

Investigating the plasticity of migration timing and roost behaviours to
environmental variability and parental care in a colonial songbird

by

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Abstract

Rapidly changing environments impact avian populations greatly. Indeed, variable weather affects the timing of crucial resource availability and behaviours of breeding birds. Migratory birds are particularly threatened by advancing springs and must adjust their migration timing to remain synchronized with spring phenology. Environmental factors such as weather variability are known to influence bird timing both during breeding and migratory periods but have rarely been investigated for their impact across migration routes. Once birds are at their breeding locations, how environmental factors influence local timing and movements has also been little examined. In this study, in a declining long-distance migrant, the purple martin (*Progne subis*), I first investigate how extrinsic (environmental), and intrinsic (morphological, migration destination) factors impact migration timing and rate. Second, I investigate the timing of parental roosting during active parental care, and how environmental and nest conditions influence this behaviour. I found that variation in destination and timing are the main influence on spring arrival date and migration rate, while to a lesser extent favourable weather promotes faster migration. The great influence of spring departure on migration rate and arrival suggests selective pressure on migration timing across routes to match with conditions at the breeding grounds. I also found that summer roosting is prominent in purple martins with colder evenings and increased parental investment increasing the odds of parents remaining at their colony at night. Overall, my findings indicate that the influence of environmental factors on movement behaviour may vary by season, with spring migration being mostly driven by intrinsic factors, while summer roosting may be most influenced by local temperature. Future research on the effects of environmental factors on migratory stopover duration and the seasonality of roosting

would further our understanding of these timing behaviours and how they may interact with advancing climate change.

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Chapter 1. A general introduction

Climate change & extreme weather

Each year, billions of birds migrate from their wintering grounds to northern latitudes to breed and have important impacts on the local ecosystems. However, northern nesters are facing multiple threats including the growing threat of climate change (North American Bird Conservation Initiative 2019). Climate change introduces a more variable climate, which is most impactful in ecosystems at northern latitudes, which have shorter intervals of summer productivity and are inherently more instable than lower latitudes (Bellard et al. 2012). A variable environment will impact breeding behaviour and success (Skagen and Adams 2012; Wiley and Ridley 2016) while migratory birds have the added challenge of migrating in this altered climate and avoiding extreme weather events which can cause mass deaths (Brown and Brown 1998; Brown et al. 2017). In Eastern North America, earlier springs caused by warming weather have been described to cause a mismatch between spring phenology and the spring arrival of migratory birds (Mayor et al. 2017; Visser and Gienapp 2019). Indeed, as the climate warms, local vegetation, and insect emergence at breeding sites with which birds need to synchronize their breeding behaviours occurs earlier over decades. Nesting birds depend on matching the rearing of nestlings with the peak insect emergence to maximize their breeding success (Kokko 1999). As such, migratory birds failing to change their arrival date may lead to population declines (Both et al. 2006).

To adjust to the rapidly changing environment, some migratory birds may change their migration timing through phenotypic plasticity in migration timing (Mayor et al. 2017). Phenotypic plasticity is an intra-individual capacity to vary responses, to changes in the

environment (Price et al. 2003). Whether phenotypic plasticity alone may be enough to consistently match migrating birds with their local phenology is uncertain and may be species-specific (Charmantier and Gienapp 2014; Bonamour et al. 2019; Radchuk et al. 2019). Moreover, increasing weather variability in spring may dampen the benefits of earlier spring arrival by reducing clutch survival with more frequent cold snaps during active breeding (Shiple et al. 2020), with some arguing that benefits of migratory species breeding at higher latitudes may be diminishing (Kubelka et al. 2022). Advancing springs do not impact all avian populations to the same extent, as a species' niche can make them more inherently sensitive and the extent of asynchrony varies geographically (Mayor et al. 2017). Resident species and short-distance migratory birds may be marginally affected as they may be able to adjust better, but for neotropical migratory birds which can travel tens of thousands of kilometres, the distance may create a larger disconnect between conditions experienced at overwintering sites, along migratory routes, and those happening at their breeding sites (Fraser et al. 2019). Aerial insectivores and shorebirds, which are two avian groups where most species exhibit long-distance migrations, are among some of the bird groups with the greatest declines (Rosenberg et al. 2019).

The environment in bird ecology

The use of environmental cues is common in nature to time crucial behaviours, like breeding or migratory behaviours. Weather can be an important environmental cue, with higher temperature influencing the timing of egg-laying (Shave et al. 2019), parental care (Wiley and Ridley 2016), and within-breeding parental movements (Saldanha et al. 2019). Other extrinsic

factors can also influence breeding behaviours such as phenology, daylength, predation risk, and parasite load.

During their spring migration, birds will attempt to reach their nesting sites as quickly and efficiently as possible (Alerstam 2011). This entails birds migrating while minimizing energy costs which is partially done by avoiding geographical obstacles, flying during favourable weather (*e.g.*, tailwinds, warmer temperatures, reduced rain), and following niche-specific favourable spring phenology (green-up) (Kokko 1999; Nilsson et al. 2013; Schmaljohann 2019). Daylength, a known cue in migration timing, may also have an important impact on diurnal species, and especially diurnal migrants, as it limits the amount of daylight available to be allocated for the bird's behaviours, including active migration (Nilsson et al. 2013; Pokrovsky et al. 2021) and refueling (Berthold et al. 2001; Klaassen et al. 2008).

A better understanding of how daily weather and other conditions may facilitate spring migration has allowed for the creation of bird migration forecasts which predicts instant local nocturnal migration intensity based on forecasted weather, timing, and location (Van Doren and Horton 2018). The use of weather radars has been used efficiently to follow large non-specific patterns of mostly nocturnal avian migration and bird movements at major roosts (Bridge et al. 2016; Van Doren and Horton 2018; Nilsson et al. 2019). More recently, the use of direct-tracking technology allowed for accurate studies of individual bird behaviours (Stutchbury et al. 2009; Bridge et al. 2013; Taylor et al. 2017; McKinnon and Love 2018). Some of these technologies use geolocation by light intensity, GPS (Global Positioning System), or radio-telemetry arrays. The spatial and temporal precision of direct tracking allows for precise individual-specific studies of bird movement (*e.g.*, migration), whether it be at major migration stopovers, departure, destination, or en route. However, studies investigate overall migration patterns with respect to

en route environmental factor as most previous research focuses on short-term environment signalling in movements at specific migration passages or relate migration to conditions at breeding ground (Gómez et al. 2014; Schmaljohann and Both 2017; Tomotani et al. 2021).

The influence of the environment on migratory bird behaviour: a case study

My study species is the purple martin (*Progne subis*) (Figure 1.1), a colonial long-distance migratory species that is widespread in North America (Figure 1.2) and which has an unusual relationship with humans. Indeed, it is one of the few bird species which is positively impacted by human interactions where the eastern subspecies (*P. s. subis*) is now entirely dependent on human-made nest cavities to nest (Jervis et al. 2019; Kelly and Hvenegaard 2022). However, purple martins, like other rapidly declining aerial insectivores (Rosenberg et al. 2019), are experiencing population losses in the extremities of their breeding range such as in Canada (Sauer et al. 2017), and the species' reliance on aging landlords who may not continue to provide this stewardship may further threaten them in the future (Jervis et al. 2019).

As long-distance migrants, purple martins travel from wintering ranges mostly in the Amazonian forest of Brazil to breeding colonies throughout eastern and central North America (Figure 1.2) , usually using flyways that cross the Gulf of Mexico using the Yucatan Peninsula (Fraser et al. 2012, 2013; Brown et al. 2021). Recognized as a social species, throughout their fall migration and wintering, purple martins gather in large nocturnal communal roosts, often reaching several thousands of individuals (Fraser et al. 2012; Bridge et al. 2016). While martins have been observed to perform nocturnal flights when crossing the Gulf of Mexico, they are strictly diurnal migrants (Lavallée et al. 2021). Because of this, daylength may be a limiting

factor for migrating purple martins, which may need to divide time to be invested in migrating and other behaviours such as foraging (Alerstam 2009; Pokrovsky et al. 2021; Lavallée et al. 2021), contrary to other passerines which mostly migrate nocturnally. The reliance of purple martins on man-made structures and high nesting site fidelity as adults (Brown et al. 2021) facilitated the construction of the largest migration direct-tracking datasets for a songbird, with over 350 individual migration tracks recorded. Using this large database, purple martins have been shown to possess high intra- and population-specific variation in migration timing (Figure 1.1) although how the environment influences this migration-wide variation has yet to be investigated (Fraser et al. 2019). Indeed, purple martin studies on migration have been mostly focused on intrinsic factors influencing migration timing.

In contrast, purple martin breeding and roosting behaviours have been better studied in relation to environmental factors. For instance, the timing of egg laying may correspond to local temperatures where martins lay earlier in warm springs and later in cool springs (Shave et al. 2019). While purple martin communal roosting has been well described during migration, anecdotal evidence suggests that this behaviour may extend to the breeding season, with both parents with active nests leaving their nesting cavity during the night (Fraser pers. obs.). First described in bank swallows (*Riparia riparia*), it appears that swallows known to form large migratory roosts commute regularly to large nocturnal communal roosts, sometimes 30 kilometres away from their colony, while they have active nests (Falconer et al. 2016; Saldanha et al. 2019). Early records show purple martins (*P. s. hesperia*) do appear to also travel to roosts during the breeding season (Cater 1944; Anderson and Anderson 1946) but have not yet been described nor have the environmental factors that may impact this behaviour been investigated. In bank swallows, participation in summer roosting was linked with meeting nestling

thermoregulatory needs, reducing predation risk, and optimizing access to prey availability among other factors (Saldanha et al. 2019).

Investigating environmental variability in migration and breeding movements

This thesis includes the present background introductory chapter (Chapter 1), two data chapters (2 and 3) to be published as research papers, and a final concluding chapter (3) that provides a synthesis of my findings and their general implications for purple martin conservation. My first data chapter (Chapter 2) investigates some environmental and intrinsic factors that may influence the spring migration rate and timing of a neotropical migrant, the purple martin. I used a large migration tracking dataset (n= 307 individual tracks) that includes birds from colonies spread throughout their eastern breeding range. This investigation will enable inferences about the ability of this species to adjust to environmental variability through space and time. My second data chapter (Chapter 3) examines the timing of summer roosting behaviour during the active breeding season in purple martin and investigates the environmental and intrinsic factors which influence this behaviour. This study allow us to uncover a yet undescribed breeding behaviour of a declining species and examine its significance for purple martin breeding success. Overall, these two studies in this thesis will provide a better understanding of how environmental factors influence purple martin behaviour and strategies in two critical seasons of their life history: spring migration and nesting.

References

- Alerstam, T. 2009. Flight by night or day? Optimal daily timing of bird migration. *J. Theor. Biol.* **258**(4): 530–536. doi:10.1016/j.jtbi.2009.01.020.
- Alerstam, T. 2011. Optimal bird migration revisited. *J. Ornithol.* **152**(S1): 5–23. Springer Verlag. doi:10.1007/s10336-011-0694-1.
- Anderson, A., and Anderson, A. 1946. Notes on the Purple Martin Roost at Tucson, Arizona. *Condor* **48**(3): 140–141. doi:10.1093/condor/48.3.140.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., and Courchamp, F. 2012. Impacts of climate change on the future of biodiversity. doi:10.1111/j.1461-0248.2011.01736.x.
- Berthold, P., Bossche, W. Van Den, Fiedler, W., Kaatz, C., Kaatz, M., Leshem, Y., Nowak, E., and Queruer, U. 2001. Detection of a new important staging and wintering area of the White Stork *Ciconia ciconia* by satellite tracking. *Ibis (Lond. 1859)*. **143**(4): 450–455. doi:10.1111/j.1474-919X.2001.tb04946.x.
- Bonamour, S., Chevin, L.M., Charmantier, A., and Teplitsky, C. 2019. Phenotypic plasticity in response to climate change: The importance of cue variation. *Philos. Trans. R. Soc. B Biol. Sci.* **374**(1768). doi:10.1098/rstb.2018.0178.
- Both, C., Bouwhuis, S., Lessells, C.M., and Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* **441**(7089): 81–83. Nature Publishing Group. doi:10.1038/nature04539.
- Bridge, E.S., Kelly, J.F., Contina, A., Gabrielson, R.M., MacCurdy, R.B., and Winkler, D.W. 2013. Advances in tracking small migratory birds: A technical review of light-level geolocation. *J. F. Ornithol.* **84**(2): 121–137. Blackwell Publishing Inc. doi:10.1111/jof.12011.
- Bridge, E.S., Pletschet, S.M., Fagin, T., Chilson, P.B., Horton, K.G., Broadfoot, K.R., and Kelly, J.F. 2016. Persistence and habitat associations of Purple Martin roosts quantified via

- weather surveillance radar. *Landsc. Ecol.* **31**(1): 43–53. doi:10.1007/s10980-015-0279-0.
- Brown, C.R., Airola, D.A., and Tarof, S. 2021. Purple Martin (*Progne subis*). *In* *Birds of the World*. Edited by P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.purmar.02.
- Brown, C.R., and Brown, M.B. 1998. Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution* (N. Y.). **52**(5): 1461–1475. doi:10.1111/j.1558-5646.1998.tb02027.x.
- Brown, C.R., O'Brien, V.A., Wagnon, G.S., Moore, A.T., and Sherry, R. 2017. Nonrandom weather-related mortality in a purple martin (*Progne subis*) roost. *Southwest. Nat.* **62**(3): 212–215. doi:10.1894/0038-4909-62.3.210.
- Cater, M.B. 1944. Roosting Habits of Martins at Tucson, Arizona. *Condor* **46**(1): 15–18. doi:10.2307/1364245.
- Charmantier, A., and Gienapp, P. 2014. Climate change and timing of avian breeding and migration: Evolutionary versus plastic changes. *Evol. Appl.* **7**(1): 15–28. doi:10.1111/eva.12126.
- Van Doren, B.M., and Horton, K.G. 2018. A continental system for forecasting bird migration. *Science* (80-.). **361**(6407): 1115–1118. American Association for the Advancement of Science. doi:10.1126/science.aat7526.
- Falconer, C.M., Mitchell, G.W., Taylor, P.D., and Tozer, D.C. 2016. Prevalence of Disjunct Roosting in Nesting Bank Swallows (*Riparia riparia*). *Wilson J. Ornithol.* **128**(2): 429–434. doi:10.1676/1559-4491-128.2.429.
- Fraser, K.C., Shave, A., de Greef, E., Siegrist, J., and Garroway, C.J. 2019. Individual Variability in Migration Timing Can Explain Long-Term, Population-Level Advances in a Songbird. *Front. Ecol. Evol.* **7**. Frontiers Media S.A. doi:10.3389/fevo.2019.00324.
- Fraser, K.C., Stutchbury, B.J.M., Kramer, P., Silverio, C., Barrow, J., Newstead, D., Mickle, N., Shaheen, T., Mammenga, P., Applegate, K., Bridge, E., and Tautin, J. 2013. Consistent

range-wide pattern in fall migration strategy of Purple Martin (*Progne subis*), despite different migration routes at the Gulf of Mexico. *Auk* **130**(2): 291–296.
doi:10.1525/auk.2013.12225.

Fraser, K.C., Stutchbury, B.J.M., Silverio, C., Kramer, P.M., Barrow, J., Newstead, D., Mickle, N., Cousens, B.F., Lee, J.C., Morrison, D.M., Shaheen, T., Mammenga, P., Applegate, K., and Tautin, J. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proc. R. Soc. B Biol. Sci.* **279**(1749): 4901–4906. doi:10.1098/rspb.2012.2207.

Gómez, C., Bayly, N.J., and Rosenberg, K. V. 2014. Fall stopover strategies of three species of thrush (*Catharus*) in northern South America. *Auk* **131**(4): 702–717. doi:10.1642/AUK-14-56.1.

Jervis, L.L., Spicer, P., Foster, W.C., Kelly, J., Bridge, E., Jervis, L.L., Spicer, P., Foster, W.C., Kelly, J., and Bridge, E. 2019. Resisting Extinction: Purple Martins, Death, and the Future. *Conserv. Soc.* **17**(3): 227–235. doi:10.4103/cs.cs.

Kelly, B.D., and Hvenegaard, G.T. 2022. Impacts of purple martin landlord stewardship activities on nest box occupancy. *Wildl. Soc. Bull.* **46**(1). doi:10.1002/wsb.1247.

Klaassen, R.H.G., Strandberg, R., Hake, M., and Alerstam, T. 2008. Flexibility in daily travel routines causes regional variation in bird migration speed. *Behav. Ecol. Sociobiol.* **62**(9): 1427–1432. doi:10.1007/s00265-008-0572-x.

Kokko, H. 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.* **68**(5): 940–950. doi:10.1046/j.1365-2656.1999.00343.x.

Kubelka, V., Sandercock, B.K., Székely, T., and Freckleton, R.P. 2022, January 1. Animal migration to northern latitudes: environmental changes and increasing threats. Elsevier Ltd. doi:10.1016/j.tree.2021.08.010.

Lavallée, C.D., Assadi, S.B., Korpach, A.M., Ray, J.D., Fischer, J.D., Siegrist, J., and Fraser, K.C. 2021. The use of nocturnal flights for barrier crossing in a diurnally migrating songbird. *Mov. Ecol.* **9**(1). BioMed Central Ltd. doi:10.1186/s40462-021-00257-7.

- Mayor, S.J., Guralnick, R.P., Tingley, M.W., Otegui, J., Withey, J.C., Elmendorf, S.C., Andrew, M.E., Leyk, S., Pearse, I.S., and Schneider, D.C. 2017. Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Sci. Rep.* **7**(1). Nature Publishing Group. doi:10.1038/s41598-017-02045-z.
- McKinnon, E.A., and Love, O.P. 2018. Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. doi:10.1642/AUK-17-202.1.
- Nilsson, C., Dokter, A.M., Verlinden, L., Shamoun-Baranes, J., Schmid, B., Desmet, P., Bauer, S., Chapman, J., Alves, J.A., Stepanian, P.M., Sapir, N., Wainwright, C., Boos, M., Górska, A., Menz, M.H.M., Rodrigues, P., Leijnse, H., Zehndjiev, P., Brabant, R., Haase, G., Weisshaupt, N., Ciach, M., and Liechti, F. 2019. Revealing patterns of nocturnal migration using the European weather radar network. *Ecography (Cop.)*. **42**(5): 876–886. doi:10.1111/ecog.04003.
- Nilsson, C., Klaassen, R.H.G., and Alerstam, T. 2013. Differences in Speed and Duration of Bird Migration between Spring and Autumn. *Am. Nat.* **181**(6): 837–845. doi:10.5061/dryad.82d4q.
- North American Bird Conservation Initiative. 2019. State of Canada's Birds 2019 report. Ottawa.
- Pokrovsky, I., Kölzsch, A., Sherub, S., Fiedler, W., Glazov, P., Kulikova, O., Wikelski, M., and Flack, A. 2021. Longer days enable higher diurnal activity for migratory birds. *J. Anim. Ecol.* **90**(9): 2161–2171. doi:10.1111/1365-2656.13484.
- Price, T.D., Qvarnström, A., and Irwin, D.E. 2003. The role of phenotypic plasticity in driving genetic evolution. doi:10.1098/rspb.2003.2372.
- Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., Adamík, P., Adriaensen, F., Ahola, M.P., Arcese, P., Miguel Avilés, J., Balbontin, J., Berg, K.S., Borrás, A., Burthe, S., Clobert, J., Dehnhard, N., de Lope, F., Dhondt, A.A., Dingemanse, N.J., Doi, H., Eeva, T., Fickel, J., Filella, I., Fossøy, F., Goodenough, A.E., Hall, S.J.G., Hansson, B., Harris, M., Hasselquist, D., Hickler, T., Joshi, J., Kharouba, H., Martínez, J.G., Mihoub, J.B., Mills, J.A., Molina-Morales, M., Moksnes, A., Ozgul, A., Parejo, D., Pilard, P.,

- Poisbleau, M., Rousset, F., Rödel, M.O., Scott, D., Senar, J.C., Stefanescu, C., Stokke, B.G., Kusano, T., Tarka, M., Tarwater, C.E., Thonicke, K., Thorley, J., Wilting, A., Tryjanowski, P., Merilä, J., Sheldon, B.C., Pape Møller, A., Matthysen, E., Janzen, F., Dobson, F.S., Visser, M.E., Beissinger, S.R., Courtiol, A., and Kramer-Schadt, S. 2019. Adaptive responses of animals to climate change are most likely insufficient. *Nat. Commun.* **10**(1): 3109. Nature Publishing Group. doi:10.1038/s41467-019-10924-4.
- Rosenberg, K. V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., Stanton, J.C., Panjabi, A., Helft, L., Parr, M., and Marra, P.P. 2019. Decline of the North American avifauna. *Science* (80-.). **366**(6461): 120–124. American Association for the Advancement of Science. doi:10.1126/science.aaw1313.
- Saldanha, S., Taylor, P.D., Imlay, T.L., and Leonard, M.L. 2019. Biological and environmental factors related to communal roosting behavior of breeding Bank Swallow (*Riparia riparia*). *Avian Conserv. Ecol.* **14**(2): art21. Resilience Alliance. doi:10.5751/ACE-01490-140221.
- Sauer, J.R., Pardieck, K.L., Ziolkowski, D.J., Smith, A.C., Hudson, M.A.R., Rodriguez, V., Berlanga, H., Niven, D.K., and Link, W.A. 2017. The first 50 years of the North American Breeding Bird Survey. doi:10.1650/CONDOR-17-83.1.
- Schmaljohann, H. 2019. The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: A cross-continental analysis. *Mov. Ecol.* **7**(1). BioMed Central Ltd. doi:10.1186/s40462-019-0169-1.
- Schmaljohann, H., and Both, C. 2017. The limits of modifying migration speed to adjust to climate change. *Nat. Clim. Chang.* **7**(8): 573–576. Nature Publishing Group. doi:10.1038/NCLIMATE3336.
- Shave, A., Garroway, C.J., Siegrist, J., and Fraser, K.C. 2019. Timing to temperature: Egg-laying dates respond to temperature and are under stronger selection at northern latitudes. *Ecosphere* **10**(12). Wiley-Blackwell. doi:10.1002/ecs2.2974.
- Shipley, J.R., Twining, C.W., Taff, C.C., Vitousek, M.N., Flack, A., and Winkler, D.W. 2020. Birds advancing lay dates with warming springs face greater risk of chick mortality. *Proc.*

- Natl. Acad. Sci. **117**(41): 25590–25594. doi:10.1073/pnas.2009864117.
- Skagen, S.K., and Adams, A.A.Y. 2012. Weather effects on avian breeding performance and implications of climate change. *Ecol. Appl.* **22**(4): 1131–1145. doi:10.1890/11-0291.1.
- Stutchbury, B.J.M., Tarof, S.A., Done, T., Gow, E., Kramer, P.M., Tautin, J., Fox, J.W., and Afanasyev, V. 2009. Tracking long-distance songbird migration by using geolocators. *Science* (80-.). **323**(5916): 896. doi:10.1126/science.1166664.
- Taylor, P.D., Crewe, T.L., Mackenzie, S.A., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C.M., Guglielmo, C.G., Hamilton, D.J., Holberton, R.L., Loring, P.H., Mitchell, G.W., Norris, D.R., Paquet, J., Ronconi, R.A., Smetzer, J.R., Smith, P.A., Welch, L.J., and Woodworth, B.K. 2017. The motus wildlife tracking system: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conserv. Ecol.* **12**(1). Resilience Alliance Publications. doi:10.5751/ACE-00953-120108.
- Tomotani, B.M., Gienapp, P., de la Hera, I., Terpstra, M., Pulido, F., and Visser, M.E. 2021. Integrating Causal and Evolutionary Analysis of Life-History Evolution: Arrival Date in a Long-Distant Migrant. *Front. Ecol. Evol.* **9**. Frontiers Media S.A. doi:10.3389/fevo.2021.630823.
- Visser, M.E., and Gienapp, P. 2019. Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* **3**(6): 879–885. Nature Publishing Group. doi:10.1038/s41559-019-0880-8.
- Wiley, E.M., and Ridley, A.R. 2016. The effects of temperature on offspring provisioning in a cooperative breeder. *Anim. Behav.* **117**: 187–195. Academic Press. doi:10.1016/J.ANBEHAV.2016.05.009.

