The impacts of phenological mismatch on reproductive success in a declining migratory aerial insectivore

by

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Abstract

Faced with the advancement of spring due to climate change, avian species must adjust their phenological timings in response. However, as the mechanisms underlying organisms' phenology widely vary, responses to altered ecological conditions may differ, which can cause a phenological mismatch resulting in population declines in migratory species. To better understand the mechanisms and effects of these mismatches, I studied the timing of breeding in a long-distance migratory songbird, the purple martin (*Progne subis*), and compared it to the timing of its key resources. I first investigated whether mistiming between purple martin breeding stages and insect emergence negatively affected reproductive success. I found direct evidence for the impact of phenological mismatch on martins' reproductive success, where greater misalignment between peak energetic demand of the nest and peak prey availability resulted in lower fledge success. Next, I investigated whether there were fine-scale differences in the environmental phenology of local breeding sites, and if so, were birds able to align the timing of nesting with this variation. I found that while peak insect variability varied widely (0-49 days) at the micro-habitat scale, nest timing did not, suggesting that birds were misaligned with available resources at this scale. Overall, my results show that phenological mismatches negatively affect migratory birds' reproductive success, and that the lack of synchronization with microhabitat variation may indicate that temperature—shown to influence the timing of egg laying—does not necessarily translate to birds' synchronization with resources at a micro-habitat scale. This rare evidence of direct effects of a mismatch of migratory songbird timing on fitness can help us better understand causes of population declines in purple martin and other aerial insectivores. Future studies should further investigate the mechanisms driving the timing of breeding, such as individual quality and carry-over effects of migration, as well as the population-level consequences of phenological mismatch in martins and other aerial insectivores.

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CHAPTER 1: General introduction

As far back as I can remember, I've always been fascinated by animals' ability to evolve and adapt to their environments. One such adaptation that intrigued me was how birds evolved flight, only to lose the trait when living on islands with reduced predation (Pan et al., 2019). Having learned about evolution with a strong emphasis on Charles Darwin's work, I always viewed evolution as a 'thing of the past,' given the millions of years it would take for a species to develop the adaptations we see today. It was on a trip to Florida that I began to realize that evolution was an ongoing process. I noticed that house sparrows (*Passer domesticus*) in Florida were physically much slimmer than the ones I saw daily in Ontario and Manitoba. In fact, house sparrows were found to have differentiated in size and colour following their introduction to North America, with birds in northern latitudes becoming larger and darker than their southern counterparts (Cohen and Dor, 2018).

The most fascinating evolutionary trait is phenotypic plasticity, a trait allowing organisms to alter their phenotype when exposed to different environments (Murren et al., 2015). This trait is believed to evolve as a result of contrasting selection pressures that arise when organisms are exposed to environmental heterogeneity. Many models have shown that plasticity is favoured in heterogeneous environments where varying 'phenotypic optima' exist across different environments encountered either within an organism's lifetime or across generations (Murren et al., 2015). One real-life example is the common shore crab (*Carcinus maenas*), which exhibits significant differences in colour and pattern depending on its life stage (adult or juvenile) and its habitat (Stevens et al., 2013). Another example is the brown antechinus (*Antechinus stuartii*), which shows plasticity in its activity patterns and use of torpor. Individuals in burned, open habitats displayed decreased activity and increased use of torpor compared to those in the control, a densely vegetated forest (Stawski et al., 2016).

With climate change impacting environments at a pace too rapid for many organisms to adapt to (Sih et al., 2011; Visser and Gienapp, 2019), phenotypic plasticity may offer a solution, enabling them to withstand these changes (Bonamour et al., 2019; Chevin et al., 2010). An example of this can be seen in the bighorn sheep (*Ovis canadensis*), which has advanced its parturition by a median of 15 days in response to environmental shifts, allowing it to better align its reproductive timing with changes in plant phenology (Renaud et al., 2019). In bighorn sheep, as well as in many other species, timing of key life events is often driven by environmental cues, with daylength and temperature being the most common (Visser and Gienapp, 2019). The reliability of these cues is crucial for phenotypic plasticity to be favoured across generations (Bonamour et al. 2019).

Climate change and timing of breeding in migratory species

Migratory animals face a particular challenge, as they must track changes across different suitable environments located in various regions of the globe (Sillett and Holmes, 2002; Newton, 2007; Visser et al., 2004). Migrations typically involve traveling between breeding and non-breeding areas, with animals moving to non-breeding locations when conditions at breeding grounds become unfavourable (Robinson et al., 2008). As climate change impacts different regions of the planet in varying ways, these two types of locations will undergo different levels of alteration (Visser et al., 2004; Horton et al., 2019; Sillett and Holmes, 2002; Newton, 2007). High-latitude regions, in particular, are experiencing the most rapid and significant climate change effects (Robinson et al., 2008).

Reproduction and growth in animals are usually timed with peaks in resource availability, ensuring that juveniles develop during optimal conditions (Visser and Both, 2005; Visser and Gienapp, 2019). However, the cues used to predict these conditions, typically being temperature and photoperiod, may not be the same as those used by food resources. If changes in cues or responses occur too slowly or quickly, there is potential for a phenological mismatch between species (Visser and Both, 2005; Visser and Gienapp, 2019). In marine animals, for instance, fluctuations in sea temperature shifted the phenology of plankton blooms by as much as 2 months (Edwards and Richardson, 2004), resulting in lower recruitment in Atlantic cod (*Gadus morhua*), as cod larvae had less zooplankton available to feed on (Beaugrand et al., 2003). While sedentary species determine breeding time through local cues, migratory species rely on climate cues from non-breeding grounds to predict optimal conditions at their breeding sites (Forchhamer et al., 2002; Visser et al., 2004). The varying magnitudes of alterations across the globe resulting from climate change prevent species from accurately predicting the ideal time to return to their breeding grounds, with long-distance migratory species often experiencing the most severe effects (Visser et al., 2004, Sanderson et al., 2006). Pied flycatchers (*Ficedula hypoleuca*), for example, experienced severe population declines resulting from a mistiming with insect prey. While the birds were found to have advanced their laying dates, they failed to advance their timing of migration, causing young to hatch during suboptimal conditions, which in turn led to a population decline of 90% in areas where resources peaked earlier (Both et al., 2006).

