Determining the impact of intrinsic and extrinsic factors throughout the annual cycle on the reproductive behaviour of a migratory songbird, Purple Martin *Progne subis*

by

Alisha Marie Ritchie

A Thesis submitted to the Faculty of Graduate Studies of

The University of Manitoba

in partial fulfilment of the requirements of the degree of

MASTER OF SCIENCE

Department of Biological Sciences

University of Manitoba

Winnipeg

Abstract

The causes of steep rates of population decline in migratory songbirds remain largely unknown. In a trans-hemispheric migratory swallow (purple martin, *Progne subis*), I examined carry-over effects from spring migration on an individual's subsequent reproductive success as well as latitudinal variation in clutch size and timing of provisioning. I show that martins that spent more days at spring migratory stopovers initiated their clutches earlier after arrival at breeding colonies, and lost fewer offspring. I found that martins at more northern latitudes provisioned their young for more hours per day but I did not find a predicted positive correlation between clutch size and latitude. Overall, I show for the first time how spatio-temporal factors during migration carry over to affect the reproductive success of individual songbirds and my results suggest that the increased risk associated with longer migration is not compensated for by higher productivity at more northern latitudes.

Acknowledgements

First, I would like to thank my advisor, Dr. Kevin Fraser, for the opportunity to conduct this research. Your guidance has been instrumental in producing a thesis that I have enjoyed working on. I would also like to convey sincere thanks to my advisory committee members, Dr. James Roth and Dr. Jason Fischer. Your feedback on my research from proposal to completion has helped improve the final thesis. My fellow Avian Behaviour and Conservation (ABC) lab members, Lawrence Lam, Amanda Shave, and Amélie Roberto-Charron, were crucial in shaping my experiences throughout this program and I will value all your friendship for a lifetime. I would like to convey a special thanks to Myrna Pearman whom was instrumental in not only getting me involved in this research but also provided a team from Ellis Bird Farm who were essential in my successful field season in Alberta. This thesis would not be what it is if it was not for Dr. Jason Fischer and his team at Disney's Animal Kingdom who collected complementary data in Florida for my project. I would like to thank Joe Siergrist for the opportunity to work with the data collected through the project MartinWatch, and the citizen scientists who recorded the data. I also extend my utmost gratitude to Larry Leonard, Kelly Applegate, Paul Mammenga, Joe Siegrist, Tim Shaheen, Nanette Mickle, James Mejeur, Anne Savage, Jason Fischer, Leslie Burgess, Jerome Jackson, and Bill Dietrich for contributions to developing such a large dataset of geolocator tracked purple martins with associated breeding information. Finally, I would not have been able to complete this project without the love and support of my family. This research would not have been possible without the financial support provided by the University of Manitoba, Alberta Conservation Association and Ellis Bird Farm. I would also like to acknowledge the travel funding from the University of Manitoba Faculty of Graduate Studies, Department of Biological Sciences, and Graduate Student Association that gave me the opportunity to present this research at national and international academic conferences.

Table of Contents

List of Tables

List of Figures

Chapter 1: General introduction

Migratory species across diverse taxonomic groups, eco-regions, and habitats are currently experiencing rapid rates of population decline world-wide relative to residents. Consequently, there is a great deal of current research on factors that may be contributing to these declines (Wilcove and Wikelski 2008). Research on migratory songbirds has explored multiple factors that may be involved to varying degrees in population declines, such as habitat loss and climate change. However, since factors impacting declines are still largely unknown and may vary from species to species, it is still unclear why many migratory species are declining more than resident species (Wilcove and Wikelski 2008, Rappole and McDonald 1994).

The annual cycle can be divided into two major seasons; a breeding season, largely associated with population growth, and a nonbreeding season, largely associated with population decline (Fretwell 1972). For migratory species, the nonbreeding season can be divided further into an overwintering period and two migration periods (fall and spring). Migratory songbirds can travel thousands of kilometers between breeding and nonbreeding grounds on migration. Events in each of these periods can have important impacts on the population both within the period it occurred and in future periods. Such events from previous seasons can have non-lethal impacts that affect an individual's future fitness, which are known as carry-over effects (Harrison et al. 2011). To better understand the population declines of migratory species, it is important to consider factors within each period of the annual cycle and the interactions between seasons; especially since research has shown that carry-over effects have the potential to magnify population declines (Norris 2005). The number of carry-over effect studies has rapidly increased as methods and technologies allow for increased and improved tracking of migratory species across multiple periods of the annual cycle.

Habitat quality and food availability were the main variables first incorporated in theoretical models of carry-over effects (Fretwell 1972, Norris 2005) and have since been the focus of recent carry-over effect research. The loss of different qualities of winter habitat not only impacts the condition of individual birds but also the number of birds that survive the winter, both of which have important impacts on per capita breeding in the following season (Norris 2005). These models of carry-over effects are beginning to be tested in natural systems through analysis of the variation in resources, how factors affect an individual's physical condition and ability to make transitions between seasons, and finally how factors result in a change in fitness (either reproductive success or survival) (Harrison et al. 2011). Habitat quality, food abundance, and body condition have been examined to evaluate how access to resources (i.e. high-quality habitat and/or abundant food source) impact fitness (Studds and Marra 2005, Harrison et al. 2011). Several migratory songbird species, such as the American Redstart (*Setophaga ruticilla*) (Cooper et al. 2015) and Wood Thrush (*Hylocichla mustelina*) (McKinnon et al. 2015), have been used to test the hypotheses developed in these models (see Harrison et al. 2011 for further examples of carry-over studies). These studies have shown that conditions at the nonbreeding grounds can impact the timing of migration, arrival at the breeding grounds, and reproductive success.

However, a little-examined aspect of carry-over effects is the influence of factors during the migration period on future reproduction. Migratory stopover sites can be defined as locations where birds pause during migration to rest and refuel essential resource stores (e.g. fat and protein) that are necessary to continue migration (Newton 2004). The quality and length of time spent at stopovers have been shown to have significant impacts on the body condition of migrants prior to departure (Nisbet and Medway 1972, Bearhop et al. 2004, Bauchinger et al.

2008), but how stopover duration carries over to impact the rest of migration and breeding remains largely unexamined (Gómez et al. 2017). The timing of migration and arrival can be a critical component of fitness (Kokko 1999). Selection should generally favour early arrival at the breeding grounds to obtain high quality territories and/or mates while not arriving too early due to the considerable risks of adverse weather and low food availability in early spring (Kokko 1999). Breeding arrival timing may be cued from thousands of kilometers away for many species, without cues of spring phenology at breeding sites (Ouwehand and Both 2017). In addition, there are potential trade-offs between the advantages of early arrival at the breeding grounds versus the higher insurance of larger energy stores gained by spending more time at stopovers (Pfister et al. 1998, Baker et al. 2004, Smith et al. 2007). The timing of arrival at the breeding grounds can impact the timing of events within the breeding season, such as egg-laying, which is involved with the seasonal declines in reproductive success of late breeding relative to other individuals of the population (Hatchwell 1991). In addition to reduced clutch size of late breeders, timing of events within the breeding season may be related to the quality of an individual; seasonal declines in reproductive success have been associated with lower provisioning rates by late breeders (Hatchwell 1991). There have been a few studies that have connected environmental conditions from predicted spring migration stopover locations to reproductive performance and timing based on mark-resight data (Schaub et al. 2011, Drake et al. 2014). However, to my knowledge, there have been no studies that have examined how specific conditions experienced at stopovers by individual birds impact their future reproduction.

For songbirds, the migratory period may pose the greatest threat to survival, as compared to the overwintering and breeding stationary periods of the annual cycle (Sillett and Holmes 2002). Migration is costly not only with respect to the time spent in flight but in some cases even

more so during stopovers (Wikelski et al. 2003, Chernetsov 2012). A study of two migratory thrush species (*Catharus ustulatus* and *C. guttatus*) showed that birds' energy expenditure is twice as high during foraging and thermoregulation at stopovers as compared to long-distance migratory flights (Wikelski et al. 2003). Conditions at migratory stopover sites may influence subsequent migration performance as well as body condition upon arrival at their destination (Chernetsov 2012). However, the carry-over effects of en route conditions (e.g. weather at stopover) and subsequent migration timing (e.g. time of departure and time spent at stopovers) on breeding has not been studied in songbirds.

Species that breed across a wide range of latitudes generally also have correspondingly broad variation in migration distance within species. Considering that migration is costly and may increase survival risk, it is generally predicted that individuals that breed farther north gain some benefit to traveling the extra distance. Breeding at more northern latitudes has been shown to be strongly correlated with larger clutches, both inter- and intraspecifically (Lack 1947). There are several long-standing hypotheses that have been posited to explain this variation in clutch size (Cooper et al. 2005). One theme of hypotheses relate to how provisioning ability may be more constrained by seasonality, predation pressure, and daylength for birds at more southern as compared to northern latitudes. Northern temperate latitudes generally have a larger peak in food abundance for insectivorous birds during the breeding season, have lower predation pressures, and have longer daylight hours. All of these factors may reduce provisioning constraints, allowing for increased provisioning levels (Cooper et al. 2005). Increase in daylight hours during the breeding season associated with increasing latitude in the northern hemisphere has been found to impact provisioning levels through allowing for longer 'work days' leading to greater chick mass (Rose and Lyon 2013) and shorter nestling periods (Sanz 1999).

Parental provisioning is an energetically expensive portion of reproduction, particularly for species with altricial young, which can have important impacts on the fledging success and future survival of offspring (Schwagmeyer and Mock 2008, Wilkin et al. 2009). A number of factors within the breeding season, in addition to breeding latitude, have been studied with respect to their impacts on parental provisioning of young. However, the impacts of past events, such as those during migration, on provisioning ability have never been examined. In the 'golden age of biologging' through the use of miniaturized tracking devices (Wilmers et al. 2015), we now have the ability to collect detailed spatio-temporal data for complete migrations of some songbirds. Combined with the advent of new ways to automate the recording of parental provisioning rates there are now unprecedented opportunities to investigate factors both from the breeding grounds and from past seasons that are influencing this aspect of reproduction (Rose 2009).

Although conditions from past events, like migration, have the potential to carry over to impact fitness, it is important to account for conditions at the breeding grounds that also impact provisioning behaviour or fitness independently of factors experienced during migration. Climatic conditions can not only impact the birds themselves, but also their insect prey abundances. Temperature is one of the most important, and may be the dominant, climatic factor impacting aerial insect abundance at a given time, although the optimal temperature varies depending on the order of insect (Glick 1939). Wind is another major factor impacting aerial insect abundance in multiple ways, such as blowing insects to unsuitable areas for reproduction, directly destroying them by blowing them into standing water and storm fronts, or reducing their activities in the air column (Glick 1939). Rose (2009) found that wind had a significant negative impact on provisioning levels of an aerial insectivore, tree swallows (*Tachycineta bicolor*).

To study carry-over effects an individual must be tracked through more than one season and the mechanisms underlying the observed difference in fitness between individuals must be understood (Harrison et al. 2011). Avian species are an ideal study system for two main reasons; 1) tracking technology is now becoming light-weight enough to track small songbirds; and 2) birds have fewer mechanisms to compensate for poor wintering conditions than mammals, meaning carry-over effects typically have a more obvious impact on bird species than mammals (Harrison et al. 2011). Using geolocators to track purple martins I examined how factors from spring migration impacted reproductive activities at the breeding grounds.

Purple martins (*Progne subis*) are long-distance migratory songbirds that fit within the functional group aerial insectivores, meaning they catch insects while in flight. Aerial insectivores are currently experiencing the steepest rates of decline of any functional group of birds in North America (Nebel et al. 2010). Since declines in migratory species are being seen in such a wide range of taxa, conservation actions need to take a more proactive approach for protecting species rather than waiting until species are threatened before studying their declines and how to protect them (Wilcove and Wikelski 2008). Purple martins are therefore an important species to study to further understand what mechanisms may be underlying the declines of migratory species and aerial insectivores (Tautin et al. 2008) since they are a declining species that is still abundant. Purple martins are colonial cavity nesters that breed in human-made artificial cavities in close proximity to humans across a wide range of latitudes in North America, reaching as far north as central Alberta and as far south as Florida. Combined, these factors make purple martins amenable for exploring the research gaps noted above in carry-over effects from migratory stopovers on reproduction and latitudinal variation in reproduction.

The second chapter of this thesis will fill a major gap in carry-over effect studies; specifically, how factors during migration carry over to influence behaviour and fitness at breeding sites. Another way in which new technologies can contribute to carry-over effect research is through the automated recording of parental provisioning rates, which provide the new opportunity to examine how carry-over effects impact parental provisioning rates and reproductive success. Previous studies have only been able to look at effects on reproductive success measured by clutch size, but not on an adult bird's ability to provision their nest. I used radio frequency identification (RFID) to record provisioning rates by remotely and non-intrusively recording when a marked individual entered and exited any monitored cavity.

Despite latitudinal trends in clutch size being a well-explored area of research there has been few studies that have examined trends within aerial insectivore species (Dunn et al. 2000), and there has been less uniformity in these trends in cavity nesting species (Orell and Ojanen 1983 [great tit *Parus major*], Järvinen 1989 [pied flycatcher *Ficedula hypoleuca*], Soler and Soler 1992 [jackdaw *Corvus monedula*], Fargallo 2004 [blue tit *Cyanistes caeruleus*]); therefore understanding latitudinal variation in clutch size of purple martins in addition to testing a long-standing hypothesis to explain this trend will be an important addition to this area of research. In the third chapter, I 1) examined variation in clutch size across latitudes using a 71,844 nest record, citizen scientist database (Purple Martin Conservation Association (PMCA)) of nesting data from across the purple martin breeding (Tautin et al. 2008), and, 2) tested if longer daylength allowed for increased provisioning activity at northern latitudes as has been hypothesized to explain why larger clutches are typically found at more northern latitudes. With the new ability to remotely record parental provisioning activity at the nest for the entire nesting period using RFID technology it is now possible to test long-standing hypotheses that have been

posited to explain latitudinal variation in clutch size, such as how activity patterns and nestling

provisioning may be constrained or modulated by variation in daylength.

References

Baker, A.J., P.M. González, T. Piersma, L.J. Niles, I.L.S. Nascimento, P.W. Atkinson, N.A. Clark, C.D.T. Minton, M.K. Peck, and G. Aarts. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. The Proceedings of the Royal Society of London B, 271: 875-882.

Bauchinger, U., T. Van't Hof, and H. Biebach. 2008. Migratory stopover conditions affect the developmental state of male gonads in garden warblers (*Sylvia borin*). Hormones and Behaviour, 54: 312-318.

Bearhop, S., G.M. Hilton, S.C. Votier, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proceedings of the Royal Society of London B (Supplement), 271: S215-S218.

Boyle, W.A., D.W. Winkler, and C.G. Guglielmo. 2012. Rapid loss of fat but not lean mass prior to chick provisioning supports the flight efficiency hypothesis in tree swallows. Functional Ecology, 26: 895-903.

Chernetsov, N. 2012. Passerine migration: stopovers and flight. Springer Science and Business Media.

Cooper, C.B., W.M. Hochachka, G. Butcher and A.A. Dhondt. 2005. Seasonal and latitudinal trends in clutch size: thermal constraints during laying and incubation. Ecology, 86: 2018-2031.

Cooper, N.W., T.W. Sherry, and P.P. Marra. 2015. Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. Ecology, 96: 1933-1942.

Drake, A., C.A. Rock, S.P. Quinlan, M. Martin, and D.J. Green. 2014. Wind speed during migration influences the survival, timing of breeding, and productivity of a Neotropical migrant, *Setophaga petechial*. PLoS ONE, 9: e97152.

Fargallo, J.A. 2004. Latitudinal trends of reproductive traits in the blue tit *Parus caeruleus*. Ardeola, 51: 177-190.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press.

Glick, P.A. 1939. The distribution of insects, spiders and mites in the air. Technical Bulletin 673, U.S. Department of Agriculture, pp. 1-150.

Gómez, C., N.J. Bayly, D.R. Norris, S.A. Mackenzie, K.V. Rosenberg, P.D. Taylor, K.A. Hobson, and C.D. Cadena. 2017. Fuel loads acquired at a stopover site influence the pace of intercontinental migration in a boreal songbird. Scientific Reports, 7: 3405.

Harrison, X.A., J.D. Blount, R. Inger, D.R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology, 80: 4-18.

Hatchwell, B.J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of common guillemots (*Uria aalge*)

Järvinen, A. 1989. Clutch-size variation in the pied flycatcher *Ficedula hypoleuca*. Ibis, 131: 572-577.

Kokko, H. 1999. Competition for early arrival in migratory birds. Journal of Animal Ecology, 68: 940-950.

Lack, D. 1947. The significance of clutch-size. Ibis, 89: 302-352.

McKinnon, E.A., C.Q. Stanley, and B.J.M. Stutchbury. 2015. Carry-over effects of nonbreeding habitat on start-to-finish spring migration performance of a songbird. PLoS ONE, 10: e0141580.

Nebel, S., A. Mills, J.D. McCracken, and P.D. Taylor. 2010. Declines of Aerial Insectivores in North America Follow a Geographic Gradient. Avian Conservation and Ecology, 5: 1-14.

Newton, I. 2004. Review: Population limitation in migrants. Ibis, 146: 197-226.

Nisbet, I.C.T. and L. Medway. 1972 Dispersion, population ecology and migration of eastern great reed warblers *Acrocephalus orientalis* wintering in Malaysia. The Ibis, 114: 451-494.

Norris, D.R. 2005. Carry-over effects and habitat quality in migratory populations. Oikos, 109: 178-186.

Orell, M. and M. Ojanen. 1983. Effect of habitat, date of laying and density on clutch size of the great tit *Praus major* in Northern Finland. Holarctic Ecology, 6: 413-423.

Ouwehand, J. and C. Both. 2017. African departure rather than migration seed determines variation in spring arrival in pied flycatchers. Journal of Animal Ecology, 86: 88-97.

Pfister, C., M.J. Kasprzyk and B.A. Harrington. 1998. Body-fat levels and annual return in migrating semipalmated sandpipers. The Auk, 115: 904-915.

Rappole, J.H. and M.V. McDonald. 1994. Cause and effect in population declines of migratory birds. The Auk, 111: 652-660.

Rose, A.P. 2009. Temporal and individual variation in offspring provisioning by tree swallows: a new method of automated nest attendance monitoring. PLoS ONE, 4: e4111.

Rose, A.P., and B.E. Lyon. 2013. Day length, reproductive effort, and the avian latitudinal clutch size gradient. Ecology, 94: 1327-1337.

Sanz, J.J. 1999. Does daylength explain the latitudinal variation in clutch size of pied flycatchers *Ficedula hypoleuca*? Ibis, 141: 100-106.

Schaub, M., H. Jakober, and W. Stabber. 2011. Demographic response to environmental variation in breeding, stopover and non-breeding areas in a migratory passerine. Ecologic, 167: 445-459.

Schwagmeyer, P.L. and D.W. Mock. 2008. Parental provisioning and offspring fitness: size matters. Animal Behaviour, 75: 291-298.

Sillett, T.S. and R.T. Holmes. 2002. Variation in survivorship of a migratory songbird through its annual cycle. Journal of Animal Ecology, 71: 296-308.

Smith, R.J., F.R. Moore, and C.A. May. 2007. Stopover habitat along the shoreline of northern Lake Huron, Michigan: emergent aquatic insects as a food resource for spring migrating landbirds. The Auk, 124: 107-121.

Soler, M. and J.J. Soler. 1992. Latitudinal: trends in clutch size in single brooded hole nesting bird species: a new hypothesis. Ardea, 80: 293-300.

Studds, C. and P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology, 86: 2380-2385.

Stutchbury, B.J.M., S.A. Tarof, T. Done, E. Gow, P.M. Kramer, J. Tautin, J.W. Fox, A. Vsevolod. 2009. Tracking long-distance songbird migration by using geolocators. Science, 323: 896-896.

Tautin, J., B. Cousens, K. Kostka, S. Kostka, and D.A. Airola. 2008. Addressing regional declines in purple martin populations. Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics, 82-87.

Wikelski, M., E. Tarlow, A. Raim, R.H. Diehl, R.P. Larkin, and G.H. Visser. 2003. Avian metabolism: costs of migration in free-flying songbirds. Nature, 423: 704-704.

Wilcove, D.S. and M. Wikelski. 2008. Going, going, gone: is animal migration disappearing. PLoS Biology, 6: e188.

Wilkin, T.A., L.E. King, and B.C. Sheldon. 2009. Habitat quality, nestling diet, and provisioning behaviour in great tits *Parus major*. Journal of Avian Biology, 40: 135-145.

Wilmers, C.C., B. Nickel, C.M. Bryce, J.A. Smith, R.E. Wheat, and V. Yovovich. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. Ecology, 96: 1741-1753.