Figures

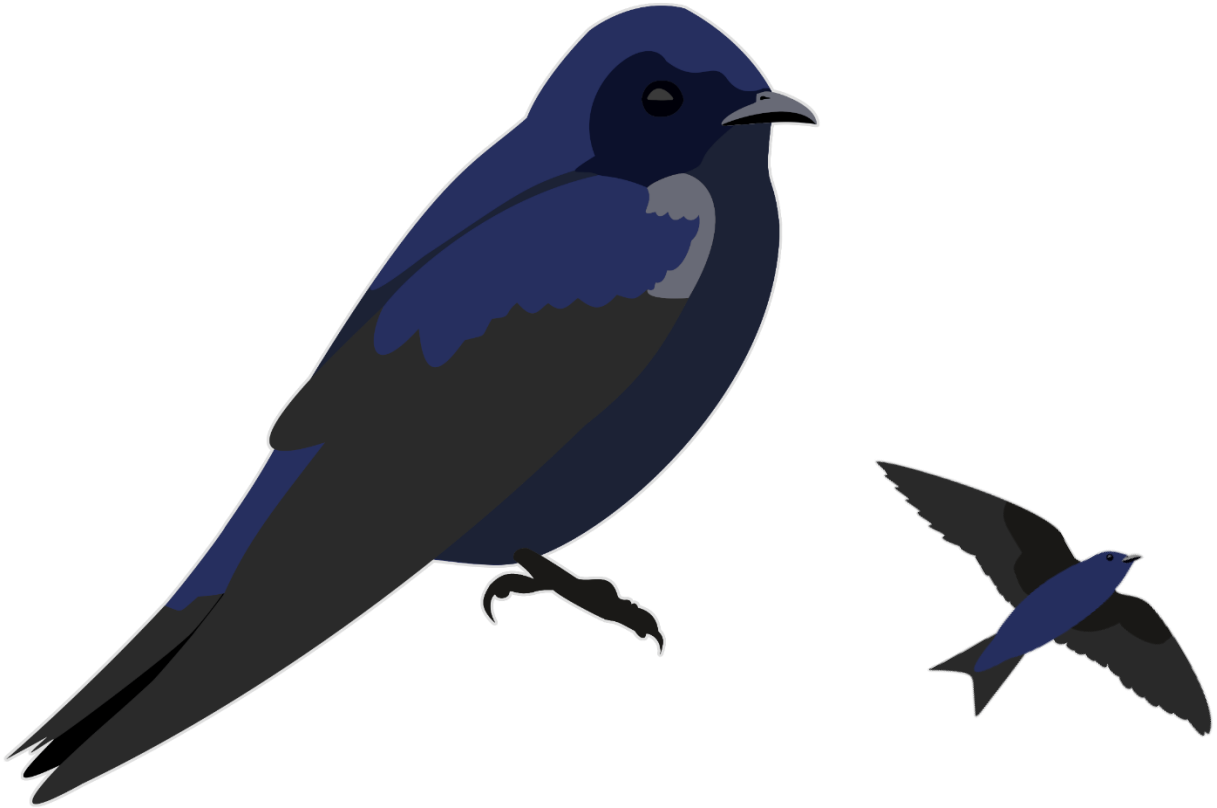


Figure 1. 1 Male purple martin (*Progne subis*), females are generally browner with pale underside.

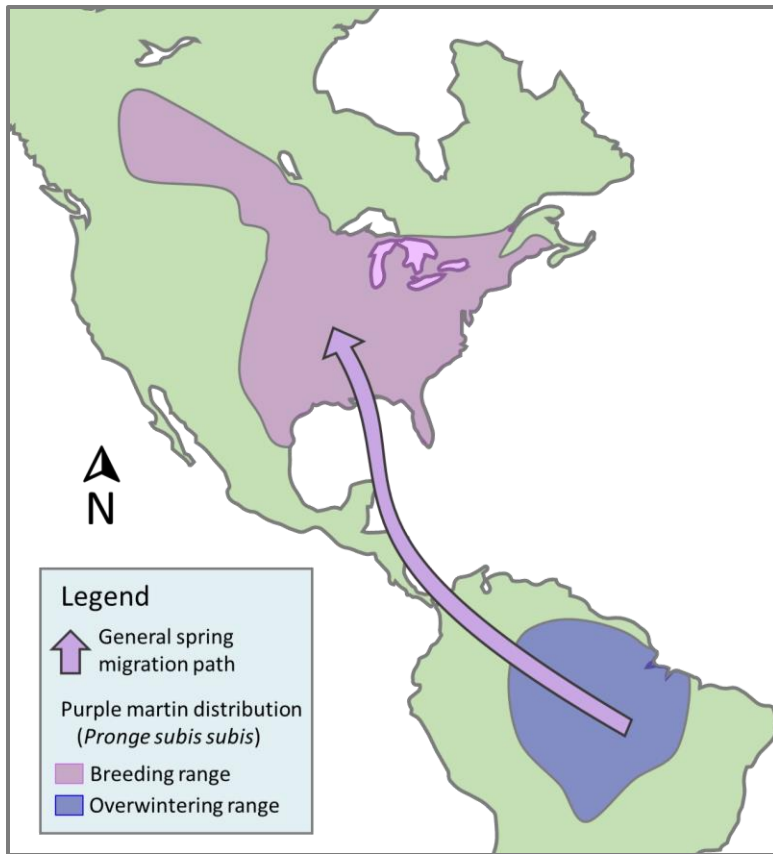


Figure 1. 2 Approximate breeding and overwintering distribution of the eastern subspecies of purple martin (*Progne subis subis*).



Figure 1. 3 The difference in migration timing in days between years of individual purple martins tracked for two consecutive years, from breeding colonies throughout Eastern North America. Lines indicate individual timing at the start of spring migration in South America, crossing the Tropic of Cancer (23.4°N), and the arrival at the bird's breeding colony in North America. A positive timing difference indicates earlier migration timing in the 2nd year as compared to the 1st year.

Chapter 2. The influence of the environment, timing, and destination on spring migration rate in a long-distance migratory songbird

Abstract

Long-distance avian migrants are threatened by a rapidly changing environment, which can induce a mismatch between favourable environmental conditions and the timing of breeding. Migrating birds must therefore greatly rely on their phenotypic plasticity in migration timing to remain synchronized with earlier occurring resources. However, how this plasticity responds to en route environmental factors and whether it may allow migratory birds to remain synchronized with advancing springs is largely unknown. The objective of this study is to investigate how weather variability (*e.g.*, temperature, precipitation, wind) and daylengths experienced along purple martin spring migration routes, individual morphological traits (*e.g.*, sex, age), as well as the departure date from wintering grounds, influence (1) migration-wide migration rate, (2) spring arrival date at the breeding grounds, and (3) variation in the migration rate of the subtropical and temperate portions of migration. We investigated arrival timing and rate using 307 individual migration tracks of purple martin (*Progne subis*) sampled from individuals across their eastern breeding range. Overall, purple martin travelled at an average rate of 400 ± 290 km/day and arrived at their colony from January 28th to June 9th. We found that birds with a faster migration rate (*i.e.*, fewer stopovers) arrived earlier at their breeding sites. We also found that later departing birds travelled faster than early departing birds. Instead of expected patterns of protandry observed in songbirds, where males migrate faster and arrive earlier than females, we found females to migrate faster and arrive earlier than males (protogyny). Departure date

explained most of the variation in migration rate but facilitating South winds and lower precipitation also induced a faster migration rate. Overall, our results suggest that migration rate may be mostly impacted by intrinsic factors tied to the phenology of breeding sites rather than by conditions experienced en route. These findings support growing evidence that selection upon spring departure date may be needed for the advancement of spring migration timing and arrival date to match advancing springs with climate change. Future research investigating how environmental conditions at stopovers contribute to overall migration rate would provide further insight into factors influencing migration timing.

Introduction

Earlier springs caused by climate change can cause a mismatch between spring phenology and spring arrival dates of migratory birds (Mayor et al. 2017; Visser and Gienapp 2019). A mismatch in spring migration timing can lead to an overall decrease in fitness (Kokko 1999), and ultimately, population decline (Both and Visser 2001; Both et al. 2006). Phenotypic plasticity in migration timing (*i.e.*, inherent variability within and among individuals) can potentially ameliorate such a mismatch and optimize arrival timing (Bonamour et al. 2019; Fraser et al. 2019). Selection on migration departure timing and pace can influence this variation in spring arrival dates, mediated by environmental conditions experienced while en route (Schmaljohann 2019; Neufeld et al. 2021), yet technological limitations and sample size have generally limited the ability to investigate these interactions in songbirds.

Migration rate, which can be defined as the kilometres travelled per day during entire seasonal migrations (McKinnon et al. 2013), may be influenced by both intrinsic and extrinsic

factors experienced while en route. The sum of days a migrating bird spends resting at a specific location during migration is referred to as stopover duration and is most strongly correlated with overall migration rate, rather than flight speed (Schmaljohann and Both 2017). Variation in this migration rate may also be caused by intrinsic factors that varies by population or from individual to individual (Nilsson et al. 2014), between demographic distinctions (*e.g.*, sex and age), or energetic condition (Alerstam 2011; González et al. 2020).

The extrinsic factor of the environment may also impact migration as birds attempt to migrate with minimal energy losses (Wikelski et al. 2003; Alerstam 2011). Weather can considerably impact migration pace, with favourable weather such as advanced spring phenology (*e.g.*, warm temperatures, increased insect availability), tailwind, and absence of precipitation supporting shorter stopovers or faster migration (Wikelski et al. 2003; Haest et al. 2020; Åkesson and Bianco 2021). Seasonal change in daylength can be a critical cue in cueing migration and may also impact migration timing generally (Berthold 1996). Longer photoperiods have been associated with a longer duration of activity in diurnal species, leading to greater foraging ability during migration and fewer stopovers in a fly-and-forage migration strategy (Berthold et al. 2001; Alerstam 2003, 2009; Pokrovsky et al. 2021). Numerous studies have examined migration timing at a specific point during migration, such as at arrival, departure, or specific stopovers. (McKellar et al. 2013; Van Doren and Horton 2018; Abdulle and Fraser 2018; Schmaljohann 2019; Conklin et al. 2021; Lomas Vega et al. 2021; Tomotani et al. 2021). However fewer have examined the entire migration (Schmaljohann and Both 2017; McKinnon and Love 2018) and studies examining the interaction between timing, rate, and en route conditions are also exceptionally rare in all birds (Haest et al. 2020).

Here, we investigated the overall effects of en route environmental variables (*i.e.*, factors such as weather that are experienced along a bird's migration routes) on spring migration rate and timing while controlling for intrinsic factors known to influence timing such as age and sex, and the migration destination (*i.e.*, geographical region of breeding colony)(Neufeld et al. 2021). In addition, we explore how both migration timing and pace may vary in a long-distance migratory bird, the purple martin (*Progne subis*). In purple martins, the plasticity of migration timing is closely intertwined with migration rate since spring arrival timing was shown to be greatly impacted by departure date from wintering grounds, while migration rate was correlated with departure date (Neufeld et al. 2021). Multiple studies show that at critical steps in migration such as spring departure date and stopovers, and throughout migration, environmental factors are tied to suitable conditions for migration (Abdulle and Fraser 2018; Galtbalt et al. 2022) and departures (Beauchamp et al. 2020; Haest et al. 2020).

This study has three aims: investigating the influence of en route environmental factors, departure timing, geographic destination, and demographic factors (age, sex) on (1) overall migration rate, (2) spring arrival date, and (3) variation in migration rate in the subtropical and temperate portions of migration. We incorporated migration data from throughout the purple martin range using a rare sample (n=307) of direct migration tracks. For the first objective (1), we expected faster migrants would arrive earlier at their breeding site (Neufeld et al. 2021). Second (2) we expected birds to be sensitive to unfavourable weather to conserve energy as cues for spring phenology timing, where colder temperatures, associated with low insect availability and late spring phenology, opposing winds, and rainy conditions would slow spring migration rate, leading to later arrival (Wikelski et al. 2003; Van Doren and Horton 2018; Haest et al. 2020). Moreover, we expected female and younger martins to migrate at a slower pace than

males, due to protandry in songbirds, and older birds, from differing level of migratory experience, and later departing birds to migrate faster to mitigate the risk of late arrival (Fraser et al. 2019; González et al. 2020).

As purple martins are nearly completely diurnal during their migration (Lavallée et al. 2021), longer daylengths as the spring migration season progresses and as birds move further north may provide more time for flights and foraging, increasing migration rate. Previous research found migratory birds to possibly accelerate as they approached their breeding sites (Alerstam 2006; Briedis et al. 2018), which may be tied to changes in daylength (Pokrovsky et al. 2021). For the third objective (3), we, therefore, investigated whether migration rate varies over the course of migration between subtropical and temperate portions of migration (*e.g.*, first and latter migration legs). Moreover, we investigated how en route environmental factors, departure timing, geographic destination, and intrinsic factors (age, sex) may affect these within-migration variations in pace.

Methods

Migration tracking dataset

We used 366 migration tracks sampled using light-level geolocators between 2007 and 2019 from adult purple martin colonies throughout the eastern breeding range (Fraser et al. 2012, 2019; Brown et al. 2021). These included samples from 27 distinct breeding colonies distributed across latitudes (26° to 53°) within the species' eastern breeding range in the states and provinces of Alberta, Manitoba, Ontario, Minnesota, South Dakota, Pennsylvania, New Jersey, Virginia,

South Carolina, Florida, and Texas (Figure 2.1). Of the original dataset, 59 birds were excluded from further analysis owing to poor quality light data resulting in biologically unrealistic migration routes, resulting in 307 migration tracks for further analysis. Of these, thirty individuals were repeat tracked on more than one migration.

Light-level geolocators (≤ 1.6 g; MK10s/12/12 s/14 s/20, British Antarctic Survey) were mounted using leg-loop harnesses made of Teflon ribbon (Fraser et al. 2012; Neufeld et al. 2021). Geolocators provided location estimates for two points per day, one at noon and one at midnight. The spatial error of these geolocators varies with the time of year and latitude, but the spatial error is estimated to be about 200 km (Fraser et al. 2012). Tags were retrieved at the same breeding colony in the spring of the following year. To maximize the likelihood of recapture, only adult (second-year and after second-year whose age was determined using plumage characteristics (Pyle 1997)) birds were tagged, meaning the spring migration tracks used in this study contain third-year (TY) and after third-year (ATY) birds.

Purple martins were grouped into 5 latitudinal groups following K-means clustering of their breeding colony latitude (Neufeld et al. 2021). We separated the K-means cluster around 35° of latitude into two distinct groups resulting in the 6 following regions named by geographical location: highest ($\sim 50^\circ$, Canadian prairies), mid interior ($\sim 45^\circ$, Great Lakes and US prairies), mid coastal ($\sim 40^\circ$, US east coast), low interior ($\sim 35^\circ$, Northern Texas), low coastal ($\sim 35^\circ$, South Carolina), and lowest regions ($\sim 30^\circ$, Gulf of Mexico coast). The separation between the low interior and low coastal regions was done on the basis that they display large differences in migration timing (Suppl. Table 2.1), and climatic characteristics according to the Koppen-Geiger Climate Classification. The resulting low interior and low coastal latitudinal

regions were classified as BSk (arid, steppe, and cold) and Cfa (no dry season and warm summers) respectively (Beck et al. 2018).

Geolocator data analysis

Spring departure from wintering grounds and spring arrival at breeding colony of migration timing was determined using the GeoLight R package (version 2.0.0; Lisovski and Hahn 2012) as described in Neufeld et al. (2021). Light data were manually verified for quality and twilight (sunrise/sunset) outliers from shade or light pollution were adjusted based on surrounding twilights. A combination of the R packages GeoLight, BASTag (version 0.1.3; Wotherspoon et al. 2016), and FLightR (version 0.5.2; Rakhimberdiev et al. 2017) were used to determine migration tracks. We calculated migration rates for each bird's subtropical and temperate region of migration. We used a bird's closest point to the Tropic of Cancer crossing (23.4° latitude) to divide each bird's subtropical and temperate migration rates. Subtropical or temperate migration leg exhibiting distance travelled of <100km and duration <1 day was excluded from further analysis. All migration track measurements and stopover analysis were done using R (version 3.6.1) in RStudio (version 1.2.1335), except for the subtropical and temperate migration rates, which were calculated in different software versions (R versions 4.1.2 and RStudio 2021.09.1+372).

Spring stopover locations and duration were estimated using the FLightR stationary.migration.summary function with a probability of displacement cut-off of 0.1 (Rakhimberdiev et al. 2017). We defined stopovers as a time of rest where a martin would take at least a day off from active migration and used a minimum stay of three twilights, equivalent to roughly 36 hours. We further refined stationary period estimates by manually inspecting each

track, and using known geolocator spatial error (Fraser et al. 2012) and maximum daily travel distances for martins (Lavallée et al. 2021) to further group stationary points (*e.g.*, points within a radius of 2° of latitude and longitude (~220 km) were considered the same stopover). We removed individual birds with a flight speed (migration rate excluding stopovers) exceeding 1000 km/day. To estimate the effect of stopovers on migration, while taking into account the wide variation in total migration duration, we divided stopover duration by total migration duration, which calculates the proportion of time a bird spent at stopovers during their spring migration.

Environmental data

Individual migration tracks were annotated with environmental variables for each of the two daily (noon and midnight) locations along the entire spring migration. Daylength was calculated using the *geosphere* R package (version 1.5.14; Forsythe et al. 1995) using daily tracking location and date to estimate that day's photoperiod (in R version 4.1.2 and RStudio 2021.09.1+372). However, this light measurement does not consider that actual daylength experienced by individual birds which may fluctuate with cloud cover, light pollution, and habitat-dependent variation in daylight (*e.g.*, tree canopy, mountain range, etc.). Temperature at two meters above ground, total hourly precipitation, and wind as meridional and zonal flows (South to North and West to East winds respectively) at ten meters above ground, were annotated using the Env-DATA System on Movebank (movebank.org) (Dodge et al. 2013) from ERA5 Hourly Data on Single Levels provided by the European Centre for Medium-Range Weather Forecasts (ECMWF) Global Atmospheric Reanalysis (Hersbach et al. 2020). Meteorological values had a spatial granularity of 0.25° (~27.75 km) and temporal granularity of one hour, with

total precipitation accumulating one hour of precipitation per location. Temperature and wind components had an inverse-distance-weighted interpolation and total precipitation had a nearest-neighbour interpolation. Wind components were used to calculate average wind speed ($\sqrt{\text{meridional wind}^2 + \text{zonal wind}^2}$) to which we added a metric of average wind favourability (*i.e.*, favourability of strength and direction to facilitate migration). This was defined where average south facilitating winds were denoted as positive and average north headwinds as negative. Although, the short temporal resolution for weather factors may not include all variation in that day's weather, those factors may be most accurate especially for periods where the tracked bird is actively migrating.

Migration data analyses

To investigate the relation between en route environmental factors, timing, and intrinsic traits with 1) overall migration rate, 2) spring arrival date, and 3) subtropical and temperate migration rates we used a mixture of Generalized Linear Mixed Models (GLMMs) using `glmmTMB` (version 1.1.2.3; Brooks et al. 2017) and Generalized Linear Models (GLMs) using base R functions (in R version 4.1.2 and RStudio 2021.09.1+372) with 95% confidence intervals. In every initial analysis, we used GLMMs with individuals and year of deployment as random effects. Individual as a factor allowed us to consider the variation between individuals as well as control for repeat tracks (n=25) of the same bird. Year of deployment as a factor allowed us to account for unknown variation between sampling years. When random effects failed to account for a meaningful proportion of the total variance (<1% of total variance), they were dropped and GLMs were used instead.

The environmental factors of wind, temperature, precipitation, daylength, and migration timing (arrival date and departure date) all had some degree of collinearity amongst them (Suppl. Figure 2.1). To estimate and limit the contribution of collinearity in our models, fixed effects were tested with Variance Inflation Factor (VIF) using the performance *r* package (version 0.8.0; Lüdecke et al. 2021). When independent variables fell below a VIF threshold of 10 (Montgomery, D.C. & Peck 1992), the most collinear variables were excluded from the specific model using biological reasoning (Zuur et al. 2010).

Overall migration rate and spring arrival models

These models used whole individual migration tracks to describe migration patterns; *i.e.*, not localized responses to environmental factors but the total of these effects on the rate and timing of the whole journey. Therefore, we used average temperature (°C), wind (m/s), and total precipitation (mm) for all points along a route, including those at stopovers. We did not use daylength as a fixed effect for both overall migration rate and arrival date models because it correlated with both timing and location of the breeding colony locations.

To investigate the effects of individual traits, timing of spring departure, and environmental factors on migration rate, we used a GLMM with overall migration rate as our response variable. As fixed effects, we used the proportion of stopovers, age, sex, departure date, temperature, wind, precipitation, and latitudinal group of destination. As a random effect, we used year of deployment while individual was omitted as a factor because of its small contribution to the model variation.