Aerial insectivore population declines

Aerial insectivores overall have experienced significant population declines, the majority of which appeared to have begun in the 1980s (Nebel et al., 2010). This group, which includes swifts, nightjars, flycatchers, and swallows, has is more likely to experience decreases compared to other passerines, with northeastern North America showing the highest probability of such declines (Nebel et al., 2010). Several theories have been proposed to explain these trends, including reductions in prey availability, deteriorating wintering ground conditions, and phenological shifts driven by climate change (Spiller and Dettmers, 2019).

Due to the increased rate at which insects respond to environmental changes compared to birds (Saalfeld et al., 2019; Visser and Gienapp, 2019), many studies have examined the effects of phenological mismatch on aerial insectivores. The mismatch has been postulated as a primary driver of population declines, but the evidence remains mixed, with some studies showing no clear impact on populations (Robinson et al., 2008). For example, Dunn et al. (2011) found that tree swallow (*Tachycineta bicolor*) egg-laying dates were not significantly associated with the peak of food abundance. Instead, laying dates were found to advance whereas insect peaks increased later on in the season (Dunn et al., 2011). Similarly, Imlay et al. (2017) showed that although Barn (*Hirundo rustica*), Cliff (*Petrochelidon pyrrhonota*), and tree Swallows with earlier laying dates had higher insect abundance during brood rearing, nestling survival and mass did not correlate with this abundance. However, Bank Swallows (*Riparia riparia*), which did not significantly advance their breeding, experienced lower reproductive success (Imlay et al., 2018).

Previous research in the Avian Behaviour and Conservation lab have examined many aspects of phenotypic plasticity in my study species, the purple martin (*Progne subis*), a declining migratory aerial insectivore affected by climate change (Jervis et al., 2019). This trait may enable the birds to adapt to shifting environmental conditions. Shave et al. (2019) and Smith and Fraser (2024) demonstrated that purple martins, like other birds (Bonamour et al., 2019), are capable of advancing their nesting and laying dates in response to temperature. Since temperature is often used as a proxy to determine insect timing (Bonamour et al., 2019), this suggests that purple martins may be able to synchronize their breeding with insect phenology.

Thesis Outline

To better understand the mechanisms underlying the response of long-distance migrants to shifts in resource phenology, it is crucial to gain more information about their plasticity and how they are affected by changing conditions. In my projects, I explored the timing of purple martin (*Progne subis*) breeding in relation to the phenology of key resources and how this timing impacts their fitness.

In Chapter 2, I aimed to determine whether purple martins experienced direct effects from phenotypic mismatches with their insect prey. To do so, I conducted insect transects throughout their breeding season to determine the timing of peak availability. I then modeled the timing of these peaks relative to the timing of purple martin breeding stages observed at field sites to determine whether mismatches impacted the birds' reproductive success. My results indicate that timing later breeding stages, such as day ten of development and fledging, closer to availability peaks increases reproductive success, providing rare evidence of direct effects of phenological mismatches on fitness.

In Chapter 3, I focused on whether there were microhabitat and purple martin phenology timing differences between field sites. Using the same transect and nest data, along with tree green-up data collected from regularly sampled tree leaves to track their development throughout the season, I compared timings at each site as well as the difference between microhabitat timing and bird timing. I found that while there were significant variations in microhabitat timing between sites, the timing of purple martins was not significantly different, remaining relatively constant across sites. These findings suggest that while purple martins time their breeding with temperature changes, temperature alone does not enable them to fine-tune their timing to varying conditions between microhabitats.

In Chapter 4, I used the knowledge gained from my previous chapters to summarize the consequences of failing to synchronize with insect peaks and the ability (or inability) of purple martins to align their timing with resource availability. I discuss how these findings relate to past research on avian species and climate change and offer suggestions for conservation applications.

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CHAPTER 2: Phenological mismatch with peak insect availability results in reduced reproductive success in a declining aerial insectivore

Abstract

Climate change is driving an advancement and increased variability in resource phenology, requiring animals to adjust their schedules in order to breed at optimal times. Migratory birds may be particularly challenged in this regard, as cues at their wintering grounds are becoming unreliable indicators of conditions at breeding grounds, and it is unclear whether they can adjust sufficiently to environmental conditions after arrival in spring. I investigated how long-distance migratory insectivores, specifically purple martins (*Progne subis*), time their breeding stages relative to insect prey availability, and whether phenological mismatches impact reproductive success. In southern Manitoba, Canada, I estimated the peak insect availability during purple martin breeding, determined how it aligned with breeding stages (egg laying, hatch, peak nest provisioning at day 10, and fledge) and modeled how the alignment affected reproductive outcomes. I found that the timing of peak nest provisioning (day 10) aligned best with peak insect availability compared to other nesting stages (egg laying or fledge). Overall, my results show that nests that better aligned with peak insect availability (i.e. showing a lower phenological mismatch) resulted in shorter duration in the nest, and greater numbers of young fledged, and a higher proportion of hatched young that successfully fledged. For example, when fledge dates were timed closer to overall insect and Odonate peaks, the time that young spent in the nest before fledging decreased. The proportion of hatched young that fledged also decreased when Odonate and Lepidopteran peaks were less aligned with fledge dates. In summary, my results demonstrate direct impacts of phenological mismatch on the reproductive success, and therefore fitness, of a declining aerial insectivore. Future research should focus on studying the

mechanisms underlying the timing of breeding stages, such as carry-over effects from migration, individual quality, and the effects of parent age. Due to the impacts of climate change on resource availability timing, understanding these phenological mismatches is crucial. My findings provide insights into the challenges faced by declining migratory songbirds and critical insights into the mechanisms of phenotypic plasticity in response to climate change.