Chapter 2: Carry-over effects from spring migration on reproduction in a long distance migratory aerial insectivore

Abstract

Migratory species can travel thousands of kilometers during the course of an annual cycle between over-wintering and breeding grounds. Previous studies have measured the carry-over impact of conditions experienced at the over-wintering grounds on reproduction, but the influence of factors experienced during migration have remained largely unstudied. With recent technological advances in biologging devices (light-level geolocators), it is now possible to track individual songbirds across their entire annual cycle providing the opportunity to examine carry-over effects from the migratory period for the first time. In a long-distance migratory songbird (purple martin *Progne subis),* I examined how factors from spring migration impacted the number of days between arrival at the breeding grounds and first egg date, clutch size, fledging success, and provisioning levels. Birds that departed their overwintering sites later and had a higher number of migratory stopovers had fewer days between arrival at breeding sites and first egg date, demonstrating a carry-over effect of migration timing and stopover on breeding timing and behaviour. The duration of migratory stopovers and environmental conditions at stopovers (windspeed and precipitation) had weak carry-over effects on the number of offspring lost during the course of the breeding season. Although no carry-over effects on provisioning levels were found, the timing of breeding had an impact on provisioning levels. Overall, my results reveal that the timing of breeding and reproductive success are influenced by spatio-temporal and environmental factors during the spring migratory period. These factors could have critical implications for purple martins and other declining aerial insectivores considering current climate change across their breeding and migratory ranges.

Introduction

For species living in seasonal environments, factors acting outside of the breeding season can carry over to impact fitness (Fretwell 1972). Most studies of carry-over effects in migratory birds have examined how non-breeding factors impact body condition, migration timing, and/or reproductive success (Norris et al. 2004, Norris 2005, Both et al. 2006a, Harrison et al. 2011). Conditions at the wintering grounds and en route that allow for early arrival at the breeding grounds can allow for earlier breeding and increased fledging success (Norris et al. 2004, Saino et al. 2004, Rockwell et al. 2012).

In American redstarts (*Setophaga ruticilla*), females that overwintered in poorer-quality habitat in Jamaica fledged two fewer offspring at the North American breeding grounds than birds originating from higher quality winter habitat, which is quite significant considering this is a single brood species with an average clutch size of 3-5 offspring per season (Norris et al. 2004). Greater rainfall that is associated with higher habitat quality and food abundance at the overwintering grounds, has also been found to be correlated with better physical condition prior to migration, earlier spring migration departure, and higher return rates to the wintering grounds in the following year (Studds and Marra 2005, 2007, 2011).

There is evidence that some species are capable of modulating migration timing, which indicates departure date cannot be used as a predictor of arrival timing for all species and highlights the potential importance of carry-over effects from factors experienced while on migratory routes, particularly at stopover sites. Although poor body condition, particularly the loss of pectoral muscle mass caused by low food availability at winter habitats was found to delay spring departure in American redstarts and inferred to delay arrival at the breeding grounds (Cooper et al. 2015), wood thrushes (*Hylocichla mustelina*) that wintered in poor habitat (dry) were found to have faster (duration) and shorter (distance) migrations to compensate for later

13

spring departures (McKinnon et al. 2015). This modulation of migration timing indicates departure cannot be used as a predictor of arrival for all species and highlights the potential importance of carry-over effects from factors experienced while on migratory routes, particularly at stopover sites. Migratory songbirds have been shown to use double the amount of energy during stopovers compared to migratory flight (Wikelski et al. 2003) highlighting the importance of stopovers on the energetics and timing of migration.

One way in which migration timing may be modulated is through different use of migratory stopovers. Conditions at migratory stopover sites can have significant impacts on body condition and migration timing in migratory birds, which is expected to have a carry-over influence on survival and reproduction (Newton 2004). Since factors at migratory stopovers, such as weather, habitat quality, and food availability can impact the body condition and survival of an individual these factors have the opportunity to impact a bird's fitness (Newton 2004). Variability in the duration of stopovers, may indicate a trade-off between the advantages of early arrival at future destinations (via shorter stopovers) with the insurance of higher fuel levels (obtained during longer stopovers) leading to increased survival (Pfister et al. 1998, Baker et al. 2004, Smith et al. 2007). Conditions at stopovers are just beginning to receive research attention as the importance of impacts that stopovers have on energetics are being realized and as technology for tracking small songbirds improves. Migratory songbirds have been shown to use double the amount of energy during stopovers compared to migratory flight (Wikelski et al. 2003), highlighting the importance of stopovers.

Research to date on carry-over effects from migratory stopovers has mostly been on shorebirds and waterfowl that use a few critical refueling sites during their migration (Newton 2004), but there has been little research on these effects in migratory songbirds that adopt a fly-

and-forage migration strategy, where stopover refueling opportunities are potentially more variable and stopover conditions may have different impacts (Alerstam and Lindström 1990, Strandberg and Alerstam 2007). A few studies have examined the connection between the duration and quality of stopovers and resulting spring body condition prior to departing the stopover in migratory songbirds (Nisbet and Medway 1972, Bearhop et al. 2004, Bauchinger et al. 2008) but they have not been able to directly link factors from stopovers to reproductive success. A study on red-backed shrikes *Lanius collurio* across years found habitat quality at broad-scale fall stopover locations had a carry-over effect on probability of successful reproduction and level of reproductive output in the following breeding season (Schaub et al. 2011). However, Schaub et al. (2011) was unable to identify specific conditions individuals experienced and how that impacted their reproduction. One of the few studies that have examined carry-over effects from migration to reproduction in a songbird found that wind and precipitation conditions experienced during spring migration best described the variation in the timing of breeding of yellow warblers (*Setophaga petechia*), which was strongly linked to annual productivity (Drake et al. 2014).

Changes in weather and/or food availability along migration may impact the route a migrant takes (Hahn et al. 2014), or the duration it must spend at stopovers before being able to continue migrating (Ahola et al. 2004). Precipitation and wind speed are important aspects of weather that have been examined in relation to stopover durations and departure decisions (Tsvey et al. 2007). Levels of precipitation experienced at long staging areas on migration have been found to impact future body condition (Sorensen et al. 2016). Warming temperature in the spring during migration and at the breeding grounds may not only impact birds during migration but also at the breeding grounds (Both 2010). There is evidence that some migrants may be able

to modulate their migration to track environmental conditions within and across continents en route to maximize their access to optimal seasonal resources throughout the migration (Tøttrup et al. 2008, Thorup et al. 2017). A theoretical investigation found that even a small reduction in maximum refueling due to suboptimal foraging at a stopover has the potential to cause a significant decrease in reproductive success (Weber et al. 1999) suggesting weather factors that impact refueling abilities of migrants are likely to have carry-over effects on reproduction.

With climate change having different effects at different latitudes, long distance migrants are faced with advancing spring phenology and peak food abundances at the breeding grounds but unreliable cues at the overwintering grounds to indicate what departure date and timing of migration are optimal. Such changes have the potential to result in mismatches between peak food abundances and provisioning requirements for young (Both and Visser 2001, Weidinger and Kral 2007). Increasing spring temperatures that advance egg laying without advancing arrival at the breeding grounds result in the interval between arrival and egg laying decreasing (Both and Visser 2001, Weidinger and Kral 2007). Migrants that arrive at the breeding grounds earlier and with greater fat stores have been shown to begin breeding earlier and have greater reproductive success (Smith and Moore 2003). However, the arrival to first egg interval is not always driven by the time it takes for an individual to obtain sufficient energy requirements. Secondary cavity nesters often have early arrival relative to egg laying due to the limited number and quality of cavities available for nesting, but can have variable lengths of time between settlement of a cavity and egg laying, with individuals that secure a cavity late having shorter periods before egg laying (Stutchbury and Robertson 1987; Morton and Derrickson 1990).

When carry-over effects on reproduction have been examined, clutch size, fledging success, or the timing of reproduction are the typical aspects of reproduction studied, although

other energetic aspects of reproduction may also be impacted. For example, parental provisioning rates may be impacted by individual condition (Tveraa et al. 1998, Markman et al. 2002, Boyle et al. 2012) and can have important fitness impacts (Schwagmeyer and Mock 2008, Wilkin et al. 2009). Thus, understanding factors contributing to variability in provisioning may provide important clues into how carry-over effects from migration may influence fitness.

Both intrinsic and extrinsic factors influencing parental provisioning rates have been examined (Wiebe and Elchuk 2003). Intrinsic factors include age (Mulder and Magrath 1994, Forslund and Part 1995), sex (Wagner et al. 1996, Daunt et al. 2001), brood size (Wagner et al. 1996, Sanz et al. 2000), and breeding latitude (Sanz 1999, Rose and Lyon 2013). Higher quality individuals are typically indicated by earlier clutch initiation (Ewald and Rohwer 1982, Perrins 1970, Rowe et al. 1994), which has also been implicated in provisioning levels (Hatchwell 1991). There have been mixed results as to how provisioning is affected by brood size, with evidence that in some species provisioning levels are modified in relation to brood size (Sanz et al. 2000) and in others provisioning does not linearly increase with brood size meaning larger broods are fed less per young (Wagner et al. 1996). Increased daylight hours at more northern latitudes may allow for longer 'work days' leading to greater chick mass (Rose and Lyon 2013) and shorter nestling periods (Sanz 1999). Extrinsic factors impacting provisioning are climatic factors, including temperature, wind speed and precipitation (Wiebe and Elchuk 2003, Hoset et al. 2004, Perez et al. 2008, Rose 2009). In addition, climatic factors have been shown to have significant implications on fitness at the breeding grounds through thermoregulatory costs (Allen and Nice 1952, Perez et al. 2008) and by impacting food availability, particularly aerial insects (Glick 1939, Rose 2009). Low temperature, high winds, and precipitation all have the potential

to reduce both aerial insect activity (Glick 1939) and provisioning activity by birds (Wiebe and Elchuk 2003, Hoset et al. 2004, Rose 2009).

New bio-logging technologies (e.g. light-level geolocators) that allow for the tracking of small (<60g) migratory songbirds during an entire annual cycle (Stutchbury et al. 2009, McKinnon et al. 2013) provide new opportunities to study migration timing and environmental factors that birds experience on migration. In combination with other new technologies that automate the recording of parental provisioning activity (radio-frequency identification tags and receivers) allowing for individual variation in provisioning to be quantified (Rose 2009), the influence of carry-over effects from spring migration on parental provisioning can be examined for the first time.

Purple martins are a Neotropical long-distance migratory aerial insectivore that journeys annually between South American overwintering sites and breeding sites in North America (Brown and Tarof 2013, Fraser et al. 2012). Purple martins are experiencing steep population declines across much of their range, particularly at more northern breeding latitudes (Nebel et al. 2010, Michel et al. 2016). By understanding how factors across the annual cycle impact fitness, we may gain a better understanding of what may be leading to the declines of purple martins.

The objective of this study was to simultaneously examine how multiple intrinsic and extrinsic factors experienced during spring migration and at the breeding grounds influence arrival to first egg interval (the number of days between spring arrival date at the breeding sites and first egg date), clutch size, fledging success, and nestling provisioning levels of the purple martin. The factors from spring migration that were examined for their potential to have carry-over effects on reproduction included environmental conditions experienced at stopovers (minimum temperature, average wind speed, sum rainfall), the length of time spent at stopovers

and the timing of migration. I also examined how factors at the breeding grounds impacted

purple martins in combination with the carryover effects they experienced, including intrinsic

factors (age, sex, breeding latitude), environmental conditions (average temperature, average

wind speed, sum rainfall), partner's provisioning, and hatch date.

Methods

Geolocator deployment, use, and analysis

Purple martins were outfitted with geolocators to track the length, timing, and location of

their spring migration to analyze potential carry-over effects from spring migration on breeding.

Geolocators were deployed at the nine locations described above and retrieved at the same

breeding sites in the following year by recapturing the birds at their nest boxes. Breeding activity

(as described below) was recorded for all birds returning with a geolocator when a nest site could

be identified (n= 79) (Table 2.1). Geolocators were deployed on purple martins using a Rappole-

Tipton leg-loop harness of Teflon ribbon (Fraser et al. 2012) and were marked with a federal leg

band and aged and sexed based on adult plumage (Pyle 1997). All geolocator models used

weighed ≤ 1.6g to meet the specification set by Guidelines to the Use of Wild Birds in Research

(Fair et al. 2010) that geolocators be less than 5% of the birds' body mass.

The light-level data from geolocators were analyzed in the program BASTrak (BASTrak

2015). The program converts data from the geolocators into light transitions where sunsets and

sunrises were assessed to determine the latitude and longitude of the bird at midnight each day,

since purple martins migrate during the day and roost at night (Fraser et al. 2012). Only

longitudes were estimated for the 15 days before and after both the fall and spring equinox since

light transitions during this period are similar across latitudes. Light transitions were assigned a

confidence interval to determine the accuracy of the locations. Locations with large intervals

were considered unreliable (typically caused by poor light data due to various types of shading) and were not used in future analyses. The remaining locations were used to map overwintering roosts, stopover sites, migration routes, distances traveled, and migration rates of each bird. Stopover sites were defined as any time that the latitude and longitude did not differ by more than two degrees (~222km) from one midnight to the next since geolocator error for purple martins was previously estimated to be at most 210km in latitude and 196km in longitude (Fraser et al. 2012). See Fraser et al. (2012) and Fraser et al. (2013) for additional methodological details.

Nest monitoring

Nest boxes were monitored through the breeding season to record breeding activity at nine locations across North America, including Alberta (52°23'24"N, -113°36'36"W), two locations in Minnesota (46°21'36"N, -94°11'24"W; 46°9'36"N, -93°43'48"W), South Dakota (45°36'36"N, -98°18'36"W), Pennsylvania (42°7'48"N, -80°5'24"W), New Jersey (40°23'24"N, -74°1'48"W), Virginia (38°36'36"N, -77°9'0"W), and two locations in Florida (28°21'12"N, -81°35'24"W; 26°8'60"N, -81°45'0"W). The breeding activity that was measured was the date the first egg was laid in a nest (nest initiation), number of eggs laid (clutch size), date eggs hatched (hatch date; chick age 0 days), number of eggs hatched (nestlings), earliest estimated date young fledged (fledge date; chick age 25 days), and the number of young that fledged from each nest (fledglings). Nest initiation and hatch date were estimated by aging chicks using a standardized set of life-sized pictures of young at each day of development (Purple Martin Conservation Association 2015) and back-calculating dates using known intervals for laying and incubation. Fledge date was estimated based on the earliest age purple martin chicks fledge (25 days) and typically survive. Fledgling number was defined as nestling number minus the number of young found dead or missing from the nest prior to the calculated earliest fledge date.

Radio frequency identification (RFID) use and analysis

     RFID was used to measure parental visits at nest cavities as an indicator of parental provisioning. RFID technology records the presence/absence of a passive integrated transponder (PIT) tag by logging the time and unique identification number associated with the PIT tag detected. Antennas, used to detect the PIT tags, were placed level with the entrance of nest cavities to record the entrances and exits of any purple martin with a PIT tag. An 8mm long PIT tag was secured to a plastic coloured leg band and the unique identification number associated with the PIT tag was recorded for the bird with that band. RFID units (composed of an antenna, computer board to log data on a SD card and batteries) were set up at the entrance of nest boxes of birds with a PIT tag (Figure A1a). RFID units were maintained with periodic battery changes and periodically downloading the data saved on a SD card in the unit.

     Purple martins were monitored with radio frequency identification (RFID) technology at two sites, Ellis Bird Farm in Alberta (52°23'27"N, 113°36'40"W) and Disney's Animal Kingdom in Florida (28°21'00"N, 81°35'15"W). In Alberta, 12 nests were monitored in 2015 from May 19 to Aug 22, and eight nests were monitored in 2016 from June 30 to August 11. In Florida, 11 nests were monitored in 2016 from May 10 to June 9. Of the 31 nests monitored, 19 (7 from Florida, 10 from Alberta in 2015, 2 from Alberta in 2016) were used in the analysis due to nests failing to hatch, both adults at the nest not being monitored, or RFID unit failure. Data recorded from June 30 to August 11, 2015 and July 1 to July 28, 2016 in Alberta, and from May 10 to June 9, 2016 in Florida were used in the analysis to focus on visitation during the nestling stage (hatch date to earliest fledge date) to estimate provisioning (i.e., number of nest visits per day). In total 38 birds were monitored from the time that eggs hatched to when young were 25 days old for a total of 680 daily provisioning estimations that were used in the analysis. For some

nests, daily provisioning estimates were not available on all days due to battery and/or antenna failure of the RFID unit.

Because RFID technology does not directly measure provisioning, nest observations were performed to determine what percentage of trips to the nest involved provisioning of young. Observations were made in the later part of the nesting period (> 14 chick age) when chicks were beginning to beg for food at the nest entrance and/or parents were bringing larger food items so provisioning events could be more accurately documented. It should be noted that this method is potentially biased if the proportion of nest visits involving provisioning changes with chick age. Six nests were simultaneously observed with binoculars from a distance of approximately 15m for 1 hour a day for 5 days. Of the 626 observed nest visits, parents brought food to the nest 75% of the time (471) (Figure A1b). Of the trips made that did not involve provisioning, 62% (96 of 155) involved nest sanitation through fecal sac removal (Figure A1c). Given that RFID data was not used to estimate the amount of food that was delivered to young, manual observation supported the use of RFID data as a good indicator of parental provisioning specifically and more generally of parental effort.

Any clock drift of the RFID unit was corrected for by taking the difference between the recorded time and the observed (actual) time at battery changes throughout the monitoring period. The average difference between recorded and actual time for the entire monitoring period was used as the correction factor for the time at which bird activity was recorded. Since RIFD only records presence or absence and not whether the event was an entrance or exit, any time more than one event for an individual bird was recorded within a minute only one event for that minute was counted. Although it is possible that a bird entered and exited in different minutes, which would result in an overestimation of provisioning, removing multiple events within a

minute was used to remove multiple events within a short time (which was assumed to be a result of the bird standing on the antenna for an extended period) to be more representative of provisioning activity. Manual observations were not made on a fine enough scale for a test of how many entrance/exit events occurred in different minutes. However, Wilkin et al. (2009) found that over 90% of Great Tits (*Parus major*) visits at their nest box were less than 30 seconds; in addition, purple martins in Oklahoma that were provisioning young were found to have foraging trips that lasted from 80-2250 seconds (Helms et al. 2016), suggesting we were not likely to be removing provisioning events. At the very least the potential overestimation of provisioning is not expected to differ among individuals, making the number of events recorded for a bird each day of the monitoring period (daily number of visits) that was used an indicator of provisioning a good relative parental effort measure.

Weather variable collection

Weather variables were collected from an online historical data source (weather underground) to estimate the conditions birds experienced during migration. The closest weather station to the location of the bird at stopovers was used to determine the weather at the time that the bird was present. The distance between the location of interest and weather stations ranged from 5km to 561km and was on average 144km apart.

Maximum, minimum, and mean temperature, average wind speed, and sum precipitation at the breeding grounds was collected on a daily basis for the periods of interest, including provisioning monitoring periods, arrival to first egg interval, and first egg to earliest estimated fledge date. Mean temperature was used for provisioning monitoring periods because provisioning levels were based on daily values so mean temperature would be more representative of the overall conditions impacting provisioning rather than the short periods at

which birds would have experienced maximum or minimum temperatures. Minimum

temperature was used for the period from arrival to first egg since early in the breeding typically

has the greatest risk of more extreme minimums that have been shown to have stronger impacts

on purple martin foraging activity than mean or maximum temperatures (Finlay 1976).

Maximum temperature was used for the date of first egg to earliest fledge date because this

period was examined in relation to the number of offspring lost where extreme heat has been

predicted to have the greatest impact on causing mortality (Allen and Nice 1952).

Minimum temperatures, average wind speed and sum precipitation was collected on a

daily basis for each stopover location. Temperatures and wind speed were averaged by the total

number of days spent on stopovers during the entire spring migration, and precipitation was

summed for the total number of days spent on stopovers.

Statistical analysis

Generalized linear models (GLMs) and generalized linear mixed models (GLMMs) (Zuur

et al. 2009) were used to examine factors from the breeding grounds and spring migration

impacting four aspects of reproduction (arrival to first egg interval, clutch size, fledging success,

provisioning) of purple martins to understand carry-over effects from spring migration. A set of

models were formed for each response variable to include a null model, a global model that

included all variables of interest, and a set of models based on *a priori* hypotheses developed

from factors discussed in the literature to have potential impacts on each response variable of

interest. Since the relative importance of the effects of different variables was the main interest

of this study each variable was centered and standardized to have a mean of 0 and a standard

deviation of 1 so they were all on the same scale and could be compared to one another (Grueber

et al. 2011). To avoid the problem of collinearity among fixed effects in models only variables

with a pairwise correlation coefficient (|r|) less than 0.7 were included together in models (Dormann et al. 2012). Since there is no agreed upon goodness-of-fit test for mixed models, model validation was visually assessed according to Zuur et al. (2009) for the global model of each response variable.