To investigate the effects of migration rate, individual traits, timing of spring departure, and environmental factors on the timing of spring arrival, we used a GLMM with spring arrival

date as our response variable. We used individual and year of deployment as random effects. The fixed effects were migration rate, age, sex, departure date, temperature, wind, precipitation, and latitudinal groups. For random effects we used both year of deployment and individual.

Subtropical and temperate models

To investigate whether birds vary their migration rate between the subtropical and temperate regions in response to intrinsic or extrinsic factors, we used three GLMMs with regional migration rate (subtropical and temperate migration rate) as our response variable. Since regional migration rate had a skewed distribution, the response variable was logged to respect our model assumptions. In the first model, our fixed effects were migration portion (subtropical or temperate), age, sex, daylength, temperature, wind, precipitation, and breeding latitudinal group. All environmental factors (daylength, temperature, wind, total precipitation) were averaged within each region, similarly to the full track analysis. Because of the inclusion of daylength as a fixed effect in subtropical and temperate models, we did not include departure date since it is collinear with daylength. As random effects we used year of deployment and omitted individual for its marginal contribution to the model's variation. We fitted two additional models for migration rate, one each for tropical and temperate migration. As we may expect differing migration rates between subtropical and temperate regions, we investigated how the same intrinsic and extrinsic factors may impact migration rate differently based on migratory regions. Here we used the same predictor variables of age, sex, daylength, temperature, wind, precipitation, and breeding latitudinal group.

Results

Overall migration track models

Of the original dataset, 307 migration tracks including 25 repeat tracks were used for our analyses. Overall, our sample had a sex ratio of about 4 males to 5 females (142 males and 160 females) and an age ratio of about 1 TY to 5 ATY (56 TY and 249 ATY) (Suppl. Table 2.1). Within the latitudinal regions, there are 74 birds in the highest, 97 in the mid interior, 55 in the mid coastal, 18 in the low interior, 16 in the low coastal, and 47 in the lowest region. While all latitudinal groups had similar migration rates ranging from 121 to 580 km/day, low coastal had on average slower migration rates and ranged from 109 to 354 km/day (Suppl. Table 2.1, Suppl. Figure 2.2). Stopovers occurred from 1 to 6 times during spring migration while stopover durations ranged from 36 hours to 47 days with stopover proportion ranging from 0.13 to 0.81. Spring migration timing varied with the latitude of breeding colony, with the wintering departure dates ranging from January 10th (Florida) to May 12th (Alberta), and arrival dates ranging from January 28th (Florida) to June 9th (Alberta) (see Suppl. Table 2.1). For overall en route weather factors for each individual, average temperature ranged from 18.5 to 28.3°C, average wind ranged from -5.0 to 2.4 m/s, and average precipitation ranged from 0.00 to 0.85 mm of rain. The daylengths that birds experienced along their migration ranged from 10.7 hours in early migrating birds breeding at low latitudes and 16.6 hours for late birds breeding at high latitudes.

Migration rate

We found a strong positive correlation between spring migration rate and the proportion of stopover days within a track (Table 2.1; Figure 2.2), where for each 10% of time invested in

stopover, the migration rate was reduced by 26.5 ± 6.2 km/day. For migration timing, on average, for every 10 days later purple martins departed from their wintering grounds, migration rate increased by 40 km/day (Figure 2.3, b). For weather factors, for each increase of 1 m/s of favourable wind experienced by martins, their migration rate increased by 10.7 ± 8.3 km/day, and for each 1 mm of total average precipitation, the migration rate decreased by -63.0 ± 47.7 days (Figure 2.4, a, b). We also found that the low coastal region (South Carolina) to be 53.1 ± 51.6 km/day slower than highest region (Canadian prairies) (Suppl. Figure 2.2). The year itself had a small effect accounting for 9.9% of the variation with a variance of 449, leaving the residual to account for the other 90.1% with a variance of 4077. For this model, the marginal R^2 was 0.41, and the conditional R^2 of 0.46 (Table 2.1).

Spring arrival date

All variables and groups considered either displayed a statistically significant effect on spring arrival date or were marginally significant ($p < 0.1$; Table 2.2). We found that the departure date had a positive effect on arrival date (where later departure led to later arrival dates at breeding sites) whereas migration rate had a negative effect (where faster rates resulted in earlier arrival dates). For migration timing, we found that on average a bird departing from its wintering ground 1 day later will have a later spring arrival of 1 ± 0.03 days (Figure 2.3, a), while an increase of about 15 km/day in migration rate will lead an earlier spring arrival of 1 ± 0.06 days. We found a surprising sex difference in migration timing as males arrive at their breeding site 1.5 ± 0.8 days later than females (protogyny) (Mills 2005). All en route weather factors and age were not significant at 95% CI but would be at 90% CI (Table 2.2). Of the total variance, individuals accounted for 48.0% of the variation with 5.7 of variance, year accounted for 1.0 %

of the variation with 0.1 of variance, and the residual accounted for the remaining 51.0% with a variance of 6.1. For this model, the marginal R^2 was 0.988, and the conditional R^2 of 0.994 (Table 2.2).

Comparing subtropical and temperate migration rates

After data cleaning, we had a total of 594 samples from 282 individual purple martins, with 288 samples in the temperate northern migration period and 306 samples in the subtropical southern migration period. Subtropical and temperate migration rate ranges from 52 to 919 km/day (Figure 2.4). We found a significant difference in the migration rate between the subtropic (South) and temperate (North) regions, with temperate region being 0.16 ± 0.13 log km/day slower than the subtropical region (Table 2.3; Figure 2.4). We also found the departure date to be a significant factor, with the temperate and subtropical migration rate increasing by 0.004 ± 0.002 log km/day for each additional day spent either in the wintering grounds or in the tropics. For weather factors, only average wind had a significant effect with regional migration rate increasing by 0.033 ± 0.017 log km/day for each one m/s increase in average favourable wind. Additionally, we found that only the low coastal region differed from the others in terms of migration rate and was 0.22 ± 0.21 log km/day less than the highest region. The random effect of year accounted for 3.2% of the variation with a variance of 0.0042, leaving the residual to account for the other 96.8% with a variance of 0.1315. For this model, the marginal R^2 was 0.16, and the conditional R^2 of 0.18 (Table 2.3).

Subtropical and temperate subset models

In the southern migration leg, we found a negative correlation between subtropical migration rate and average temperature (Table 2.3). Subtropical migration rate decreases by -0.054 ± 0.035 log km/day for each degree Celsius in average temperature, and the subtropical migration rate for the highest region was significantly different from the mid coastal, low coastal, and the lowest regions, by -0.14 ± 0.12 log km/day, -0.62 ± 0.21 log km/day, and -0.38 ± 0.22 log km/day respectively. Daylength was not significant while temperature was controlled. In the northern migration leg, we found a positive correlation between temperate migration rate with both average daylength and average wind. Temperate migration rate increased by 0.149 ± 0.128 log km/day for each hour of daylength and increases by 0.031 ± 0.022 log km/day for each one m/s of average favourable wind. Notably, in the temperate region, we found a difference in migration rates between sexes, with males migrating -0.130 ± 0.096 log km/day less than females. We also found that in the temperate region, there were no significant differences between latitudinal groups and the reference group of the highest region.

Discussion

In one of the few studies that incorporate en route environmental factors to investigate overall patterns of migration behaviour, we investigated the influence of intrinsic and extrinsic factors on spring migration rate and timing, using 307 migration tracks of purple martins, in a series of population-wide analyses. We had three main hypotheses whose important results were: (1) departure date from wintering grounds and stopover duration may drive most of the variation in migration rate, while favourable en route weather promotes faster migration rate to a lesser

extent, (2) earlier spring arrival date at the breeding colony was driven by earlier departure date, faster migration rate, breeding location (latitude), and sex, with no measurable carry-over effect of en route weather, and (3) migration rate within the temperate region was not faster than in the subtropical region as predicted. Notably, our findings also indicate that females within the temperate region migrate faster within the temperate region and arrive earlier at breeding sites than males (protygyny) (Mills 2005), in contrast to the expected pattern of protandry previously reported in this species (Morton and Derrickson 1990). Overall, our findings show support for spring migration (both rate and timing) in long-distance migrants being driven mostly by intrinsic factors rather than environmental factors encountered en route. This aligns with results from earlier work, including a meta-analysis of migration rate in songbirds, that suggested that advances in timing required under new conditions with climate change would be constrained by selection on spring departure date (Schmaljohann and Both 2017; Schmaljohann 2019). Our findings of slower migration in the temperate zone as compared to migration rate through the tropics at the beginning of migration also contradict predictions under the sprint-to-the-finish hypothesis (Briedis et al. 2018).

Migration rate

Our results suggest that spring migration rate depended heavily on intrinsic factors such as departure date, proportion of stopovers, and migration destination (latitude of breeding location), whereas environmental factors influenced rate to a lesser extent. The impact of the number of stopover days on overall migration rate is not surprising as longer stopovers have been associated with slower migration rates in other studies (Nilsson et al. 2013; Schmaljohann 2019). Our result that birds departing later from their wintering grounds had faster migration

rates may indicate an intrinsically cued difference in rate between early and later departing birds, rather than that later birds encounter improved migratory conditions that increased their pace. When considering latitudinal groups, stopover, and environmental factors, we did not find that groups at higher latitudes increased migration rate as previously described (Neufeld et al. 2021). However, we found that the low coastal latitudinal region displayed a slower migration rate than the other regions, which may reflect smaller scale, more regional impacts on rate that could be further investigated in future studies. The high variation in migration rate we found, coupled with the minimal effect of environmental factors, aligns with inferences made by Schmaljohann and Both (2017), who suggested that since migration rates may vary little en route, selection on departure date may be required for birds to advance their timing in response to climate change.

We found overall that earlier departing and faster-migrating martins arrive earlier at their breeding colonies. Yet, later departing martins migrate faster, which may indicate that later departing martins may be under strong selection to travel at faster rates, to arrive at similar times to earlier departing birds, as arrival date may be critical to fitness (Kokko 1999). This has been described in Swainson's thrush (*Catharus ustulatus*) where earlier departing birds migrated slower than later departing birds, although both groups arrived at their breeding sites at a similar date (González et al. 2020). These patterns may also be related to condition-dependent strategies, where birds that depart later are better prepared for migration with higher fuel loads (*i.e.*, better conditions)(González et al. 2020).

Supporting the idea that migration rate is directly influenced by days of rest along the migration route (Nilsson et al. 2014; Schmaljohann and Both 2017), we found that martins with higher stopover proportions display a slower migration rate. This aligns with previous work with varied groups of birds showing that stopover duration, rather than the modulation of pace in the

air, has the largest impact on overall migration rate and duration (Schmaljohann and Both 2017). It would be valuable to explore how en route environmental factors influence migration either stopover duration or stopover proportion in purple martins (Beauchamp et al. 2020). For instance, cold snaps, which aerial insectivores such as purple martins are sensitive to (Brown 1976), are associated with induced stopovers (Alerstam 2011). Total stopover duration is suggested to be a better estimate of the general migration pace than migration rate, as it may be a bigger limiting factor than a hypothesized more constant migration rate (Schmaljohann and Both 2017; Haest et al. 2020).

Sex differences in migration timing and rate

Our findings indicate that during the temperate portion of spring migration, purple martin females migrated faster than males and arrived earlier at their breeding sites than males. Protogyny, where females migrate earlier than males may be a more common behaviour in fall for songbirds (Mills 2005), or in some shorebird species in spring (Oring and Lank 1982; Reynolds et al. 1986). Moreover, earlier spring arrival for females is contrary to predictions for songbirds generally, where strong selection on male arrival for territorial or nest site defence may promote protandry (Kokko 1999); a pattern also found previously for purple martins (Morton and Derrickson 1990). Our study is the first that we are aware of to find protogyny in travel speeds in a songbird.

Arrival timing

Our results showed that the spring arrival date was especially influenced by intrinsic factors, with little influence of environmental factors while birds were en route. As expected, we

found that faster and earlier departing birds arrive earlier at their breeding colony. Moreover, we found latitudinal and sexual differences in arrival with more southern latitudinal regions arriving earlier than northern ones and females arriving earlier than males.

Because of the variability of en route weather along migration routes and its effect on migration efficiency and stopover duration (Nilsson et al. 2013; Haest et al. 2020), migration timing is usually assumed to vary depending on these en route conditions (Both 2010; Conklin et al. 2021; Neufeld et al. 2021). For instance, in pied flycatchers (*Ficedula albicollis*), another long-distance migratory songbird species, population-wide advancements in spring departure date from wintering grounds, did not result in earlier arrival dates, which was inferred to be the result of unmeasured en route environmental factors constraining migration pace (Both 2010). Further contrasting our finding of no effect of environment on timing, a study on six trans-Saharan long-distance songbirds found that environmental conditions during stopovers contributed to most of the variation observed in migration timing (Haest et al. 2020). The lack of impact of extrinsic factors on arrival date and their minimal impact on migration rate in purple martins supports the idea that migration rate cannot be increased, and that rate and timing are mainly impacted by departure date and destination (Schmaljohann and Both 2017). As such, in the event of early springs, purple martins may not be able to increase their migration pace in response to favorable en route environmental cues. Indeed, in response to a record-setting early and warm spring in 2012, purple martins did not advance their migration timing (Fraser et al. 2013). Therefore, changes to maintain an optimal arrival date with climate change may induce selection pressure for martins to depart for spring migration earlier.

Weather

Although contrary en route environmental factors have been associated with a reduced ability to adjust to changing springs negating the effect for earlier departures (Both 2010), we found that extrinsic factors did not affect spring arrival and had only small effects on the migration rate. We found that as predicted, impeding weather, such as headwinds and precipitation, slowed migration rate. Optimal migration strategies for energy selection would result in avoidance of contrary weather conditions for active migration (Alerstam 2011). Facilitating winds in contrast would allow purple martins to cover greater grounds for the same duration of time and cross geographical barriers while saving energy (Abdulle and Fraser 2018). Migrating common swifts (*Apus apus*), another aerial insectivore, were shown with GPS tracking to take advantage of tailwinds to greatly increase their flight speed. Similarly, avoiding migrating during precipitation may avoid thermoregulatory losses and the additional weight from rain (Alerstam 2011).

Temperature can act as an invaluable environmental factor when investigating spring migration. Bird thermoregulatory needs increase as temperature decreases, a situation that birds and especially aerial insectivores may avoid (Alerstam 2011). Indeed, when temperatures drop below 13°C, flying insects decrease in activity, and prevent aerial insectivores from foraging (Brown 1976). Inversely, higher temperatures may be a proxy of insect abundance and advanced local spring phenology. As purple martins are diurnal migrants, and fly-and-forage during migration (Alerstam 2009; Shave et al. 2019), higher prey availability during migration may allow martins to migrate faster. While we found no effect of average temperature on overall and temperate migration rate, it did have an impact on subtropical migration rate, a portion of spring migration where the temperatures and seasonality are most constant. Contrary to our

expectations, we found a negative correlation where warmer average temperatures encountered correlated with slower migrating birds. Possibly, higher temperatures impact the bird's willingness to migrate but may also be because most stopovers surrounding the Gulf of Mexico may be located in warmer regions within the subtropical region. Possibly, higher temperatures at tropical latitudes reduced travel rates if birds were avoiding thermoregulatory costs of higher temperatures which exacerbates heat generation excess produced while flying (Bryant 2008).

Variation in temperate and subtropical migration portions

Migrating birds are hypothesized to increase their daily flight speed as they approach their breeding site during spring migration, owing to spring phenology patterns and selection for earlier arrival via intraspecific competition (Alerstam 2006). However, when all intrinsic and extrinsic factors were kept constant, our results show that the subtropical migration rate was faster than the temperate migration rate, contradicting predictions under the hypothesis of a sprint-to-the-finish strategy. In contrast to our results, the pied flycatcher displayed migration rate increases in the last portion of their migration (Briedis et al. 2018). Other studies report finding no change in migration rate along migration routes (*e.g.*, Nilsson et al. 2013). Varying degrees of geographic barriers or species-specific natural history may increase stopover needs at differing parts of spring migration (Alerstam 2011), thus inducing differing migration rates at different portions of migration. Moreover, the location of main stopovers within a migration may vary, for instance, in relation to migration barriers, and thereby influence migration rate. For example, we found that purple martin spring stopovers are mostly located before crossing the Gulf of Mexico. This is unlikely to have influenced our results regarding slower temperate rates, as these stopovers would be included in the southern portion of migration, thus slowing rates in this section. In their study, Briedis et al. (2018) exclude all stopover locations associated with the

Sahara Desert from their last migration leg, thus overrepresenting stopovers in the first portion of their migration and relatively increasing the temperate migration rate. Further research on how distance to the breeding site influences rate in the presence of environmental factors such as daylength may be needed to properly investigate the sprint to the finish hypothesis.

Daylength

As predicted, our findings indicate that longer average daylength increased the temperate migration rate, as expected for a diurnal migrant that must fly and forage within daylight hours (Alerstam 2009; Shave et al. 2019). Daylength did not influence the subtropical migration rate, although at these latitudes daylength varies little as compared to more northern latitudes. Direct tracking of osprey (*Pandion haliaetus*) and white stork (*Ciconia Ciconia*), two diurnal migrants, found them to combine foraging and migration by allocating daylight hours to forage before or after active migration (Berthold et al. 2001; Klaassen et al. 2008). However, the effect of daylength on migrating passerines had not yet been studied. Since temperature was collinear with daylength, it is not possible to conclude the influence of daylength on migration rate. However, future studies looking at how daily flight distances may be predicted by daylength while considering the intrinsic and other environmental factors at play may be best to estimate the effect of daylength on migration pace and strategy.

Conclusion and implications

The purple martin, like other aerial insectivores, has exhibited population declines in recent years (Sauer et al. 2017; Rosenberg et al. 2019). For its conservation, it is imperative to better understand how various environmental factors can help or impede this migrating species

as it tackles a changing environment. Overall, our results show that intrinsic factors of departure date and destination have the largest influence on migration rate and arrival dates, with little influence of en route environmental factors. This suggests that these migratory birds may be under selective pressure to depart earlier from wintering grounds to remain synchronized with advancing springs with climate change and that changes in migration rate are unlikely to have a strong influence on arrival timing, as has been suggested in recent studies (Schmaljohann and Both 2017). We also found unexpected sex-specific migration strategies, where females migrated faster and arrived earlier than males (protogyny), which could be explored further in future studies. We did not find support for the sprint-to-the-finish hypothesis, where rates of travel increase near breeding sites. As stopover duration was found to play an important role migration rate, further studies should investigate how environmental factors may influence stopover duration, to further our understanding of how climate change may influence migration timing.

References

- Abdulle, S.A., and Fraser, K.C. 2018. Does wind speed and direction influence timing and route of a trans-hemispheric migratory songbird (purple martin) at a migration barrier? *Anim. Migr.* **5**(1): 49–58. Walter de Gruyter GmbH. doi:10.1515/ami-2018-0005.
- Åkesson, S., and Bianco, G. 2021. Wind-assisted sprint migration in northern swifts. *iScience* **24**(6). Elsevier Inc. doi:10.1016/j.isci.2021.102474.
- Alerstam, T. 2003. Bird Migration Speed. *In Avian Migration. Edited by P. Berthold, E. Gwinner, and E. Sonnenschein.* Springer Berlin Heidelberg, Berlin, Heidelberg. pp. 253–267. doi:10.1007/978-3-662-05957-9_17.
- Alerstam, T. 2006. Strategies for the transition to breeding in time-selected bird migration. *Ardea* **94**(3): 347–357.
- Alerstam, T. 2009. Flight by night or day? Optimal daily timing of bird migration. *J. Theor. Biol.* **258**(4): 530–536. doi:10.1016/j.jtbi.2009.01.020.
- Alerstam, T. 2011. Optimal bird migration revisited. *J. Ornithol.* **152**(S1): 5–23. Springer Verlag. doi:10.1007/s10336-011-0694-1.
- Beauchamp, A.T., Guglielmo, C.G., and Morbey, Y.E. 2020. Stopover refuelling, movement and departure decisions in the white-throated sparrow: The influence of intrinsic and extrinsic factors during spring migration. *J Anim Ecol* **89**: 2553–2566. doi:10.1111/1365-2656.13315.
- Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., and Wood, E.F. 2018.

- Present and future köppen-geiger climate classification maps at 1-km resolution. *Sci. Data* **5**. doi:10.1038/sdata.2018.214.
- Berthold, P. 1996. Circadian and Circannual Rhythms. *In* Control of Bird Migration, 1st edition. Springer Netherlands.
- Berthold, P., BOSSCHE, W. VAN DEN, FIEDLER, W., KAATZ, C., KAATZ, M., LESHEM, Y., NOWAK, E., and QUERNER, U. 2001. Detection of a new important staging and wintering area of the White Stork *Ciconia ciconia* by satellite tracking. *Ibis* (Lond. 1859). **143**(4): 450–455. doi:10.1111/j.1474-919X.2001.tb04946.x.
- Bonamour, S., Chevin, L.M., Charmantier, A., and Teplitsky, C. 2019. Phenotypic plasticity in response to climate change: The importance of cue variation. *Philos. Trans. R. Soc. B Biol. Sci.* **374**(1768). doi:10.1098/rstb.2018.0178.
- Both, C. 2010. Flexibility of Timing of Avian Migration to Climate Change Masked by Environmental Constraints En Route. *Curr. Biol.* **20**(3): 243–248. doi:10.1016/j.cub.2009.11.074.
- Both, C., Bouwhuis, S., Lessells, C.M., and Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* **441**(7089): 81–83. Nature Publishing Group. doi:10.1038/nature04539.
- Both, C., and Visser, M.E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**(6835): 296–298. doi:10.1038/35077063.
- Briedis, M., Hahn, S., Krist, M., and Adamík, P. 2018. Finish with a sprint: Evidence for time-

selected last leg of migration in a long-distance migratory songbird. *Ecol. Evol.* **8**(14): 6899–6908. John Wiley and Sons Ltd. doi:10.1002/ece3.4206.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., and Bolker, B.M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**(2): 378–400. doi:10.32614/rj-2017-066.

Brown, C.R. 1976. Minimum temperature for feeding by Purple Martins. *Wilson Bull.* **88**(4): 672–673.

Brown, C.R., Airola, D.A., and Tarof, S. 2021. Purple Martin (*Progne subis*). *In* *Birds of the World*. Edited by P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.purmar.02.

