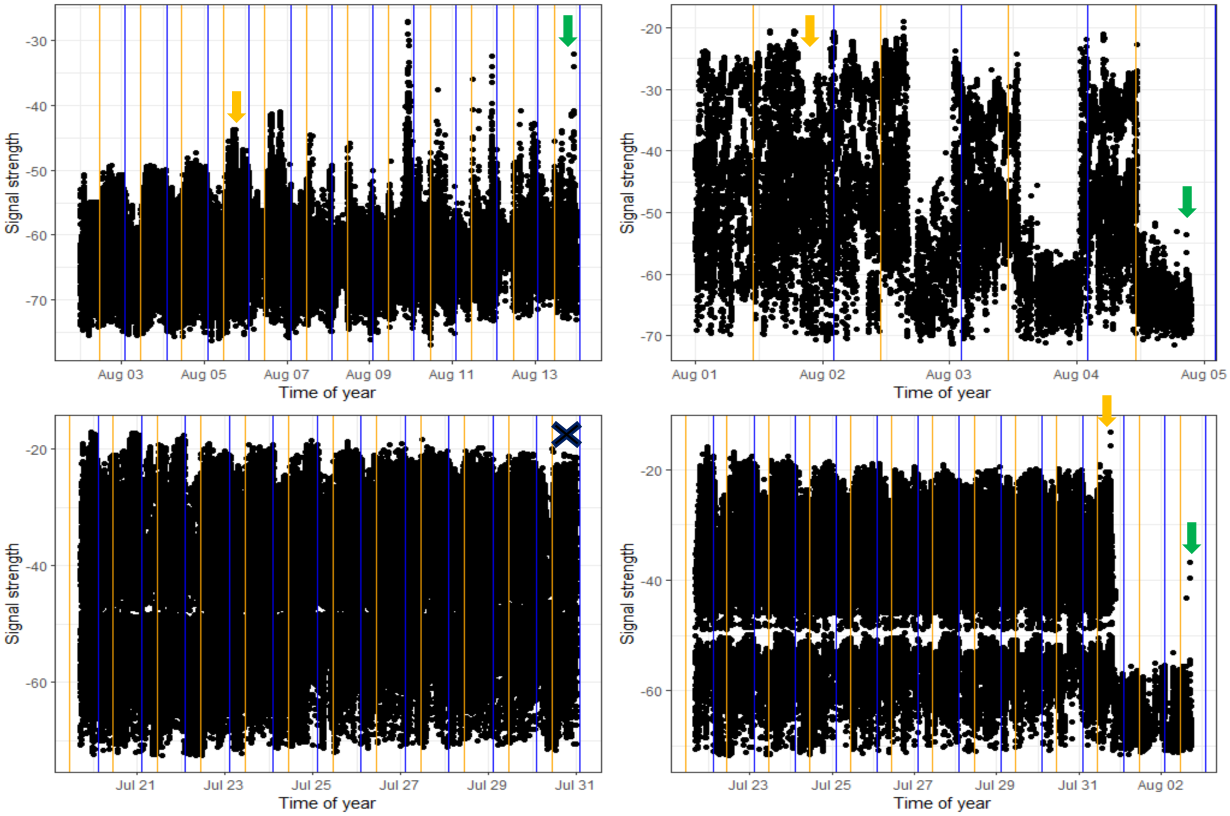