Factors impacting arrival to first egg interval:

Spring migration and breeding ground factors were included in analyses of effects on the arrival to first egg interval. Since not all individuals used in this analysis were tracked during the same years (n=7) nor from the same colony (n=9), random effects for year and colony were included in model comparisons to determine which should be included. The global fixed effect model was compared with no random factors, one random factor, or both random factors. Based on model comparison with ΔAICc the best model was the one including only year as a random factor. Therefore, GLMMs with year as a random factor were used to examine the impacts that aspects of spring migration have on the arrival to first egg interval for an individual (n=64). In the case of Florida and Minnesota, which each had two colony sites located close to one another (Table 2.1), individuals were grouped into one colony site for the analysis (i.e. colony n=7). A zero-truncated negative binomial error distribution fit by Laplace approximation of maximum likelihoods was used because of the impossibility of the arrival to first egg interval being zero (i.e. having both events occur on the same date) and the data was over-dispersed count data.

Six models were fit with fixed effects from both the spring migration and breeding grounds: 1) a null model that only included the random effect; 2) a breeding ground weather model that included sum precipitation from arrival to first egg; 3) a spring stopover weather model that included sum precipitation and average wind speed experienced at stopovers; 4) a spring migration timing model that included the departure date from the wintering grounds and

breeding latitude; 5) a spring stopover model that included the number of days spent at stopovers; 6) a global model that included all variables included in the previous models. Although age may impact the arrival to first egg interval there were not enough birds from each age class from each colony to include this as a factor in these models.

Factors impacting clutch size:

Only spring migration factors were included in analyses of effects on clutch size since a larger dataset of geolocator tracked individuals with known clutch size but unknown first egg date or chick age were available; therefore, conditions at the breeding grounds could not be determined for this analysis. The same procedure as described for the analysis of factors impacting the arrival to first egg interval was used to determine if years and/or colony should be included as random effects. Based on comparison of ΔAICc the best model was the one including neither year nor colony as random factors in the model. Therefore, GLMs with a zero-truncated Poisson error distribution fit by Laplace approximation of maximum likelihoods were used to examine if factors from spring migration influence clutch size (n=79) since it was count data without failed nesting attempts (i.e. the only way there could be a zero-clutch size) recorded.

Six models were fit using the following fixed effects: 1) a null model that included no effects; 2) a spring migration timing model that included departure date from the wintering grounds and arrival date at the breeding grounds; 3) a spring migration model that included the distance traveled and the number of days spent at stopovers during spring migration; 4) an intrinsic model that included age, sex and breeding latitude; 5) a spring stopover weather model that included the sum precipitation, average wind speed, and average temperature experienced at stopovers; 6) a global model that included all variables included in the previous models.

Factors impacting fledging success:

The impacts of spring migration and breeding ground conditions on the number of offspring lost (i.e. number of eggs that did not hatch and/or young that died; n=64) was examined with a GLM since a comparison of ΔAICc indicated that the global model with neither year nor colony as a random effect was better than including either as random effects. A zero-inflated negative binomial error distribution fit by Laplace approximation of maximum likelihoods was used to deal with the over-dispersed count data with a large number of zeros.

Seven models were fit with fixed effects from both the breeding grounds and spring migration: 1) a null model that included no effects; 2) a breeding ground weather model that included the average maximum temperature and sum precipitation from first egg to earliest estimated fledge date; 3) a spring stopover weather model that included the average wind speed and sum precipitation experienced at stopovers; 4) a spring stopover model that included the number of days spent at stopovers; 5) a spring migration timing model that included the departure date from the wintering grounds and the breeding latitude; 6) a breeding timing model that included the arrival to first egg interval; 7) a global model that included all variables included in the previous models. Although age may impact fledging success there were not enough birds from each age class from each colony to include this as a factor in these models.

Factors impacting provisioning:

Spring migration and breeding ground factors were included in the analysis of effects on provisioning. To examine the factors at the breeding grounds impacting total daily provisioning levels, estimated from number of visits at the nest (n=680) I used GLMMs fit by Laplace approximation of maximum likelihood. Individual (n=38) was included as a random effect in all models to account for the lack of independence of the repeated measures of daily visits by each

individual from hatch date to when chicks were 25 days old. I used a negative binomial error distribution because daily provisioning was determined to be over-dispersed.

Five models were created: 1) a null model that included only the random effect; 2) a breeding quality model that included the hatch date relative to the colony, number of nestlings, and provisioning level of the partner; 3) a breeding weather model that included the daily mean temperature, average wind speed, and sum precipitation; 4) an intrinsic model that included sex and breeding colony. There were not enough birds in the second-year age class to compare with the after second year age class, so this variable was not used; 5) a global model that included all variables included in the previous models. Although age may impact the provisioning level of an individual there were not enough birds from each age class from each colony to include this as a factor in these models.

GLMs with negative binomial error distribution were used to examine how past events from spring migration impact nest provisioning levels. Thirteen purple martins were tracked with geolocators and monitored with RFID the breeding season after returning with a geolocator. Due to RFID unit failure, all of these individuals were not monitored for the same length of time so RFID data was summed from chick age 4-14 (days) for 11 birds and from chick age 15-25 (days) for 8 birds to examine potential carry over effects of spring migration on provisioning. Sum provisioning from the first half and the second half of the nestling period were used as response variables to maximize the sample size and examine if carry-over effects manifest differently through the breeding season. This analysis had no random effects since a sum of the same portion of the nestling period for each individual was only included in the analysis once.

Seven models were fit using fixed factors from both the breeding grounds and spring migration period: 1) a null model that included no effects; 2) a breeding quality model that only included provisioning level of the partner since it was found to have the greatest effect of the factors in the breeding quality model for daily provisioning level; 3) a breeding weather model that only included the sum precipitation from the nestling period of interest since it was found to have the greatest effect of the factors in the breeding weather model for daily provisioning level; 4) a spring stopover model that included the number of days spent at stopovers; 5) a timing model that included the date of departure from the wintering grounds and the arrival to first egg interval; 6) a spring stopover weather model that included the sum precipitation experienced at stopovers; 7) a global model that included all variables included in the previous models.

Due to the small sample size, all the weather variables experienced at spring migration stopovers could not be used in the analysis of carry-over effects on provisioning. Only sum precipitation was used since precipitation from nonbreeding (Studds and Marra 2007, 2011) and migration (Sorensen et al. 2016) have been shown to have significant impacts on the timing of migration and body condition of migratory songbirds. The same variables and model set up was used for early and late nestling period as the early nestling period. However, since there was a smaller sample size for the late nestling period the breeding ground model and the migration model, which explained the least amount of variation from the early nestling period, were removed from the analysis of the late nestling period, for a total of five models.

For each response variable, model comparison was based on information criterion. Akaike Information Criterion with a correction for small sample sizes (AICc) was used to determine the top models (ΔAICc < 6) and these were model averaged due to uncertainty in the best model when there were multiple top models (Symonds and Moussalli 2011, Burnham et al.

2011, Grueber et al. 2011). Model averaging with shrinkage was used to determine which factors among the top models were having the strongest effects (Symonds and Moussalli 2011, Burnham et al. 2011, Grueber et al. 2011). Akaike model weights (w_i) were used to determine the relative support of each model. Although there are potential biases with using Akaike Information Criterion for mixed models in terms of the interpretation of random effects (Liang et al. 2008, Greven and Kneib, 2010), these effects were not of central interest to the research questions of this study I did not anticipate this would influence the main interpretation of my results.

To run GLMs with a negative binomial error distribution the package "MASS" was used (Venables and Ripley 2002). All GLMMs with a negative binomial error distribution were run using the "lme4" package (Bates et al. 2015) and the "numDeriv" package (Gilbert and Varadhan 2016) was used to solve warnings associated with these models. Models with either a zero-truncated Poisson or zero-inflated negative binomial error distribution were fit using the package "glmmADMB" (Fournier et al. 2012). Packages "AICcmodavg" (Mazerolle 2016) and "MuMIn" (Barton 2016) were used for model selection with AICc of the negative binomial GLMMs and the zero-truncated/inflated models respectively. All analyses were conducted in 3.3.1 R (R Core Team 2016).

Results

Factors impacting the interval between arrival and first egg:

The global model of factors impacting arrival to first egg interval was the only model with support ($w_i = 1.00$) suggesting there is more variation in this interval than can be explained by the variables included in this analysis (Table 2.2). Four variables had model averaged parameter estimates with confidence intervals that did not span zero, suggesting these variables have an effect on the length of the arrival to first egg interval. Date of departure from the

overwintering grounds (-0.3619±0.0575) (Figure 2.1a) and the number of days spent on stopovers (-0.0597±0.0289) both had a negative effect (Figure 2.1b), whereas latitude of breeding colony (0.2112±0.0597) (Figure 2.1c) and sum precipitation at the breeding grounds from arrival to first egg (0.1566±0.0280) had positive effects on the length of the arrival to first egg interval (Figure 2.1d).

Factors impacting clutch size:

The null model was the top model ($w_i = 0.74$) in the analysis of factors from spring migration impacting clutch size (Table 2.2), and all parameters had confidence intervals that spanned zero indicating no effects (Table 2.3). There is no evidence that factors from spring migration are having carry-over effects on the clutch size of purple martins.

Factors impacting fledging success:

There was a high degree of model uncertainty in the analysis of factors impacting the fledging success, with only one model, the global model, not included in the top models at a cut-off of ΔAICc < 6. The breeding ground weather model ranked as the top model ($w_i = 0.56$) followed by the spring stopover model ($w_i = 0.15$) and spring stopover weather model ($w_i = 0.10$) before the null model ($w_i = 0.09$) (Table 2.2) indicating that the number of stopover days and the weather experienced at stopovers explained slightly more variation in the data than the null model. Number of stopover days and spring stopover precipitation and windspeed all had negative parameter estimates but confidence intervals that spanned zero indicating they were not influencing fledging success. Two factors in the top models had model averaged parameter estimates that had confidence intervals that did not span zero; breeding grounds average maximum temperature had a positive effect (0.3107±0.1546) and breeding grounds sum precipitation had a negative effect (-0.3200±0.1510) on the number of young lost (Table 2.3).

Factors impacting provisioning:

There was more variation in daily provisioning than could be explained by the variables examined as indicated by the global model ($w_i = 1.00$) being the top model. Neither the breeding quality model nor the breeding weather model were good predictors of daily provisioning but were better than the null model, with the intrinsic model having the lowest ranking (Table 2.2). Of the standardized estimates from the top model, there were four variables with confidence intervals that did not span zero indicating they had an effect on provisioning; daily provisioning level of an individual's partner had a positive effect (0.4047 ± 0.0304) and sex had a positive effect (males: 0.2917 ± 0.0959) on provisioning level whereas scaled hatch date had a negative effect (-0.2190 ± 0.0651) and sum precipitation had a negative effect (-0.0998 ± 0.0253) on provisioning levels (Table 2.3).

There was no evidence of carry-over effects on provisioning early in the nestling period (chick age 4-14 days) as the top models ($\Delta AICc < 6$) were all related to breeding ground effects. The best model was the breeding ground weather model ($w_i = 0.72$), with some support for the second ranked model which was the breeding quality model ($w_i = 0.23$) (Table 2.2). Partner provisioning level had a positive effect (0.4103 ± 0.2626) and was the largest effect of the model averaged parameter estimates of the top models for sum provisioning early in the nestling period. Although all of the variables had a confidence interval that spanned zero indicating no effect (Table 2.3).

There was not strong evidence for carry-over effects on provisioning during the latter part of the nestling period (chick age 15-25 days). The null model was the best model ($w_i = 0.53$) with the breeding quality model a close second ($w_i = 0.40$) (Table 2.2). Further the only model that was not in the top models was the global model, presumably due to over-parametrization

associated with the small sample size and large number of variables in the global model. All variables had confidence intervals that spanned zero (Table 2.3) meaning variables had no effect on the sum provisioning during the late nestling period. Despite no effects being found, the small sample size prevents any conclusions from being made on carry-over effects from spring migration on provisioning, neither in the early nor late part of the nestling period.

Discussion

My results demonstrate for the first time a carry-over influence of spring migration timing and stopover behaviour on subsequent reproduction in a migratory songbird. I found that birds with a later spring migration departure date and a greater number of stopover days had fewer days between their arrival date and first egg date. Arrival to first egg interval was also shorter for individuals breeding at lower latitudes (except for birds breeding at Florida colonies) and that experienced lower levels of precipitation at the breeding grounds. There was some weak evidence that greater number of stopover days and weather (wind speed and precipitation) at stopovers had carry-over effects on the number of offspring lost during the course of the breeding season, in that the model with number of stopover days and the model with stopover weather were ranked among the top models, above the null model. However, the only factors that were found to have an effect on fledging success of purple martins were higher maximum temperature and lower precipitation at the breeding grounds.

Timing of events both on the breeding grounds and from spring migration were important factors in the reproductive activities of purple martins. Birds that departed the wintering grounds later had a shorter arrival to first egg interval at the breeding grounds. In addition, birds with young that had a later hatch date relative to other birds in the colony had lower provisioning

33

levels, potentially due to late breeders often being poor quality, and/or inexperienced, individuals and therefore poorer at provisioning.

Carry-over effects on reproduction

Arrival to First Egg Interval

Breeding timing has been well documented as an important factor influencing clutch size and probability of recruitment (Perrins 1970, Rowe et al. 1994). Purple martins that arrived late at the breeding grounds had shorter intervals to egg laying (Figure 2.2). This interval may serve as a buffer, with which migrants have some flexibility in the timing of first egg date after they have completed migration. Since birds with a shorter arrival-first egg interval did not have lower provisioning or lose more offspring, the duration of this interval may not have direct or immediate fitness costs, but longer-term effects on adults or young, for example reduced survival to the following breeding season, requires further investigation.

If birds have higher food availability at stopover sites than they would have if they arrived early at the breeding grounds it may be beneficial for later migrants to spend more time at stopovers. There have been accounts of large numbers of purple martins starving at the breeding grounds because they arrived too early and were exposed to prolonged cold snaps resulting in low to no food availability (Allen and Nice 1952). Although competition and depleted food resources at stopovers are often discussed as factors influencing migrants to minimize time spent at stopovers (Moore and Yong 1991), these factors may not be strong driving forces for purple martins. While geographical and seasonal variation in food availability in the Amazon and along migratory routes is poorly understood (Stutchbury et al. 2016), food may be less of a limiting resource for migrating aerial insectivores as they can forage in flight even when food is at low densities while searching for stopover locations with greater food

resources. In addition, there was weak evidence of stopover duration during spring migration impacting the number of offspring lost, suggesting the refueling taking place at stopovers can influence future breeding performance. However, I found no significant effect of arrival to first egg interval on clutch size or fledge success, which seems to indicate that purple martins can use the arrival to first egg interval as a buffer during which they can modify its length to maintain optimal first egg date while not negatively impacting reproductive success. Purple martins were found to be constrained by their breeding timing, as indicated by individuals with nests that hatched late among the colony having lower provisioning levels, potentially due to reduced food availability and/or lower individual quality. If later nests experience lower food availability it would be adaptive for later arriving birds to minimize the arrival to first egg date interval to avoid, or reduce, further delay of the timing of the nest.

Greater levels of precipitation a bird experienced at the breeding grounds during the arrival to first egg interval was found to increase the length of this period. Given that weather is closely related to insect abundance (Glick 1939), the association between poor weather and breeding timing was likely the result of low food availability causing individuals to take longer to get into breeding condition. Although precipitation is potentially beneficial for increasing future food availability as purple martins mainly rely on aerial insects with an aquatic life stage (Walsh 1978, Jones et al. in prep), this study has shown that the precipitation experienced can also have negative impacts on three aspects of reproduction including arrival to first egg interval, provisioning, and number of offspring lost.

Although this analysis showed a positive effect of breeding latitude on the length of arrival to first egg interval, suggesting that martins breeding at more northern latitudes had longer intervals, Florida was a clear exception to this trend and southern colonies were not well

represented in this dataset (Figure 2.3). Considering the strong positive correlation between arrival date and breeding latitude (northern breeders arrive later at breeding grounds) (Figure 2.2) it is unlikely that this latitudinal trend in arrival to first egg interval is representative of the entire purple martin breeding range. The positive trend found could suggest that purple martins at northern latitudes are more constrained in their ability to shorten this interval due to greater energy requirements of longer migration and time constraints due to the shorter breeding season with increasing latitude; particularly females that need to generate the resources to produce eggs. In addition, the finding that longer stopovers enabled shorter arrival to first egg intervals would further support that the positive trend between latitude and arrival to first egg interval may be due to northern birds being more time constrained, as it suggests that greater energy stores accumulated at stopovers allow for faster clutch initiation. However, since southern latitudes were not represented in this analysis apart from Florida, which showed the longest intervals, it is likely that breeding range wide the length of this interval shortens with increasing latitude due to shorter breeding seasons at more northern latitudes.

Fledging Success

There was a high degree of model uncertainty amongst the fledging success models but the model that included spring stopover days and the model that included weather factors experienced at stopovers had stronger support than the null model. Weather conditions at stopovers have been shown to have important impacts on energy expenditures at stopovers and the decision of when to depart stopovers (Wikelski et al. 2003, Tsvey et al. 2007). Overall refueling at stopovers appear to have the potential to not only important for an individual's ability to complete migration but also their ability to successfully raise young.

The variables that impacted the number of offspring lost were the average maximum temperature and the sum precipitation at the breeding grounds from first egg to earliest estimated fledge date. Purple martins with nests that experienced higher maximum temperatures and lower precipitation lost more offspring. Allen and Nice (1952) report extreme weather as one of the main reasons for partial or complete nest failure. Cold, rainy days resulted in low food availability and hot weather that drove nestlings from their nests prematurely, leading to falling from the nest box and abandonment (Allen and Nice 1952).

Although increased rainfall reduced provisioning levels on a daily basis, the greater number of offspring lost with lower rainfall throughout the breeding season suggests that precipitation has important impacts on food availability both on a short term and long-term basis through the breeding season. Allen and Nice (1952) reported that nestlings leaving the nest in an effort to escape heat are a common occurrence although most of these occurrences were during extreme heat waves above 32˚C. However, there were sites in this study, such as the most northern site in Alberta, that had no days above 32˚C, yet maximum temperature was still found to have an effect. This result suggests that higher temperatures (not specific to extreme heat waves) are having a greater negative effect on nest survival than reported in the 1950s. Further, the colony that had the greatest offspring loss relative to the average maximum temperature experienced (i.e. the farthest below the line of best fit) was the most northern colony where population trends are declining. The colony with the least offspring loss relative to average maximum temperature experienced (i.e. the farthest above the line of best fit) (Figure 2.4) was the most southern colony where population trends tend to be stable or even increasing (Michel et al. 2016). This may suggest that southern birds are better adapted to higher maximum temperatures. Considering the importance of weather, increasing temperatures and decreasing

precipitation due to climate change could lead to detrimental impacts on purple martins through negative effects on food availability and offspring mortality, which may be part of the reason behind their patterns of declines as a species across their breeding range. Dunn et al. (2011) suggest that aerial insectivores may not face a large fitness cost associated with climate change causing a mismatch in prey abundance as has been found in some species because they rely on a food source that is abundant or without a strong seasonal peak; however, these results suggest climate change may negatively impact purple martins in other ways.

Provisioning & Clutch Size

I found no evidence for carry-over effects on provisioning levels in the purple martin. Variables impacting sum provisioning during the first half of the nestling period (chick age 4-14) included those based on breeding ground factors but none of the model averaged parameters were found to have an effect. Sum provisioning during the second half of the nestling period (chick age 15-25) was not found to be impacted by any variables included in this analysis.

Despite all the migration models examined in relation to clutch size being in the top models at an AICc cut-off of 6, the null model was the top model and had much stronger support indicating that variation in the data was better explained by including no variables than including factors from migration.

Breeding ground factors impacting provisioning

Evidence of four factors at the breeding grounds impacting the parental provisioning of purple martins was found. The provisioning level of an individual's partner was found to have the strongest effect followed by sex, timing of hatch date relative to the colony (scaled hatch date), and daily sum precipitation in decreasing order of effect size.

Although this was not an manipulative study, the increase in provisioning with increased partner provisioning suggest that purple martins have a matching response rather than a compensatory response as has been found for other species. For example, an experimental study on supplemented broods of house sparrows (*Passer domesticus*) found that both parents increased provisioning of supplemented broods, with males showing a greater increase than females (Mock et al. 2005). The strength of this effect suggests that carry-over effects impacting an individual through timing of breeding and their condition influencing their breeding performance is compounded by pairing with a mate that may be similarly in poor breeding condition.

Greater provisioning of males compared to females found in purple martins could be a result of the greater pre-hatching energetic requirements of females reduce their ability to have high provisioning levels (Mock et al. 2005), or 2) paternal provisioning is a sexually selected trait that impacts a male's social status. The 'status hypothesis' suggest that the cost of not reducing parental provisioning when an individual has low confidence of paternity (i.e. provisioning young not genetically related) by male purple martins could be beneficial through increased social status the following breeding season (Wagner et al. 1992, 1996).