Bryant, D.M. 2008. Heat stress in tropical birds: behavioural thermoregulation during flight. *Ibis* (Lond. 1859). **125**(3): 313–323. doi:10.1111/j.1474-919X.1983.tb03117.x.

Conklin, J.R., Lisovski, S., and Battley, P.F. 2021. Advancement in long-distance bird migration through individual plasticity in departure. *Nat. Commun.* **12**(1). doi:10.1038/s41467-021-25022-7.

Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S.C., Kays, R., Douglas, D., Cruz, S., Han, J., Brandes, D., and Wikelski, M. 2013. The environmental-data automated track annotation (Env-DATA) system: Linking animal tracks with environmental data. *Mov. Ecol.* **1**(1). BioMed Central Ltd. doi:10.1186/2051-3933-1-3.

- Van Doren, B.M., and Horton, K.G. 2018. A continental system for forecasting bird migration. *Science* (80-.). **361**(6407): 1115–1118. American Association for the Advancement of Science. doi:10.1126/science.aat7526.
- Forsythe, W.C., Rykiel, E.J., Stahl, R.S., Wu, H. i., and Schoolfield, R.M. 1995. A model comparison for daylength as a function of latitude and day of year. *Ecol. Modell.* **80**(1): 87–95. doi:10.1016/0304-3800(94)00034-F.
- Fraser, K.C., Shave, A., de Greef, E., Siegrist, J., and Garroway, C.J. 2019. Individual Variability in Migration Timing Can Explain Long-Term, Population-Level Advances in a Songbird. *Front. Ecol. Evol.* **7**. Frontiers Media S.A. doi:10.3389/fevo.2019.00324.
- Fraser, K.C., Stutchbury, B.J.M., Silverio, C., Kramer, P.M., Barrow, J., Newstead, D., Mickle, N., Cousens, B.F., Lee, J.C., Morrison, D.M., Shaheen, T., Mammenga, P., Applegate, K., and Tautin, J. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proc. R. Soc. B Biol. Sci.* **279**(1749): 4901–4906. doi:10.1098/rspb.2012.2207.
- Galtbalt, B., Batbayar, N., Sukhbaatar, T., Vorneweg, B., Heine, G., Müller, U., Wikelski, M., and Klaassen, M. 2022. Differences in on-ground and aloft conditions explain seasonally different migration paths in Demoiselle crane. *Mov. Ecol.* **10**(1). BioMed Central Ltd. doi:10.1186/s40462-022-00302-z.
- González, A.M., Bayly, N.J., and Hobson, K.A. 2020. Earlier and slower or later and faster: Spring migration pace linked to departure time in a Neotropical migrant songbird. *J. Anim. Ecol.* **89**(12): 2840–2851. Blackwell Publishing Ltd. doi:10.1111/1365-2656.13359.

- Haest, B., Hüppop, O., and Bairlein, F. 2020. Weather at the winter and stopover areas determines spring migration onset, progress, and advancements in Afro-Palearctic migrant birds. *Proc. Natl. Acad. Sci. U. S. A.* **117**(29): 17056–17062. doi:10.1073/pnas.1920448117.
- Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers, D., Simmons, A., Soci, C., Abdalla, S., Abellan, X., Balsamo, G., Bechtold, P., Biavati, G., Bidlot, J., Bonavita, M., De Chiara, G., Dahlgren, P., Dee, D., Diamantakis, M., Dragani, R., Flemming, J., Forbes, R., Fuentes, M., Geer, A., Haimberger, L., Healy, S., Hogan, R.J., Hólm, E., Janisková, M., Keeley, S., Laloyaux, P., Lopez, P., Lupu, C., Radnoti, G., de Rosnay, P., Rozum, I., Vamborg, F., Villaume, S., and Thépaut, J.N. 2020. The ERA5 global reanalysis. *Q. J. R. Meteorol. Soc.* **146**(730): 1999–2049. doi:10.1002/qj.3803.
- Klaassen, R.H.G., Strandberg, R., Hake, M., and Alerstam, T. 2008. Flexibility in daily travel routines causes regional variation in bird migration speed. *Behav. Ecol. Sociobiol.* **62**(9): 1427–1432. doi:10.1007/s00265-008-0572-x.
- Kokko, H. 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.* **68**(5): 940–950. doi:10.1046/j.1365-2656.1999.00343.x.
- Lavallée, C.D., Assadi, S.B., Korpach, A.M., Ray, J.D., Fischer, J.D., Siegrist, J., and Fraser, K.C. 2021. The use of nocturnal flights for barrier crossing in a diurnally migrating songbird. *Mov. Ecol.* **9**(1). BioMed Central Ltd. doi:10.1186/s40462-021-00257-7.
- Lisovski, S., and Hahn, S. 2012. GeoLight-processing and analysing light-based geolocator data

in R. doi:10.1111/j.2041-210X.2012.00248.x.

Lomas Vega, M., Fransson, T., and Kullberg, C. 2021. The effects of four decades of climate change on the breeding ecology of an avian sentinel species across a 1,500-km latitudinal gradient are stronger at high latitudes. *Ecol. Evol.* **11**: 6233. doi:10.1002/ece3.7459.

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., and Makowski, D. 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *J. Open Source Softw.* **6**(60): 3139. doi:10.21105/joss.03139.

Mayor, S.J., Guralnick, R.P., Tingley, M.W., Otegui, J., Withey, J.C., Elmendorf, S.C., Andrew, M.E., Leyk, S., Pearse, I.S., and Schneider, D.C. 2017. Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Sci. Rep.* **7**(1). Nature Publishing Group. doi:10.1038/s41598-017-02045-z.

McKellar, A.E., Marra, P.P., Hannon, S.J., Studds, C.E., and Ratcliffe, L.M. 2013. Winter rainfall predicts phenology in widely separated populations of a migrant songbird. *Oecologia* **172**(2): 595–605. doi:10.1007/s00442-012-2520-8.

McKinnon, E.A., Fraser, K.C., and Stutchbury, B.J.M. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. *Auk* **130**(2): 211–222. doi:10.1525/auk.2013.12226.

McKinnon, E.A., and Love, O.P. 2018. Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. doi:10.1642/AUK-17-202.1.

Mills, A.M. 2005. Protogyny in Autumn Migration: Do Male Birds "Play Chicken"? *Auk*

122(1): 71–81. doi:10.1093/auk/122.1.71.

Montgomery, D.C. & Peck, E.A. 1992. *Introduction to Linear Regression Analysis*. Wiley, New York.

Morton, E.S., and Derrickson, K.C. 1990. The Biological Significance of Age-Specific Return Schedules in Breeding Purple Martins. *Condor* **92**(4): 1040–1050.

Neufeld, L.R., Muthukumarana, S., Fischer, J.D., Ray, J.D., Siegrist, J., and Fraser, K.C. 2021. Breeding latitude is associated with the timing of nesting and migration around the annual calendar among Purple Martin (*Progne subis*) populations. *J. Ornithol.* **162**(4): 1009–1024. Springer Science and Business Media Deutschland GmbH. doi:10.1007/s10336-021-01894-w.

Nilsson, C., Klaassen, R.H.G., and Alerstam, T. 2013. Differences in Speed and Duration of Bird Migration between Spring and Autumn. *Am. Nat.* **181**(6): 837–845. doi:10.5061/dryad.82d4q.

Nilsson, J.-Å., Brönmark, C., Hansson, L.-A., and Chapman, B.B. 2014. Individuality in movement: the role of animal personality. *In Animal Movement Across Scales. Edited by L.-A. Hansson and S. Akesson*. OUP Oxford, Oxford, England. doi:10.10910.1093/acprof:oso/9780199677184.003.0006.

Oring, L.W., and Lank, D.B. 1982. Sexual selection, arrival times, philopatry and site fidelity in the polyandrous spotted sandpiper. *Behav. Ecol. Sociobiol.* **10**(3): 185–191. doi:10.1007/BF00299684.

- Pokrovsky, I., Kölzsch, A., Sherub, S., Fiedler, W., Glazov, P., Kulikova, O., Wikelski, M., and Flack, A. 2021. Longer days enable higher diurnal activity for migratory birds. *J. Anim. Ecol.* **90**(9): 2161–2171. doi:10.1111/1365-2656.13484.
- Pyle, P. 1997. *Identification Guide to North American Birds: Columbidae to Ploceidae*. Slate Creek Press, Bolinas, Calif.
- Rakhimberdiev, E., Saveliev, A., Piersma, T., and Karagicheva, J. 2017, November 1. FLIGHTR: an R package for reconstructing animal paths from solar geolocation loggers. *British Ecological Society*. doi:10.1111/2041-210X.12765.
- Reynolds, J.D., Colwell, M.A., and Cooke, F. 1986. Sexual selection and spring arrival times of red-necked and Wilson's phalaropes. *Behav. Ecol. Sociobiol.* **18**(4): 303–310. doi:10.1007/BF00300008.
- Rosenberg, K. V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., Stanton, J.C., Panjabi, A., Helft, L., Parr, M., and Marra, P.P. 2019. Decline of the North American avifauna. *Science* (80-.). **366**(6461): 120–124. American Association for the Advancement of Science. doi:10.1126/science.aaw1313.
- Sauer, J.R., Pardieck, K.L., Ziolkowski, D.J., Smith, A.C., Hudson, M.A.R., Rodriguez, V., Berlanga, H., Niven, D.K., and Link, W.A. 2017. The first 50 years of the North American Breeding Bird Survey. doi:10.1650/CONDOR-17-83.1.
- Schmaljohann, H. 2019. The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: A cross-continental analysis. *Mov. Ecol.* **7**(1). BioMed Central Ltd. doi:10.1186/s40462-019-0169-1.

- Schmaljohann, H., and Both, C. 2017. The limits of modifying migration speed to adjust to climate change. *Nat. Clim. Chang.* **7**(8): 573–576. Nature Publishing Group.
doi:10.1038/NCLIMATE3336.
- Shave, A., Garroway, C.J., Siegrist, J., and Fraser, K.C. 2019. Timing to temperature: Egg-laying dates respond to temperature and are under stronger selection at northern latitudes. *Ecosphere* **10**(12). Wiley-Blackwell. doi:10.1002/ecs2.2974.
- Tomotani, B.M., Gienapp, P., de la Hera, I., Terpstra, M., Pulido, F., and Visser, M.E. 2021. Integrating Causal and Evolutionary Analysis of Life-History Evolution: Arrival Date in a Long-Distant Migrant. *Front. Ecol. Evol.* **9**. Frontiers Media S.A.
doi:10.3389/fevo.2021.630823.
- Visser, M.E., and Gienapp, P. 2019. Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* **3**(6): 879–885. Nature Publishing Group.
doi:10.1038/s41559-019-0880-8.
- Wikelski, M., Tarlow, E.M., Raim, A., Diehl, R.H., Larkin, R.P., and Visser, G.H. 2003. Costs of migration in free-flying songbirds. *Nature* **423**(6941): 704. Oxford Univ. Press.
doi:10.1038/423704a.
- Wotherspoon, S., Sumner, M., and Lisovski, S. 2016. BASTag: Basic data processing for light based geolocation archival tags. R package version 0.1.3.
- Zuur, A.F., Ieno, E.N., and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**(1): 3–14. doi:10.1111/j.2041-210x.2009.00001.x.

Tables and figures

Table 2. 1 Result summary of generalized linear mixed model (GLMM) migration strategy and en route weather experienced over overall spring migration rate of purple martins

Fixed effects	Estimate	Lower 95% confidence interval	Higher 95% confidence interval
Stopover proportion	-265.285	-327.747	-202.823
TY (comp. to ATY)	-3.210	-23.036	16.615
Male (comp. to female)	-2.871	- 17.776	12.034
Departure date (days)	0.822	0.168	1.476
Average temperature (°C)	-2.922	-7.976	2.132
Average wind (m/s)	10.676	2.363	18.988
Average precipitation (mm)	-63.027	-110.692	-15.363
Mid interior region *	-14.630	-40.593	11.332
Mid coastal region *	-12.178	-42.534	18.178
Low interior region *	6.455	-36.827	49.737
Low coastal region *	-53.141	-104.714	-1.568
Lowest region *	-3.410	-61.893	55.074
Random effects	Variance	Standard deviation	% of variation
Year deployed	449	21.19	9.92
Residual	4077	63.86	90.08
Total variance	4526		
GLMM R ²			
Marginal R ²	0.405		
Conditional R ²	0.464		

*Region compared to the reference group of the highest region

Table 2. 2 Result summary of the generalized linear mixed model (GLMM) of the migration strategy and en route weather experienced over the timing of spring arrival of purple martins to their breeding colonies

Fixed effect	Estimate	Lower 95% confidence interval	Higher 95% confidence interval
Migration rate (km/day)	-0.067	-0.071	-0.062
Third-year birds (comp. to ATY)	0.907	-0.118	1.932
Male (comp. to female)	1.483	0.666	2.299
Departure date (days)	0.974	0.940	1.008
Average temperature (°C)	0.242	-0.016	0.500
Average wind (m/s)	-0.417	-0.863	0.029
Average precipitation (mm)	2.317	-0.229	4.864
Mid interior region *	-5.087	-6.315	-3.858
Mid coastal region *	-6.659	-8.155	-5.162
Low interior region *	-8.196	-10.462	-5.930
Low coastal region *	-4.968	-7.666	-2.270
Lowest region *	-12.821	-15.847	-9.795
Random effects	Variance	Standard deviation	% of variation
Individuals	5.725	2.393	48.0
Year deployed	0.118	0.343	1.0
Residual	6.083	2.466	51.0
Total variance	11.926		
GLMM R ²			
Marginal R ²	0.988		
Conditional R ²	0.994		

*Region compared to the reference group of the highest region

Table 2. 3 Result summary of generalized linear mixed models (GLMM) for the log of spring subtropical and temperate migration rate of purple martin migration.

Overall subtropical versus temperate model			
Fixed effects	Estimate	Lower 95% confidence interval	Higher 95% confidence interval
Temperate (comp. to subtropical)	-0.157	-0.286	-0.029
TY (comp. to ATY)	-0.038	-0.116	0.041
Male (comp. to female)	-0.032	-0.092	0.028
Departure date (days)	0.004	0.002	0.007
Average temperature (°C)	-0.010	-0.025	0.005
Average wind (m/s)	0.033	0.016	0.050
Average precipitation (mm)	-0.038	-0.178	0.103
Mid interior region *	-0.087	-0.186	0.012
Mid coastal region *	-0.019	-0.135	0.098
Low interior region *	-0.040	-0.211	0.131
Low coastal region *	-0.220	-0.427	-0.012
Lowest region *	-0.011	-0.240	0.217
Random effects	Variance	Standard deviation	% of variation
Year deployed	0.0042	0.0646	3.19
Residual	0.1273	0.3568	96.81
Total variance	0.1315		
GLMM R²			
Marginal R ²	0.158		
Conditional R ²	0.185		

Subtropic migration portion only – Relatively controlled daylength and temperature

Fixed effects	Estimate	Lower 95% confidence interval	Higher 95% confidence interval
TY (comp. to ATY)	0.002	-0.093	0.097
Male (comp. to female)	0.032	-0.041	0.105
Average daylength (hours)	-0.057	-0.303	0.189
Average temperature (°C)	-0.054	-0.088	-0.019
Average wind (m/s)	0.027	-0.005	0.060
Average precipitation (mm)	-0.132	-0.321	0.057
Mid interior region *	-0.073	-0.176	0.030
Mid coastal region *	-0.144	-0.267	-0.021
Low interior region *	-0.103	-0.284	0.078
Low coastal region *	-0.624	-0.839	-0.410
Lowest region *	-0.382	-0.606	-0.158
Random effects	Variance	Standard deviation	% of variation
Year deployed	0.0007	0.0267	0.71
Residual	0.0979	0.3129	99.29
Total variance	0.0986		
GLMM R ²			
Marginal R ²	0.179		
Conditional R ²	0.185		

Temperate migration portion only – Daylength and temperature varying with date and latitude

Fixed effects	Estimate	Lower 95% confidence interval	Higher 95% confidence interval
TY (comp. to ATY)	-0.074	-0.199	0.052
Male (comp. to female)	-0.130	-0.226	-0.034
Average daylength (hours)	0.149	-0.021	0.276
Average temperature (°C)	0.000	-0.020	0.020
Average wind (m/s)	0.031	0.009	0.054
Average precipitation (mm)	-0.048	-0.269	0.172
Mid interior region *	-0.093	-0.276	0.091
Mid coastal region *	0.084	-0.137	0.304
Low interior region *	-0.094	-0.407	0.218
Low coastal region *	-0.107	-0.457	0.243
Lowest region *	-0.062	-0.463	0.339
Random effects	Variance	Standard deviation	% of variation
Year deployed	0.0071	0.08418	4.30
Residual	0.1580	0.39747	95.70
Total variance	0.1651		
GLMM R ²			
Marginal R ²	0.195		
Conditional R ²	0.229		

*Region compared to the reference group of the highest region

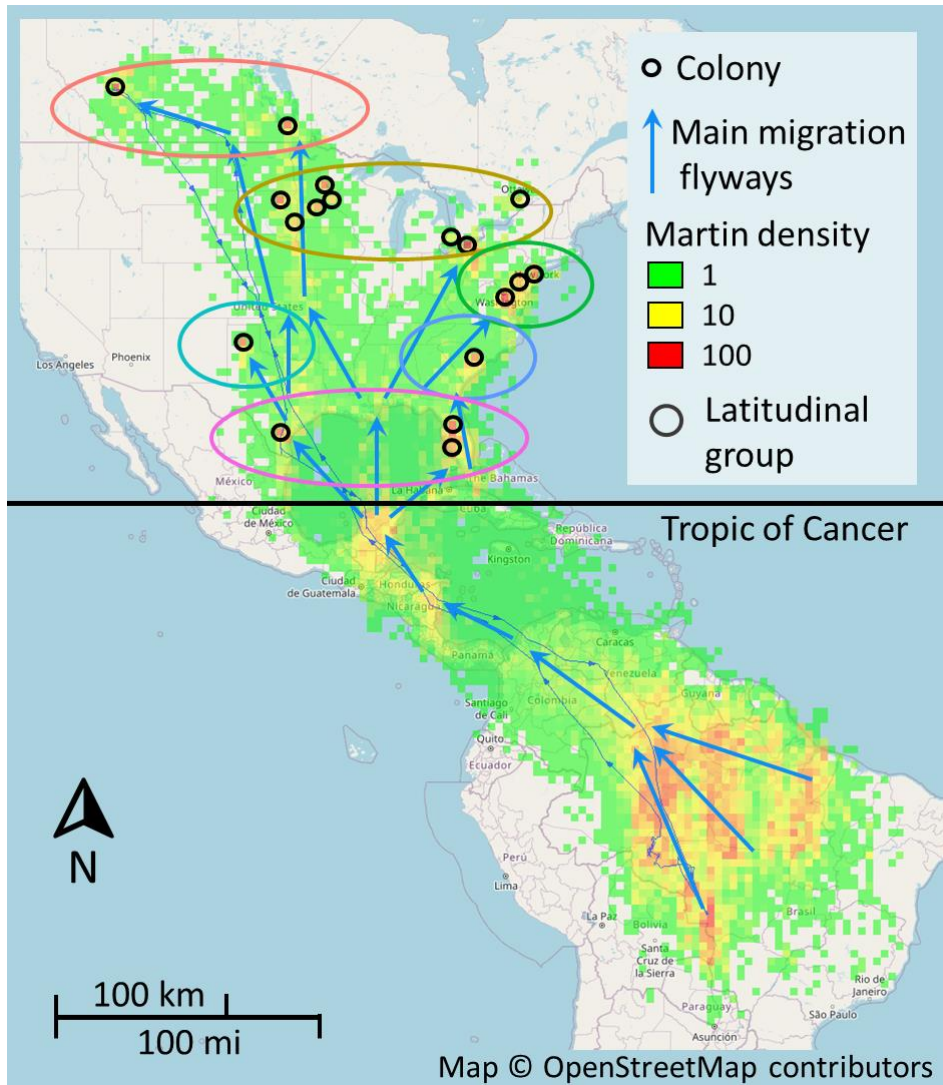


Figure 2. 1 Map of breeding colonies sampled in study with their respective latitudinal groups, with animal density and main spring migration flyways.

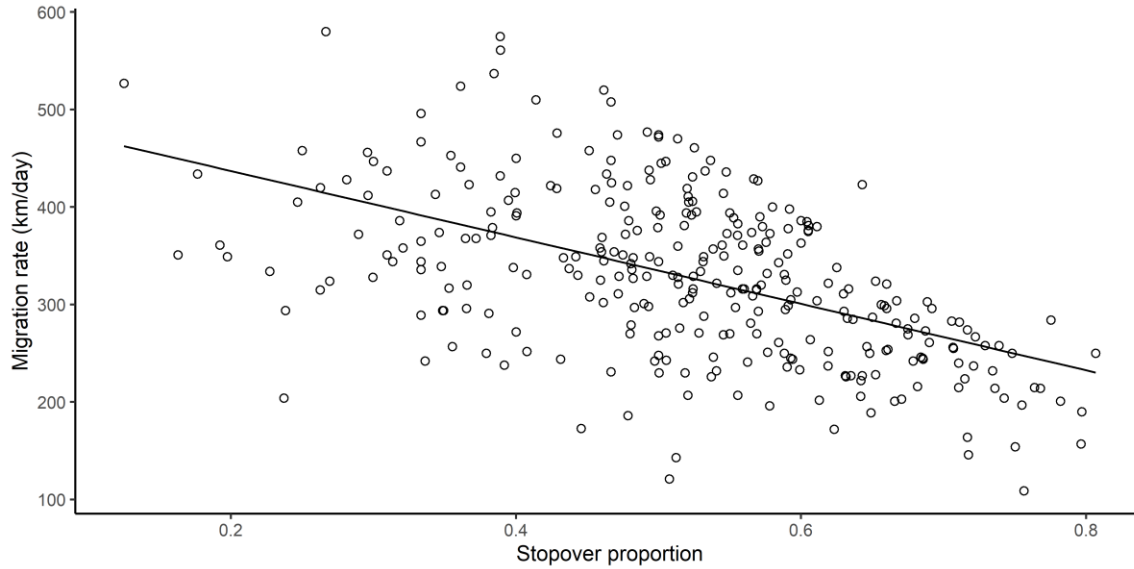


Figure 2. 2 Linear correlation between the total duration of spring stopover duration and resulting migration rate in purple martins.