Introduction

To maximize individual fitness and survival, animals need to time their phenology – the seasonal timing of life-cycle events – with limited yearly periods during which environmental conditions are most advantageous. This is particularly true for energetically demanding activities such as reproduction; if this life-cycle event were to take place outside of the 'window' of favourable conditions (i.e. a period of high resource abundance), parents and offspring could both experience significant fitness consequences (Visser and Gienapp, 2019; Parmesan and Yohe, 2003). Despite having evolved to meet these time constraints, animals must now face the added challenge of having their ecological conditions altered by climate change. The phenology of organisms across many taxonomic groups has shifted in response to this global phenomenon, albeit not at the same rates (Visser and Gienapp, 2019; Kharouba et al., 2018). This disparity may be attributed to the different mechanisms underlying the phenology of various organisms. As the time windows for many species are determined by the phenology of other species at different trophic levels, differences in phenological response rates could result in a mismatch (Visser and Gienapp, 2019; Kharouba et al., 2018; Visser and Both, 2005).

It is crucial for birds to optimize their access to resources to meet the high energetic costs of nest provisioning (Visser et al., 2004). Optimal hatch dates may occur a few days before seasonal food peaks, allowing chicks better access to food over a longer period, especially when their energetic demands are highest (Visser et al., 2006; Lepage et al., 1998). Birds may use environmental cues during egg formation to time their egg-laying, as they have a predictive value for when food will be plentiful later in the season. Egg-laying cues, such as temperature and photoperiod, may combine to trigger a physiological response that results in egg laying (Bonamour et al., 2019; Visser et al., 2011; Schaper et al., 2012; Guillemette et al., 2024). However, as the environment varies from year to year, so does the relative value of different cues, causing birds to lay at different times (Visser et al., 2004). In arctic-nesting shorebirds such as American Golden Plover (*Pluvialis dominica*), Baird's Sandpiper (*Calidris bairdii*) and White-rumped Sandpiper (*Calidris fuscicollis*), hatching occurred earlier in the 2000s than in 1954, and synchrony with food resources was especially low between the years 2005 and 2008 (McKinnon et al., 2012). Throughout all years, however, chicks experienced increased growth rates when hatches were timed before peak periods of arthropod abundance (McKinnon et al., 2012). In Snow Geese (*Anser caerulescens*), birds synchronized hatch dates with peak food abundance, as food availability during egg formation may have served as a cue for geese to anticipate when food would be abundant later in the summer (Lepage et al., 1998).

If peak food resources and energetic demand in the nest are mismatched, the nutritional stress caused by parents' limited ability to deliver food may cause nestlings to experience slower growth and maturation (Kouba et al., 2015). Nestling development would be particularly impacted if these food shortages coincided with more energetically demanding periods, which may prolong time spent in the nest (Kouba et al., 2015; Freeman et al. 2020), although further studies are needed to test the direct relationship between food peak mismatches and time spent in the nest. Wing length growth, for instance, strongly predicts nest departure timing in species like

Tengmalm's owls (*Aegolius funereus*), great tits (*Parus major*), and tree swallows (*Tachycineta bicolor*), with higher growth rates correlating to shorter nestling periods (Kouba et al., 2015; Michaud and Leonard, 2000; Radersma et al., 2011). Leaving the nest earlier comes with the benefit of reducing the risk of nestlings being preyed upon by nest predators (Kouba et al., 2015). This is also applicable to parents, as they too would be less exposed to nest predators by spending less time in the nest (Turcotte-van de Rydt, 2022). Parents would further benefit from the expedited growth of their nestlings by spending less time and energy on feeding them (Michaud and Leonard, 2000).

Migratory birds face the added challenge of needing to shift their migration timing to reach breeding grounds and match the emergence of key resources (Visser et al., 2004; Mayor et al., 2017). As climate change affects the globe's regions differently, this problem is exacerbated for long-distance migrants, which, from their wintering grounds, lack environmental cues indicating an earlier spring at their breeding sites (Visser et al., 2004; Both et al., 2010; Horton et al., 2019). Spring migration timing is mostly driven by inherent circannual schedules, which can be cued at their wintering grounds by seasonal changes in photoperiod (Visser et al., 2004; Jones and Creswell, 2009; Singh et al. 2021).

If mistimed spring arrival impacts the timing of nesting through unreliable cues at wintering grounds, there is an increased potential for a phenological mismatch (Visser et al., 2004; Jones and Creswell, 2009; Horton et al., 2019). A mismatch between prey abundance and nesting timing may cause migratory birds to face low breeding success, leading to population declines (Visser et al., 2004). For instance, the pied flycatcher (*Ficedula hypoleuca*) population in the Netherlands declined by 90% over two decades in areas with the earliest food peaks. While the birds were found to have advanced their laying dates, their spring arrival timing had not changed, limiting their ability to further align with the advancement of spring (Both et al. 2006; Both and Visser, 2001). American wood warblers may also experience mismatches, as their wintering grounds had not warmed to the same degree as their breeding areas, which likely resulted in them arriving after their food resources had peaked (Strode, 2003; Mayor et al., 2017). However, there have been few studies of the direct consequences of phenological mismatch on reproductive success for migratory passerines.

Aerial insectivores in North America have experienced significant population declines (Spiller and Dettmers, 2019; Fraser et al., 2012). While they face a multitude of threats, such as habitat loss, road mortality and pollution (Nebel, 2010), climate change is believed to be the most important driver of these declines (Hansen et al., 2006). In tree swallows, reductions in insect availability led to decreased clutch sizes, fewer fledglings, and poorer body conditions (Quinney et al., 1986; Hussell and Quinney, 1987; McCarty and Winkler, 1999). Other studies suggest this may have been caused partly by warmer temperatures, resulting in earlier emergences and peaks (Visser et al., 2006; Bartomeus, 2011). However, few studies have shown a direct connection between the alignment of insect peaks and the reproductive output of birds, let alone aerial insectivores. Certain aerial insectivores exhibit high plasticity in response to changing environmental conditions, with purple martins (*Progne subis*), for example, adjusting their laying dates to earlier times in response to increasing temperatures (Shave et al., 2019; Smith and Fraser, 2024). Furthermore, previous research with purple martins suggests that populations and individuals can flexibly adjust the timing of their egg laying to local environmental conditions, laying earlier in warmer years and later in cooler years (Shave et al., 2019; Smith and Fraser, 2024; Bani Assadi et al., *under review*). This flexibility is presumed to allow birds to align their nesting timing with the availability of insect prey. This suggests that aerial insectivores may be able to recover and sufficiently synchronize their breeding with insect emergence.