Individuals with earlier scaled hatch date having higher parental provisioning levels may suggest parental provisioning levels are an underlying mechanism impacting breeding success in relation to the timing of breeding. Timing of clutch initiation (first egg date) has been shown to have important impacts on fledging success of American redstarts (Norris et al. 2004). Birds with nests that hatched later had lower provisioning levels, which could indicate that earlier breeders were better able to match nestling rearing with peak food resources and as such can provision at a higher level. Alternatively, late breeders have been shown to have reduced clutch size, reduced

offspring survival, but higher adult survival (Brown and Brown 1999), suggesting late breeders may reduce energy put into provisioning late nests since the offspring potentially have lower survival rates while increasing their own survival to the next breeding season. However, this result may also be explained as late breeders being lower quality and/or inexperienced, thus having lower provisioning abilities. Further research would be needed to determine which of these explanations, or if both, are impacting the higher provisioning levels early breeders are capable of providing their offspring.

Precipitation had a negative effect on levels of provisioning in that purple martins visited their nests less frequently on days with greater amounts of rain. Climate change and changing spring phenology is giving rise to potential mismatches between timing of peak food abundance and peak food requirements (Both and Visser 2001, Both et al. 2006b), which may be magnified by lowered provisioning levels in poor weather. Although food abundance was not examined in this study, Walsh (1978) found that the use of certain insect families for provisioning young by purple martins significantly differed between years in association with weather trends. It is possible that the changes in purple martin provisioning associated with weather found in this study is also related to food availability, but future studies are needed to differentiate the impacts of weather versus food availability on purple martin provisioning.

The difference in latitude between the colony sites in Alberta and Florida did not have an effect on provisioning level of purple martins. In addition, mean temperature, average wind speed, and brood size did not have an effect on provisioning either. Despite past studies which found purple martins provision larger broods at higher levels (Finlay 1971), the number of young being fed did not have an effect on the level of provisioning by purple martins relative to the other factors examined in this study. If purple martins were bringing different amounts of food

per trip to accommodate the differences in number of young they were feeding it could explain why we did not find an increase in provisioning level of larger broods. Walsh (1978) found that purple martins brought larger food boluses as chicks aged as a way of meeting the higher energetic requirements of the brood, suggesting this would also be a feasible strategy for purple martins meeting higher energy requirements of larger broods.

Conclusions

The results of this study suggest that the breeding activities of purple martins are impacted by both factors at the breeding grounds and carry-over effects from spring migration. Until recent developments of tracking technology it had not been possible to track individual songbirds during an entire annual cycle. Using relatively fine scale estimations of locations and timing of events on spring migration determined from light-level geolocators this study has shown that carry-over effects from spring migration are impacting purple martins throughout the breeding season, from influencing the arrival to first egg interval to affecting the number of offspring lost during the course of the breeding season. Further, factors at the breeding grounds may further increase these carry-over effects. Late breeders had reduced provisioning levels, which in combination with the positive trend in partner provisioning levels, may compound the effects of poor quality parents on offspring quality and success. Purple martins were affected by timing of multiple events and weather experienced through the spring migration and breeding season; these factors could have critical implications for the species and other aerial insectivores considering current climate change, the associated shifts in spring phenology, and the impacts that weather at the breeding grounds have on fledging success.

Factors from spring migration that were found to impact breeding activity included the time of departure on spring migration, the number of stopovers and the weather experienced at

the stopovers. At the breeding ground, the provisioning level of an individual's partner had the largest effect on an individual's provisioning rate, but the timing of breeding, environmental conditions and parental sex also affected provisioning levels. Unlike some species, purple martins were not found to change the level of provisioning with respect to brood size. However, this study was unable to address whether the amount of food being delivered differed with brood size.

This study highlights the importance of understanding the influence of specific conditions an individual experiences over multiple portions of the annual cycle. With advancements in technology that allow for fine-scale tracking of songbirds across an annual cycle, potential compounding effects and trade-offs between portions of the annual cycle, such as the wintering grounds and migratory stopover sites (Gunnarsson et al. 2005, Schaub et al. 2011, Tøttrup et al. 2012), can be better understood with future research (Senner et al. 2014).

Tables and figures

Table 2.1 Purple martin geolocator deployment sites and years with associated breeding data for the year the geolocator was retrieved.

State/Province	Latitude	Longitude	Number of Geolocators Retrieved with Corresponding Clutch data / First Egg Date + number Fledged data	Years Geolocators Deployed
Alberta	52.39	-113.61	27/25	2012-2015
Minnesota	46.36	-94.19	2/2	2013
	46.16	-93.73	1/1	2011
South Dakota	45.61	-98.31	6/6	2011-2013
Pennsylvania	42.13	-80.09	9/9	2007, 2009, 2011
New Jersey	40.39	-74.03	6/6	2011
Virginia	38.61	-77.15	4/4	2011-2012
Florida	28.37	-81.59	22/9	2013
	26.15	-81.75	2/2	2013

Table 2.2 Model ranking of the global, null, and *a priori* hypothesis models for each response variable based on Akaike information criteria corrected for small sample sizes (AICc). The number of parameters in each model (K), AICc, ΔAICc and the AICc model weights (w_i) are reported for each model fit. The variables included in each *a priori* hypothesis model are included in brackets. The global model includes every variable included in *a priori* hypothesis models for that response variable.

Response Variable	Model	K	AICc	ΔAICc	w_i
Arrival to first egg interval (n=7)**	Global Model	9	389.7	0.00	1.00
	Breeding Ground Weather Model (Sum Precipitation)	4	409.2	19.42	0.00
	Spring Migration Timing Model (Spring Depart + Breeding Latitude)	5	416.5	26.80	0.00
	Spring Stopover Model (No. of Stopover Days)	4	447.8	58.05	0.00
	Null Model	3	450.4	60.63	0.00
	Spring Migration Weather Model (Sum Precipitation + Avg. Wind Speed)	5	455.0	65.25	0.00
Clutch Size (n=79)	Null Model	1	287.3	0.00	0.74
	Spring Migration Timing Model (Spring Depart + Arrival)	3	291.5	4.17	0.09
	Spring Migration Model (Distance + No. of Stopovers)	3	291.6	4.26	0.09
	Spring Migration Weather Model (Mean Temp + Avg. Wind Speed + Sum Precipitation)	4	292.9	5.58	0.05
	Intrinsic Model (Age + Sex + Breeding Latitude)	4	293.6	6.22	0.03
	Global Model	10	309.7	22.31	0.00
Offspring lost (n=64)	Breeding Ground Weather Model (Sum Precipitation + Max. Temperature)	5	191.7	0.00	0.56
	Spring Stopover Model (No. of Stopover Days)	4	194.4	2.69	0.15
	Spring Migration Weather Model (Avg. Wind Speed + Sum Precipitation)	5	195.2	3.49	0.10
	Null Model	3	195.4	3.70	0.09
	Spring Migration Timing Model (Spring Depart + Breeding Latitude)	5	195.9	4.16	0.07
	Breeding Timing Model (Arrival to First Egg Interval)	4	197.6	5.94	0.03
	Global Model	11	200.6	8.92	0.01
Daily provisioning (n=38)**	Global Model	11	5736.92	0.00	1.00
	Breeding Quality Model (Partner Visits + No. of Nestlings + Scaled Hatch Date*)	6	5769.22	32.31	0.00

	Breeding Weather Model (Mean Temperature + Avg. Wind Speed + Sum Precipitation)	6	5933.64	169.72	0.00
	Null Model	3	5976.87	239.95	0.00
	Intrinsic Model (Sex + Breeding Colony)	5	5978.99	242.07	0.00
Early sum provisioning (chick age 4-14 days) (n=11)**	Breeding Quality Model (Partner Visits)	3	148.51	0.00	0.71
	Breeding Ground Weather Model (Sum Precipitation)	3	150.81	2.30	0.23
	Null Model	2	155.17	6.66	0.03
	Timing Model (Spring Depart + Arrival to First Egg Interval)	3	155.79	7.28	0.02
	Spring Migration Weather Model (Sum Precipitation)	3	157.01	8.51	0.01
	Spring Stopover Model (No. of Stopovers)	3	158.79	10.29	0.00
	Global Model	7	217.74	69.23	0.00
Late sum provisioning (chick age 15-25 days) (n=8)**	Null Model	2	110.61	0.00	0.53
	Breeding Quality Model (Partner Visits)	3	111.18	0.57	0.40
	Spring Migration Timing Model (Spring Depart)	3	116.09	5.48	0.03
	Spring Migration Weather Model (Sum Precipitation)	3	116.16	5.55	0.03
	Global Model	6	199.51	88.89	0.00

* Scaled Hatch Date = timing of breeding relative to colony; i.e. time from first egg laid at the colony to hatch date of an individual's nest

**All arrival to first egg interval models included year as a random effect; all provisioning models included individual as a random effect

Table 2.3 Parameter estimates of variables included in the top models for each response variable. Model averaged estimates with shrinkage reported when multiple top models at a cut-off of ΔAICc < 6. The unconditional standard error and the 95% unconditional confidence intervals are reported for model averaged estimates. Bolded parameters estimates are those that have confidence intervals that don't cross zero.

Response Variable	Parameter	Estimate	Std. Error	Lower CI	Upper CI
Arrival to first egg interval	*(Intercept)*	*3.2186*	*0.0265*	*3.1667*	*3.2705*
	Wintering Grounds Departure	**-0.3619**	**0.0575**	**-0.4745**	**-0.2492**
	Latitude of Breeding Grounds	**0.2112**	**0.0597**	**0.0943**	**0.3282**
	Number of Days at Stopovers	**-0.0597**	**0.0289**	**-0.1163**	**-0.0032**
	Spring Stopover Avg. Wind Speed	0.0102	0.0275	-0.0437	0.0641
	Spring Stopover Sum Precipitation	0.0037	0.0254	-0.0460	0.0534
	Breeding Sum Precipitation	**0.1566**	**0.0280**	**0.1017**	**0.2114**
Clutch size	*(Intercept)*	*1.5676*	*0.0522*	*1.4636*	*1.6716*
	Arrival at Breeding Grounds	-0.0125	0.1337	-0.9569	0.6954
	Wintering Grounds Departure	0.0123	0.1336	-0.6965	0.9555
	Distance of Spring Migration	0.0002	0.0162	-0.1047	0.1088
	Number of Stopover Locations	0.0004	0.0162	-0.1026	0.1108
	Spring Stopover Precipitation	-0.0018	0.0147	-0.1508	0.0757
	Spring Stopover Avg. Wind Speed	-0.0016	0.0137	-0.1409	0.0748
	Spring Stopover Avg. Mean Temp.	0.0004	0.0117	-0.0982	0.1146
Offspring lost	*(Intercept)*	*0.0608*	*0.1707*	*-0.2804*	*0.4021*
	Breeding Maximum Temp.	**0.3107**	**0.1546**	**0.0013**	**0.6202**
	Breeding Sum Precipitation	**-0.3200**	**0.1510**	**-0.6221**	**-0.0178**
	Stopover Days	-0.3017	0.1701	-0.6420	0.0385
	Spring Stopover Sum Precipitation	-0.6568	0.4226	-1.5024	0.1889
	Spring Stopover Avg. Wind Speed	-0.0123	0.1578	-0.3280	0.3034
	Wintering Grounds Departure	0.5823	0.2967	-0.0114	1.1759
	Latitude of Breeding Grounds	-0.5970	0.3024	-1.2022	0.0082
	Arrival to First Egg Interval	-0.0290	0.1536	-0.3363	0.2783
Daily provisioning	*(Intercept)*	*3.1946*	*0.0795*	*3.0350*	*3.3539*
	Breeding Mean Temp.	0.0819	0.0462	-0.0088	0.1725
	Breeding Avg. Wind Speed	-0.0463	0.0284	-0.1019	0.0096
	Breeding Sum Precipitation	**-0.0998**	**0.0253**	**-0.1486**	**-0.0493**
	Number of Nestlings	-0.0529	0.0643	-0.1816	0.0765
	Scaled Hatch Date*	**-0.2190**	**0.0651**	**-0.3486**	**-0.0890**
	Partner Visits	**0.4047**	**0.0304**	**0.3456**	**0.4648**
	Sex (Male)**	**0.2917**	**0.0959**	**0.0974**	**0.4829**
	Breeding Colony** (Florida)	0.1151	0.1534	-0.1874	0.4191

Early sum provisioning (chick age 4-14 days)	*(Intercept)*	*5.8558*	*0.1402*	*5.5810*	*6.1306*
	Breeding Sum Precipitation	-0.1197	0.2260	-0.5626	0.3233
	Partner Visits	0.4103	0.2626	-0.1043	0.9249
Late sum provisioning (chick age 15-25 days)	*(Intercept)*	*5.7394*	*0.1787*	*5.3892*	*6.0897*
	Partner Visits	0.1774	0.2435	-0.2998	0.6546
	Wintering Grounds Departure	-0.0024	0.0388	-0.0785	0.0737
	Spring Stopover Sum Precipitation	0.0016	0.0395	-0.0758	0.0791

* Scaled Hatch Date = timing of breeding relative to colony; i.e. time from first egg laid at the colony to hatch date of an individual's nest)