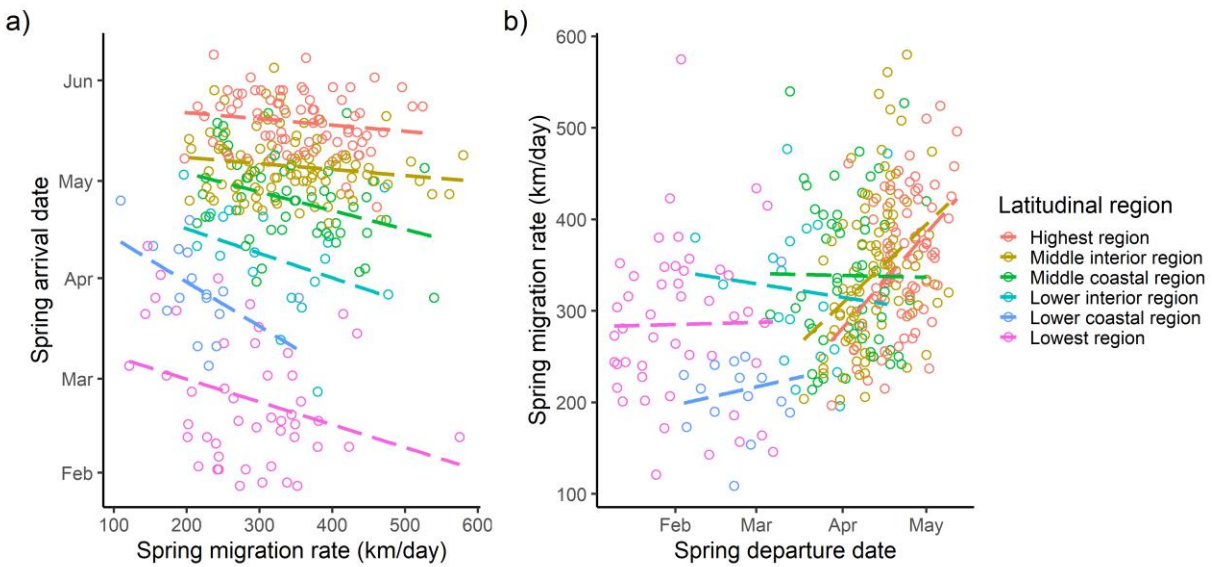


Figure 2. 3 Latitudinal destination (a) and departure date (b) drives most of the variation in spring migration rate in purple martins. Birds arriving earlier at their breeding site (a) or departing later exhibit a faster rate during migration (b). Coloured open circles represent individual timing and rate data derived through direct tracking by using light-level geolocators.

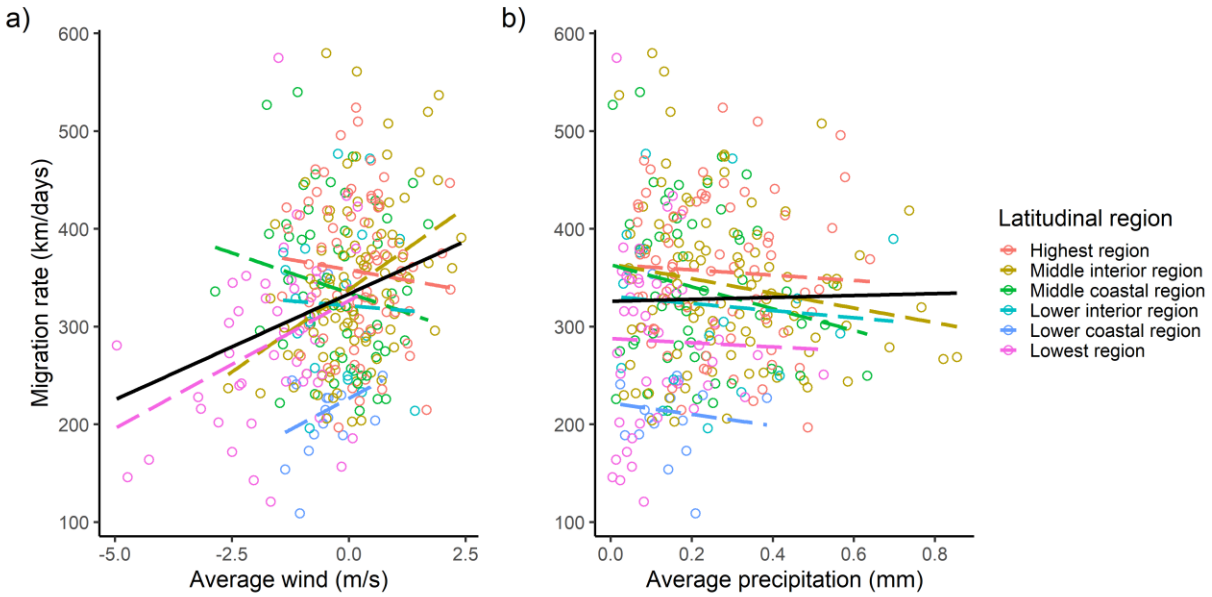


Figure 2. 4 Correlation of spring migration rate with average en route (a) wind and (b) precipitation in purple martins.

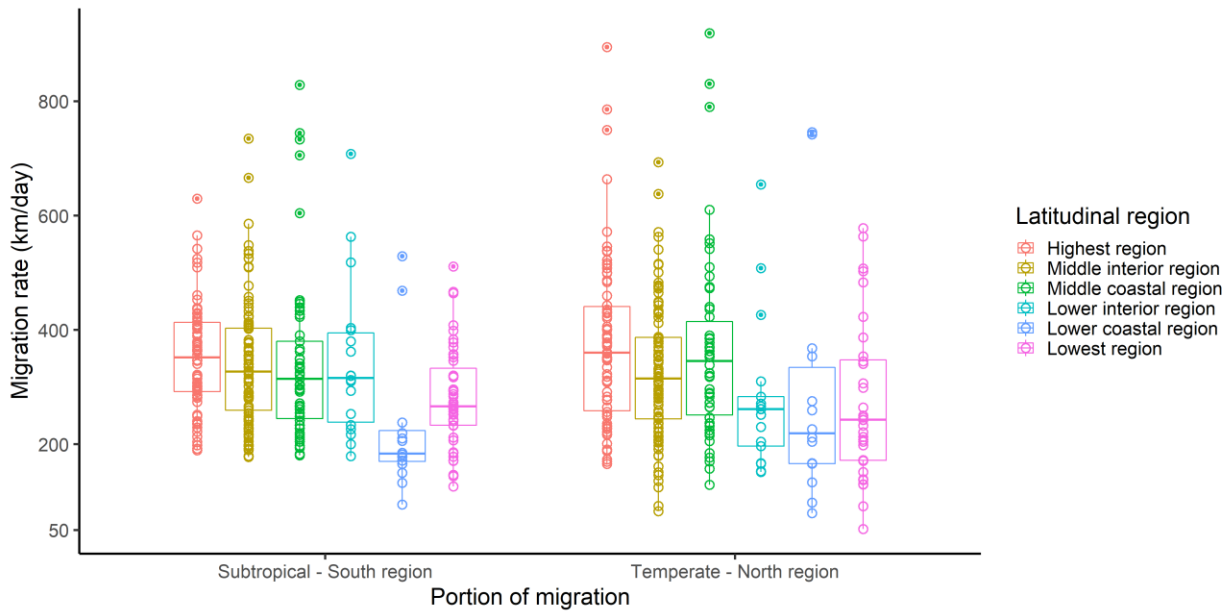
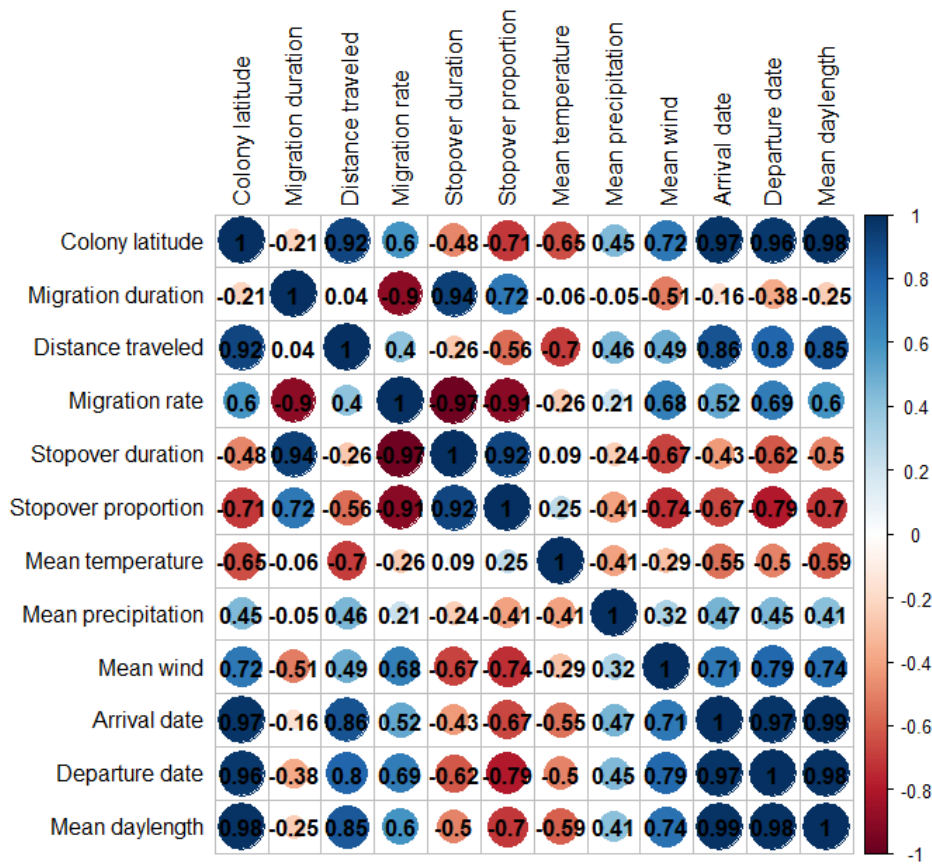


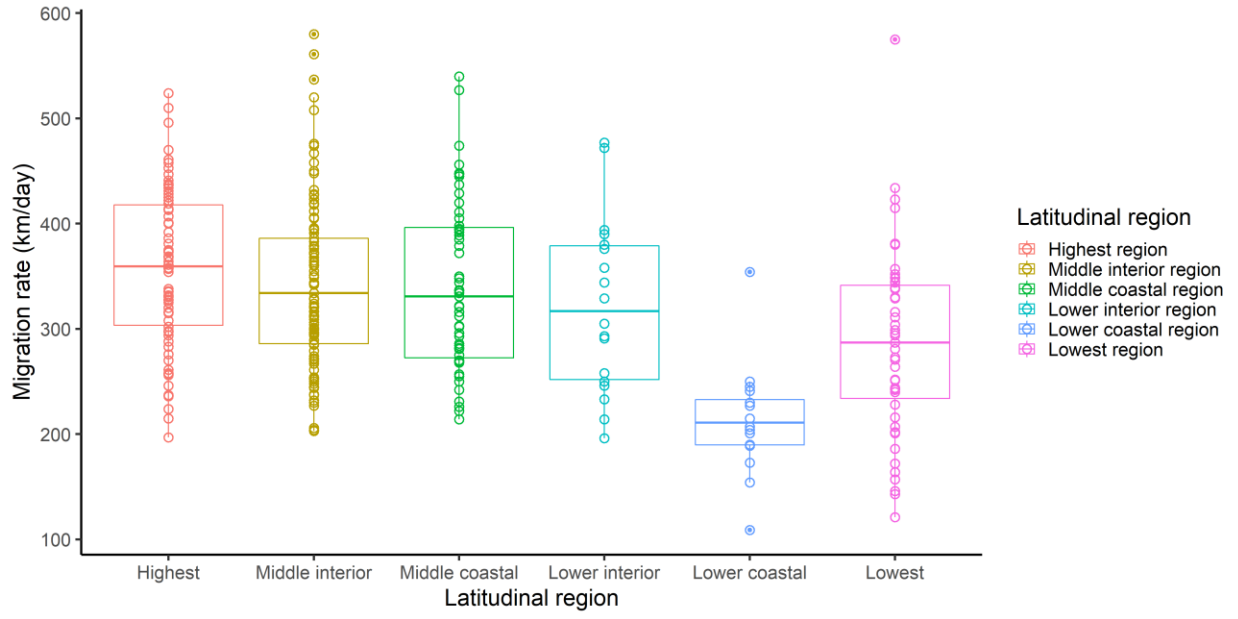
Figure 2. 5 Subtropical and temperate migration rate variation by latitudinal region, shows statistical outliers which were included in subtropical and temperate migration models.

Supplemental Table 2. 1 Geolocator purple martin spring migration summary by latitudinal groups.

Latitudinal region	Highest	Mid interior	Mid coastal	Low interior	Low coastal	Lowest	Overall	
n	74	97	55	18	16	47	307	
Males	33	39	28	9	9	24	142	
Females	41	55	25	9	7	23	160	
ATY	57	77	39	16	16	44	249	
TY	17	18	16	2	0	3	56	
Departure date	Maximum	12 May	9 May	1 May	17 Apr.	18 Mar.	7 Mar.	12 May
	Average	22 Apr.	12 Apr.	3 Apr.	15 Mar.	24 Feb.	2 Feb.	29 Mar.
	Minimum	28 Mar.	18 Mar.	6 Mar.	8 Feb.	4 Feb.	10 Jan.	10 Jan.
Arrival date	Maximum	9 Jun.	5 Jun.	22 May	3 May	25 Apr.	11 Apr.	9 Jun.
	Average	19 May	5 May	25 Apr.	7 Apr.	29 Mar.	23 Feb.	22 Apr.
	Minimum	23 Apr.	18 Apr.	26 Mar.	26 Feb.	5 Mar.	28 Jan.	28 Jan.
Migration rate (km/day)	Maximum	524	580	540	477	354	575	580
	Average	356.3	342.2	338.6	322.6	213.5	285.3	328.4
	Minimum	197	203	214	196	109	121	109
Stopover duration (days)	Maximum	30.95	29.5	22.47	19.87	46.89	25.11	46.89
	Average	13.55	11.7	11.68	13.82	21.45	11.87	12.75
	Minimum	3.18	2.77	1.5	5.13	7.5	3.5	1.5



Supplemental Figure 2. 1 Pearson correlation plot of all independent variables.



Supplemental Figure 2. 2 Purple martin spring migration rate by latitudinal region.

Chapter 3. Influence of the environment and parental investment on roosting behaviour in nesting swallows

Abstract

The purple martin (*Progne subis*), a declining colonial and aerial insectivore, is known for its large fall migratory and wintering communal roosts. However, little is known of the actual start timing of these roosts. Incidental and historical observations support that purple martin may roost away from their breeding colony at night during the active breeding season, a newly described behaviour in a related species, the bank swallow (*Riparia riparia*), where parents occasionally roost communally in wetlands. Our objectives were to verify the extent of roosting away from the nest during active breeding and to investigate the environmental, morphological, and nest-specific factors that may influence this behaviour in purple martins. Using radio telemetry, we monitored 25 adult martins at three breeding colonies located in central Canada during the active breeding season (July-August). We found evidence of nocturnal roosting away from the breeding colony (over 1.5 km away) for parents (21 of 25 birds) with active nests with nestlings, with, on average, parents leaving the breeding colony 70% of nights. Roosting at the nest may be influenced by the thermoregulatory needs of nestlings, as we found that colder evening temperatures increased the likelihood of parents passing the night at their colony. We also found that larger broods increased the odds the parents remained at the colony at night, suggesting roosting in the nest may be associated with a higher parental investment with more nestlings to feed or defend. We did not find that roosting away was influenced by the sex of the parent nor by nestling age. Further research on roosting behaviour during the breeding season could focus on movement to and from the roost to better understand roost formation, location,

timing, and size. Roosting sites during the breeding season may be part of the critical habitat required by purple martins and fully understanding the ecology of decreasing species is key for their conservation.

Introduction

Animals forming large gatherings are of common occurrence in the wild, although they have been only observed in certain species and groups (*e.g.*, primates, fish, sakes, birds). These social groups evolved for benefits gained from the proximity with others, in rare cases reaching altruism (Beauchamp 1999). Such communal gatherings can be for a variety of social behaviours, including accessing resources of limited availability, herding, mating, hibernation, and roosting. Swallows in the family Hirundinidae are known to form large nocturnal roosts forming post-breeding in fall and at their wintering ranges (Bridge et al. 2016; Brown et al. 2021). These nocturnal roosts are a gathering of usually a single species which form in the hour before sunset at a single location where birds pass the night and disperse in the hour preceding daybreak (Bridge et al. 2016; Brown et al. 2021). Roosts can be quite large, occasionally reaching over several hundred thousand individuals, with birds travelling up to 80 kilometres to reach their roost (Russell and Gauthreaux 1999; Brown et al. 2021; Lalla et al. in revision). Studying the temporal and spatial dynamics of large post-breeding and migratory roosts has been facilitated by remote sensing using weather surveillance radars (Bridge et al. 2016). Roosting locations in migration are used for periods of several days to weeks and can coincide with migratory stopovers (Russell and Gauthreaux 1999; Bridge et al. 2016). Swallow roosts sites

occur in a multitude of habitats, ranging from agricultural lands, forests, wetlands, and urban areas (Bridge et al. 2016; Brown et al. 2021).

While this gregarious behaviour has drawbacks (*e.g.*, increased visibility to predators, disease spread, intraspecific competition), the benefits are multiple (Beauchamp 1999). Communal roosting behaviour may arise to mitigate energetic and thermoregulatory demands (Beauchamp 1999). For example, prolonged cold snaps drove migrating tree swallows (*Tachycineta bicolor*) to roost in large numbers in small nests cavities, likely to mitigate energy losses (Stutchbury and Robertson 1990). By perching toward the center of a roost, long-tailed tits (*Aegithalos caudatus*) can minimize energy loss during colder nights (Hatchwell et al. 2009). Having numerous birds at one roost will also provide safety in numbers. Larger flocks lower the likelihood of predation as predators are more readily spotted and may be confused by too numerous prey (Beauchamp 1999). Finally, although still debated with some supporting research on hooded crows (*Corvus corone*) (Sonerud et al. 2001), large roosts are hypothesized to act as information centers where crucial information such as favourable foraging areas is shared amongst individuals (Ward and Zahavi 1973).

These advantages could be conferred to roosting birds in all seasons, but most evidence for communal roosting in Hirundinidae is during the post-breeding and over-wintering periods. Emerging evidence suggests that communal roosting behaviour may also occur during the breeding season while adult birds have active nests. In a species known for its large migratory roosts, the bank swallow (*Riparia riparia*), two studies detailed the behaviour of breeding adults leaving their nesting colony during the night to roost in nearby rural areas and marshes (Falconer et al. 2016; Saldanha et al. 2019), and recorded night travels up to 30 kilometres from their breeding colony (Falconer et al. 2016). A prominent behaviour in bank swallows, nocturnal

roosts occurred in tracked parents on about 70% of nights (Saldanha et al. 2019), although there was high individual variation in the extent of the behaviour (Falconer et al. 2016). From their results, Saldanha et al. (2019) hypothesized that the timing of bank swallow communal roosting during the nesting period appeared to follow the thermoregulatory needs of the offspring based on nest characteristics (*e.g.*, nestling age, brood size) and relative humidity. They also suggested that these roosting behaviours may help to reduce predation risk for roosting adults (both at the colony and the roost), avoid high parasite loads in nests, and optimize foraging efficiency where roost locations may be near optimal foraging locations. All of these remain to be tested further in bank swallow and other Hirundinidae.

Purple martins (*Progne subis*) are a long-distance migratory swallow that are experiencing population declines in the extremities of their breeding range (Sauer et al. 2017), and as such, it becomes increasingly important to investigate undocumented behaviours and their underlying causes. Like other swallows, martins commonly roost in large numbers post-breeding (Brown et al. 2021). In purple martins, communal migratory roosts may occur in a multitude of habitats, ranging from agricultural lands, forests, to urban areas. About half of these roosting sites may be used repetitively in subsequent years, with birds having greater site fidelity for roosts in urban areas and those surrounded by water (Bridge et al. 2016). More persistent roosts in more island-like habitats may be influenced by the reduction in predation level, as these sites may be more difficult for predators to access (Fournier et al. 2019), which may also be the case for urban roosts. This social behaviour extends to their wintering range in Brazil where purple martins overwinter in cities, forests, and wetlands (Fraser et al. 2012). However, like bank swallows (Falconer et al. 2016; Saldanha et al. 2019), they may also roost communally beginning within the breeding season. Incidental observations of *P. s. subis* (Fraser, pers. obs.)

and historical reports of *P. s. hesperia* (Cater 1944; Anderson and Anderson 1946) found breeding purple martins were absent from their breeding colony at night. Male purple martins were generally less present at their nest than females, although females may sleep outside of their nest cavity when nestlings reached 13 days old (Brown 1980). When absent from their nesting cavity, both parents were assumed to sleep in unoccupied cavities or nearby trees when not in the nest cavity (Brown 1980) but it is also possible that they travel further and/or joined communal roosts. Late-summer roosting sites (called post-breeding or pre-migratory roosts) have been observed in purple martins, but have been assumed to only be formed of fledged and non-breeding adults (Morton and Patterson 1983; Russell and Gauthreaux 1999). However, the extent, timing of formation, destination, and causes of nocturnal departures while parental birds have active nests have yet to be investigated in purple martins. Identifying the underlying causes of breeding roosting behaviour and the location of roosting sites away from the breeding colony during the active breeding season may be important as they are likely part of the habitat requirements of these colonial species (Saldanha et al. 2019).

The objective of this study was to investigate the extent of roosting away from the nest cavity and/or the breeding colony during active parental care in purple martins. We also sought to examine the influence of environmental variation (*e.g.*, weather), sex of the parent, and nest characteristics on purple martin decisions to roost at or away from their breeding colony. We predicted adult purple martins to remain in the breeding colony at night based on the thermoregulatory needs of their nestlings (Saldanha et al. 2019), staying when nestlings are younger, less numerous in a nest, and during cooler ambient temperatures. Based on prior observations (Brown 1980; Saldanha et al. 2019) and higher investment in offspring for females

(Stutchbury and Morton 1995; Kokko and Jennions 2008), we predicted females would roost away from their nest cavities less often than males.

Methods

In the summer of 2021, we monitored three colonies of purple martins (*P. s. subis*) in Southern Manitoba (Figure 3.1 for map). The sites were: Oak Hammock Marsh (OHM; 50.17, -97.13; large marsh bordered by open farmland and short grass prairie), which had two martin nest boxes supporting 15 martin breeding pairs, FortWhyte Alive (FWA; 49.82, -97.23; a forested park with large artificial ponds situated in a semi-urban area), which had two martin nest boxes supporting 25 breeding pairs, and a private residence in Howden (49.73, -97.13; semi-residential farmland with small marshes along the Red River), which had three martin nest boxes supporting 50 breeding pairs. All houses shared the same design with 14 available nest compartments in each, with 3-4 cavities stacked vertically and each stack facing in a different direction. Each colony was visited every other day for nest monitoring and trapping activities.