In current literature, there is a distinct gap in knowledge about whether avian species, such as migrants and aerial insectivores, experience direct consequences to their reproductive success when they fail to synchronize their breeding with peak insect abundance. It is also unclear whether birds align their breeding stages with the peaks of different food sources. To understand how aerial insectivores time their reproduction, I investigated the reproductive timing and success of the purple martin (*Progne subis*). This declining species was studied by monitoring their nests and insect prey availability at breeding sites in southern Manitoba.

My first objective was to determine whether aerial insectivores aligned different reproductive stages (egg laying, hatch, peak nest provisioning, or fledge dates) with peak insect availability. Previous studies have shown that aerial insectivores such as the Purple Martin (*Progne subis*), feed their young a wide variety of insects, such as Dipterans, Lepidopterans and Odonates. While Hymenopterans are fed to young as well, they are most prevalent in adult diets (Dunoyer et al., 2024; Forsman et al., 2012). In addition to this, larger or more chitinous insects were shown to be better suited for older nestlings (Kaya et al., 2015; Dunoyer et al., 2024; Walsh, 1978). Furthermore, nestling energetic demands are expected to peak during the period at which chick growth rates are highest, typically around day ten in purple martins due to the development of wings and feathers (Allen et al., 1952; Poulin and Brigham, 2001). I therefore hypothesized that aerial insectivores align periods of peak energetic demand with the peak availability of insects, prioritizing the intake of smaller, softer insects, during early nestling stages (as they are easier to digest), and larger, more chitinous insects during later developmental stages (Dunoyer et al., 2024; Forsman et al., 2021). I predicted that hatch dates would more closely match Diptera and Lepidoptera peaks and that day 10 post-hatch dates would align with Odonata and overall insect availability. I also predicted that fledge dates would be closer to peak Hymenoptera availability, as adults are known to eat more insects of this order than nestlings, suggesting that this insect group may be an important food source for recently fledged young (Dunoyer et al., 2024). My second objective was to determine whether aligning nesting stages with insect peaks plays a vital role in aerial insectivore reproductive success and fitness. I hypothesized that aligning key life stages with insect peaks is crucial for reproductive success, as synchronization allows parents to provision young to meet the high energy demands of development (Allen et al., 1952; Poulin and Brigham, 2001). Specifically, I predicted that aligning the period where energy requirements are expected to be the highest (i.e. day 10 post-hatch, when nestling growth rates peak) with the peak availability of insect prey would increase the proportion of hatched birds that fledge as well as the total number of nestlings fledged. I also predicted that nests more aligned with peak prey would result in a decrease in the amount of time spent in the nest before fledging (i.e. because more food would result in faster growth rates and an earlier fledge). This research addresses an important research gap by providing direct tests of how mismatch with the availability of prey resources may impact the reproductive success of migratory songbirds, specifically in declining populations of aerial insectivores believed to be impacted by climate change. Understanding these direct effects is crucial for informing conservation efforts and predicting potential future declines in populations due to advancements in insect emergence.

Methods

Study sites and study species

The breeding colonies used in the study were located at four different field sites located near Winnipeg, in Manitoba, Canada. These sites include a private backyard south of Winnipeg (49.74°N, 97.13°W), FortWhyte Alive (FWA), a wildlife preserve and recreation area in the city of Winnipeg (49.82°N, 97.23°W), Oak Hammock Marsh (OHM), a marsh located north of Winnipeg (50.17°N, 97.13°W) and Pointlands (PL), located on the University of Manitoba campus (49.81°N, 97.13°W). The purple martin (*Progne subis*) is a long-distance diurnal migrant that travels 7, 000 to 12, 000 km each spring from its wintering grounds in South America to breeding grounds in North America (Turcotte-van de Rydt et al., 2023). As an aerial insectivore, its diet consists of many flying insects including Odonates, Hymenopterans, Dipterans and Lepidopterans (Dunoyer et al., 2024). This species' abundance in Manitoba and preference for nesting in man-made houses makes it an ideal subject for this research.

Nest monitoring

All nest data collection adhered to guidelines provided by the Purple Martin Conservation Association' 'Project Martinwatch' (Purple Martin Conservation Association [PMCA], 2017). Nests were visited every 2-3 days during the breeding period with the dates of important reproductive stages such as first egg laid, hatch date, and fledge dates being recorded. As female purple martins typically lay one egg per day, first egg dates were determined by subtracting the number of eggs present in the nest from the nest-check date. Using hatch dates, I was also able to calculate the date at which nestlings reached the age of 10 days. In addition to these dates, the number of eggs, hatchlings, and fledged young were also documented. I determined the age and sex of parents through visual observations using binoculars or by capturing the birds from their nestboxes, with plumage characteristic being used to determine age categories (after second year

– ASY, or second year – SY) (Pyle, 1997). All data collection procedures followed the guidelines of the University of Manitoba’s Animal Care Committee, which approved the methods used in this experiment (Animal Care Protocol Number F23-001-1).