** Estimate for categorical variable with two groups is based on comparison of a group to a reference group, for example comparison of males to the reference group females. When applicable, the model being compared to the reference group is included in brackets.
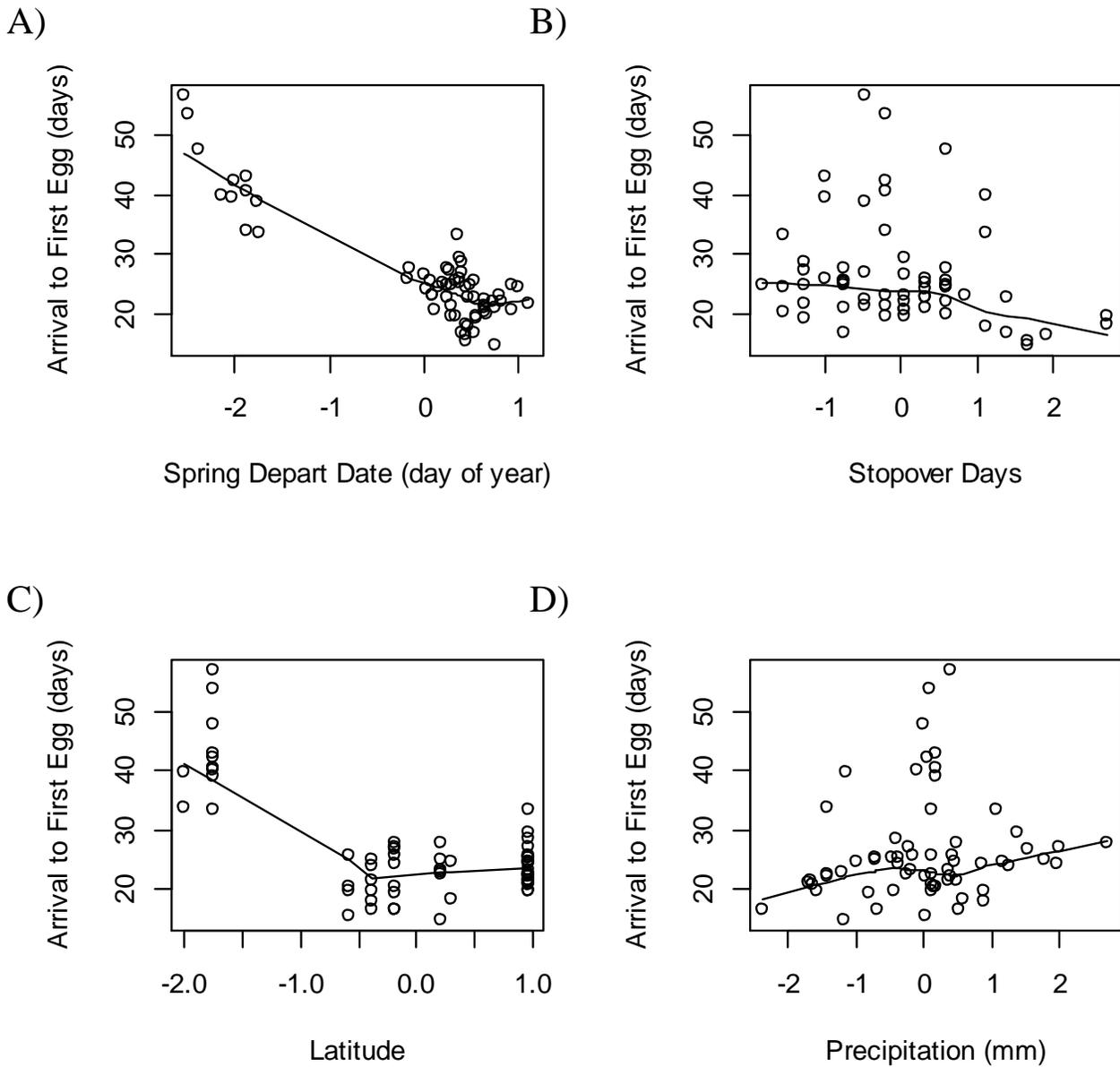
Figure 2.1 The impacts of spring departure date (a), stopover days (b), latitude (c), and average precipitation at the breeding grounds (d) on predicted values of arrival to first egg date derived from the global generalized linear mixed model (top model in Table 2.2), with locally weighted smoothing (LOESS) trend lines.
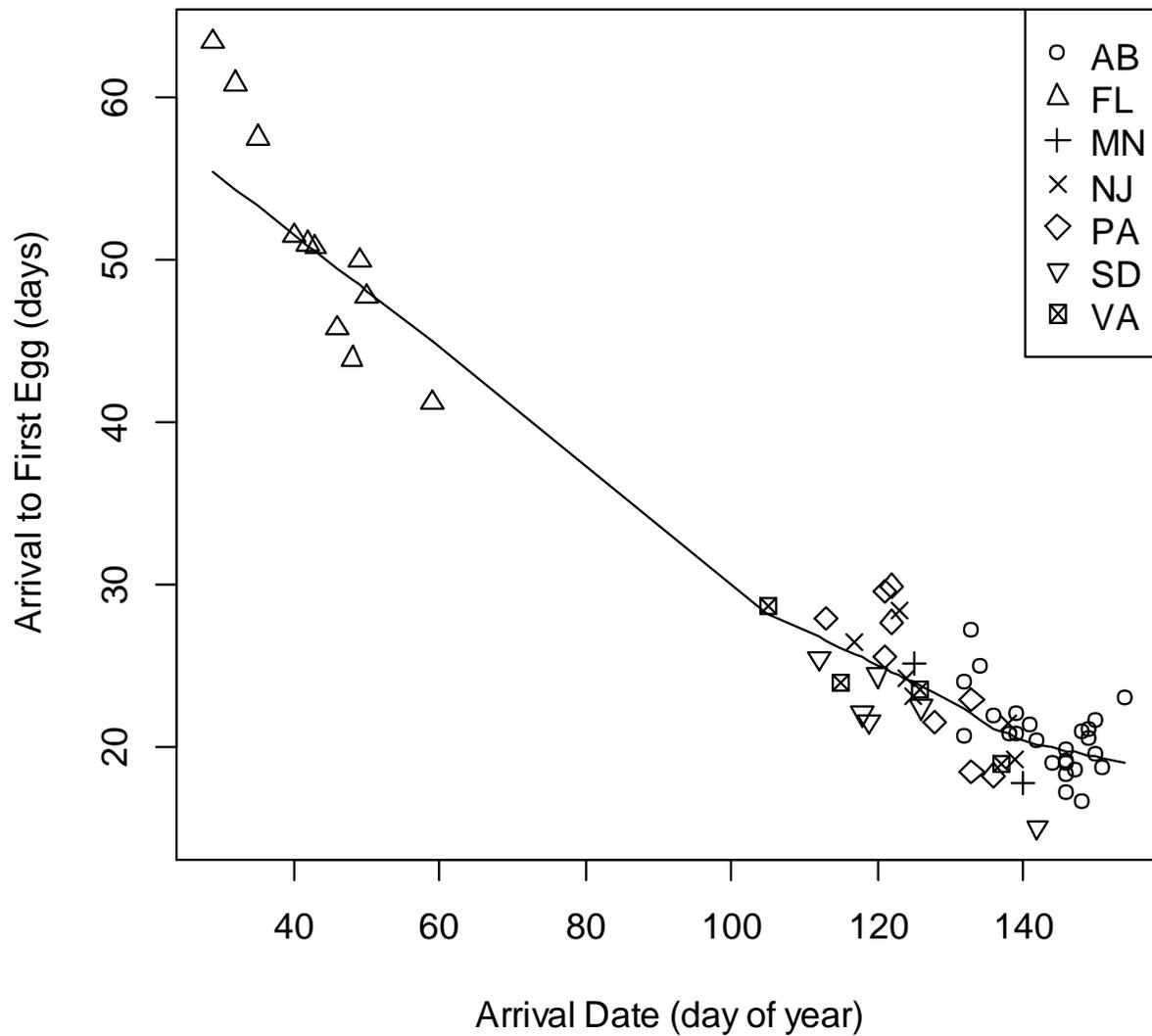
Figure 2.2 Scatterplot of arrival to first egg interval versus arrival date based on predicted values of global generalized linear mixed model (Table 2.2) with locally weighted smoothing trend line. Colony indicated by shapes identified in legend; AB=Alberta (n=25), FL=Florida (n=11), MN=Minnesota (n=3), NJ=New Jersey (n=6), PA=Pennsylvania (n=9), SD=South Dakota (n=6), VA=Virginia (n=4).
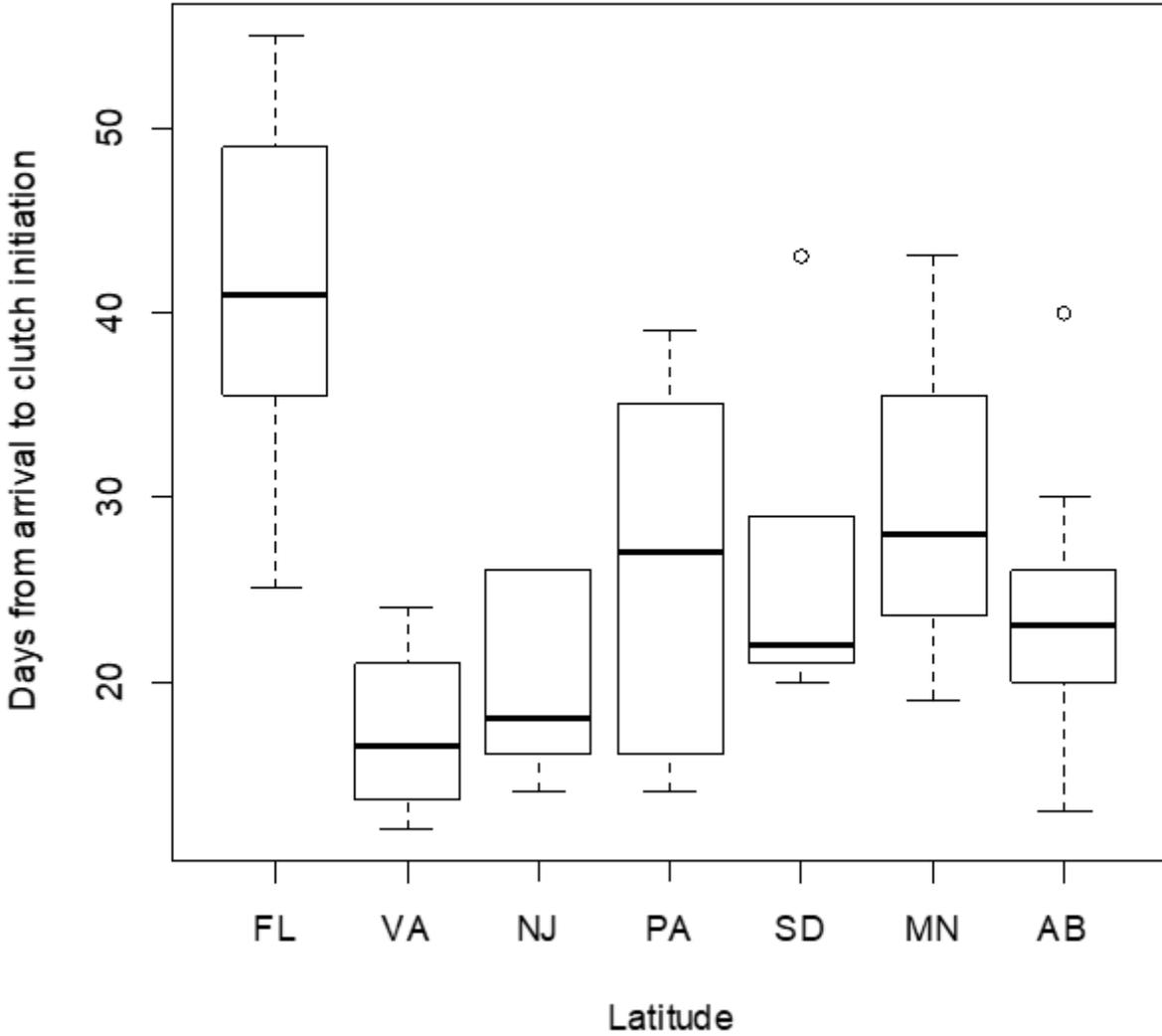
Figure 2.3 Boxplot of breeding timing (number of days from arrival to first egg date) of purple martins at seven colonies. From south to north (left to right) boxes represent FL=Florida (n=11), VA=Virginia (n=4), NJ=New Jersey (n=6), PA=Pennsylvania (n=9), SD=South Dakota (n=6), MN=Minnesota (n=3), AB=Alberta (n=25). X-axis in order of increasing latitude but not to scale.
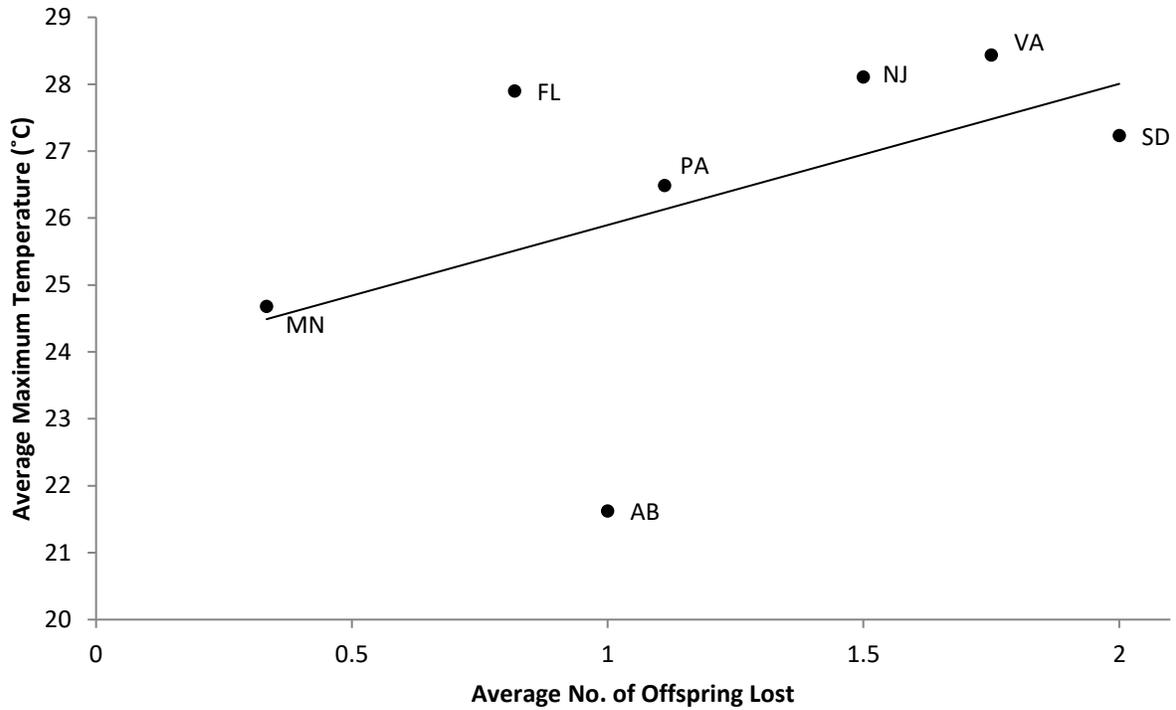
Figure 2.4 Scatterplot with linear trend line of the average number of purple martin offspring lost in relation to the average maximum temperature experienced from the first egg to earliest estimated fledge date for each individual at seven colonies; MN=Minnesota (n=3), FL=Florida (n=11), AB=Alberta (n=25), PA=Pennsylvania (n=9), NJ=New Jersey (n=6), VA=Virginia (n=4), SD=South Dakota (n=6).

References

Ahola, M., T. Laaksonen, K. Sippola, T. Eeva, K. Rainio, and E. Lehikoinen. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. Global Change Biology, 10: 1610-1617.

Alerstam, T. and Ȧ. Lindström. 1990. Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner E. (eds) Bird Migration. Springer, Berlin, Heidelberg, 331-351.

Allen, R.W., and M.M. Nice. 1952. A study of the breeding biology of the purple martin (Progne subis). The American Midland Naturalist, 47: 606-665.

Baker, A.J., P.M. González, T. Piersma, L.J. Niles, I.L.S. Nascimento, P.W. Atkinson, N.A. Clark, C.D.T. Minton, M.K. Peck, and G. Aarts. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. The Proceedings of the Royal Society of London B, 271: 875-882.

Barton, K. 2016. MuMIn: Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn

BASTrak. 2015. British Antarctic Survey. http://www.biotrack.co.uk/m-series-bastrack-software.php [Accessed 30 October 2015]

Bates, D., M. Maechler, B. Bolker, S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 671, 1-48. doi:10.18637/jss.v067.i01.

Bauchinger, U., T. Van't Hof, and H. Biebach. 2008. Migratory stopover conditions affect the developmental state of male gonads in garden warblers (*Sylvia borin*). Hormones and Behaviour, 54: 312-318.

Bearhop, S., G.M. Hilton, S.C. Votier, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proceedings of the Royal Society of London B (Supplement), 271: S215-S218.

Both, C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. Current Biology, 20: 243-248

Both, C., S. Bouwhuis, C.M. Lessells and M.E. Visser. 2006b. Climate change and population declines in a long-distance migratory bird. Nature Letters, 441: 81-83.

Both, C., J.J. Sanz, A.V. Artemyev, B. Blaauw, R.J. Cowie, A.J. Dekhuizen, A. Enemar, A. Järvinen, N.E.I. Nyholm, J. Potti, P.A. Ravussin, B. Silverin, F.M. Slater, L.V. Sokolov, M.E. Visser, W. Winkel, J. Wright, and H. Zang. 2006a. Pied Flycatchers *Ficedula hypoleuca*

travelling from Africa to breed in Europe: Differential effects of winter and migration conditions on breeding date. Ardea, 94: 511–525.

Both, C., and M.E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature, 411: 296-298.

Boyle, W.A., D.W. Winkler, and C.G. Guglielmo. 2012. Rapid loss of fat but not lean mass prior to chick provisioning supports the flight efficiency hypothesis in tree swallows. Functional Ecology, 26: 895-903.

Brown, C.R. and M.B. Brown. 1999. Fitness components associated with laying date in the cliff swallow. The Condor, 101: 230-245.

Brown, C.R. and S. Tarof. 2013. Purple Martin (Progne subis), The Birds of North America. P.G. Rodewald, Ed. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna-org.uml.idm.oclc.org/Species-Account/bna/species/purmar

Burnham, K.P., D.R. Anderson, and K.P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations and comparisons. Behavioral Ecology and Sociobiology, 65: 23-35.

Cooper, N.W., T.W. Sherry, and P.P. Marra. 2015. Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. Ecology, 96: 1933-1942.

Daunt, F., P. Monaghan, S. Wanless, M.P. Harris, and R. Griffiths. 2001. Sons and daughters: age-specific differences in parental rearing capacities. Functional Ecology, 15: 211-216.

Dormann, C.F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carre, J.R. Garcia Marquez, B. Gruber, B. Lafourcade, P.J. Leitao, T. Munkemuller, C. McClean, P.E. Osborne, B. Reineking, B. Schroder, A.K. Skidmore, D. Zurell, and S. Lautenbach. 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography, 36: 27-46.

Drake, A., C.A. Rock, S.P. Quinlan, M. Martin, and D.J. Green. 2014. Wind speed during migration influences the survival, timing of breeding, and productivity of a Neotropical migrant, *Setophaga petechial*. PLoS ONE, 9: e97152.

Dunn, P.O., D.W. Winkler, L.A. Whittingham, S.J. Hannon, and R.J. Robertson. 2011. A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore? Ecology, 92: 450-461.

Ewald, P.W., and S. Rohwer. 1982. Effects of supplemental feeding on timing of breeding, clutch-size and polygyny in red-winged blackbirds *Agelaius phoeniceus*. Journal of Animal Ecology, 51: 429-450.

Fair, J., E. Paul, and J. Jones, Eds. 2010. Guidelines to the Use of Wild Birds in Research. Washington, D.C.: Ornithological Council.

Finlay, J.C. 1971. Breeding biology of purple martins at the northern limit of their range. The Wilson Bulletin, 83: 255-269.

Finlay, J.C. 1976. Some effects of weather on purple martin activity. The Auk, 93: 231-244.

Forslund, P., and T. Pärt. 1995. Age and reproduction in birds- hypotheses and tests. Trends in Ecology and Evolution, 10: 374-378.

Fournier, D.A., H.J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. Maunder, A. Nielsen and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software, 27: 233-249.

Fraser, K.C., B.J.M. Stutchbury, C. Silverio, P.M. Kramer, J. Barrow, D. Newstead, N. Mickle, B.F. Cousens, J.C. Lee, D.M. Morrison, T. Shaheen, P. Mammenga, K. Applegate, and J. Tautin. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. Proceedings of the Royal Society B, 279: 4901-4906.

Fraser, K.C., B.J.M. Stutchbury, P. Kramer, C. Silverio, J. Barrow, D. Newstead, N. Mickle, T. Shaheen, P. Mammenga, K. Applegate, E. Bridge, and J. Tautin. 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: 291-296.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press.

Gilbert, P. and R. Varadhan. 2016. numDeriv: Accurate Numerical Derivatives. R package version 2016.8-1. https://CRAN.R-project.org/package=numDeriv

Glick, P.A. 1939. The distribution of insects, spiders and mites in the air. Technical Bulletin 673, U.S. Department of Agriculture, pp. 1-150.

Greven, S. and T. Kneib. 2010. On the behaviour of marginal and conditional AIC in linear mixed models. Biometrika, 94: 773-789.

Grueber, C.E., S. Nakagawa, R.J. Laws, and I.G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology, 24: 699-711.

Gunnarsson, T.G., J.A. Gill, J. Newton, P.M. Potts and W.J. Sutherland. 2005. Seasonal matching of habitat quality and fitness in a migratory bird. Proceeding of the Royal Society B, 272: 2319-2323.

Hahn, S., T. Emmenegger, S. Lisovski, V. Amrhein, P. Zehtindjiev, and F. Liechti. 2014. Variable detours in long-distance migration across ecological barriers and their relation to habitat availability at ground. Ecology and Evolution, 4: 4150-4160.

Harrison, X.A., J.D. Blount, R. Inger, D.R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology, 80: 4-18.

Hatchwell, B.J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of common guillemots (*Uria aalge*)

Hoset, K.S., Y. Espmark, A. Moksnes, T. Haugan, M. Ingebrigtsen, and M. Lier. 2004. Effect of ambient temperature on food provisioning and reproduction success in snow buntings *Plectrophenax nivalis* in the high arctic. Ardea, 92: 239-246.

Liang, H., H. Wu, and G. Zou. 2008. A note on conditional AIC for linear mixed-effects models. Biometrika, 95: 773-778.

Markman, S., B. Pinshow, and J. Wright. 2002. The manipulation of food resources reveals sex-specific trade-offs between parental self-feeding and offspring care. Proceedings: Biological Sciences, 269: 1931-1938.

Mazerolle, M.J. 2016. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-4. http://CRAN.R-project.org/package=AICcmodavg.

McKinnon, E.A., K.C. Fraser, and B.J.M. Stutchbury. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. The Auk, 130: 211-222.

McKinnon, E.A., C.Q. Stanley, and B.J.M. Stutchbury. 2015. Carry-over effects of nonbreeding habitat on start-to-finish spring migration performance of a songbird. PLoS ONE, 10: e0141580.

Michel, N.L., A.C. Smith, R.G. Clark, C.A. Morrissey, and K.A. Hobson. 2016. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography, 39:774-786.

Mock, D.W., P.L. Schwagmeyer, and G.A. Parker. 2005. Male house sparrows deliver more food to experimentally subsidized offspring. Animal Behaviour, 70: 225-236.

Moore, F.R. and W. Yong. 1991. Evidence of food-based competition among passerine migrants during stopover. Behavioural Ecology and Sociobiology, 28:85-90.

Morton, E.S. and K.C. Derrickson. 1990. The biological significance of age-specific return schedules in breeding purple martins. The Condor, 92: 1040-1050.

Mulder, R.A., and M.J.L. Magrath. 1994. Timing of prenuptial molt as a sexually selected indicator of male quality in superb fairy-wrens (*Malurus cayaneus*). Behavioural Ecology, 5: 393-400.

Nebel, S., A. Mills, J.D. McCracken, and P.D. Taylor. 2010. Declines of Aerial Insectivores in North America Follow a Geographic Gradient. Avian Conservation and Ecology, 5: 1-14.

Newton, I. 2004. Review: Population limitation in migrants. Ibis, 146: 197-226.

Nisbet, I.C.T. and L. Medway. 1972 Dispersion, population ecology and migration of eastern great reed warblers *Acrocephalus orientalis* wintering in Malaysia. The Ibis, 114: 451-494.

Norris, D.R. 2005. Carry-over effects and habitat quality in migratory populations. Oikos, 109: 178-186.

Norris, D.R., P.P. Marra, T.K. Kyser, T.W. Sherry, and L.M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society B, 271: 59-64.

Perez, J.H., D.R. Ardia, E.K. Chad, and E.D. Clotfelter. 2008. Experimental heating reveals nest temperatures affects nestling condition in tree swallows (*Tachycineta bicolor*). Biology Letters, 4: 168-471.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis, 112: 242-255.

Pfister, C., M.J. Kasprzyk and B.A. Harrington. 1998. Body-fat levels and annual return in migrating semipalmated sandpipers. The Auk, 115: 904-915.

Purple Martin Conservation Association [online]. 2015. Laminated Photos and Prognosticator. Available from https://www.purplemartin.org/shop/product/lmpprog/laminated-martin-photos-and-prognosticator/ [accessed on 03/11/2015]

Pyle, P. 1997. Identification guide to North American birds slate creek press. Bolinas CA.

R Core Team [online]. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. [Accessed 28 Sept 2016].

Rockwell, S.M., C.I. Bocetti, and P.P. Marra. 2012. Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's warbler (*Setophaga kirtlandii*). The Auk, 129: 744-752.

Rose, A.P. 2009. Temporal and individual variation in offspring provisioning by tree swallows: a new method of automated nest attendance monitoring. PLoS ONE, 4: e4111.

Rose, A.P., and B.E. Lyon. 2013. Day length, reproductive effort, and the avian latitudinal clutch size gradient. Ecology, 94: 1327-1337.

Rowe, L., D. Ludwig, and D. Schluter. 1994. Time, condition, and the seasonal decline of avian clutch size. American Naturalist, 143: 698-722.

Saino, N., T. Szép, M. Romano, D. Rubolini, F. Spina, and A.P. Møller. 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. Ecology Letters, 7: 21-25.

Sanz, J.J. 1999. Does daylength explain the latitudinal variation in clutch size of pied flycatchers *Ficedula hypoleuca*? Ibis, 141: 100-106.

Sanz, J.J., J.M. Tinbergen, J. Moreno, M. Orell, and S. Verhulst. 2000. Latitudinal variation in parental energy expenditure during brood rearing in the great tit. Oecologia, 122: 149-154.

Schaub, M., H. Jakober, and W. Stauber. 2011. Demographic response to environmental variation in breeding, stopover and non-breeding areas in a migratory passerine. Oecologia, 167: 445-459.

Schwagmeyer, P.L. and D.W. Mock. 2008. Parental provisioning and offspring fitness: size matters. Animal Behaviour, 75: 291-298.

Senner, N.R., W.M. Hochachka, J.W. Fox, and V. Afanasyev. 2014. An exception to the rule: carry-over effects do not accumulate in a long-distance migratory bird. PLoS ONE, 9: e86588. Doi:10.1371/journal.pone.0086588.

Smith, R.J. and F.R. Moore. 2003. Arrival fat and reproductive performance in a long-distance passerine migrant. Oecologia, 134: 325-331.

Smith, R.J., F.R. Moore, and C.A. May. 2007. Stopover habitat along the shoreline of northern Lake Huron, Michigan: emergent aquatic insects as a food resource for spring migrating landbirds. The Auk, 124: 107-121.

Sorensen, M.C., G.D. Fairhurst, S. Jenni-Eiermann, J. Newton, E. Yohannes, C.N. Spottiswoode. 2016. Seasonal rainfall at long-term migratory staging sites is associated with altered carry-over effects in a palearctic-African migratory bird. BMC Ecology, 16: 41-41.

Strandberg, R. and T. Alerstam. 2007. The strategy of fly-and-forage migration, illustrated for the osprey (*Pandion haliaetus*). Behavioural Ecology and Sociobiology, 61: 1865-1875.