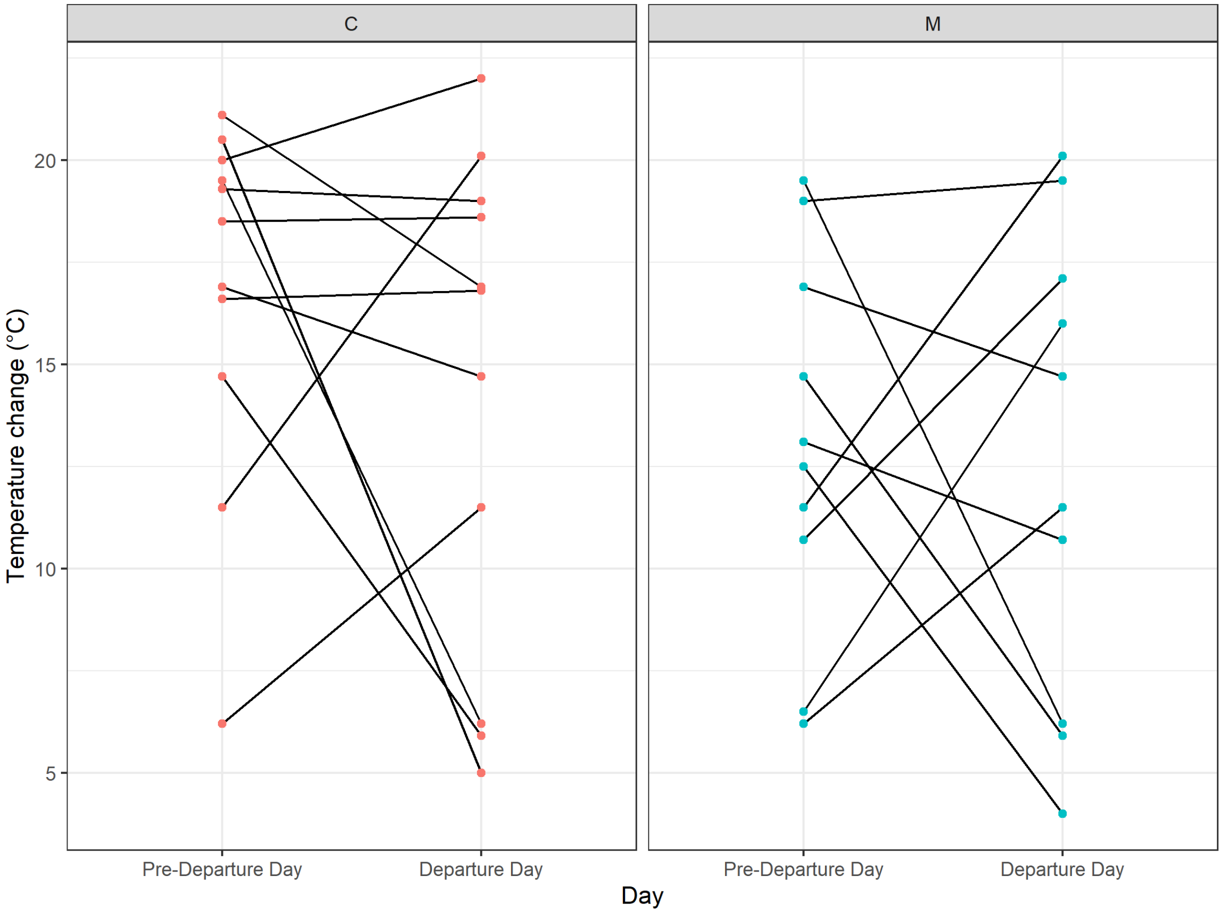
Supplementary Material