Insect monitoring

Insect availabilities were measured every other day from 8:00 to 16:00 from the start of May to mid-August, in 2017, 2021, 2023 and 2024 through transect surveys located within a 250 m distance of purple martin colonies. Transects were 100 m in length and were completed in 15 minutes, with surveyors walking at a constant speed of 0.4 km/h. Two surveyors conducted transects: one was responsible for counting and identifying all flying insects within their frontal view, while the other recorded the data, noting the number of insects observed from each order. All flying insects observed were identified to order, with the exception of data recorded in 2017, when only Odonate dates were recorded. Since there was no distance limit for counting insects, these methods come with the caveat that larger insects may be seen at a farther distance than smaller ones, potentially creating a sampling bias towards bigger insects. Transects were conducted only once upon visiting each site on any given day, and the same locations were used each time (within 150 meters of purple martin houses, in areas with a high observed insect density). As these methods reflect prey availability to birds on a specific day rather than the overall abundance over the summer, weather effects were not directly controlled for. The reasoning is that weather impacts would already influence insect availability on any given day and therefore are captured in the data. Furthermore, since prey is sampled every 1-3 days, this sampling frequency provides a reliable index of prey availability over the nesting period, accounting for short-term weather fluctuations.

Statistical methods

Peak insect availability dates

To determine peak insect availability dates, quadratic models were fitted to the transect data, using similar methods outlined in Saalfeld et al. (2019). The response variable in each of those models was the number of insects in a given order observed, whereas the independent variable was the date converted to Julian date. The peak date was then determined by calculating the maximum value of each model's predictions. This method was repeated for four study sites during 2023 and 2024, but for only 3 of those sites during 2021 and 2017, as martin houses at PL had only been installed in 2021 and were not occupied by martins in that season.

While I assessed peak insect availability for all insects observed over the summer, I calculated additional peak dates for 4 specific insect orders: Lepidoptera, Diptera, Odonata and Hymenoptera. Special focus was put on these insect groups due to them potentially serving as important food sources during different life stages (Dunoyer et al., 2024; Forsman et al., 2012). The orders Diptera and Lepidoptera are predicted to increase the number and proportion of young fledged from the nest and decrease the time spent in the nest prior to fledging if their peaks are timed closer to purple martin hatch dates, as their smaller and softer bodies would benefit small, young nestlings (Dunoyer et al., 2024). The orders Odonata and Hymenoptera, in contrast, are better suited for older nestlings due to their tough chitinous bodies, and larger size in the case of Odonates (Kaya et al., 2015; Dunoyer et al., 2024; Walsh, 1978). Nestling diets were found to contain significantly more Odonates than adults, whereas Hymenopterans were more frequently detected in adult diets, leading to the prediction that fledge numbers and proportions will increase, and that time spent in the nest would decrease, if day 10 and fledge dates are timed with Odonate and Hymenopteran peaks, respectively (Dunoyer et al., 2024). In the case of timing with fledge, this would suggest that older nestlings, beyond day 10, would benefit more from Hymenopterans, rather than fledged young.

Alignment of life stages with insect peaks

Using the ‘glmmTMB’ package (version 1.1.10 in R (version 4.4.1) in RStudio (version 2024.09.0+375, R Core Team, 2024), I determined whether there were significant differences in life stage timing relative to peak insect availability. I fitted five Gaussian general linear models, one for each insect group, examining the time difference between the dates of each life stage and the corresponding peak insect availability date. Life stage (egg laying, hatching, day 10 of development and fledging)served as the independent variable, while the difference in time served as the response variable. The age of the parents was included as a fixed effect, while site, year and nest ID were included as random effects (Table 1).

Next, to determine which insect peak aligned the closest to each nest stage, I calculated the median date of each life stage at a given site and year and subtracted its corresponding insect peak date to obtain a median difference from each site. I then averaged these differences to determine which insect group had its peak closest to each life stage, where the smallest time difference across all life stages would indicate the closest alignment with the insect peak. I used egg laying, hatch, and day ten date data from all four years. Fledge dates, however, were only collected in 2021 and 2023 (Supplemental Table 1).

Effect of breeding timing relative to peak availability on reproductive success

Using the ‘glmmTMB’ package (version 1.1.10 in R (version 4.4.1) in RStudio (version 2024.09.0+375, R Core Team, 2024), I fitted a total of 60 general linear models, all of which used different combinations of response variables and independent variables.

The response variables included the proportion and number of successfully fledged young, and the time young spent in the nest prior to fledging. The proportion of fledged young standardizes the rate of successful fledges to the number of eggs laid and may indicate more about the success of provisioning young post-hatch, whereas the number of fledged young provides the total reproductive output per bird and would include resources incorporated from egg laying to fledge. The number of fledged young was determined by monitoring the number of birds that fledged from a nest, done by subtracting the number of observed deaths throughout the season, until the fledging period, from the number of observed hatches. The proportion of young fledged was determined by dividing the number of young fledged by the number of eggs laid in a given nest. The time spent in the nest was measured in days from the date of first hatch to the date of first fledge.

The independent variables were the difference in time between the peak date of a given insect group (all insects, Lepidopterans, Dipterans, Odonates and Hymenopterans) and the date of occurrence of life stages at each nest (egg laying, hatch, day 10 of development and fledging). As combining insect groups and life stages in the same model resulted in overfitting and multicollinearity, I opted to instead study these variables independently in their own separate models. I converted the differences in time to their absolute – or positive – values, which would allow me to study how closeness to peak affects reproductive success by determining whether a given stage date was closer to insect peaks (smaller values, closer to zero) or further away from the peak (larger values).

To test the effects of independent variables on the proportion of fledged young, I used binomial models, whereas Poisson models were used to model the number of fledged young and the time duration to fledge.

All models included the age of parents as a fixed effect, as older birds (after second year – ASY) have been shown to arrive earlier at breeding sites and may therefore have an increased ability to time themselves with peak dates compared to younger birds (second year – SY) (Morton and Derrickson, 1990). The different categories used in the models include ASY-ASY, ASY-SY, SY-ASY and SY-SY, with the first age position indicating the age of males, and the second position indicating the age of females. For example, an ASY-SY grouping would indicate an older, after second year male, and a younger, second year female. Site and year, on the other hand, were included as random effects. The overall model structure was kept consistent across analyses to ensure that model results were comparable to one-another. While interactions terms between date differences and age of parents were originally included in the models, ANOVAs performed to assess their significance revealed that they did not enhance the models' performances. All interaction terms were thus excluded from the models.