Studds, C. and P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology, 86: 2380-2385.

Studds, C. and P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Climate Research, 35: 115-122.

Studds, C. and P. Marra. 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. Proceedings of the Royal Society B, 278: 3437-3443.

Stutchbury, B.J.M. and R.J. Robertson. 1987. Do nest building and first egg dates reflect settlement patterns of females? The Condor, 89: 587-593.

Stutchbury, B.J.M., S.A. Tarof, T. Done, E. Gow, P.M. Kramer, J. Tautin, J.W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. Science, 323: 896-896.

Stutchbury, B.J.M., R. Siddiqui, K. Applegate, G.T. Hvenegaard, P. Mammenga, N. Mickle, M. Pearman, J.D. Ray, A. Savage, T. Shaheen, and K.C. Fraser. 2016. Ecological causes and consequences of intertropical migration in temperate-breeding migratory birds. The American Naturalist, 188.S1: S28-S40.

Symonds, R.E. and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology, 65: 13-21.

Thorup, K., A.P. Tøttrup, M. Willemoes, R.H.G. Klaassen, R. Strandberg, M.L. Vega, H.P. Dasari, M.B. Araújo. 2017. Resource tracking within and across continents in long-distance migrants. Science Advances, 3: e1601360.

Tøttrup, A.P., K. Thorup, K. Rainio, R. Yosef, E. Lehikoinen, and C. Rahbek. 2008. Avian migrants adjust migration in response to environmental conditions en route. Biology Letters, 4: 685-688.

Tøttrup, A.P., R.H.G. Klaassen, R. Strandberg, K. Thorup, M.W. Kristensen, P.S. Jørgensen, J. Fox, V. Afanasyev, C. Rahbek, and T. Alerstam. 2012. The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. Proceedings of the Royal Society B, 279: 1008-1016.

Tsvey, A., V.N. Bulyuk, and V. Kosarev. 2007. Influence of body condition and weather on departures of first-year European robins, *Erithacus rubecula*, from an autumn migratory stopover site. Behavioural Ecology and Sociobiology, 61: 1665-1674.

Tveraa, T., B.E. Saether, R. Aanes, and K.E. Erikstad. 1998. Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. Journal of Animal Ecology, 67: 699-704.

Venables, W. N. and B.D. Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

Wagner, R.H. 1992. Confidence of paternity and parental effort in razorbills. Auk, 109: 556-562.

Wagner, R.H., M.D. Schug, and E.S. Morton. 1996. Confidence of paternity, actual paternity and parental effort by purple matins. Animal Behaviour, 52: 123-132.

Walsh, H. 1978. Food of nestling purple martins. The Wilson Bulletin, 90: 248-260.

Weber, T.P., A.I. Houston, and B.J. Ens. 1999. Consequences of habitat loss at migratory stopover sites: a theoretical investigation. Journal of Avian Biology, 30: 416-426.

Weidinger, K. and M. Kral. 2007. Climatic effects on arrival and laying dates in a long-distance migrant, the collared flycatcher *Ficedula albicollis*. Ibis, 149: 836-847.

Wiebe, K.L. and C.L. Elchuk. 2003. Correlates of parental care in northern flickers *Colaptes auratus*: do the sexes contribute equally while provisioning young? Ardea, 91: 91-101.

Wikelski, M., E. Tarlow, A. Raim, R.H. Diehl, R.P. Larkin, and G.H. Visser. 2003. Avian metabolism: costs of migration in free-flying songbirds. Nature, 423: 704-704.

Wilkin, T.A., L.E. King, and B.C. Sheldon. 2009. Habitat quality, nestling diet, and provisioning behaviour in great tits *Parus major*. Journal of Avian Biology, 40: 135-145.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev and G.M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Science and Business Media.

Chapter 3: Latitudinal effects on reproductive effort of purple martins (*Progne subis*)

Abstract

There is strong evidence that clutch size increases with latitude in many avian species, which has led to several groups of hypotheses to explain this pattern. One hypothesis is that increased daylight at higher latitudes may allow for increased provisioning to meet the greater energy requirements of larger broods. However, trends in geographical variation with clutch size are not universal across species and quantifying provisioning rates continuously to test the daylight hypothesis has been difficult until recent developments in technology. A 20-year data set collected by citizen scientists of clutch sizes (n=71,844) across the breeding range of a trans-hemispheric migratory songbird, the purple martin (*Progne subis*), provides an opportunity for a robust examination of the geographic variation in clutch size (latitude: 54.47°N to 25.53°N, longitude: -122.81°W to -70.48°W). Radio-frequency identification technology was used to examine differences in foraging activity through automated recording of activity at nest boxes at a northern (52.39°N) and southern (28.37°N) purple martin colony. I found a decrease in clutch size with increasing latitude and longitude across the breeding range. Purple martins at the northern colony on average began provisioning later relative to sunrise and ended earlier relative to sunset compared to southern birds, but due to longer day length, had greater overall longer provisioning time and used a smaller percent of the available daylight. I also found differences in the daily nest visitation between northern and southern breeders; birds had higher nest visitation through the first part of the nestling period in the north whereas in the later part of the nestling period southern birds had higher nest visitation. Although there were differences in activity patterns, this study was unable to clearly identify fitness benefits that northern birds may obtain by incurring the greater costs of longer migration.

Introduction

Life history studies have long recognized that clutch sizes tend to be larger at more northern latitudes than at more southern, tropical latitudes (Lack 1947). There is support for both intrinsic and extrinsic factors that impact clutch size. Jetz et al. (2008) examined the global patterns of clutch size of over 5000 bird species showing that intrinsic factors are largely constrained by phylogenetic patterns but when clade membership was accounted for, extrinsic factors were stronger predictors of variation in clutch size than intrinsic factors.

One set of hypotheses based on extrinsic factors that may explain this geographic variation in clutch size is centered around constraints on the ability of parents to bring food to young due to factors such as seasonality, predation risk, and daylength (Cooper et al. 2005). Greater seasonality at northern latitudes means that invertebrate prey will have a shorter but larger peak in abundance. Therefore, northern breeders should be able to provide for more offspring with this greater peak in food (Chown et al. 2002). There is evidence that the seasonality of an environment over the course of an annual cycle has a more important impact on latitudinal variation in clutch size than the absolute resource availability during the breeding season (Jetz et al. 2008).

Predation risk typically is greater at more southern, tropical latitudes and can limit clutch size if higher rates of food delivery make nests more conspicuous to predators (Skutch 1949). Relative predation pressure can even be assessed by some birds, allowing them to modulate their clutch size, egg size, and provisioning rates according to perceived predation risk (Fontaine and Martin 2006). Since northern latitudes have longer daylight hours during the breeding season, birds at northern latitudes have more time to feed and so should be able to provide for larger clutches (Finlay 1971). However, northern breeders typically do not use the same proportion of

available daylight hours for foraging as southern breeders, suggesting that northern breeders are either not limited by food delivery to young or are limited in other ways from using the extra daylength they have available to them (Sanz et al. 2000, Rose and Lyon 2013).

Although the majority of work on geographical variation in clutch size has focused on latitudinal variation there is evidence that clutch size varies longitudinally as well (Klomp 1970). Generally clutch size increases longitudinally from coastal to central regions of a continent (Lack 1947, Klomp 1970, Slagsvold 1982). There are fewer hypotheses that have been posited to explain the longitudinal variation relative to latitudinal variation; regional differences in food availability are generally suggested to explain longitudinal variation but little work has been done explaining longitudinal differences in clutch size (Klomp 1970, Lepage and Lloyd 2004).

Despite a considerable body of research which shows linear increases in clutch size with increasing latitude, there is evidence that increases in clutch size with increasing latitude is less common among cavity nesters (Slagsvold 1982), suggesting that factors influencing clutch size are acting differently on open-cup nesters versus cavity nesters. A curvilinear trend in clutch size with latitude has been reported in the cavity-nesting blue tit (Fargallo 2004) and pied flycatcher (Sanz 1997). There was no trend between clutch size and latitude, but there was an effect of habitat type and laying date on clutch size of the great tit (Orell and Ojanen 1983) and pied flycatcher (Järvinen 1989). The reverse trend was found in the jackdaw, where clutch size decreased with latitude (Soler and Soler 1992).

This study examines geographical variation in clutch size and tests how differences in daylength at a northern versus a southern breeding colony impact activity patterns of a cavity-nester, the purple martin. Purple martins breed across a wide range of latitudes in North America,

reaching as far north as central Alberta and as far south as Florida (Brown and Tarof 2013).

Although Finlay (1971) found no variation in clutch size of purple martins the full breeding

range was not represented in the study. Purple martins nest in artificial cavities that are often

maintained by citizen scientists. This has allowed the Purple Martin Conservation Association to

generate a dataset of 71,844 clutch size records across their breeding range (Tautin et al. 2008),

providing an excellent opportunity for a robust examination of geographic variation in clutch

size as the largest dataset to my knowledge to examine latitudinal variation in clutch size for a

single species. New radio frequency identification (RFID) technology, which allows for the

automation and continuous recording of provisioning activity of birds at the nest, was used to

record how purple martin activity patterns varied relative to daylength at a northern versus a

southern colony. This study will add to limited research on how daily activity patterns vary with

latitude, which is only now being examined as technology has allowed for automated, continuous

recording of birds' activity from sunrise to sunset. Since the main nest predators of purple

martins have been suggested to be owls and snakes (Brown and Tarof 2013), both of which are

difficult to observe predation events, and some purple martin landlords use predator prevention

methods to reduce predation I did not examine how predation pressures impact purple martin

clutch size.

Through monitoring of purple martins with geolocators at a northern colony in Alberta

and a southern colony in Florida we have found that birds breeding at northern colonies on

average travel more than 4000km farther on each fall and spring migration compared to southern

breeding birds and spend more than a month longer on fall migration (Fraser unpublished data).

Considering the migratory period may pose the greatest threat to survival, as compared to

stationary periods of the annual cycle (Sillett and Holmes 2002), I predict there would be a

benefit to incurring the greater cost of longer migrations. Increased fitness via increased reproductive success through larger clutch sizes and/or increased provisioning offspring, potentially leading to higher quality offspring, are the potential benefits for northern birds that I examined in this study.

I will determine: 1) if there are differences in clutch size relative to latitude and longitude of purple martins nesting across their breeding range based upon a 20-year citizen-science dataset (n= 71,844 nests), and 2) if purple martins breeding farther north, where there are a greater number of daylight hours in the breeding season than southern latitudes, spend more time provisioning young or show increased nest visitation.

Methods

The Purple Martin Conservation Association (PMCA) has created a 20-year database of 71,844 nesting records for purple martins breeding across North America (Table 3.1) through citizen scientists recording nesting information at the purple martin nest boxes they manage. Nest boxes at breeding sites were monitored through the breeding season to record the number of eggs laid in each nest of the breeding colonies. Nesting data at colonies in Alberta and Florida, where purple martins were monitored with RFID, were added to the PMCA data.

Measuring provisioning rates

New technology in avian research, RFID, was used as a measure of birds' visitation patterns to their nest cavities as an indicator of parental provisioning. RFID technology records the presence/absence of a passive integrated transponder (PIT) tag by logging the time and unique identification number associated with the PIT tag detected. Antennas, used to detect the PIT tags, were placed level with the entrance of nest cavities to record the entrances and exits of any purple martin with an 8mm long PIT tag secured to a plastic coloured leg band (Figure A1a).

RFID technology was used to record the time of first and last activity, the number of visits at the nest, and the total foraging time (time of last activity – time of first activity). RFID data from the hatch date (chick age 0 days) to earliest predicted fledge date (chick age 25 days) were analyzed to include only days that birds were provisioning young.

Because RFID technology cannot differentiate whether the activity at the nest was for the purpose of provisioning young, manual observation of nests was used to determine how many trips to the nest involved provisioning. Using binoculars at a distance of approximately 15 meters, 6 nests were simultaneously observed for 1 hour a day over the course of 5 days to determine the appropriateness of using activity patterns recorded by RFID to infer provisioning activity. Roughly 75% (471 observed trips with food of a total 626 observed trips) of visits by parents had observable food in their mouth (Figure A1b). Of the trips made that did not involve provisioning over half involved nest sanitation through fecal sac removal (96/155) (Figure A1c). Given that RFID data was not used to estimate the amount of food that was delivered to young, manual observation supported the use of RFID data as a good indicator of parental provisioning or at least parental effort/care.

RFID units were maintained with periodic battery changes, which were also used to check for clock drift, and periodically downloading the data saved on a SD card in the unit. Any clock drift of the RFID unit was corrected for by taking the difference between the recorded time and the observed (actual) time at battery changes throughout the monitoring period. The average difference between recorded and actual time for the entire monitoring period was used as the correction factor for the time at which bird activity was recorded. Since RIFD only records presence or absence and not whether the event was an entrance or exit, the data was truncated to reduce potential overestimation of provisioning. This was particularly important for events when

birds remained perched on the antenna resulting in multiple visits logged in a very short period

of time. Any time more than one event for an individual bird was recorded within a minute, only

one event for that minute was counted. Manual observations were not made on a fine enough

scale for a test of how many entrance/exit events occurred in different minutes, but Wilkin et al.

(2009) found that over 90% of Great Tit (*Parus major*) visits at their nest box were less than 30

seconds. In addition, purple martins in Oklahoma that were provisioning young were found to

have foraging trips that lasted from 80-2250 seconds (Helms et al. 2016) suggesting we were not

likely to be removing provisioning events. At the very least this potential overestimation of

provisioning is not expected to differ between individuals, making this a good relative parental

effort measure. Nest visitation was designated as the number of events recorded in a day for

each bird on each day of the monitoring period and was used an indicator of provisioning.

Statistical analyses

Geographical variation in clutch size of purple martins was analyzed using a zero

truncated Poisson generalized linear mixed model (GLMM) since clutch size was under-

dispersed count data that had no zeros (Zuur et al. 2009). Year and colony site were included in

the model as random effects. Clutch size data collected from 54.47˚N to 25.53˚N latitude and

from -122.81˚W to -70.48˚W longitudes were used to determine if purple martin clutch size

varies with latitude and longitude.

The number of events recorded in a day (nest visitation), total time during which there

was activity in a day (foraging time), time of first activity from sunrise, and last activity from

sunset at the nest were calculated from the RFID data at a northern site in Alberta (52.39˚N, -

113.61˚W) and a southern site in Florida (28.37˚N, -81.59˚W) were used to determine if

provisioning was impacted by number of daylight hours (daylength). Daylength was collected

from an online data source (Weather Underground). I used linear mixed models (LMM) fit by Laplace approximation of maximum likelihood with individual as a random effect and with sex and the interaction between chick age/colony with each of the variables in the interaction individually included as fixed effects to determine their effects on the timing of first activity, last activity, foraging time, and percent of daylight hours used by purple martins. The same random and fixed factors were included in a generalized linear mixed model (GLMM) with a negative binomial error distribution, fit by Laplace approximation of maximum likelihood, to examine latitudinal variation in nest visitation due to over-dispersion of this variable. The chick age/colony interaction was included in models because the latitude of the colony an individual was breeding at and the timing of breeding within the colony affected the amount of daylight birds had to provision chicks of a given age. All northern birds were feeding young after the summer solstice (Jun 25 – Aug 14 2015, summer solstice= Jun 21; Jun 30 – Aug 6 2016, summer solstice= Jun 20) meaning they had decreasing daylight as chicks aged whereas all southern birds were feeding young before the summer solstice (May 10 - Jun 9 2016; summer solstice = Jun 20) meaning they had increasing daylight as chicks aged.

Generalized linear mixed models with a zero-truncated Poisson error distribution were fit using the package "glmmADMB" (Fournier et al. 2012), while LMMs and negative binomial GLMMs were run using the "nlme" package (Pinheiro et al. 2016). All analyses were conducted in 3.3.1 R (R Core Team 2016).

Results

There was a statistically significant negative linear relationship between clutch size and both latitude and longitude (Table 3.2), but the quadratic relationships between clutch size and latitude and longitude were not significant. Clutch sizes were larger in the south than the north

and larger in the west than the east, with a difference in mean clutch size of about half an egg across the range (Figure 3.1).

There were differences in activity patterns between a northern and southern colony but no differences in any of the measures of activity patterns between males and females (Table 3.3). In addition, the chick age/colony site interaction did not have significant impacts on any activity patterns, including time of first activity, last activity, foraging time, percent of daylight hours used, and nest visitation (Table 3.3). Chick age was a significant factor influencing time of first activity, total foraging time, nest visitation, and percent of daylight used (Table 3.3). Foraging began later and total daily foraging times shortened as chicks aged, leading to a shorter percent of daylight being used and less visits were made to the nest as chicks aged (Table 3.3). Colony site was a significant factor impacting the time of first and last activity, total foraging time, and the percent of daylight used (Table 3.3). Foraging began earlier and ended later at the southern colony (Figure 3.2a,b) leading to a greater percent of daylight being used (Figure 3.2d). However, since northern breeders had longer daylight hours they had longer daily foraging times (Figure 3.2c). Despite these differences in activity patterns there was no difference in the number of daily visits to the nest between colonies (Figure 3.2e).

Discussion

My results show a trend in latitudinal and longitudinal variation in clutch size of purple martins breeding across 29 degrees of latitude and 52 degrees of longitude. A negative trend in both latitude and longitude indicated that clutch sizes are larger in the south than the north and larger in the west than the east. Although the longitudinal results support trends reported in the literature that clutch sizes increase from coastal to central longitudes (Lack 1947, Klomp 1970, Slagsvold 1982), whereas the latitudinal results are opposite to the trends most commonly

reported in the literature that clutch size increases with increasing latitude (Lack 1947, Jetz et al. 2008). These results indicate that the lack of a latitudinal trend in clutch size of purple martins between Alberta and Michigan as reported by Finlay (1971) was likely a result of the entire range not being included. Further, since the difference in clutch size found was small it would have been difficult to detect without such a large dataset (71,844 nest records). Foraging activity patterns were impacted by chick age. Birds showed reduced foraging, both in terms of time of foraging as well as number of trips made to the nest, as chicks aged. I also found latitudinal differences in activity patterns between birds breeding at a northern versus southern colony. Northern birds began foraging later relative to sunrise and ended earlier relative to sunset meaning they were using a smaller percentage of available daylight. However, since northern birds had longer daylengths available they foraged for about an hour longer than southern birds.

The decrease in clutch size at higher latitudes suggest there may be different fitness benefits to breeding farther north to offset the costs of longer migrations. Alternatively, the decrease in clutch size with increasing latitude could suggest that the longer migrations that northern breeders make are not having a greater cost that needs to be compensated for.

While increasing clutch size with latitude has been demonstrated both intra- and interspecifically in many avian species (Lack 1947), exceptions have been found. Cavity nesters in particular appear to have greater variation in latitudinal trends in clutch size, which may indicate that factors impacting clutch size are acting differently on cavity nesters (Slagsvold 1982), including purple martins. Trends range from linear increases in clutch size with increasing latitude (tree swallow, Dunn et al. 2000; great tit, Hõrak et al. 1995), curvilinear trend in clutch size with latitude (blue tits, Fargallo 2004; pied flycatchers, Sanz 1997), no trend between clutch size and latitude (great tits, Orell and Ojanen 1983; pied flycatchers, Järvinen 1989), and

decreasing clutch size with latitude (jackdaw, Soler and Soler 1992). Life history traits (Orell and Ojanen 1983, Järvinen 1989, Soler and Soler 1992, Fargallo 2004) and egg size/clutch size trade-offs (Soler and Soler 1992) have been suggested as explanations of the greater variation in latitudinal trends in clutch size of cavity nesting species.

Predation pressures acting differently on open-cup nesters versus cavity-nesters has been suggested to be involved with opposite latitudinal trends in clutch size. The decreasing latitudinal trend in clutch size found in the cavity nesting jackdaw was suggested to be influenced by predation pressures acting on nest site selection rather than the clutch size (Soler and Soler 1992). Since the quality of the nest site impacts the predation risk of the nest regardless of the clutch size; narrow openings and deep cavities will reduce the ability of predators to access the nest regardless of a greater number of trips made to the nest to provision more chicks making the nest more conspicuous. Therefore, cavity nesters may not be constrained at southern latitudes by an increase in predation pressures to the same degree as open-cup nesters (Soler and Soler 1992). Differences in predation pressures from those on open-cup nesters could be having a large effect on purple martins since they are colonial cavity nesters that may also benefit from colony predator mobbing to further reduce predation risk (Stutchbury 1991, Davis and Brown 1999). There is relatively little published on predation pressures on purple martins and how it varies across latitudes, although owls and snakes are likely the most common and significant source of predation on both adults and nestlings at the nest (Brown and Tarof 2013). In addition, purple martin nests can be destroyed by nest competitors, primarily house sparrows (*Passer domesticus*) and European starlings (*Sturnus vulgaris*) (Brown and Tarof 2013). However, given the prevalence of these invasive species across North America the degree to which nest competitors destroy nests are unlikely to vary with latitude, but may be influenced by the practices of the

landlord based on if they evict invasive nest competitors or not. Although snake populations are smaller in the upper mid-west and northeast of the United States and all of Canada as compared to the rest of the purple martin range, since purple martins rely on human-made cavities that often have predator guards to prevent/reduce predation there may not be a significant difference in predation pressure across latitudes. Finally, as a colonial cavity nester they do not increase their predation risk if they make more trips to the nest to provision larger clutches. Without this constraint northern and southern birds may not show the typical trend in clutch size since southern birds could have larger clutches without increased predation costs.