Supplemental Table 3.1. Experimental results from the egg manipulation treatments (control or delay juveniles), showing lower hatching in delayed clutches.

Treatment	**Number of nests**	**Number of eggs laid**	**Number hatched**	**Number fledged**	**Percent of eggs which hatched**	**Percent of young which fledged**
Control	18	88	66	49	75.0	74.2
Delayed	17	95	23	20	24.2	87.0
Untouched	55	252	176	131	69.8	74.4



Supplemental Figure 3.1. Four examples of the signal strength of tag detections graphs used in order to determine fledge and departure dates. Yellow arrows indicate first fledge date and green arrows represent departure date when the tag is no longer detected, the X indicated the bird never fledged or departed, due to tag failure or nest predation.



Supplemental Figure 3.2. The change in temperature C˚, from minimum to maximum temperature, on the pre-departure day compared to the departure day, separated by control (above in pink, n = 12) and delayed birds (below in blue, n = 11). Each line shows the change in temperature from the day before each juvenile departed the colony (pre-departure) to the day each juvenile departed the colony (departure).

Chapter 4

General Discussion: Adjusting to our changing climate

Lakesha H. N. Smith

© Katie Smith

Introduction

The reoccurring theme throughout this thesis is to provide a greater understanding of how long-distance migrants may adjust parts of their life cycle to acclimate to their changing climate. Migrants may adjust the timing of migratory stages through an evolutionary response by inheriting genetic material with the aid of additive genetic variation (Pulido et al., 2001) or by more of a plastic response, such as the ontogenetic effect of photoperiod during juvenile development while in the nest (see Chapter 3). Other flexible responses may occur in response to changing environmental conditions faced at the wintering grounds (Gordo et al., 2005), en route (Turcotte-van de Rydt, 2022), and/or at breeding grounds (see Chapter 2, Both & Visser, 2001; Shave et al., 2019) via phenotypic plasticity. There are many ways in which migratory birds may be able to adjust; however, there are also many barriers preventing them from acclimating. For instance, low levels of additive genetic variation within the population may prevent the adjustment of migratory timing. Alternatively, if unfavourable environmental conditions are encountered at the wintering grounds, en route, or upon arrival at the breeding grounds these may hinder the ability to properly acclimate. The annual life cycle of a long-distance migrant is indeed complex and will vary between years, populations, and individuals.

In this thesis, I addressed two parts within the complex annual cycle of a long-distance migrant, the purple martin, to further our understanding of how birds may acclimate to their rapidly changing environment. In this final chapter, I will summarize the main findings of each chapter and discuss future avenues of research questions that stem from each chapter. Then I will explain the connection between the two chapters and discuss what it might mean for purple martins, and other long-distance migrants. After, the benefits and pitfalls of direct tracking technology will be briefly examined in the context of tracking migratory birds. I will conclude with how this thesis contributed to the wider understanding of migration and breeding timing.

Flexibility in the arrival-breeding interval

Chapter 2 focused broadly across the entire eastern breeding range of purple martins from as far South as Florida to Alberta in the North to determine the flexibility within the arrival-breeding interval. Purple martins were found to have fairly long arrival-breeding intervals which on average were about 28 days long, with shorter intervals in the North and longer intervals in the South. The arrival-breeding interval exhibited phenotypic plasticity to changing environmental conditions in spring and was not constrained by carry-over effects from migration. Throughout the breeding range, warmer spring temperatures had a similar effect by shortening the length of the arrival-breeding interval most likely by enabling birds to lay eggs earlier. Precipitation also was found to influence the length of the arrival-breeding interval but had differing effects depending on the region. In the northern region, purple martins had shorter intervals with increasing levels of rainfall while the southern region had longer intervals with more rainfall. Both local environmental conditions of temperature and precipitation strongly influenced the length of the interval which demonstrated phenotypic plasticity existing within the interval.

Carry-over effects from migration, *i.e.* migration rate and stopover duration, were not found to constrain the length of the arrival-breeding interval. This may be due to the long arrival-breeding interval purple martins have which may give them more than enough time to recover energy stores after arrival and therefore not see any carry-over effects from migration. Since the arrival-breeding interval was flexible to local conditions and unconstrained by carry-over effects from migration it makes sense that fledge success was not influenced by the arrival-breeding interval. In other words, the majority of purple martins were able to lay eggs to match favourable breeding conditions resulting in consistent fledging success. So, currently, it appears that purple martins can reduce potential phenological mismatch with their environment through the adjustment of the length of the arrival-breeding interval.

Future research

Two new questions to be addressed by future studies arose out of Chapter 2. The variable influence of precipitation on the arrival-breeding interval was particularly interesting and of importance in aerial insectivores. To my knowledge, there has not been a study looking at how the time of day in which the rainfall occurs may help or hinder the breeding success of aerial insectivores. Since purple martins along with other aerial insectivores are one of the groups of birds in steep decline it is critical to thoroughly examine all that may influence their ability to breed successfully (Rosenberg et al., 2019; Spiller & Dettmers, 2019). In locations where rain falls more often during the day, for example in the south-eastern United States, the purple martins are likely hindered by their ability to forage (Prat & Nelson, 2014). While in the central prairies in Canada, rainfall occurs more commonly at night and may increase food availability while allowing plenty of diurnal foraging (Chakravarti & Archibold, 1993). Future research could be directed toward determining if the timing of rainfall has varying effects on aerial insectivores foraging which could be confirmed with additional research to understand the mechanisms by which precipitation influences birds. In addition, studies on how the time of precipitation influences diurnal versus nocturnal aerial insectivores would show more patterns of how precipitation may influence the timing of avian breeding.