Adult purple martins were targeted for capture once their nestlings were aged 10 ± 2 days post-hatch between the 5th and 29th of July. Birds were trapped as they entered their nest cavities using drop door traps or by blocking the entrance with an extendable pole. The sex and age (second-year or after second-year) of each martin were determined using plumage characteristics (Pyle 1997). We tagged 44 purple martins (20 males and 24 females from 28 nests) with radiotelemetry nanotags using leg-loop harnesses made of polypropylene thread (Lotek NTQB2-4-2S; 0.90g without a harness and ~1.10g with, and Lotek NTQB2-3-2; 0.62g without a harness and ~0.75g with), with 8 tags deployed at OHM, 8 at FWA, and 28 at Howden. Tags were below

the recommended 5% of total bird body mass (Fair et al. 2010). All tags had a signalling frequency of 30 seconds, and their functionality was verified before their installation.

An automated radio-telemetry receiver station (Sensorgnome, with two Yagi 9 element and a J-pole -omnidirectional- antennas) as part of the Motus Wildlife Tracking System was installed at each study site to detect nanotag signals within a ~15km range (Taylor et al. 2017). Once radio tags were installed, colonies were visited every other night when tracked nests were active (from July 7th to August 12th) to determine the presence or absence of tagged adults using a hand-held radio receiver (Lotek SRX1200M) attached to a Yagi 3 Elements antenna.

The handheld antenna was used within 20 meters (OHM and Howden) or 500 to 1100 meters (FWA) away from martin houses where tagged birds had active nests (the estimated detection range of the antenna is around 1.5km based on detections from a fixed position around FWA). Visits occurred an hour after sunset (10:30 pm to 1:30 am CDT) to ensure that these diurnally active birds had made a roosting decision for the night and lasted >20 minutes. To ensure that trapping and tagging did not affect measured roosting behaviours, we delayed the first checks until >24 hours (*i.e.*, 2nd night) after capture. Night visits were made on the same day following a nest check, to ensure the number of nestlings matched adult presence data (where we assume these likely remained the same between daily nest check and nightly check and were confirmed at the subsequent nest check).

From the original 44 radio nanotags deployed, 19 individuals were excluded where their tags ceased to be detected by the automated receiver stations within 48 hours (before the first night visit) (n=16), where a tag was never detected by the automated receiver stations (n=1), where a tag prematurely fell off the bird at the colony grounds (n=1), or where a tag had

inconsistent signalling emissions suggesting a faulty tag (n=1). From the resulting 25 working tags, 7 worked for 4 days (providing the opportunity for 1 nightly check), and 10 tags worked for over a week (3 nightly checks each), with 4 tags remaining functional until nestlings fledged (14-23 days; supporting 6 - 9 nightly checks each). Overall, 25 tags carried by 12 males and 13 females (5 from OHM, 5 from FWA, and 15 from Howden) resulted in data from 83 nightly visits that could be used for further analysis.

To estimate how environmental factors experienced by parent purple martins may influence roosting behaviour, we used hourly ambient temperature and precipitation obtained from Environment and Climate Change Canada for the Winnipeg International Airport weather station using the `weathercan` R package (version 0.6.2; LaZerte and Albers 2018). The average, maximum, and minimum ambient temperature, and the total precipitation were measured in the interval of 17:00 and 05:00 CDT, to encapsulate the time of decision for leaving to roost in the evening, and the conditions during the night. Additionally, nest cavity temperature was monitored using temperature sensor dataloggers (iButtonLink DS1921G-F5#; hourly sampling $\pm 1^\circ\text{C}$ accuracy). The sensors were mounted above the nests, on the cavity wall opposite to the entrance to minimize air currents.

For our analyses, we used Generalized Linear Mixed-effects Model (GLMM) with `glmmTMB` (version 1.1.2.3; Brooks et al. 2017) (in R 4.1.2 and RStudio 2021.09.1+372) and a critical p-value of 5%. To investigate the relation between weather, morphological traits, and nest characteristics to the roosting behaviour of purple martins we used a GLMM with a binomial distribution and a logit link. Our response variable was the nocturnal presence (noted as 1) or absence (noted as 0) of tracked birds at their breeding colony, with absences being birds roosting elsewhere, at a presumed communal roosting site. As fixed effects, we used maximum

ambient temperature, which usually occurs before sunset and may better represent environmental conditions at the time when parents are making roosting decisions, and sex, as males and females have different levels of parental investments, which may impact levels of care and therefore roosting behaviour. We included the age of nestlings as a fixed effect, because of the prediction that changing thermoregulatory needs as birds age may influence roosting within or outside of the nest cavity, and brood size may change the in-nest environment and thermoregulatory input required of parents. We used individuals as a random effect to control for repeated measures and to consider the potential for individual (*i.e.*, personality) differences in roosting behaviour. Precipitation and parent age were not included in the model as rain occurred only once during the month-long study and there were only 4 second-year birds with the remainder being after-second year. While temperature was not collinear with other independent variables, both age of nestlings and the number of nestlings were inversely correlated (Suppl. Figure 3.1). Variance Inflation Factor (VIF) using the performance R package (version 0.8.0; Lüdtke et al. 2021) was used to verify the effect of collinearity in our models using a VIF threshold of 5 (Zuur et al. 2010). To estimate the error of the model and the contribution of the random effects to the model's variance, both the marginal and conditional coefficient of determination were measured using the theoretical R^2 (Nakagawa et al. 2017).

Results

Overall, parent purple martins on average roosted away from their nest 70% of the time, with lots of variation amongst individuals but not between sexes (Figure 3.2). Brood size varied between 1 to 6 with a median of 5, while nestling age in the sample varied between 9 to 30 days,

with a greater representation of younger birds (<19 days) due to tag failures (Suppl. Figure 3.2). Daily, maximum ambient temperature varied between 20.3°C to 33.4°C with the difference between maximum and minimum nightly temperatures varying from 6.5°C to 20.1°C (Suppl. Figure 3.3).

In our GLMM of the influence of weather, morphology, and nest characteristics on the presence of purple martins at their colony during the night, we found that both maximum ambient temperature and the number of nestlings had a significant effect on the choice of roosting at or away from the colony (Table 3.1). We found that with each degree increase in maximum ambient temperature, the odds of roosting at the colony decreased by 0.26 [0.41, 0.06], while for each additional nestling present in the nest, the odds of roosting at the colony increased by 1.72 [0.12, 5.60] (Figure 3.4, a, b). Neither the sex of the parent nor the age of nestlings had a significant impact on the odds of roosting in adult martins (Table 3.1; Figure 3.2), in contrast to predictions. The random effect of individual had a standard deviation of about 5.01. Our model accounted for 29.7 % of the variation without random effects and 60.7% of the variation with the random effect of individual.

Discussion

Our results indicate that parents roosting away from their nests during the active nesting period is a common occurrence in purple martins. In contrast to predictions, we did not find that higher investment in offspring by females resulted in a greater propensity for roosting in the nest cavity as compared to males. Surprisingly, we did not find that parents were more likely to roost away from their nest when they had younger nestlings. Instead, we found that adult martins may

use evening temperatures as a cue to adjust their behavioural response to their own or their nestling's thermoregulatory needs. We also found that, generally, larger broods increased the odds of the parents remaining at the colony at night, which may indicate that the level of parental investment may also impact this behaviour; a novel result that could be explored further in future studies.

We found that the odds of roosting away from the nest increased with the maximum ambient temperature. This may relate to the thermoregulatory needs of the nestlings (Saldanha et al. 2019), where parents use ambient temperature as a cue, with colder evenings resulting in a parent bird choosing to roost in the nest cavity. Surprisingly, we did not find that age of nestlings influenced the decision to roost away from the colony. We predicted that the age of nestlings should influence the decision to roost within or away from the nest since parents may need to brood nestlings at night until they are able to self-thermoregulate at around 10 days old (Marsh 1980). It may be possible that one untracked parent remained in the nest cavity while the other was absent while chicks were at a younger age, but as short-lived tags prevented us from monitoring adult pairs effectively, we cannot verify such parental coordination. From the few tags which did work, we found no apparent trend (Suppl. Figure 3.4). Our results may also have been influenced by an unusually warm and dry summer in all of our sites, which reduced the need for brooding behaviour by parent birds. Further, most of the radio-telemetry tags were deployed on parents when nestlings were around 10 days old, around the time nestlings can self-thermoregulate, potentially limiting our ability to detect adult presence when birds were younger. An early study found female purple martins stopped roosting within their nests when nestlings reached 13-16 days old and males even earlier (Brown 1980), which is consistent with parents remaining to brood before nestlings can thermoregulate. Further research during cooler summers

or at other geographic locations with different environmental pressures, and while tracking both parents, could help to further explore these patterns.

In further contrast to the notion that roosting away from the nest may be driven in part by the thermoregulatory demands of nestlings as found in bank swallows (Saldanha et al. 2019), we found that parents were more likely to roost in their nest when they had a higher brood size. A visual data exploration confirmed that nestlings do indeed increase average nightly nest temperature independently of ambient temperature (Suppl. Figure 3.5), so adult birds may not be more likely to roost elsewhere when nests were warmer and with more nestlings as predicted for thermoregulatory nestling needs. One possibility is that the positive relationship between larger brood size and a parent bird choosing to roost at its nest may relate to higher parental investment, where a bigger clutch size may lead to increased investment in parental care. A bird roosting at its nest may be better able to defend the nest against nocturnal (*e.g.*, owls) or diurnal predators (*e.g.*, Accipiter hawks). Further, larger nests would have a higher requirement for foraging and adults with larger brood sizes may not have time to travel to the communal roosting location and back and provide the same level of nest provisioning.

We found no influence of sex on the likelihood of roosting, in contrast to our predictions that owing to greater parental investment by females in gametes (Kokko and Jennions 2008) and high rates of extra-pair paternity in this species (Møller and Birkhead 1993; Stutchbury and Morton 1995), that females would be more likely to stay at the nest overnight than males. Although both male and female purple martins are known to contribute to parental care, females have a greater investment overall and only females incubate the eggs (Brown 1980; Stutchbury and Morton 1995; Brown et al. 2021). Considering the sexual difference in parental investment

in purple martins which is similar to bank swallows (Saldanha et al. 2019), we expected to find females to remain in the nest more often than males.

Our results show a high individual variation in roosting away from the colony. The large variation in roosting between individuals leads us to suspect that unaccounted individual-specific factors are probably at play and contribute to this individual-level variation. Individual personality (*i.e.*, the different behavioural responses to set stimuli) is known to impact most behaviours, including sociability (Réale et al. 2007) and may have contributed to the variation we observed. Incidental observations of general purple martin behaviour suggest there may be a high variation in purple martin behaviour, notably in responses to capture (Turcotte-van de Rydt pers. obs.), which may relate to population variation along a shy-bold continuum (Réale et al. 2007). Since cavities trapped were chosen randomly, and since the capture of targeted individuals was nearly guaranteed, we assume that we would have a high success of capturing birds across the shy-bold continuum. However, personality has yet to be studied in purple martins. Parent age and breeding experience could also impact roosting behaviour. Unfortunately, the exact age of purple martins is impossible to determine by physical characteristics alone and we lacked previous breeding experience of tracked parents. In martins, as in some other passerines, second-year birds may invest less in parent care (Wagner et al. 1997), but we did not have enough nests with second-year parents, to be able to examine this in our study. Purple martin nests may also be impacted to varying degrees by various ectoparasites, which can be particularly abundant in nests (Brown et al. 2021), which could affect parental attendance at the nest. Indeed, the extent of parasite infection may limit a bird's survival, its breeding success, and provisioning to nestlings (Davidar and Morton 1993; Wagner et al. 1997). We were not able to test the influence of ectoparasites as properly estimating the parasite load of

nests may have impacted the roosting behaviour we were measuring, but this could be explored in future studies with treatment and control nests. There are few environmental factors known to influence post-breeding roosting behaviour and participation that were not considered in this study such as wind, roost habitat, and night illumination (moon phase and cloud cover) (Russell and Gauthreaux 1999; Fraser et al. 2013; Saldanha et al. 2019) but which could be explored in future research.

An important note is that this study assumes that observed absences from the breeding site at night are associated with parents attending communal, nocturnal roosts. From our methods, we can establish that the tracked birds that were absent from their nesting area do not pass the night at the colony or in its nearby proximity otherwise they would have been detected by our hand-held receiver. Further, from the passive Motus receivers located at each of our colonies, we found that 11 out of 15 birds nesting at the Howden colony were detected flying through the 15-kilometre detection radius of the FWA colony receiver at dusk and dawn, occasionally spending the night in the detection radius (Suppl. Figure 3.61). This confirms that birds were not roosting close to their colonies, as suggested by Brown (1980). However, direct evidence of multiple purple martins congregating at a single roost and the location of such roosts has yet to be discovered in Manitoba. It is uncertain whether bank swallows do roost communally during parental care (Falconer et al. 2016; Saldanha et al. 2019), although Saldanha et al. (2019) assumed bank swallows did do so when they detected multiple birds in marshes (by using a Motus receiver array) that they concluded were suitable communal roosting sites. From the existence of large pre-migratory roosts in purple martins and summer roosting behaviours of bank swallows, we suspect that purple martins do gather at communal roosting sites, even if not all the individuals roost at the same location. Discerning the location of the roost and studying its

relationship with the nearby breeding colonies may allow us to better define this summer roosting behaviour and its role in purple martin breeding ecology. Further research using either radar data or precise tracking devices may assist in detecting specific movement paths and potential roost sites.

Conclusion

We found that purple martin with active nests routinely roosted away from their breeding colony during the night; a behaviour shared with bank swallow, another colonially breeding species and member of the Hirundinidae family. As such, summer roosting behaviour may be shared with other related species and ones also known for their large migratory roosts, but this requires further investigation. Our results lead us to conclude that parental investment may be the leading drive behind communal roosting for purple martins, with external evening temperatures adding to the roosting decision based on the thermoregulatory needs of nestlings or parents. Further study on nest conditions from earlier nesting stages, movements from roosts, and its habitat may allow us to better understand the pressure to participate in communal roosting during the breeding season and inform conservation efforts towards these social aerial insectivores. Considering purple martins use large communal roosts at night post-breeding in the fall migration and at the overwintering grounds (Brown et al. 2021), and during breeding in late summer, there is very little time within a purple martin's annual cycle where nocturnal communal roosts are not used. The high frequency of summer communal roosting participation amongst purple martins we found may indicate the importance of this roosting behaviour for the breeding success of purple martins. As such, these roosting habitats would need to be considered in breeding habitat conservation planning for this declining species.

References

- Anderson, A., and Anderson, A. 1946. Notes on the Purple Martin Roost at Tucson, Arizona. *Condor* **48**(3): 140–141. doi:10.1093/condor/48.3.140.
- Beauchamp, G. 1999. The evolution of communal roosting in birds: origin and secondary losses. *Behav. Ecol.* **10**(6): 675–687. doi:10.1093/beheco/10.6.675.
- Bridge, E.S., Pletschet, S.M., Fagin, T., Chilson, P.B., Horton, K.G., Broadfoot, K.R., and Kelly, J.F. 2016. Persistence and habitat associations of Purple Martin roosts quantified via weather surveillance radar. *Landsc. Ecol.* **31**(1): 43–53. doi:10.1007/s10980-015-0279-0.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., and Bolker, B.M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**(2): 378–400. doi:10.32614/rj-2017-066.
- Brown, C.R. 1980. Sleeping Behavior of Purple Martins. *Condor* **82**(2): 170. doi:10.2307/1367472.
- Brown, C.R., Airola, D.A., and Tarof, S. 2021. Purple Martin (*Progne subis*). *In* *Birds of the World*. Edited by P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.purmar.02.
- Cater, M.B. 1944. Roosting Habits of Martins at Tucson, Arizona. *Condor* **46**(1): 15–18. doi:10.2307/1364245.
- Davidar, P., and Morton, E.S. 1993. Living with Parasites : Prevalence of a Blood Parasite and Its Effect on Survivorship in the Purple Martin. *Auk* **110**(1): 109–116.
- Fair, J., Paul, E., and Jones, J. 2010. *Guidelines to the Use of Wild Birds in Research*. Washington, D.C.
- Falconer, C.M., Mitchell, G.W., Taylor, P.D., and Tozer, D.C. 2016. Prevalence of Disjunct Roosting in Nesting Bank Swallows (*Riparia riparia*). *Wilson J. Ornithol.* **128**(2): 429–

434. doi:10.1676/1559-4491-128.2.429.

- Fournier, A.M. V., Shave, A., Fischer, J., Siegrist, J., Ray, J., Cheskey, E., MacIntosh, M., Ritchie, A., Pearman, M., Applegate, K., and Fraser, K. 2019. Precise direct tracking and remote sensing reveal the use of forest islands as roost sites by Purple Martins during migration. *J. F. Ornithol.* **90**(3): 258–265. doi:10.1111/jofo.12298.
- Fraser, K.C., Stutchbury, B.J.M., Kramer, P., Silverio, C., Barrow, J., Newstead, D., Mickle, N., Shaheen, T., Mammenga, P., Applegate, K., Bridge, E., and Tautin, J. 2013. Consistent range-wide pattern in fall migration strategy of Purple Martin (*Progne subis*), despite different migration routes at the Gulf of Mexico. *Auk* **130**(2): 291–296. doi:10.1525/auk.2013.12225.
- Fraser, K.C., Stutchbury, B.J.M., Silverio, C., Kramer, P.M., Barrow, J., Newstead, D., Mickle, N., Cousens, B.F., Lee, J.C., Morrison, D.M., Shaheen, T., Mammenga, P., Applegate, K., and Tautin, J. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proc. R. Soc. B Biol. Sci.* **279**(1749): 4901–4906. doi:10.1098/rspb.2012.2207.
- Hatchwell, B.J., Sharp, S.P., Simeoni, M., and McGowan, A. 2009. Factors influencing overnight loss of body mass in the communal roosts of a social bird. *Funct. Ecol.* **23**: 367–372. doi:10.1111/j.1365-2435.2008.01511.x.
- Kokko, H., and Jennions, M.D. 2008. Parental investment, sexual selection and sex ratios. doi:10.1111/j.1420-9101.2008.01540.x.
- LaZerte, S.E., and Albers, S. 2018. weathercan: Download and format weather data from Environment and Climate Change Canada. *J. Open Source Softw.* **3**(22): 571. doi:10.21105/joss.00571.
- Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., and Makowski, D. 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *J. Open Source Softw.* **6**(60): 3139. doi:10.21105/joss.03139.
- Marsh, R.L. 1980. Development of Temperature Regulation in Nestling Tree Swallows. *Condor*

82(4): 461–463. Available from <https://about.jstor.org/terms>.

- Møller, A.P., and Birkhead, T.R. 1993. Certainty of paternity covaries with paternal care in birds. *Behav. Ecol. Sociobiol.* **33**(4): 261–268. doi:10.1007/BF02027123.
- Morton, B.Y.E.S., and Patterson, R.M. 1983. Kin Association, Spacing, and Composition of a Post-Breeding Roost of Purple Martins. *J. F. Ornithol.* **54**(1): 36–41.
- Nakagawa, S., Johnson, P.C.D., and Schielzeth, H. 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* **14**(134): 20170213. Royal Society Publishing. doi:10.1098/rsif.2017.0213.
- Pyle, P. 1997. *Identification Guide to North American Birds: Columbidae to Ploceidae*. Slate Creek Press, Bolinas, Calif.
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T., and Dingemanse, N.J. 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**(2): 291–318. doi:10.1111/j.1469-185X.2007.00010.x.
- Russell, K.R., and Gauthreaux, S.A. 1999. Spatial and temporal dynamics of a Purple Martin pre-migratory roost. *Wilson Bull.* **111**(3): 354–362.
- Saldanha, S., Taylor, P.D., Imlay, T.L., and Leonard, M.L. 2019. Biological and environmental factors related to communal roosting behavior of breeding Bank Swallow (*Riparia riparia*). *Avian Conserv. Ecol.* **14**(2): art21. Resilience Alliance. doi:10.5751/ACE-01490-140221.
- Sauer, J.R., Pardieck, K.L., Ziolkowski, D.J., Smith, A.C., Hudson, M.A.R., Rodriguez, V., Berlanga, H., Niven, D.K., and Link, W.A. 2017. The first 50 years of the North American Breeding Bird Survey. doi:10.1650/CONDOR-17-83.1.
- Sonerud, G.A., Smedshaug, C.A., and Bråthen. 2001. Ignorant hooded crows follow knowledgeable roost-mates to food: Support for the information centre hypothesis. *Proc. R. Soc. B Biol. Sci.* **268**(1469): 827–831. doi:10.1098/rspb.2001.1586.

Stutchbury, B.J., and Morton, E.S. 1995. The Effect of Breeding Synchrony On Extra-Pair Mating Systems in Songbirds. *Behaviour* **132**(9–10): 675–690. doi:10.1163/156853995X00081.

Stutchbury, B.J., and Robertson, R.J. 1990. Do Tree Swallows Use Nest Cavities as Night Roosts during Territory Establishment ? *J. F. Ornithol.* **61**(1): 26–33.

Taylor, P.D., Crewe, T.L., Mackenzie, S.A., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C.M., Guglielmo, C.G., Hamilton, D.J., Holberton, R.L., Loring, P.H., Mitchell, G.W., Norris, D.R., Paquet, J., Ronconi, R.A., Smetzer, J.R., Smith, P.A., Welch, L.J., and Woodworth, B.K. 2017. The motus wildlife tracking system: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conserv. Ecol.* **12**(1). Resilience Alliance Publications. doi:10.5751/ACE-00953-120108.

Wagner, R.H., Davidar, P., Schug, M.D., and Morton, E.S. 1997. Do blood parasites affect paternity, provisioning and mate-guarding in purple martins? *Condor* **99**(2): 520–523. doi:10.2307/1369959.

Ward, P., and Zahavi, A. 1973. THE IMPORTANCE OF CERTAIN ASSEMBLAGES OF BIRDS AS “INFORMATION-CENTRES” FOR FOOD-FINDING. *Ibis (Lond. 1859)*. **115**(4): 517–534. doi:10.1111/j.1474-919X.1973.tb01990.x.

Zuur, A.F., Ieno, E.N., and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**(1): 3–14. doi:10.1111/j.2041-210x.2009.00001.x.