Results

Alignment between peak prey availability and nesting stage

The Gaussian general linear models comparing relative timing between life stages and insect peaks showed significant differences between life stages ($p < 0.001$) (Supplemental Table 1).

The peak of overall insect availability aligned the most closely with day 10 post-hatch, where day 10 varied from insect peak by an average of -4.18 days, with the negative value indicating that day 10 dates typically occurred before insect peaks. Peak availability aligned less closely with hatch (-14.45 days) and fledge (14.29 days), and least with first egg-laying date (-34.60 days, Table 1, Figure 1). At a finer scale, I found that peak availability for Dipterans and Lepidopterans (i.e. smaller, softer-bodied prey) did not align most closely with hatch date (-7.95 and -16.45 days, respectively), but instead with day ten by -2.05 and -6.45 days, respectively. Peak availability of Odonates did not support my prediction that it would align the most closely with peak nest provisioning dates (day 10), where its peak differed from median day 10 by 10.08 days, and aligned the most closely with hatch date (0.08 days). Despite this, it should be noted that due to the use of median dates in my analysis, there is likely some overlap between the earliest day 10 dates and Odonate peaks. Finally, Hymenopteran peak dates aligned more closely with median fledge dates as predicted, with an average difference of 12.00 days (Table 1 and Figure 1).

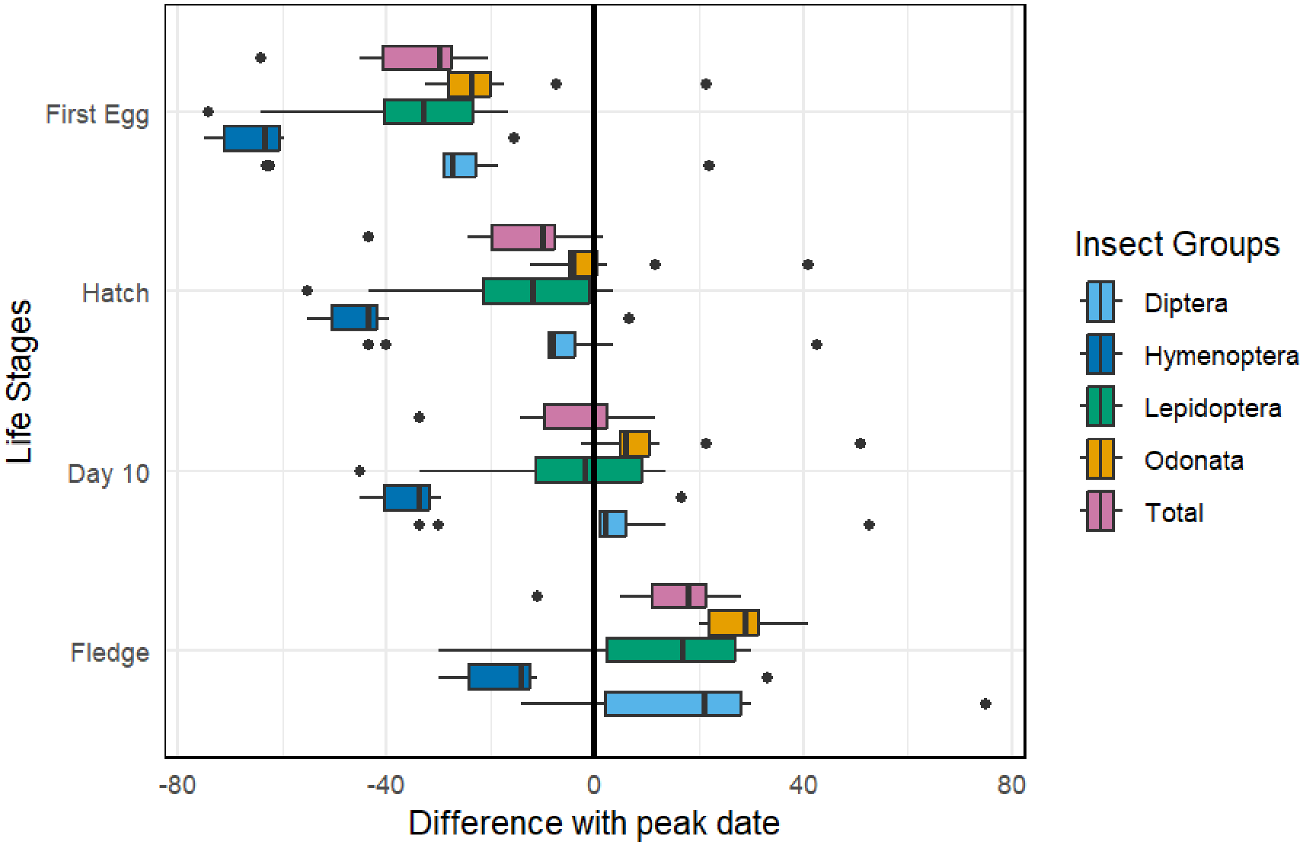

Figure 1. Boxplot demonstrating the difference in days between median date of life stages (including the date of first egg laid, first hatch, first reach of day ten of development and first fledge) at four different field sites over three years (four for Odonata) and their respective insect peak date. The closer a life stage mean estimate is to zero (accentuated by the vertical black line), the closer is to its corresponding peak insect date.

Table 1. Differences in days between the timing of four purple martin life stages (first egg, hatch, day 10, and fledge) and the peaks of five insect groups (all insects, Lepidoptera, Diptera, Odonata, and Hymenoptera). The values represent the averaged differences in timing, calculated from the median life stage dates for each field site (Private Site, FWA, OHM, and PL) and year combination (2017, 2021, 2023, and 2024). Insect peak dates were also averaged across sites and years. The lowest estimates are bolded to highlight the closest alignment of insect peaks with life stages.