Another interesting question briefly mentioned in Chapter 2 is about the length of the arrival-breeding interval. Purple martins appeared to have longer intervals than other long-distance migrants, which may be the reason they can flexibly react to new environmental conditions. However, a previous study on European pied flycatchers (*Ficedula hypoleuca*) found the short arrival-breeding interval to be constrained by arrival date (Both & Visser, 2001). This led me to wonder if the length of the interval may help indicate whether the arrival-breeding interval of birds is flexible if long or constrained if short. Further research could conduct a meta-analysis on all known arrival-breeding interval lengths of many long-distance migrants to determine if longer intervals are generally more flexible and thus associated with higher breeding success than in species with shorter less flexible intervals. If birds with shorter intervals are typically more constrained in timing, then they will face larger barriers adjusting to climate change and may need to be prioritized in conservation efforts.

Ontogenetic effect on migration timing

In Chapter 3, the influence of the ontogenetic effect on the development of migration timing in juvenile purple martins was examined in a fine-scale study located in Winnipeg, MB. The timing of migration in passerine species is largely influenced by endogenously controlled rhythms and inherited timing which set circadian (daily) and circannual (yearly) rhythms (Berthold, 1996). Yet, an ontogenetic effect where the photoperiod a juvenile was exposed to while in the nest has been more recently suggested to set migratory timing allowing more rapid adjustment of migratory schedules (Both, 2010). As predicted, control and delayed juveniles spent similar durations as nestlings and post-fledging resulting in delayed birds leaving about four days later than controls, supporting the role of an ontogenetic effect on departure timing. However, there are a few caveats to consider in the interpretation of these results: the small sample size, the small manipulation of 4 days, and the parental care overlap with the post-fledging period. However, even with the caveats, this study was important in increasing our understanding of how smaller adjustments of photoperiod may influence the migratory schedule of wild birds.

Future research

Many avenues for further research stemmed from Chapter 3, the most obvious is to determine if the ontogenetic effects on timing carries over into the next year. Originally this study was meant to follow the juveniles into the next year to determine if the timing carries over to spring arrival. However, we found there to be high levels of juvenile dispersal and in the following spring none of the tagged juveniles returned. Only one juvenile from a control nest was found breeding in the same cavity it hatched in the previous year. Therefore, to determine if the ontogenetic effects carry over into the next year, I would recommend switching to a species which has a lower rate of juvenile dispersal or conducting this study in an area with known high juvenile return rates. Another method to study the ontogenetic effect in our study system would be to wait until migration technologies advance further bringing lightweight tags (refer to Migration technology section below). With these tracking technologies, future work would be able to determine when the bird arrives at breeding grounds which would allow studies to determine if the ontogenetic effect carried over to the following year.

Another observation of mine which may require many future studies is related to the timing of egg-laying which appeared to be the same within houses and differed between houses within the same colony. I have not come across a study investigating the variable timing between houses and believe this could be investigated in future studies. One potential explanation may be that early arriving purple martins gather in the same house choosing the best housing location within the colony and occupy all available cavities. Or, synchronizing timing among colony mates may work as a strategy for protecting young from predators as purple martins will often mob predators that fly too close to their houses (Brown et al., 2021). If purple martins nest around the same time, then they may have juveniles at the same time making for more adults mobbing predators potentially increasing nesting success. Another reason purple martins all lay around at the same time may be due to individuals within the same house being exposed to the same micro-habitats. The phenology may slightly differ between houses resulting in different amounts of green leaves and aerial insects which may drive timing since purple martins require fresh leaves to line their cup before laying eggs. Or, it may be an unknown social cue which signals birds within the same house to begin nesting and laying eggs around the same time. Purple martins have been known to be a highly social species and during the late summer commonly form roosts ranging in the thousands (Brown et al., 2021). Previous studies suggest that social behaviour breaks down at the breeding grounds, however, purple martins may remain social by forming communal roosts away from their colony while raising young (Turcotte-van de Rydt, 2022). Social aspects within houses of nest initiation, egg laying, and departure timing have been little studied and may be an area for future studies. Altogether this provides many potential avenues for future studies on what factors may influence egg-lay timing in purple martins.