Figures and tables

Table 3. 1 Result summary of the generalized linear mixed-effects model (GLMM) of the weather, morphology, and nest characteristics over the presence of purple martins roosting at their breeding colony during active parental care.

Fixed effects	Estimate (log-odds ratio)	Estimate (odds ratio)	Lower 95% confidence interval	Higher 95% confidence interval
Maximum ambient temperature (°C)	-0.296	0.743	0.590	0.937
Male *	-0.062	0.940	0.136	6.507
Age of nestlings (days)	-0.034	0.966	0.838	1.115
Brood size	1.000	2.718	1.120	6.597
Random effects	Standard deviation (odds ratio)		Lower 95% confidence interval	Higher 95% confidence interval
Individuals	5.01		1.98	40.52
GLMM Theoretical R ²				
Marginal R ²	0.297			
Conditional R ²	0.607			

*Male compared to the reference group of female

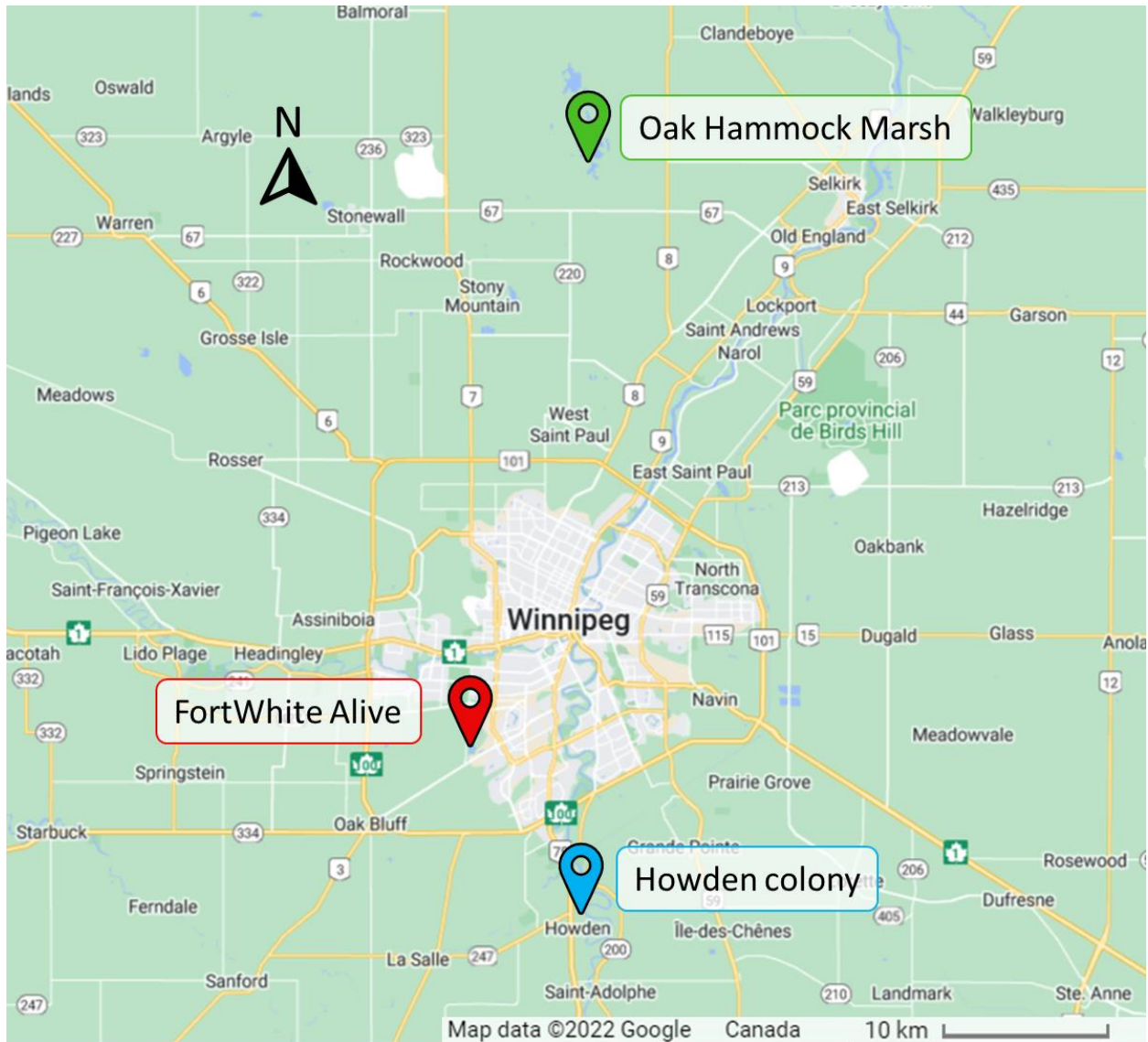


Figure 3. 1 Map of the three breeding colony locations relative to each other.

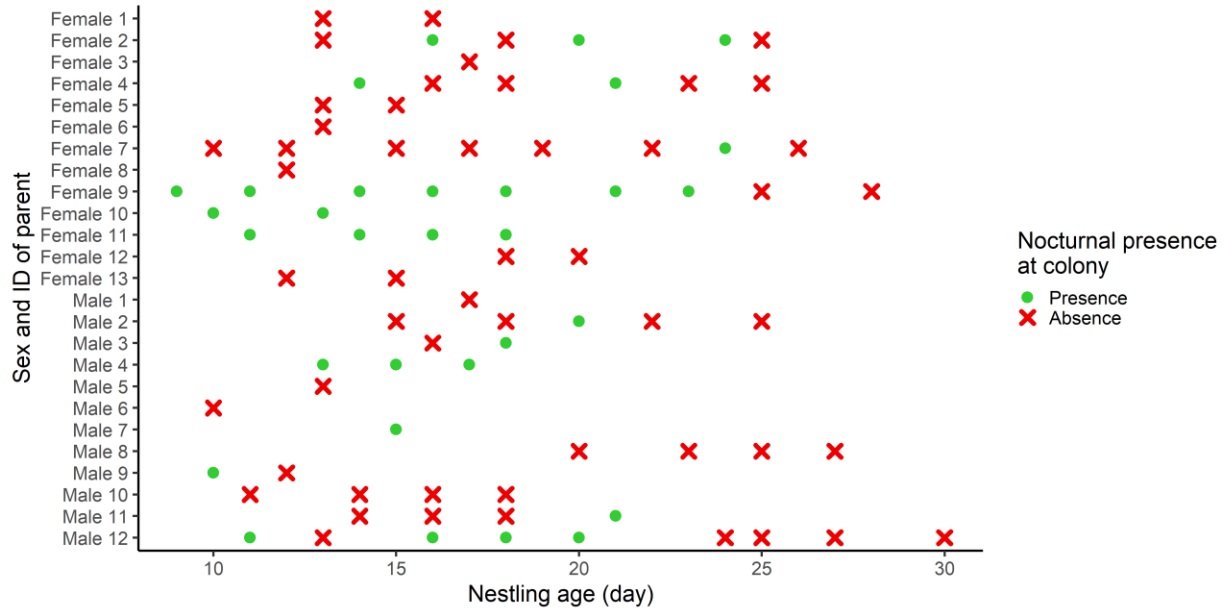


Figure 3. 2 Presence and absence as well as sex are indicated for individuals identified on the y-axis versus the age of nestlings, displays varying roosting strategies amongst individuals regardless of sex although more present on average when nestlings are younger.

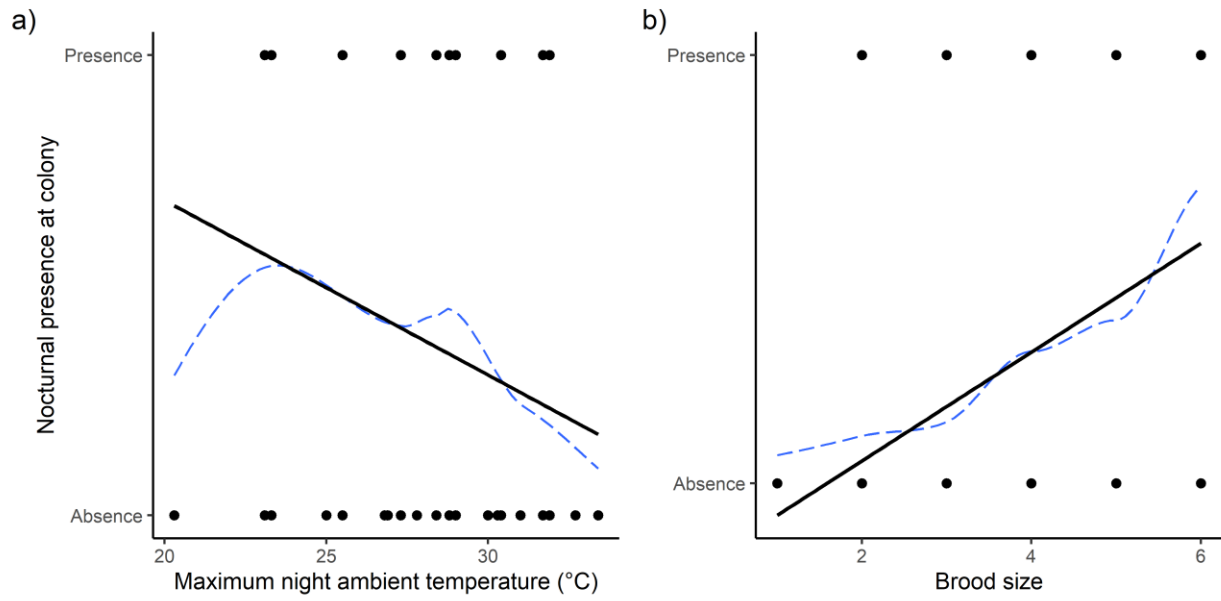
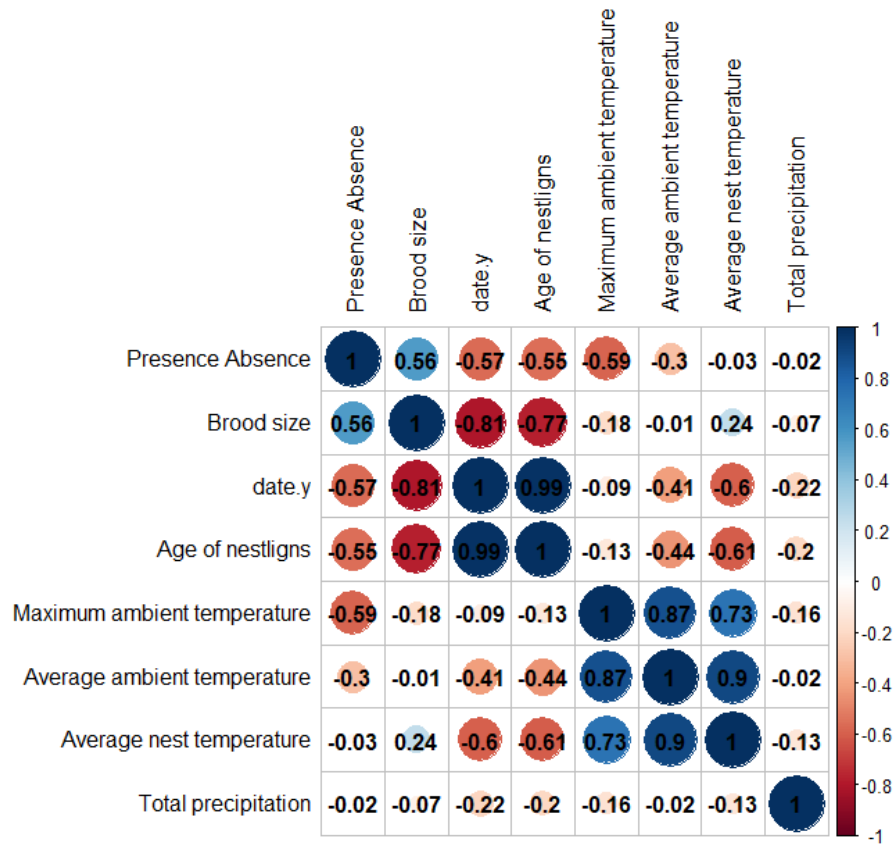
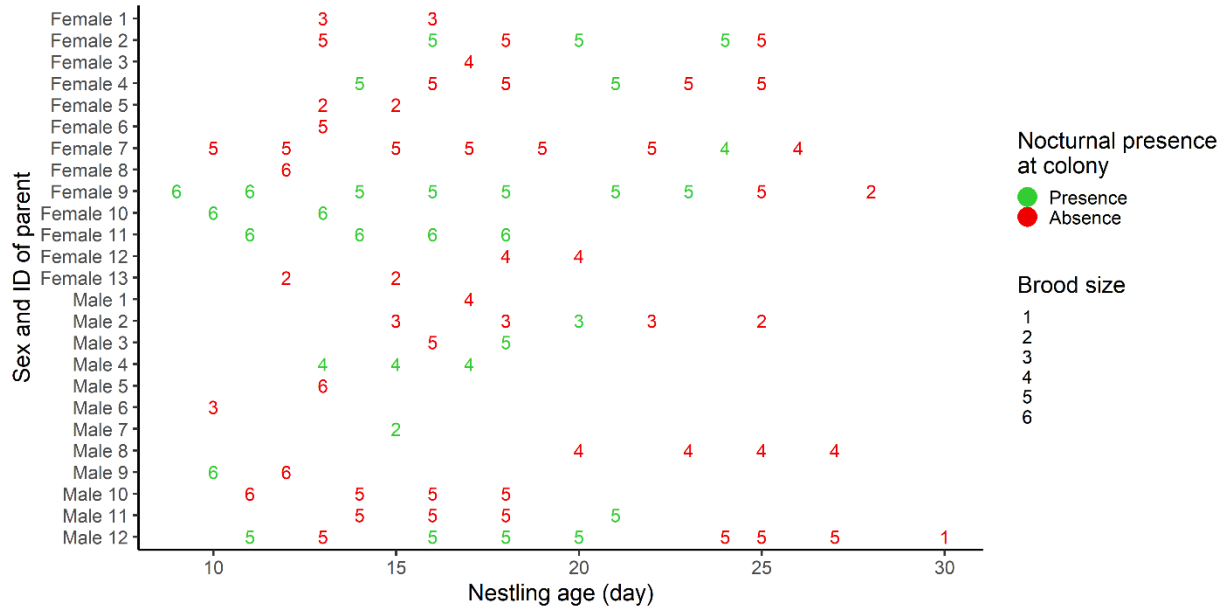


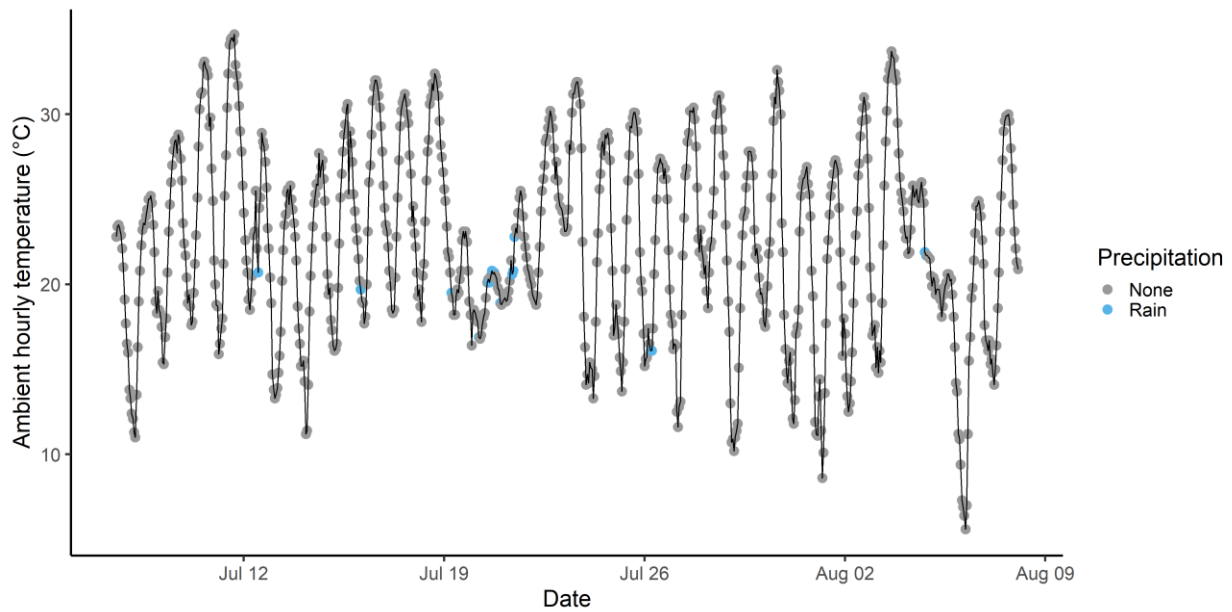
Figure 3.3 Nocturnal roosting away or at the colony during active parental care of adult purple martins with (a) maximum ambient temperature and (b) brood size. The solid black line representing a linear regression and the dashed line representing a best fit.



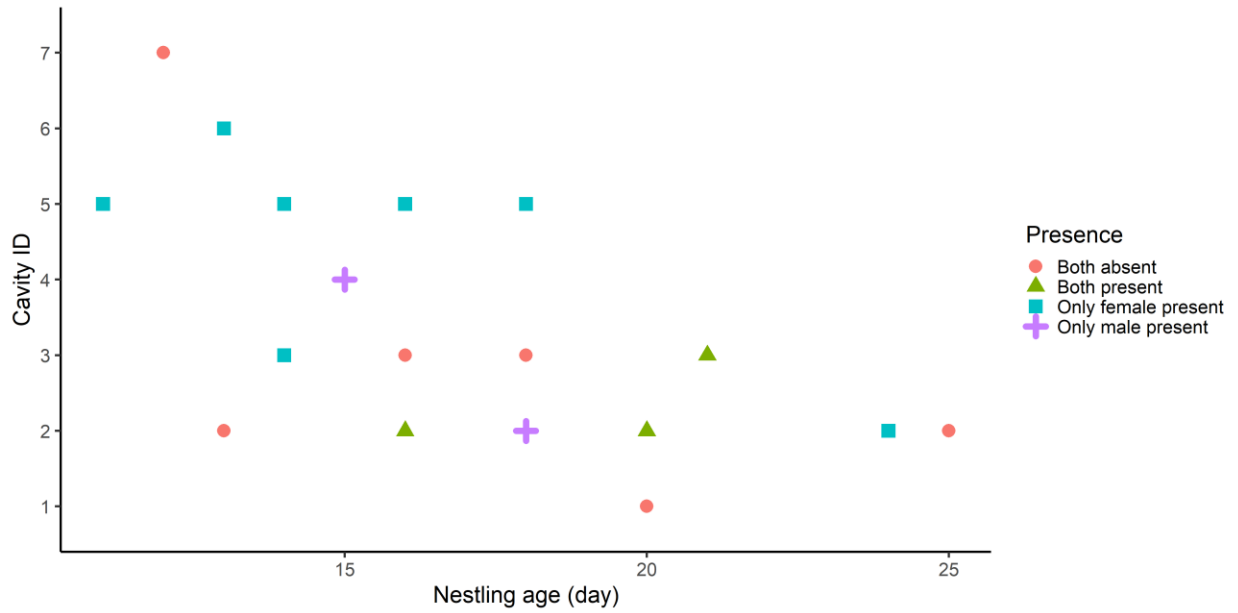
Supplemental Figure 3. 1 Pearson correlation of our various independent variables.



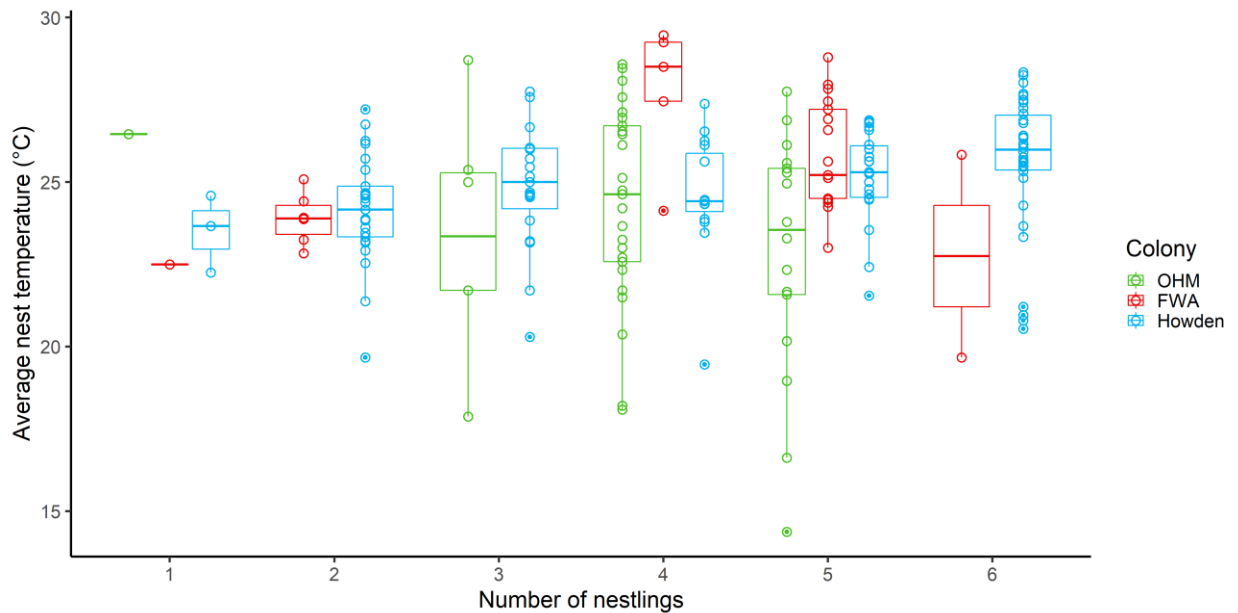
Supplemental Figure 3. 2 Change of brood size and presence and absence in different nesting individuals in relation to the age of nestlings, displaying decreasing numbers of nestlings over time with no clear difference in the nocturnal presence between sexes or with the age of nestlings.