	First Egg		**Hatch**		**Day 10**		**Fledge**	
Insect Group	Estimate	Standard Error	Estimate	Standard Error	Estimate	Standard Error	Estimate	Standard Error
All insects	-34.60	4.04	-14.45	4.00	**-4.18**	4.00	14.29	4.97
Lepidoptera	-36.60	6.04	-16.45	6.17	**-6.45**	6.17	10.86	8.59
Diptera	-28.10	7.49	-7.95	7.45	**2.05**	7.45	20.29	11.36

Odonata	-20.08	3.92	**0.08**	3.84	10.08	3.84	28.14	2.82
Hymenoptera	-61.00	5.39	-40.85	5.53	-30.85	5.53	**-12.00**	7.94

Impact of difference from peak on reproductive success

Duration in the nest

Models examining the alignment of egg laying, hatch and day 10 of nestling development with insect peaks did not show any significant effects on time spent in the nest ($p > 0.05$, Supplemental Tables 2-4, Figure 2). Modeling the difference between fledge dates and peaks, however, revealed varying effects depending on insect groups. Time spent in the nest was found to significantly decrease when fledge dates were timed closer to overall insect peaks ($p = 0.016$) and Odonate peaks ($p = 0.015$, Supplemental Table 5, Figure 2). The other insect groups showed no significant differences in time spent in the nest. The age of parents had no significant effect on the length of time spent in the nest ($p > 0.05$, Supplemental Tables 2-5).

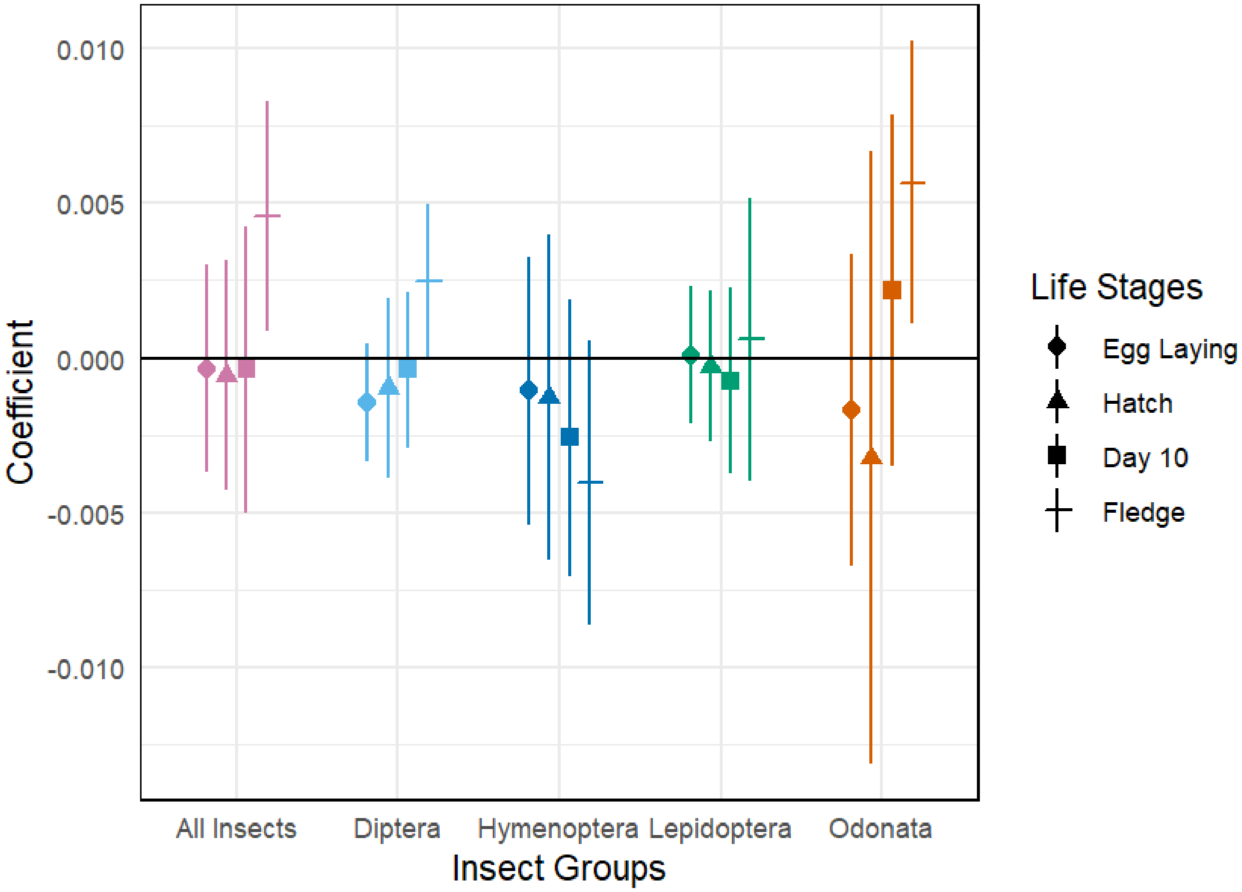

Figure 2. Coefficients from a generalized linear mixed model showing the relationship between the time taken to fledge (measured by subtracting hatch date from fledge date) and the difference in dates between various purple martin life stages (first egg date, hatch date, date nestlings reach day 10 post-hatch of and fledge) and the dates of insect peak availabilities. The shapes represent the coefficient estimates, whereas the whiskers represent the 95% confidence intervals. There is a significant relationship between the variables when the confidence intervals do not overlap with zero (accentuated by the black line). Values represent absolute differences in days between nesting stage and peak availability of each insect prey type. Positive coefficient value estimates indicate that life stages occurring closer to peak insect prey dates results in a lower amount of time spent in the nest whereas negative coefficient values indicate that life stages occurring further from peak insect prey dates result in a lower amount of time spent in the nest (indicating these insect groups may not be important for fledge success).