Adjusting to their changing environment

Altogether it appears that purple martins have phenotypic plasticity within their arrival-breeding interval, allowing them to shorten the interval by laying eggs earlier in warmer springs (refer to Chapter 2). The flexibility which allowed for earlier egg-laying may then cause the early-born juveniles to be exposed to earlier photoperiods, via the ontogenetic effect, which may set earlier migratory timing (refer to Chapter 3). If early timing carries over into adulthood it would result in earlier arrival the next year which may allow the advancement of breeding and migratory timing. These together may be a mechanism that may allow long-distance migrants to keep up with their changing environment.

However, if this is true then it may have negative consequences on migratory species with short arrival-breeding intervals that are constrained by the arrival and/or carry-over effects from migration. Species with short intervals may not be able to advance their timing with the changing environmental conditions and lay their eggs later than early arrivers and may produce juveniles with later migratory schedules, creating a negative feedback loop. What complicates this idea further is that the flexibility of the arrival-breeding interval may vary by species. Even within the same species, it may vary by population due to the different environmental conditions experienced throughout the breeding range (refer to Chapter 2; Both et al., 2006). In addition, even if birds have endogenous cues urging them to begin migration early, environmental conditions en route may block their ability to arrive earlier at breeding grounds (Both, 2010; Ouwehand et al., 2017). The study of wild migratory birds is indeed complex and this thesis has contributed to further understanding of methods migratory birds may use to adjust to their environment.

Migration technology

One of the reasons the study of wild migratory birds has become possible is due to direct tracking technology advancing at a rapid pace. In Chapter 2 I used light-level geolocators to create spring migratory tracks to determine arrival, migration rate, and stopover duration. Light-level geolocators detect the ambient light, or the lack of light, to estimate the geographic location of an animal throughout its migration (Lisovski & Hahn, 2012). The benefits of light-level geolocators are that they are very light, some less than 0.5 g, allowing them to be placed on small passerines while also being more cost-effective than other types of tags (Lisovski et al., 2020). In addition, they can be programmed to last long enough to collect points throughout the entire annual cycle. However, there are also some pitfalls associated with light-level geolocators. To get the data the bird with the light-level geolocator needs to be captured again to retrieve the device and then processed through multiple packages in R, which can be time consuming. Weather conditions and vegetation cover can darken the ambient light decreasing the accuracy of determining accurate locations and creating large amounts of spatial error (Lisovski & Hahn, 2012). However, purple martins are open air foragers, so shading caused by vegetation may not hinder the accuracy of the migration tracks since the average latitudinal error varys between 49-60km (Fraser et al., 2012; Neufeld et al., 2021). In addition, since we used geolocators to obtain arrival dates they should be particularly accurate because upon arrival at breeding grounds they enter cavities creating clear shaded patterns. Although there are pitfalls there are many advantages and ways that the data can be applied to solving pressing questions (such as in Chapter 2) therefore making light-level geolocators a useful tool for collecting migratory movements.

In Chapter 3 I used radio-telemetry tags (hereafter "Motus tags") which emit signals that were picked up by the radio-telemetry receivers (hereafter "Motus tower") that were part of the Motus Wildlife Tracking System to determine when juveniles fledged and departed the colony. The Motus network is found throughout North and South America which allows for individuals to be potentially tracked throughout their annual cycle. The benefits of Motus tags are that they are lightweight (less than 0.21g) and retrieval of the device is unnecessary since the data will be collected by a tower and then uploaded onto motus.org allowing you to see the migration route (Taylor et al., 2017). Again, there are some pitfalls as Motus towers are not found everywhere, therefore while being more precise in the locations captured than in light-level geolocators they may not produce as detailed migration routes as those collected by geolocators. In addition, the build of the Motus tag may also be important to consider along with the life history of a bird. For example, purple martins are cavity nesters meaning that they are constantly going in and out of the cavity during the breeding season. If the antenna on the Motus tag is on top of the tag it may constantly hit the top of the entrance or be bent inside the cavity possibly resulting in the antenna breaking off resulting in the tag failing to emit signals. Therefore, special care in the choice of tag design may allow for more detections in cavity-nesting species.