An egg size/clutch size trade-off may also be involved in the lack of a latitudinal increase in clutch size; producing larger eggs rather than more eggs may be a way for northern birds to allocate a limited amount of energy most efficiently to deal with colder and more variable weather (Lack 1967, Soler and Soler 1992). Inverse relationships between egg size and clutch size have been found both within and between geographic sites (Martin et al. 2006). The negative trend in clutch size with latitude found in jackdaws was also suggested to be influenced by an egg size/clutch size trade-off (Soler and Soler 1992). Since increasing egg size is an energetically cheaper strategy for increasing reproductive success over increasing clutch size (Lack 1967, Soler and Soler 1992), this may be involved in the decreasing latitudinal trend in clutch size. A meta-analysis of egg size and offspring quality found strong support that larger eggs were associated with higher juvenile survival (Krist 2011), suggesting this strategy would be an alternative way of increase reproductive success instead of increasing clutch size. Pied flycatchers exhibited a trade-off between egg size and clutch size during 'poor' years when temperatures were cold during the pre-laying and egg-laying period (Järvinen 1996). However, this trade-off disappeared during 'good' years with warm temperatures during pre-laying and

egg-laying leading to a positive relationship between egg size and clutch size (Järvinen 1996). Considering a negative latitudinal trend in clutch size was found for purple martins, differences in egg size rather than differences in clutch size deserves investigation in the future.

The decreasing trend in clutch size with increasing latitude could also be due to greater time and/or energy constraints on birds breeding farther north. Purple martins breeding at more northern latitudes not only have longer migrations from the overwintering grounds to reach their breeding grounds (Fraser et al. 2012) but also have shorter breeding seasons. Since northern breeders have shorter breeding seasons they may have less flexibility to recover from migration and get into breeding condition, which could lead to smaller clutches if females are in poorer condition after longer migrations and/or late nest initiation. Declines in clutch size through the season, in relation to first egg date, have been well documented. With climate change impacting the timing of various aspects of the annual cycle, particularly for migratory species, it is becoming more difficult for insectivorous birds to time breeding to match peak food abundances (Both and Visser 2001, Laaksonen et al. 2006). The degree of decreases in clutch size through the season can vary with latitude (Orell and Ojanen 1983). Since laying smaller clutches allows for earlier hatch dates relative to larger clutches with the same first egg date (i.e. fewer days spent laying eggs), this may be a strategy that is more important for northern breeding species that have more constrained breeding seasons to over come late clutch initiation (Orell and Ojanen 1983). Incorporating seasonal variation in the timing of breeding (first egg date) is likely to be an important variable for future research understanding this decreasing trend in clutch size of purple martins.

Timing of foraging was found to be influenced by chick age as well as the latitude. Greater seasonality and food availability at northern latitudes could allow for greater food

72

delivery per foraging trip, which has been linked to latitudinal trends in clutch size (Evans et al. 2005). Decreases in foraging times and nest visitation with chick age suggest that purple martins may have greater food availability in the later portion of the nestling period, allowing the energetic demands of chicks to be met in a shorter time and with fewer trips to the nest.

Purple martins at the northern and southern edges of their breeding range were found to have different timing at which they began and ended foraging relative to sunrise and sunset. At the southern colony, purple martins' first recorded activity was closer to and more often prior to sunrise than birds at the northern colony, and southern birds' last activity was also closer to or after sunset compared to northern birds. The provisioning results support the day length hypothesis, which predicts northern birds should provision for longer because of the increased daylight hours to accommodate larger clutches. However, since northern birds were not found to have larger clutches, the benefit of longer daylight may be impacting another aspect of fitness that was not analyzed. The higher percentage of daylight hours used by southern birds than northern birds suggests that southern birds are constrained by the number of daylight hours and therefore have to maximize their use of what is available. Northern birds did forage for an hour longer than southern birds, suggesting that although they are benefiting from the increased daylight availability, there are other factors that are constraining their foraging time.

Ambient temperatures unfavourable to foraging could prevent northern birds from earlier and later foraging because of greater brooding requirements of chicks and/or lower food availability (Sanz et al. 2000, Avery and Krebs 1984). Aerial insects are impacted by temperature such that there is a temperature threshold below which they can no longer fly (Taylor 1963). Consequently, there may be reduced food availability in the morning or evening when cool temperatures reduce the foraging efficiency of purple martins early or late in the day.

The diapause and emergence of dragonflies, one of purple martins' main food sources (Jones et al. in prep), has been shown to be impacted by differences in daylight and temperature at different latitudes (Flenner et al. 2010). Apart from a rare account of a dragonfly flying below an ambient temperature of 10°C (May 1995), dragonflies generally begin flying at a minimum ambient temperature around 14°C (Hilfert-Ruppell 1998, Sformo and Doak 2006); in the interior of Alaska, for example, a variety of dragonflies (which can be found across all or at least in parts of the purple martin's range) have minimum flight temperatures that ranged from 14-22°C (Sformo and Doak 2006). Considering that the temperature at sunrise at the northern site (11.86±0.10°C) was on average about 9°C cooler than the southern site (20.83±0.10°C) this is likely to have important impacts on food availability for purple martins early in the morning. Differences in activity patterns of dragonflies in relation to temperature at northern and southern purple martin colonies may result in purple martins shifting foraging activity patterns to mirror those of their primary prey. Although neither food availability nor activity patterns of dragonflies were collected in this study, temperature may be a potentially limiting factor impacting the time of first activity by northern birds to a greater degree than southern birds through impacts on food availability and warrants further research.

Given that differences in the total number of visits at the nest are predicted to indicate food limitations (Rose and Lyon 2013), differences in food availability appear to have a greater impact on purple martins through the breeding season rather than between colonies since nest visitation varied with chick age but not between colonies. Differences in the timing of foraging but not the level of nest visitation was also found in tree swallows (Rose and Lyon 2013). However, future research on differences in food availability and food delivery to nestlings are needed to determine if northern purple martins are bringing a greater total weight of food, either

through more prey items or larger prey items, to chicks or not. Understanding food delivery to offspring, and future survival of offspring, would inform whether northern and southern purple martins are equally able to meet energy requirements of chicks or if differences in activity patterns, particularly nest visitation, found in this study are impacting the quality of offspring fledged.

Conclusions

This research showed that there is geographic variation in clutch size and latitudinal variation in activity patterns of purple martins. Using a large (71,844 nest records), 20-year citizen-science dataset of clutch size across the breeding latitude of a widely distributed Nearctic-Neotropical songbird, I tested for geographical variation in clutch size. By using new nest monitoring technology (RFID) I was able to further this investigation by also examining variation in activity patterns across latitude and their relation to daylength. Purple martins were found to have larger clutches in the south and the west (interior of the continent). Although not common, decreases in clutch size with increasing latitude as have been found in a few other cavity-nesting species, which have been posited to be due to differences in predation pressures and/or egg size/clutch size trade-offs. The opposite trend in clutch size with increasing latitude may be in part due to ecological pressures acting differently on clutch size of cavity-nesting species versus open-cup nesting species.

Northern birds had longer daily foraging times due to the increased daylight hours available to them at higher latitudes during the temperate spring-summer. Birds breeding at the southern colony began foraging earlier and ended foraging later, using a greater percentage of the available daylight hours, which suggests they may be constrained by daylength. Without evidence of differences in nest visitation but differences in activity patterns found between

75

northern and southern colonies purple martins appear to be equally capable of meeting optimal energetic demands of offspring, simply accomplishing it in different ways due to different constraints (temperature constrains on northern birds, daylight constraints on southern birds). Future studies examining food abundance and/or food delivery to nestlings and the survival or condition of fledglings are necessary to understand the fitness consequences of the differences in activity patterns found, particularly in nest visitation. Overall, since southern birds had larger clutch sizes, have shorter migrations, and showed no obvious disadvantage in provisioning ability they appear to have greater fitness than northern birds; however, survival rates across the breeding range are needed to fully test fitness differences of purple martins across their breeding latitudes.

Tables and figures

Table 3.1 Colony locations across North America from 1995-2013 in the Purple Martin Conservation Association (PMCA) data set.

State/Province	Years of Martins recorded
Indiana	1995-2013
Texas	1995-2013
Alberta	1996-2007, 2009-2013
Alabama	1995-2002, 2004-2011, 2013
Arkansas	1996-2000, 2002, 2004-2013
Connecticut	2009-2011, 2013
Florida	1995-2013
Georgia	1998-2011
Iowa	1995-2003, 2005-2011, 2013
Kansas	1995-2013
Kentucky	1995-2013
Louisiana	1995, 1997-2011, 2013
Massachusetts	2000-2001, 2003-2007, 2009-2011, 2013
Manitoba	2010
Maryland	1995-2013
Michigan	1995-2013
Minnesota	1995-2013
Missouri	1995-2013
Mississippi	1996-1998, 2000-2001, 2004, 2006-2007, 2010, 2012-2013
North Carolina	1995-2011
North Dakota	1995, 1997-1998, 2000-2007, 2009-2011
Nebraska	1996-2001, 2004, 2007-2009, 2011, 2013
New Jersey	1995-1998, 2000-2013
New York	1995-2013
Ohio	1995-2013
Oklahoma	1995-2011
Ontario	1995-2013
Oregon	2005-2007, 2013
Pennsylvania	1995, 1997-2013
Quebec	1995
Rhode Island	2001-2004, 2006-2008, 2010
South Carolina	1995, 1997-2013
South Dakota	1998-2006, 2008-2011, 2013
Saskatchewan	1998, 2001, 2009-2013
Tennessee	1995-2013
Illinois	1995-2013
Delaware	1995-2011, 2013
Virginia	1995, 1997-2013
Vermont	2008-2011, 2013

Washington	2010, 2013
Wisconsin	1995-1998, 2000-2013
West Virginia	2002-2005, 2007

Table 3.2 Results of zero truncated Poisson generalized linear mixed model analysis of clutch size variation in relation to geographic location using a 20-year data set (n=71844) representing the entire breeding range (PMCA data). Colony and year were included in the model as random effects.

Fixed Effect	Estimate	Std Error	P value
Latitude	-2.81396	0.60773	<0.0001
Latitude^2	1.21424	0.64340	0.0591
Longitude	-3.35520	0.64563	<0.0001
Longitude^2	-0.41070	0.59116	0.4872

Table 3.3 Results of linear mixed models used to examine timing of first and last activity at the nest, total daily foraging time, and the percentage of daylight hours used. Results of generalized linear mixed model of total daily visits at the nest, based on RFID data collected at a northern (Alberta) and southern (Florida) site. Predictor variables included in each model were sex and the interaction between chick age, daylight, and colony site. Individual was included as a random effect in each model.

| Response Variable	Fixed Effect	Estimate	Standard Error	P-value
First Activity (min after sunrise)	*Intercept*	*48.58343*	*3.944196*	*<0.0001*
	Sex (M)	1.77048	5.324215	0.7412
	Colony (FL)	**-55.48233**	**6.353622**	**<0.0001**
	Chick Age	**7.38838**	**1.744660**	**<0.0001**
	Colony (FL) : Chick Age	-0.49190	4.395842	0.9109
Last Activity (min before sunset)	*Intercept*	*39.45217*	*3.268288*	*<0.0001*
	Sex (M)	2.62379	4.447802	0.5586
	Colony (FL)	**-31.53501**	**5.647828**	**<0.0001**
	Chick Age	2.32330	1.874424	0.2156
	Colony (FL) : Chick Age	5.86224	4.693343	0.2121
Foraging Time (min)	*Intercept*	*859.1241*	*8.582671*	*<0.0001*
	Sex (M)	-12.0424	11.471089	0.3001
	Colony (FL)	**-50.0913**	**13.507276**	**0.0006**
	Chick Age	**-34.7172**	**3.733019**	**<0.0001**
	Colony (FL) : Chick Age	11.9135	9.253321	0.1984
Visits at Nest	*Intercept*	*3.57474*	*0.11999*	*<0.0001*
	Sex (M)	-0.11127	0.15976	0.4861
	Colony (FL)	0.28936	0.17565	0.0995
	Chick Age	**-0.19875**	**0.03006**	**<0.0001**
	Colony (FL) : Chick Age	-0.10207	0.07696	0.1847
Percent of Daylight Hours Used	*Intercept*	*89.10535*	*0.8358616*	*<0.0001*
	Sex (M)	-1.28376	1.1200254	0.2585
	Colony (FL)	**9.93201**	**1.3439951**	**<0.0001**
	Chick Age	**-1.71356**	**0.3997871**	**<0.0001**
	Colony (FL) : Chick Age	-1.58199	0.9852499	0.1088
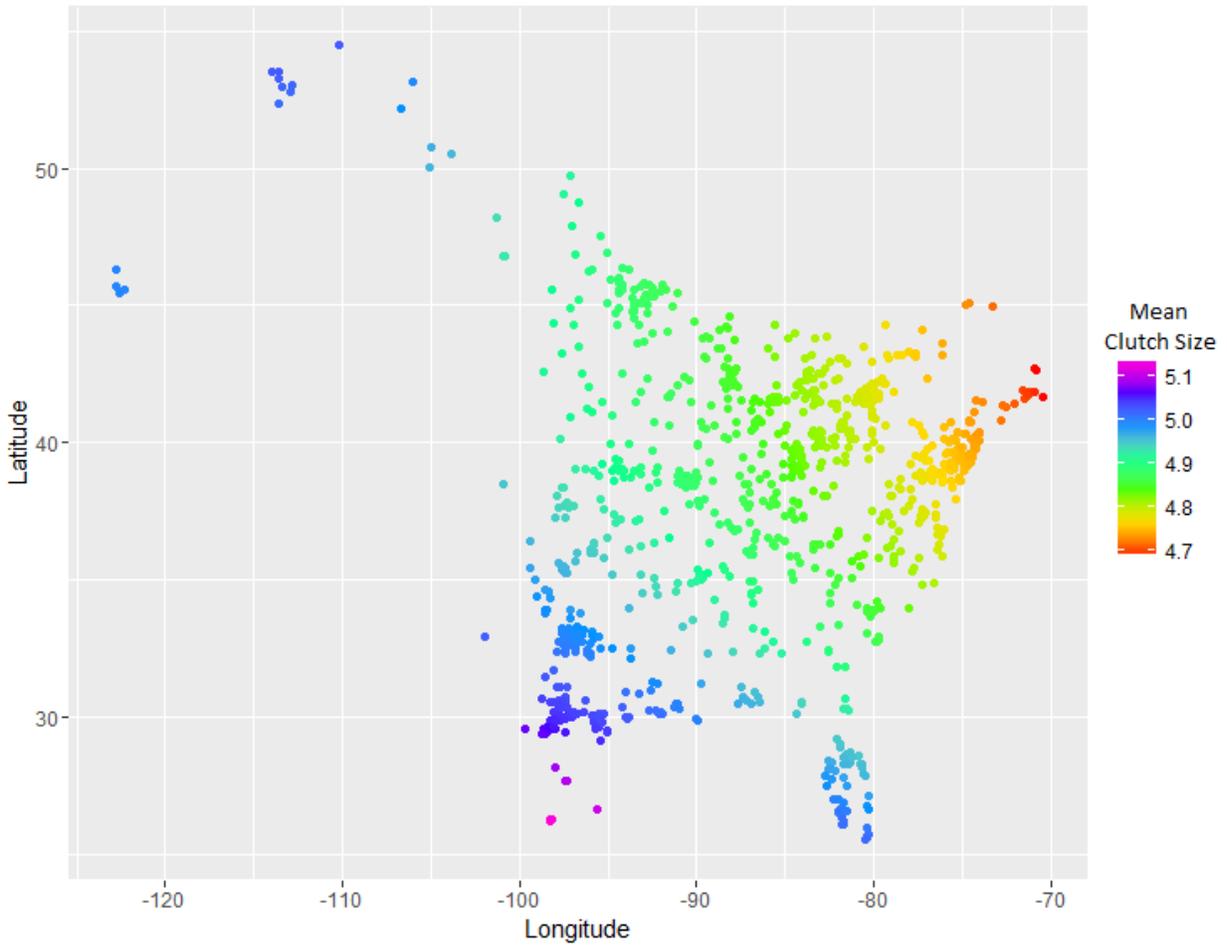
Figure 3.1 Mean clutch size based on predicted values from generalized linear mixed model with year and colony site as random factors including quadratic terms for both latitude and longitude. Based on PMCA data set and nesting data from northern and southern colony monitored with RFID.
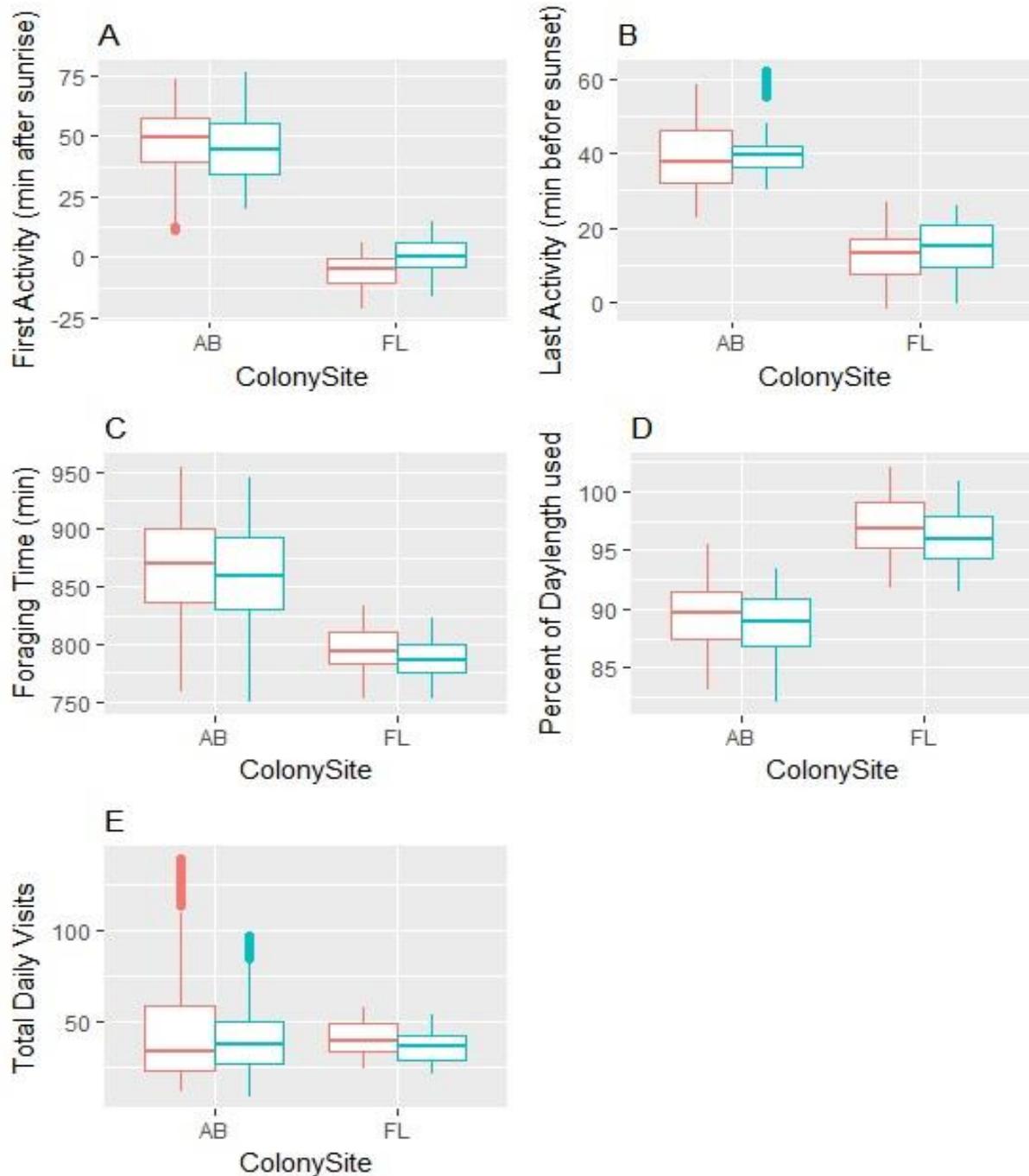
Figure 3.2 Boxplots showing median and interquantile range with outliers, derived from the predicted values of the mixed models ran for each response variable, of five aspects of foraging activity at a northern site in Alberta (AB) and a southern site in Florida (FL) colony of males (blue) and females (red). (A) time of first activity within three hours of sunrise measured in minutes from sunrise, (B) last activity within three hours of sunset measured in minutes from sunset, (C) total time foraging (last activity-first activity) that was greater than 2/3 of the available daylight, (D) percent of available daylight used, and (E) total daily visits at the nest.