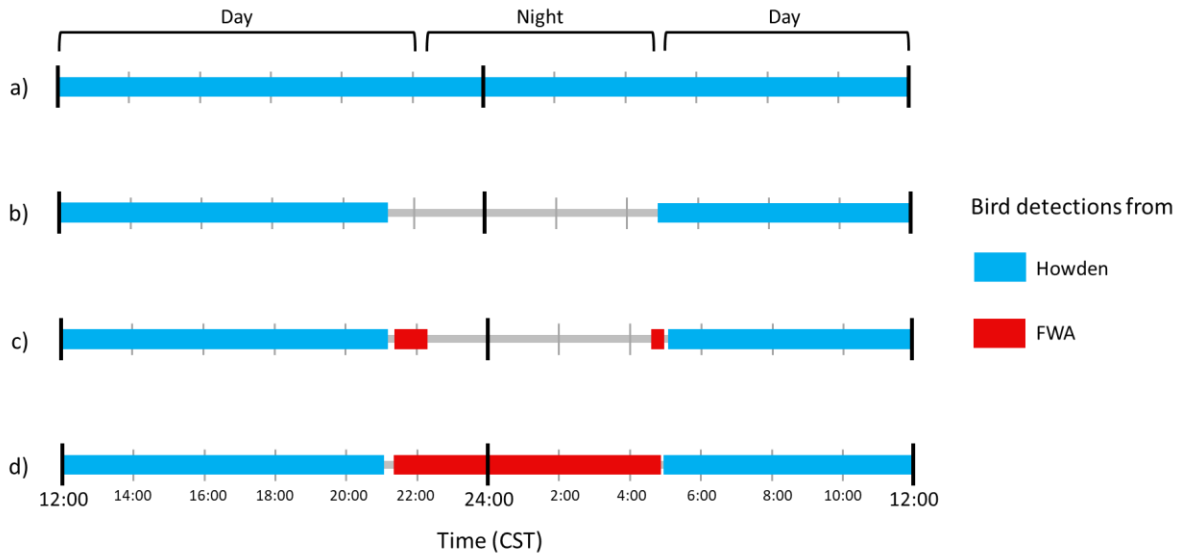
Supplemental Figure 3. 3 Circadian variation of the ambient temperature during the duration of the study with the effect of the few days of precipitation.



Supplemental Figure 3. 4 Presence and absence of both parents from the same cavity on the same night.



Supplemental Figure 3. 5 Average nest temperature increases in the nest cavities with more numerous nestlings and colony-specific nest temperature differences, likely due to house orientation and surrounding habitat.



Supplemental Figure 3. 6 Possible detection patterns over 24 hours of radio-tracked parents nesting at Howden by receivers of about 15 km of range located at their nesting breeding colony and the nearby colony of FWA. With (a) showing detections of a bird remaining at its colony all night, (b) detections of a bird roosting away from its colony all night, (c) detections of a bird roosting away from its nesting colony at night, but which flew through the detection range of another colony’s receiver to reach its roosting site, and (d) detections of a bird roosting away from its nesting colony at night, but within the range of another colony's receiver.

Chapter 4. Overall discussion

The environmental influence on spring migration rate and arrival date

In Chapter 2, I contributed to the few studies published to date that have studied environmental factors that may influence migration timing and rate of songbirds across their full migratory routes by using direct tracking (Schmaljohann and Both 2017; McKinnon and Love 2018). For this investigation, I used a rare sample of 307 individual spring migration tracks for purple martin. My results indicated that both spring migration rate and arrival date at the breeding colony were mainly impacted by the timing of migration initiation and by the latitude of the breeding destination. Timing across migration, therefore, seems geared to the specific phenology of the breeding destination and, in comparison, is only minimally impacted by weather conditions experienced while en route. These results suggest that the selection to keep arrival dates of long-distance migrants synchronized with earlier occurring spring phenology, driven by climate change, may select for earlier departure dates from the wintering grounds. Our findings were consistent with other studies which suggested that the actual migration speed may not be plastic (adjustable) as birds attempt to limit their time spent in migration (Schmaljohann and Both 2017).

In addition to timing, I found migration rate to be mainly impacted by stopover duration and departure date, where birds that had longer stops had a slower overall migration rate and later departing birds travelled faster than those that departed earlier. Environmental factors influenced migration rate, albeit to a lesser degree than timing and stopovers, with southern winds facilitating a faster rate and higher precipitation decreasing the rate. However, my analysis suggested that departure date from overwintering grounds and stopover duration have the

greatest effect on the overall migration rate. The significance of timing in migration may indicate that later departing martins may be selected to travel at faster speeds to catch up to and arrive at breeding sites at a similar time to earlier-departing migrants, which is observed in other long-distance migrants (González et al. 2020). The relationship between stopover duration and migration rate indicated that intrinsic and extrinsic factors influencing stopovers may be an important component of migration rate (Schmaljohann and Both 2017) and by proxy, migration timing. Further study on stopover duration during spring migration and the various factors influencing it may allow us to better understand how, for instance, environmental factors can be tied to timing.

We found evidence of different migration strategies between subtropical (below 23.4° of latitude) and temperate (above 23.4° of latitude) migration, with migration rate being slower overall in the temperate region than in the subtropical region. Our findings refute the idea of a sprint to the finish where birds accelerate their migration in the temperate region as they reach their breeding grounds (Briedis et al. 2018). We also found further differences in migration strategy between groups. For instance, in the second half of the migration, females migrated faster than males with no latitudinal effect. In the first half of the migration, most southern colonies displayed a slower migration rate, with only temperature influencing rate. These potential sex-based and regional patterns require further investigation.

The environmental influence on roosting behaviour of nesting pairs

In Chapter 3, I confirmed the occurrence of nesting purple martins roosting away from their breeding colony during the night. I also investigated some environment and nest-specific

factors which influence this behaviour, thereby providing a greater understanding of this newly described summer nightly roosting behaviour during active breeding in social swallows. Using individually tracked parents ($n=25$), I found that, purple martins leave their nest cavity during active parental care; on average 70% of nights. The high level of participation in this behaviour is shared with the bank swallow, another colonial swallow (Falconer et al. 2016; Saldanha et al. 2019), and may indicate that this may be further shared with other social Hirundinidae, especially if they are known for communal roosting generally.

The participation in nocturnal roosting was seemingly driven by the increased thermoregulatory needs of either the adult or the nestlings, cued by colder evening temperatures, and increased parental investment from larger brood size, which drove parents to remain in the nest cavity at night. Summer roosting away from nests when parental attendance was not needed for the thermoregulatory requirements of the nestlings would be consistent with Saldanha et al. (2019), although they found the opposite trend with larger brood size correlating with more absences from nests. We found no effect of sex on roosting, which was contrary to expectations or findings in similar species (Saldanha et al. 2019). Indeed, roosting away from the nest implies having less investment in the nest, which is expected from males with the presence of extra-pair copulation and gamete theory (Stutchbury and Morton 1995; Kokko and Jennions 2008).

Considering how prevalent roosting away from the nest appears to be, it may imply a fitness increase at the roosting sites (*e.g.*, better habitat and food, lower predation, fewer ectoparasites than in nests). Our results suggest that when roosting away from the breeding colony, swallows travelled over 15 kilometres. The energetic costs of such evening and morning displacements to roosts must be outweighed by the benefits of roosting away for it to be ecologically suitable. While roosting behaviour requires further study, our study increased our

knowledge of the intrinsic habitat needed by nesting purple martins, especially if roosting locations (or displacement between colony and roost site) allow parents proximity to safer and higher quality habitat with higher food resources. Notably, we found high individual-specific variation which may indicate an impact of personality in martins. However, a larger sample size would be necessary to entertain the effect of personality on this summer roosting behaviour. Although this is inconclusive in bank swallows (Falconer et al. 2016; Saldanha et al. 2019), evidence of smaller post-breeding communal roosts during the breeding season (Russell and Gauthreaux 1999) may indicate that parents roosting away from their nest are likely to participate in communal roosting. But the location of adult roosts and whether communal roosting occurs in summer roosting during active parental care remains to be determined.

Future research on roosting during active parent care should investigate the location and habitat of roosting sites, timing, and significance of roosts for the species, as well as verify the presence of similar summer roosting behaviours in other social birds. Moreover, I recommend that future studies start monitoring parents from an earlier date in the breeding season to investigate the start of this roosting behaviour, and the formation of pre-migratory roosts.

The environment in spring and summer behaviours

The environment is important as a cue for specific behaviours during the day and throughout the year (*e.g.*, migration timing), but it can also be a limiting factor for birds as it may impede certain behaviours. During the spring migration, the environment experienced en route by migrating birds, had little impact on the overall migration outcome. Although we found that migration efficiency is somewhat affected by weather, which is consistent with bird migration

observations and theories of energy-limited migration (Alerstam 2011), the environment had a much lesser impact on a route-long scale on arrival date, which was more greatly impacted by departure timing and geographic destination (likely a proxy for spring phenology). Therefore, weather may affect migrating birds on smaller scales and during stopovers, with birds compensating over the full journey to arrive at similar times. Birds would depend on changes to the departure timing to maintain migration and arrival synchronization with spring phenology (Schmaljohann and Both 2017; Schmaljohann 2019). Investigating how these environmental factors relate to spring stopover duration (which paces migration rate) may allow us to better predict how climate change may impede bird migration, as stopovers are associated with required stops from either contrary weather or refuelling (Gómez et al. 2014; Schmaljohann and Both 2017).

Once migrating birds arrive at their breeding range, they initiate their nesting behaviours. As we found that purple martins frequently roosted away from their nest, this suggests individuals may gain from this behaviour, via higher survival, minimizing effects of ectoparasites in the nest, or from roosting sites located in a higher quality habitat (Saldanha et al. 2019). As climate change induces extreme weather and on average warmer temperatures, the extent of participation in roosting away I found for purple martins may change as their temperature cues are altered by new conditions. Overall migrating martins try to limit their presence or movements in energetically costly environments (*e.g.*, thermoregulatory costs, precipitation), and take advantage of supportive environmental conditions during their migration and roosting (Alerstam et al. 2003).

Theoretical and instrumental limitations

While investigating migration, this study assumes that the date of spring arrival is crucial for the breeding success of purple martins as seen in other species (Kokko 1999; Both and Visser 2001), and as such, meeting such date would have a strong selective pressure (Kokko 1999). However, further studies may be needed to establish a fitness increase with the arrival date for purple martins. Indeed, in this species, birds of lower latitudes appear to have a larger spread of arrival dates compared to Alberta birds (Suppl. Table 2.1) (Fraser *unpub.* paper). The variation in arrival dates could indicate that the intensity of the selective pressure may vary amongst latitudes as the window of optimal breeding conditions may shorten with northern latitudes (Fraser *unpub.* paper). As such the arrival timing may be of greater importance at higher latitudes.

Moreover, purple martins appear to have a relatively long arrival-breeding interval (*i.e.*, the time between spring arrival at the breeding site and the first lay egg) during which adults occupy cavities and establish territories (Shave et al. 2019; Brown et al. 2021), which was also found to be very plastic (Smith, *unpub.* paper). Considering this, the actual arrival timing may not be as crucial for purple martins nest timing as may be theoretically predicted (Kokko 1999). However, purple martin arrival timing may still be critical to fitness in ways other than the timing of nesting. In purple martins, nest cavities are a limiting resource and mates need to successfully acquire and defend such cavities amid intraspecific and interspecific competition (Brown et al. 2021). Birds arriving at their breeding colony earlier can select better nesting cavities and occupy cavities before resident cavity nesters such as the invasive European starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*) start breeding (Brown et al. 2021). Further study would be needed to estimate the importance and relationship between

purple martin arrival date and the arrival breeding interval, how it relates to breeding success, and the effect of intraspecific and interspecific competition.

Using direct tracking to follow bird movements allows for an increase in the accuracy of the study of behaviour. These are convenient tools have within the instrumental uncertainties which must be considered when designing a study using such technologies. The light-level geolocator tracking dataset used (Chapter 2) works well when broader-scale position estimates are sufficient, but studies requiring higher precision (*e.g.*, less than the ~100 km of accuracy provided by light-level geolocation data) may require the use of different technology. While time-consuming, greater data quality can be achieved by taking precautions such as using an explicit and transparent analysis protocol (see methods Chapter 2) that incorporates prior biological knowledge and uses available R packages and inspection of daily light data.

Likely instrumental failure occurred during the roosting study (Chapter 3) with many radio telemetry tags ceasing to be detected by automated radio receiver towers within 48 hours after deployment, and only 10 tags lasting over 7 days (see methods Chapter 3). These failures were unexpected considering the success of these tags in other projects and on the same species (Taylor et al. 2017; Bani Assadi and Fraser 2021). Failures appeared to stem from tags stopping emitting signals, possibly due to damage dealt as martins move in nest cavities while providing for their nestlings. On a recaptured bird during the study period, we removed a radio tag which had ceased to emit signals after less than a week of deployment. The following year, two birds were recaptured with their radio tags still harnessed although the antennas had fallen off. This could indicate that these tag failures may be caused by the tag's antenna, located on the back portion of the tag, snapping off with contact with the nest's opening as the birds repetitively enter and exit their cavity. Similar antenna failures have been observed before in cavity nesters

albeit in other tag models (Pegan et al. 2018). Overall, I would not recommend using this specific model of radiotelemetry tag on adult cavity nesters during active breeding. Although many tags failed and prevented us to contrast both parents' behaviour together, we still had robust and interesting results.

Conservation application of research findings

The lack of sensitivity of purple martins to en route environmental conditions may limit acclimation to climate change at the breeding grounds, and the selection process to change departure date may be slow (Schmaljohann and Both 2017). The reliance on an intrinsic process for migration timing may render such migratory species increasingly vulnerable to advancing springs as the phenotypic mismatch may be accentuated over time if the selective change is unable to keep up with rapidly advancing springs (Radchuk et al. 2019). Although this process may be difficult to integrate into active conservation plans, understanding how different groups or species respond may help inform future conservation decisions.

Hirundinidae swallows' high reliance on communal roosting nearly year-round underline the ecological importance of this behaviour on individual fitness. Although I did not confirm whether martins roosting away from their breeding colony gather at communal roosts rather than disperse at night, the presence of pre-migratory roosts, and evidence in bank swallows (Saldanha et al. 2019), suggests that they do. The fact they roost at large distances away from their nest indicates the displacements outweigh the costs of flying away and the reduced parental care to their nestlings, whether it be from improved survival or increased foraging ability at or along the way to the roosting sites. Based on this, it is likely that roosting habitat, and notably ones during

breeding, are part of the intrinsic habitat on which social swallows like the purple martin depend on. As such, finding and protecting such roosting sites may be important and would complement protections at nesting sites.

Significance and conclusion

In Chapters 2 and 3, I investigated how the environment may impact movement behaviours in purple martins, both in spring migration and during roosting in the active breeding season. Birds can be greatly impacted by their environment because it acts both as a behavioural cue and a challenge birds must overcome, which has important ramifications on individual fitness. With an increasingly variable environment, understanding how birds rely on and are impacted by their environment is important when predicting population declines and designing better conservation projects. New technologies allow us to track birds more accurately in their migration and confirm their presence, or absence, with certainty. At the same time, the progress in information and remote sensing systems allows us to readily estimate the environmental conditions they experience from an unprecedented amount of readily available high-quality data.

Birds may become threatened as they must tackle a changing environment, as extrinsic factors, such as weather, greatly impacts behaviours. The changing environment may reduce the survival, and fitness of birds, by affecting behaviour either cued by the changing environment (*e.g.*, summer roosting) or changing circumstances during an endogenously driven behaviour (*e.g.*, spring migration). My findings indicate that the level to which birds rely on their environment varies by season. With spring migration timing being mostly driven by endogenous factors in departure date and latitudinal region, weather impacts migration strategy to a lesser

extent to avoid energetic losses. While summer roosting decision being both driven by temperature for thermoregulatory gains, and by nest conditions for greater nestling survival.

In conclusion, the present thesis has contributed to a better understanding of how migratory species respond to variable intrinsic and extrinsic factors, which may allow us to better predict bird behaviours strategy and allow us to forecast declines and direct research into factors which can be relevant for conservation. Moreover, studying declining species' behaviours, especially breeding-related, allows us to better understand the species' ecology, and unknown habitat requirements (or circumstances), which can induce new possible conservation interventions. My findings provide a better understanding of long-distance migrants and summer roosting behaviours. More broadly the impact of environmental factors on these behaviours contributes to pre-existing studies on large migration trends and provides support to summer roosting being more widespread in social Hirundinidae. In the future, more studies may look at the en route environment of long-distance migrants to investigate whether our findings are consistent amongst species and see how factors may influence stopover duration. Looking at the evolutionary significance of summer roosting in social swallows, its formation, and roosts habitats contribute to the species' ecology, and potentially greater habitat requirements, which can induce new possible conservation interventions and better understand the decline of these social species.

References

- Alerstam, T. 2011. Optimal bird migration revisited. *J. Ornithol.* **152**(S1): 5–23. Springer Verlag. doi:10.1007/s10336-011-0694-1.
- Alerstam, T., Hedenström, A., and Åkesson, S. 2003. Long-distance migration: Evolution and determinants. *In Oikos*. pp. 247–260. doi:10.1034/j.1600-0706.2003.12559.x.
- Bani Assadi, S., and Fraser, K.C. 2021. The Influence of Different Light Wavelengths of Anthropogenic Light at Night on Nestling Development and the Timing of Post-fledge Movements in a Migratory Songbird. *Front. Ecol. Evol.* **9**(October): 1–10. doi:10.3389/fevo.2021.735112.
- Both, C., and Visser, M.E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**(6835): 296–298. doi:10.1038/35077063.
- Briedis, M., Hahn, S., Krist, M., and Adamík, P. 2018. Finish with a sprint: Evidence for time-selected last leg of migration in a long-distance migratory songbird. *Ecol. Evol.* **8**(14): 6899–6908. John Wiley and Sons Ltd. doi:10.1002/ece3.4206.
- Brown, C.R., Airola, D.A., and Tarof, S. 2021. Purple Martin (*Progne subis*). *In Birds of the World*. Edited by P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.purmar.02.
- Falconer, C.M., Mitchell, G.W., Taylor, P.D., and Tozer, D.C. 2016. Prevalence of Disjunct Roosting in Nesting Bank Swallows (*Riparia riparia*). *Wilson J. Ornithol.* **128**(2): 429–434. doi:10.1676/1559-4491-128.2.429.
- Gómez, C., Bayly, N.J., and Rosenberg, K. V. 2014. Fall stopover strategies of three species of thrush (*Catharus*) in northern South America. *Auk* **131**(4): 702–717. doi:10.1642/AUK-14-56.1.
- González, A.M., Bayly, N.J., and Hobson, K.A. 2020. Earlier and slower or later and faster: Spring migration pace linked to departure time in a Neotropical migrant songbird. *J. Anim.*

- Ecol. **89**(12): 2840–2851. Blackwell Publishing Ltd. doi:10.1111/1365-2656.13359.
- Kokko, H. 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.* **68**(5): 940–950. doi:10.1046/j.1365-2656.1999.00343.x.
- Kokko, H., and Jennions, M.D. 2008. Parental investment, sexual selection and sex ratios. doi:10.1111/j.1420-9101.2008.01540.x.
- McKinnon, E.A., and Love, O.P. 2018. Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. doi:10.1642/AUK-17-202.1.
- Pegan, T.M., Craig, D.P., Gulson-Castillo, E.R., Gabrielson, R.M., Kerr, W.B., MacCurdy, R., Powell, S.P., and Winkler, D.W. 2018. Solar-powered radio tags reveal patterns of post-fledging site visitation in adult and juvenile Tree Swallows *Tachycineta bicolor*. *PLoS One* **13**(11). doi:10.1371/journal.pone.0206258.
- Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., Adamík, P., Adriaensen, F., Ahola, M.P., Arcese, P., Miguel Avilés, J., Balbontin, J., Berg, K.S., Borrás, A., Burthe, S., Clobert, J., Dehnhard, N., de Lope, F., Dhondt, A.A., Dingemanse, N.J., Doi, H., Eeva, T., Fickel, J., Filella, I., Fossøy, F., Goodenough, A.E., Hall, S.J.G., Hansson, B., Harris, M., Hasselquist, D., Hickler, T., Joshi, J., Kharouba, H., Martínez, J.G., Mihoub, J.B., Mills, J.A., Molina-Morales, M., Moksnes, A., Ozgul, A., Parejo, D., Pilard, P., Poisbleau, M., Rousset, F., Rödel, M.O., Scott, D., Senar, J.C., Stefanescu, C., Stokke, B.G., Kusano, T., Tarka, M., Tarwater, C.E., Thonicke, K., Thorley, J., Wilting, A., Tryjanowski, P., Merilä, J., Sheldon, B.C., Pape Møller, A., Matthysen, E., Janzen, F., Dobson, F.S., Visser, M.E., Beissinger, S.R., Courtiol, A., and Kramer-Schadt, S. 2019. Adaptive responses of animals to climate change are most likely insufficient. *Nat. Commun.* **10**(1): 3109. Nature Publishing Group. doi:10.1038/s41467-019-10924-4.
- Russell, K.R., and Gauthreaux, S.A. 1999. Spatial and temporal dynamics of a Purple Martin pre-migratory roost. *Wilson Bull.* **111**(3): 354–362.
- Saldanha, S., Taylor, P.D., Imlay, T.L., and Leonard, M.L. 2019. Biological and environmental factors related to communal roosting behavior of breeding Bank Swallow (*Riparia riparia*).

- Avian Conserv. Ecol. **14**(2): art21. Resilience Alliance. doi:10.5751/ACE-01490-140221.
- Schmaljohann, H. 2019. The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: A cross-continental analysis. *Mov. Ecol.* **7**(1). BioMed Central Ltd. doi:10.1186/s40462-019-0169-1.
- Schmaljohann, H., and Both, C. 2017. The limits of modifying migration speed to adjust to climate change. *Nat. Clim. Chang.* **7**(8): 573–576. Nature Publishing Group. doi:10.1038/NCLIMATE3336.
- Shave, A., Garroway, C.J., Siegrist, J., and Fraser, K.C. 2019. Timing to temperature: Egg-laying dates respond to temperature and are under stronger selection at northern latitudes. *Ecosphere* **10**(12). Wiley-Blackwell. doi:10.1002/ecs2.2974.
- Stutchbury, B.J., and Morton, E.S. 1995. The Effect of Breeding Synchrony On Extra-Pair Mating Systems in Songbirds. *Behaviour* **132**(9–10): 675–690. doi:10.1163/156853995X00081.
- Taylor, P.D., Crewe, T.L., Mackenzie, S.A., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C.M., Guglielmo, C.G., Hamilton, D.J., Holberton, R.L., Loring, P.H., Mitchell, G.W., Norris, D.R., Paquet, J., Ronconi, R.A., Smetzer, J.R., Smith, P.A., Welch, L.J., and Woodworth, B.K. 2017. The motus wildlife tracking system: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conserv. Ecol.* **12**(1). Resilience Alliance Publications. doi:10.5751/ACE-00953-120108.