Part of my study was to determine if birds arrived the following spring but the high juvenile dispersal resulted in no detections the next year. New technologies are emerging and becoming miniaturized with longer battery life that may allow better tracking of juveniles to determine arrival dates in the following year. For instance, Lotek GPS tags with ARGOS capabilities are currently too large to put on small passerines, however, once miniaturized they would be an excellent option for tracking migration. GPS tags are expensive, however, in exchange they would provide live and precise GPS points that do not require tag retrieval or birds to return to natal colonies with receivers. If this technology can become as lightweight as Motus and light-level geolocators they could provide so much valuable information. Information that could be used for understanding if the ontogenetic effect of migration timing carries over into the next year, or more broad questions related to climate change. While migration technology is exciting and novel it should always be done keeping in line with ethical considerations as we work to help not hinder or harm the species we study.

Concluding remarks

The study of the avian annual cycle and how birds may respond to their changing environmental conditions is complex and difficult to study but is also incredibly captivating. This thesis has covered from how purple martins contain flexibility within their arrival-breeding interval throughout their breeding range, to learning about how migration timing may be set in juveniles.

Therefore, my thesis contributes to a small piece in the complex puzzle of how wild long-distance migrants may be acclimating to climate change. Many new questions have arisen out of my studies creating many avenues for future studies to address. Put simply, the avian world continues to be a diverse, complex, and fascinating area of study.

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Appendix I.

Supplementary Material 1. Egg Manipulation Procedure

Note: These methods are an adaptation from Ouwehand et al. 2017

Materials

- Ziplock containers (large and twist to seal)
- 100% Sheep wool or 100% cotton
- Fake replicate eggs
- Real purple martin eggs
- Plastic bag
- Trowel
- Medium sized rocks
- Egg Manipulation Templates
- Egg Manipulation Sheet
- Pencil

Location					
House		Side		Cavity	
Nest type					
First egg-lay date					
Date clutch completed					
Clutch size					
Date to return nest					

Figure 1. Egg Manipulation Template.

Methods

Prepare Beforehand

1. Get 6 Ziplock containers (large and twist to seal) and fill the container to the top with 100% sheep wool.
2. Place a plastic bag and an Egg Manipulation Template, see Figure 1 (aka. Template), on top of the wool and seal lid shut.
3. Repeat for each container.
4. Put the 6 filled containers back into the box they came in, add the fake eggs and trowel on top.
5. Bring this into the field once egg laying begins.
6. At the end of the day make sure to make more containers if you used some during the day.

Figure 2. Materials: 3 large containers filled with wool and Egg Manipulation Template as well as dummy eggs, trowel, and box.**A total of 50 nests, 25 controls and 25 manipulated from Oak Hammock Marsh (OHM), FortWhyte Alive (FWA), and Clifton's Residence will be used in the study.**

Day 1 Egg Lay Instructions

1. Bring read kit/box mentioned above out into the field around egg laying.
2. Once you find a nest with an egg check the Martinwatch Nest Data Sheet to see which nest type it is (C – control, M – manipulated, N – Night study). If it is N do not touch the egg as it is not part of this study. For C and M nest types continue with steps below.
3. Take out the premade container and open the lid, take out the Template and plastic bag. Remove half the wool from the container (put inside plastic bag).
4. Very carefully using your thumb and middle finger pick up the real egg from the nest and put it into the container half filled with wool and add the rest of the wool on top. Make sure eggs are in the center of the container not touching the plastic of the container.
5. Take out one fake egg and place it into the nest.
6. The scribe will record on the Template the location, cavity number, nest type, date the first egg was laid, and also records the information on the Egg Manipulation Sheet.
7. Once the Template is filled out it will be placed on top of the wool and the container will be tightly sealed. And place in a safe place for now.
8. Continue checking the rest of the nests in the house, repeat steps 2-7 for every new nest found.
9. Put the container in a plastic bag, and twist to seal it close.
10. In the chosen spot at each site (marked by rocks) used the trowel to dig a hole that is the size of the container. Make sure the top of the container is just below the surface of the soil.
11. Put the container wrapped in the plastic bag carefully into the ground.
12. Cover the top with soil and place rock overtop as a marker.