References

Avery, M.I. and J.R. Krebs. 1984. Temperature and foraging success of great tits *Parus major* hunting for spiders. Ibis, 126: 33-38.

Both, C. and M.E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Letters to Nature, 411: 296-298.

Brown, C.R. and S. Tarof. 2013. Purple Martin (Progne subis), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna-org.uml.idm.oclc.org/Species-Account/bna/species/purmar.

Chown, S.L., A. Addo-Bediako, and K.J. Gaston. 2002. Physiological variation in insects: large-scale patterns and their implications. Comparative Biochemistry and Physiology Part B, 131: 587-602.

Cooper, C.B., W.M. Hochachka, G. Butcher and A.A. Dhondt. 2005. Seasonal and latitudinal trends in clutch size: thermal constraints during laying and incubation. Ecology, 86: 2018-2031.

Davis, J.A. and C.R. Brown. 1999. Costs of coloniality and the effect of colony size on reproductive success in purple martins. The Condor, 101: 737-745.

Dunn, P.O., K.J. Thusius, K. Kimber and D.W. Winkler. 2000. Geographic and ecological variation in clutch size of tree swallows. The Auk, 117: 215-221.

Evans, K.L., R.P. Duncan, T.M. Blackburn and H.Q.P. Crick. 2005. Investigating geographic variation in clutch size using a natural experiment. Functional Ecology, 19: 616-624.

Fargallo, J.A. 2004. Latitudinal trends of reproductive traits in the blue tit *Parus caeruleus*. Ardeola, 51: 177-190.

Finlay, J. 1971. Breeding biology of purple martins at the northern limit of their range. The Wilson Bulletin, 83: 255-269.

Flenner, I., O. Richter, and F. Suhling. 2010. Rising temperature and development in dragonfly populations at different latitudes. Freshwater Biology, 55: 397-410.

Fontaine, J.J. and T.E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology letters, 9: 428-434.

Fournier, D.A., H.J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. Maunder, A. Nielsen and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software, 27: 233-249.

Helms, J.A., A.P. Godfrey, T. Ames, and E.A. Bridge. 2016. Predator foraging altitudes reveal the structure of aerial insect communities. Scientific Reports, 6: 28670.

Hilfert-Ruppell, D. 1998. Temperature dependence of flight activity of odonatan by ponds. Odonatologica, 27: 45-59.

Hõrak, P., R. Mänd, I. Ots and A. Leivits. 1995. Egg size in the great tit *Parus major*: individual, habitat and geographic differences. Ornis Fennica, 72: 97-114.

Järvinen, A. 1989. Clutch-size variation in the pied flycatcher *Ficedula hypoleuca*. Ibis, 131: 572-577.

Järvinen, A. 1996. Correlation between egg size and clutch size in the pied flycatcher *Ficedula hypoleuca* in cold and warm summers. Ibis, 138: 620-623.

Jetz, W., C.H. Sekercioglu, K. Böhning-Gaese. 2008. The worldwide variation in avian clutch size across species and space. PLoS Biology, 6: e303.

Klomp, H. 1970. The determination of clutch-size in birds a review. Ardea, 58: 1-124.

Krist, M. 2011. Egg size and offspring quality: a meta-analysis in birds. Biological reviews, 86: 692-716.

Laaksonen, T., M. Ahola, T. Eeva, R.A. Väisänen, and E. Lehikoinen. 2006. Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. Oikos, 114: 277-290.

Lack, D. 1947. The significance of clutch-size. Ibis, 89: 302-352.

Lack, D. 1967. The significance of clutch-size in waterfowl. Wildfowl, 18: 125-128.

Lepage, D. and P. Lloyd. 2004. Avian clutch size in relation to rainfall seasonality and stochasticity along an aridity gradient across South Africa. Ostrich, 75: 259-268.

Martin, T.E., R.D. Bassar, S.K. Bassar, J.J. Fontaine, P. Lloyd, H.A. Mathewson, A.M. Niklison, and A. Chalfoun. 2006. Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. Evolution, 60: 390-398.

May, M.L. 1995. Dependence of flight behavior and heat production on air temperature in the green darner dragonfly *Anax junius* (Odonata: Aeshnidae). The Journal of Experimental Biology, 198: 2385-2392.

Michel, N.L., A.C. Smith, R.G. Clark, C.A. Morrissey, and K.A. Hobson. 2016. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography, 39:774-786.

Orell, M. and M. Ojanen. 1983. Effect of habitat, date of laying and density on clutch size of the great tit *Parus major*. Holarctic Ecology, 6: 413-423.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and R Core Team. 2016. _nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-128, <URL: http://CRAN.R-project.org/package=nlme>.

R Core Team [online]. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. [Accessed 28 Sept 2016].

Rose, A.P. and B.E. Lyon. 2013. Day length, reproductive effort, and the avian latitudinal clutch size gradient. Ecology, 94: 1327-1337.

Sanz, J.J. 1997. Geographic variation in breeding parameters of pied flycatcher *Ficedula hypoleuca*. Ibis, 139: 107-114.

Sanz, J.J., J.M. Tinbergen, and J. Moreno. 2000. Latitudinal variation in parental energy expenditure during brood rearing in the great tit. Oecologia, 122: 149-154.

Sformo, T. and P. Doak. 2006. Thermal ecology of interior Alaska dragonflies (Odonata: Anisoptera). Functional Ecology, 20: 114-123.

Sillett, T.S. and R.T. Holmes. 2002. Variation in survivorship of a migratory songbird through its annual cycle. Journal of Animal Ecology, 71: 296-308.

Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish? Ibis, 91: 430-455.

Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. Oecologia, 54: 159-169.

Soler, M. 1988. Egg size variation in the Jackdaw *Corvus monedula* in Granada, Spain. Bird Study, 35: 69-76.

Soler, M. and J.J. Soler. 1992. Latitudinal trends in clutch size in single brooded hole nesting bird species: a new hypothesis. Ardea, 80: 293-300.

Stutchbury, B.J. 1991. Coloniality and breeding biology of purple martins (*Progne subis hesperia*) in saguaro cacti. The Condor, 93: 666-675.

Tautin, J., B. Cousens, K. Kostka,, S. Kostka, and D.A. Airola. 2008. Addressing regional declines in purple martin populations. Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics, 82-87.

Taylor, L.R. 1963. Analysis of the effect of temperature on insects in flight. Journal of Animal Ecology, 32: 99-117.

Weather Underground [online]. Historical Weather. www.wunderground.com/history [Accessed 06 November 2015].

Wilkin, T.A., L.E. King, and B.C. Sheldon. 2009. Habitat quality, nestling diet, and provisioning behaviour in great tits *Parus major*. Journal of Avian Biology, 40: 135-145.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev and G.M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Science and Business Media.

Chapter 4: Synthesis and conclusion

This thesis has examined the impacts of several intrinsic and extrinsic factors, from two portions of the annual cycle, on reproduction in purple martins. I have shown that purple martin reproduction is impacted by factors from spring migration in combination with conditions at the breeding grounds (Chapter 2). In addition, this research has shown that purple martins have a decrease in clutch sizes with increasing latitude and differences in activity patterns between a northern and southern colony representing approximately the farthest edges of the breeding range (Chapter 3). By using light-level geolocators to track purple martins on their spring migration and radio frequency identification (RFID) technology to automatically record parental activity at the nest (a proxy for provisioning levels), I was able to address factors impacting reproduction that have not been examined previously. A 20-year dataset collected by citizen scientists across the purple martin range allowed for a robust analysis of geographic variation in clutch size that was able to detect a trend that had not been found in previous analysis of purple martin clutch size variation across latitude (Finlay 1971). This research also adds to our understanding of latitudinal trends in clutch size of cavity nesting species, which have shown greater variation in clutch size trends than open-cup nesters that are not fully understood.

Due to the difficulties associated with tracking small migratory songbirds this, is the first time, to my knowledge, that the specific conditions an individual experienced on migration has been linked to reproductive performance. The few carry-over effect studies that have examined spring migration factors have relied on estimated stopover conditions that birds experienced without detailed spatio-temporal information of individual migrations (Schaub et al. 2011, Drake et al. 2014). By using data derived from geolocators, my results show that the timing of departure on spring migration and the time spent at stopovers have impacts on the arrival to first

egg interval. Late departures and/or longer stopovers were associated with shorter arrival to first

egg intervals, which may limit the ability of a bird to recover from migration and prepare for

breeding. Trade-offs between the advantages of early arrival at the breeding grounds and the

higher insurances of greater energy stores acquired through longer stopovers may be influencing

purple martins (Pfister et al. 1998, Baker et al. 2004, Smith et al. 2007). As is the general pattern

for migratory songbirds (Kokko 1999), early arrival for purple martins appears to be very

important considering nests that hatched earlier were provisioned at higher rates. The impacts of

hatch date on provisioning was compounded because birds that exhibited higher provisioning

rates tended to be social mates. The positive relationship between pair mate provisioning rates

suggest that lower quality individuals were unlikely to obtain a pair mate that would compensate

for their lower provisioning. There was weak evidence that conditions at stopovers and stopover

duration impacted the number of offspring lost during the breeding season. However, of the

factors examined, maximum temperature and the amount of precipitation at the breeding grounds

had the strongest impacts on the number of offspring lost. Environmental conditions at the

breeding grounds were also shown to have important impacts on the length of the arrival to first

egg interval and daily provisioning levels. Overall, these results suggest that drying through the

breeding season and warming temperatures, particularly at the northern portion of the breeding

range, associated with climate change have the potential to have important impacts on purple

martins, with respect to timing of breeding, provisioning ability, and reproductive success.

I showed latitudinal variation in several aspects of reproduction, including the length of

arrival to first egg interval and timing of provisioning, and clutch size. Purple martins breeding

farther north were found to have longer arrival to first egg intervals, potentially due to greater

constraints on ability to shorten this interval. However, had the analysis included more southern

breeders, a decrease in the length of the arrival to first egg interval likely would have been found given the length of the interval of birds breeding in Florida and arrival trends.

Using a large dataset (71,844 nest records), which was representative of the purple martin breeding range, I found a decrease in clutch size with increasing latitude and longitude that a previous paper examining clutch size variation by latitude (Finlay 1971) did not detect. The decreases in clutch size with increasing latitude found may suggest that there is an alternative fitness benefit for northern breeders to offset the higher costs associated with the longer migrations they must complete, or that the longer migrations are not having a major cost on more northern birds that they need to offset. Differences in egg size instead of clutch size could be involved in the negative trend found that require further research; egg size/clutch size trade-offs are a potential strategy for increasing fitness since increasing egg size rather than clutch size is an energetically cheaper way of increasing reproductive success at northern latitudes that typically have colder and more variable weather (Lack 1967, Soler and Soler 1992).

I showed that purple martins breeding near the northern edge of the breeding range provision for more hours per day due to the longer daylight available to them despite beginning foraging later relative to sunrise and ending earlier relative to sunset compared to birds breeding in the south. In addition, I showed that birds breeding at the northern colony had higher nest visitation early in the nestling period whereas birds breeding at the southern colony had higher nest visitation later in the nestling period. These differences in activity patterns could be the result of different constraints on birds breeding in the north versus the south; my results suggest northern birds are potentially constrained by lower ambient temperatures resulting in lower food availability whereas southern birds may be constrained by daylight availability. Considering the greater population declines seen in the northern portion of the purple martin range (Michel et al.

2016), the lack of apparent fitness benefits at higher latitudes may be involved in this variation in population declines if northern birds are experiencing higher costs associated with longer migrations without increased reproductive success.

To build upon this research, analyzing food availability and the level of food delivery to nestlings are excellent future research directions. Due to purple martins routinely foraging 150 meters above the ground, with average maximum foraging heights reaching 849±362 meters (Helms et al. 2016), there has been very little work on quantifying prey availability, particularly that is representative of where purple martins are foraging. There are also potential differences in prey utilization across latitudes; in Manitoba dragonflies appear to be the main insects brought to nestlings (Jones et al. in prep) whereas in Oklahoma ants were found to be the main insects brought to nestlings (Helms et al. 2016). Understanding differences in prey utilization may be particularly useful for explaining differences in clutch size across longitudes in addition to latitudinal differences. The use of RFID technology helped with inferring provisioning levels but does not provide data on the amount of food that was actually brought to nestlings. Purple martins have been shown to bring different amounts of food per provisioning trip based on the age of chicks to meet increasing energy requirements of older chicks (Walsh 1978), which could have implications on the inferences that can be made from my results. Although there were differences in nest visitation between northern and southern breeders, each showed higher nest visitation at different portions of the nestling period. The lack of evidence in this study for fitness benefits of breeding farther north point toward the potential of an egg size/clutch size trade-off in purple martins that warrants future research. A trade-off between egg size and clutch size has not been examined in purple martins but could explain why northern birds were found to have a small decrease in clutch size. Anecdotally, there appeared to be considerable variation in egg size

and shape at the northern colony where I carried out field work, such that I could visually detect it, which selection could act on to lead to differences in egg size across latitudes.

In addition, future research to build upon this study could better address the impacts of spring migration on provisioning levels. Due to the small sample size of birds that were tracked on their spring migration and during provisioning it was not possible to make conclusions about how past events impacted parental provisioning. However, since purple martins were found to be impacted by carry-over effects and parental provisioning is an energetically costly portion of reproduction that has not been examined in carry-over effect studies it warrants further investigation.

Overall, this research has shown that the reproduction of purple martins, a declining long-distance Neotropical migrant, is impacted by carry-over effects from spring migration and there is latitudinal variation in aspects of their reproduction. This thesis contributes to current carry-over research by analyzing for the first time how specific conditions an individual bird experienced during spring migration impacted its reproduction. It also adds to research on latitudinal variation in clutch size by being one of the few studies that have tested how provisioning varies in relation to differences in daylight availability across latitude. The results of this research have added to the current knowledge on a declining species through addressing the factors influencing their reproductive success and have highlighted areas of future research.

References

Baker, A.J., P.M. González, T. Piersma, L.J. Niles, I.L.S. Nascimento, P.W. Atkinson, N.A. Clark, C.D.T. Minton, M.K. Peck, and G. Aarts. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. The Proceedings of the Royal Society of London B, 271: 875-882.

Drake, A., C.A. Rock, S.P. Quinlan, M. Martin, and D.J. Green. 2014. Wind speed during migration influences the survival, timing of breeding, and productivity of a Neotropical migrant, *Setophaga petechial*. PLoS ONE, 9: e97152.

Finlay, J. 1971. Breeding biology of purple martins at the northern limit of their range. The Wilson Bulletin, 83: 255-269.

Helms, J.A., A.P. Godfrey, T. Ames, and E.A. Bridge. 2016. Predator foraging altitudes reveal the structure of aerial insect communities. Scientific Reports, 6: 28670.

Kokko, H. 1999. Competition for early arrival in migratory birds. Journal of Animal Ecology, 68: 940-950.

Lack, D. 1967. The significance of clutch-size in waterfowl. Wildfowl, 18: 125-128.

Michel, N.L., A.C. Smith, R.G. Clark, C.A. Morrissey, and K.A. Hobson. 2016. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography, 39:774-786.

Pfister, C., M.J. Kasprzyk, and B.A. Harrington. 1998. Body-fat levels and annual return in migrating semipalmated sandpipers. The Auk, 115: 904-915.

Schaub, M., H. Jakober, and W. Stauber. 2011. Demographic response to environmental variation in breeding, stopover and non-breeding areas in a migratory passerine. Oecologia, 167: 445-459.

Smith, R.J., F.R. Moore, and C.A. May. 2007. Stopover habitat along the shoreline of northern Lake Huron, Michigan: emergent aquatic insects as a food resource for spring migrating landbirds. The Auk, 124: 107-121.

Soler, M. and J.J. Soler. 1992. Latitudinal trends in clutch size in single brooded hole nesting bird species: a new hypothesis. Ardea, 80: 293-300.

Walsh, H. 1978. Food of nestling purple martins. The Wilson Bulletin, 90: 248-260.

Appendix A
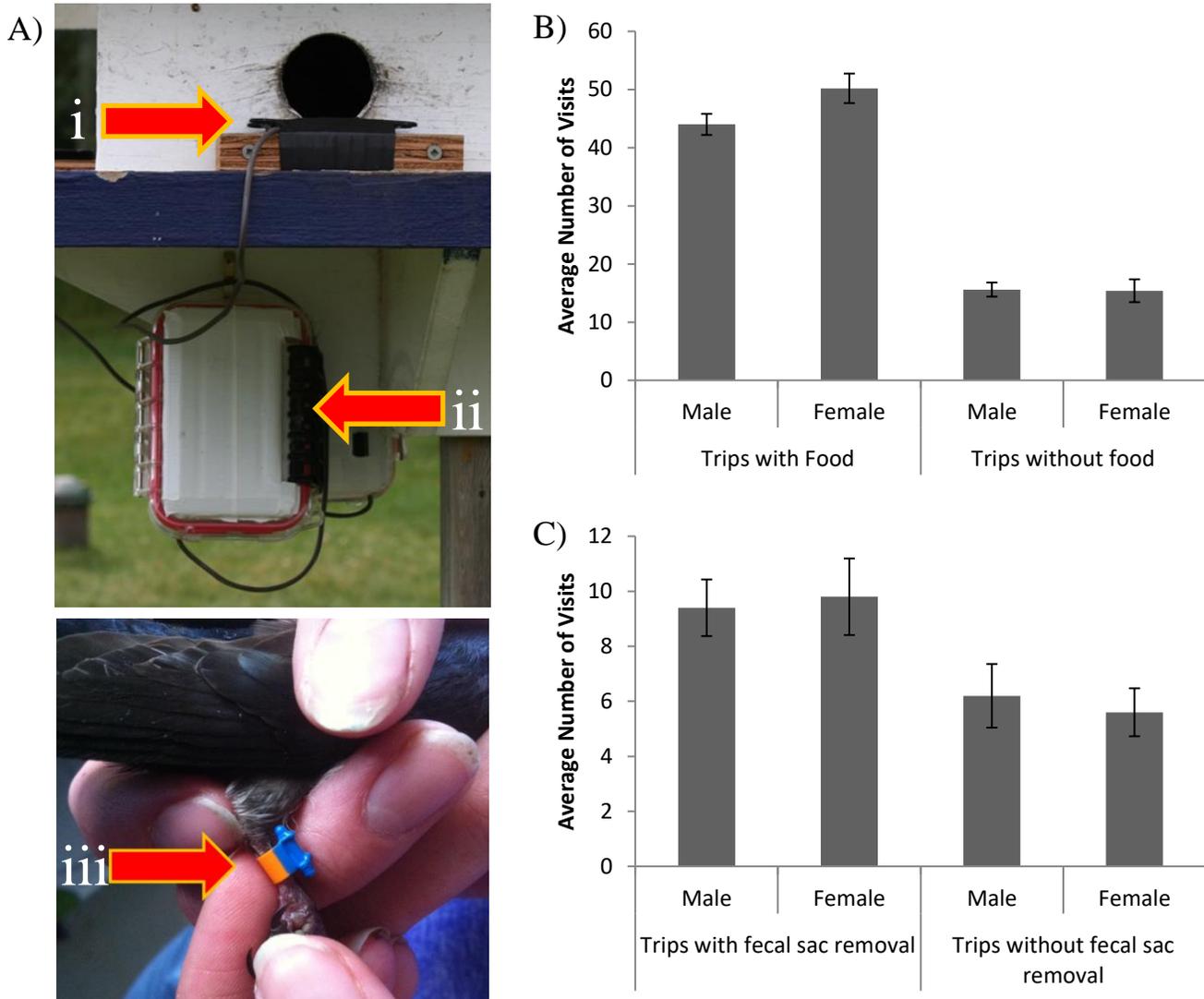
Figure A1. (a) Photos depicting the main components of radio frequency identification (RFID) technology; i- Antenna on a wood spacer block to have antenna at level of cavity entrance that records the time and unique identification number associated with each PIT tag detection, ii- RFID unit with computer board which logs events on a SD card, powered by rechargeable batteries, held within weather tight container, iii- PIT tag secured to plastic coloured leg band coated with liquid rubber. (b) Bar plot showing the average number of visits by male and female purple martins when either a provisioning event or no provisioning event occurred. (c) Bar plot showing the average number of visits that did not involve a provisioning event that involved fecal sac removal or no fecal sac removal by male and female purple martins. Values for (b) and (c) are averages of simultaneous observations of six nest cavities for one hour periods per day over the course of five days late in the nestling period when provisioning events were easily observed due to larger food items being brought and nestlings begging at the nest cavity entrance.