13. Take a picture of the Egg Manipulation Sheet and send it to the group so the other team has the up to date information.

Figure 3. Left - a purple martin egg in nest, middle - shows step 4 and 6, right - shows step 10 and 11.

<u>Day 2-3-4-5-6 Egg Laying Instructions</u>

1. Check the C and M nests every day after 10am to make sure the eggs have been laid for the day.
2. Dig up the container(s) buried before lowering the house, take it/them out of the bag and have them ready.
3. Once the nest check is done remove the newly laid real egg from the nest and replace it with a fake egg. *Make sure you are removing the REAL EGG (the real egg is slightly more beige colored and less oval shaped than fake egg) not the fake one!*
4. Carefully put the egg into the container with the other egg or eggs from the same cavity then cover with wool.
5. On the template add a mark for the number of eggs (e.g. I I I means 3 eggs) and reseal the container.
6. Repeat steps 3-5 for each C or M nest with eggs.
7. Wrap the container in the plastic bag again and put it back in the ground where it was before. Cover with dirt and mark with rock.

Note: If a fake egg is not centred or has been pushed out of the nest bowl it should be moved back into the middle with the rest of the eggs.

Figure 4. Left – shows container wrapped in plastic, middle – shows hole that will fit the container and rock used to cover it, right – red arrow indicates location of rock where the eggs are buried for house 1 at OHM.

Day Last Egg Laid Instructions

1. Dig up the container(s) buried before lowering the house, take it out of the bag and have them ready.
2. Once you check a nest and there is NO NEW EGG LAID that day you can write on the Template and Egg manipulation sheet the last egg lay date (Which would have been the day before) as well as the complete clutch size (~~IIII~~ means 5 eggs).
3. You will NOT take out any eggs from the nest and you do NOT need to touch the eggs in the container. There should only be fake eggs in the nest at this point.
4. Wrap the container in the plastic bag again and put it back in the ground where it was before. Cover with dirt and mark with rock.
5. The following day again dig up the eggs and have them ready.
6. CONTROL NESTS - If there is no egg laid today then for the C nests remove the dummy eggs from the nest and carefully replace the real eggs into the nest. Write on the Egg manipulation Sheet the date the real eggs were returned to nest, place a checkmark to confirm the eggs have been returned to the nest and add initials of the people who returned the eggs to the nest. Done with the Control nests here, no more touching eggs needed.
7. MANIPULATED NESTS - If there is no egg laid today for the M nests leave dummy eggs in nest. Write on the Templated and Egg manipulation Sheet the date eggs to be

returned to nest. Which is 6 days after the last egg laid date. Look at Figure 5 example below.

8. MANIPULATED NESTS - Wrap the container within the plastic bag again and put it back in the ground where it was before. Cover with dirt and mark with rock.
9. MANIPULATED NESTS – On the date that the eggs are to be returned to the nest, dig up container, remove the fake eggs from the nest and carefully place the real eggs back into the nest. Write on the Egg manipulation Sheet, put a checkmark to confirm the eggs have been returned to the nest and add Initials of the people who returned the eggs to the nest. Done with the Manipulated nests here.

Sunday	Monday	Tuesday	Wednesday	Thursday	Friday	Saturday
3	4 1 egg First egg lay date	5 2 eggs	6 3 eggs	7 4 eggs	8 5 eggs Date clutch complete	9 5 eggs (Day 1)
10 5 eggs (Day 2) C eggs returned to nest	11 5 eggs (Day 3)	12 5 eggs (Day 4)	13 5 eggs (Day 5)	14 5 eggs (Day 6) M eggs returned to nest	15	16

Figure 5. An example of the control (C) and manipulated (M) nests and when to return the real eggs back to the nest. In this example M eggs would be returned to the nest on the 14th (Day 6).