Proportion of young fledged

When egg laying and hatch dates were more closely aligned with Lepidopteran peaks, fledge proportions were found to significantly decrease ($p_{Egg\ Laying} < 0.001$, $p_{Hatch} = 0.039$, Supplemental

Tables 6-7, Figure 3). All other models examining egg laying and hatch date differences were otherwise insignificant. The alignment of day ten with insect peaks revealed insignificant results across all taxonomic insect groups ($p > 0.05$, Supplemental Table 8, Figure 3). Aligning fledge dates with Lepidopteran and Odonate peaks revealed a significant increase in the proportion of young that fledged ($p_{Lepidoptera} = 0.006$, $p_{Odonata} = 0.032$), whereas alignment with Hymenopteran dates resulted in a significant decrease ($p = 0.009$). The Dipteran and overall insect models revealed insignificant results ($p > 0.05$, Supplemental Table 9, Figure 3).

The age of parents was found to have significant effects, with SY-SY pairings specifically decreasing the proportion of fledged young in the egg-laying, hatch and day 10 models ($p > 0.05$). The random effects explained approximately 41.3% of the variation in the models, with the marginal R^2 ranging from 0.047 to 0.161, and the conditional R^2 ranging from 0.362 to 0.581 across models (Supplemental Tables 6-9).

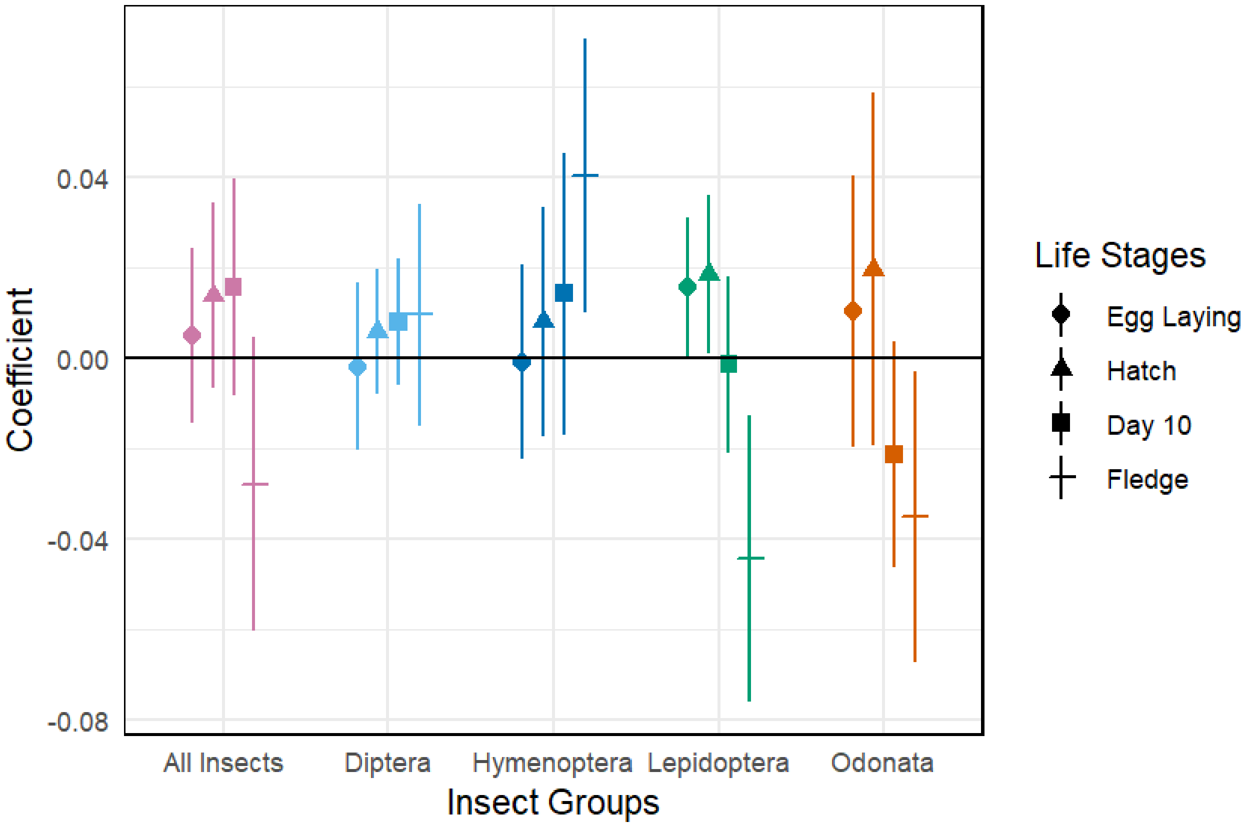

Figure 3. Coefficients from a generalized linear mixed model showing the relationship between the proportion of young fledged and the difference in dates between various purple martin life stages (first egg date, hatch date, date nestlings reach day 10 post-hatch of and fledge) and the dates of insect peak availabilities. The shapes represent the coefficient estimates, whereas the whiskers represent the 95% confidence intervals. There is a significant relationship between the variables when the confidence intervals do not overlap with zero (accentuated by the black line). Values represent absolute differences in days between nesting stage and peak availability of each insect prey type. Negative coefficient values indicate that life stages occurring closer to peak insect prey dates result in a higher proportion of hatched young that successfully fledge, whereas positive coefficient value estimates indicate that life stages occurring further from peak insect prey dates results in a higher proportion (indicating these insect groups may not be important for fledge success).

Number of young fledged

Models examining the degree of alignment between insect peaks and nesting stages (egg laying and hatch) did show any significant differences in fledge numbers ($p > 0.05$, Supplemental Table 10-11, Figure 4). Closer alignment between day 10 and Odonate peaks resulted in significant increases in fledge numbers (*p* = 0.039), while other models examining day 10 were found to have insignificant results (*p* > 0.05, Supplemental Table 12, Figure 4). Aligning fledge dates with Hymenopteran peaks resulted in significant declines in fledge numbers (*p* = 0.006, Supplemental Table 13, Figure 4). Otherwise, models examining fledge alignment relative to peaks of remaining insect groups revealed no significant differences in number of fledged young. The age of parents was found to have significant effects in only some of the egg-laying, hatch, and day 10 models, with SY-SY pairings specifically decreasing the proportion of fledged young in (*p* > 0.05, Supplemental Tables 6-9).

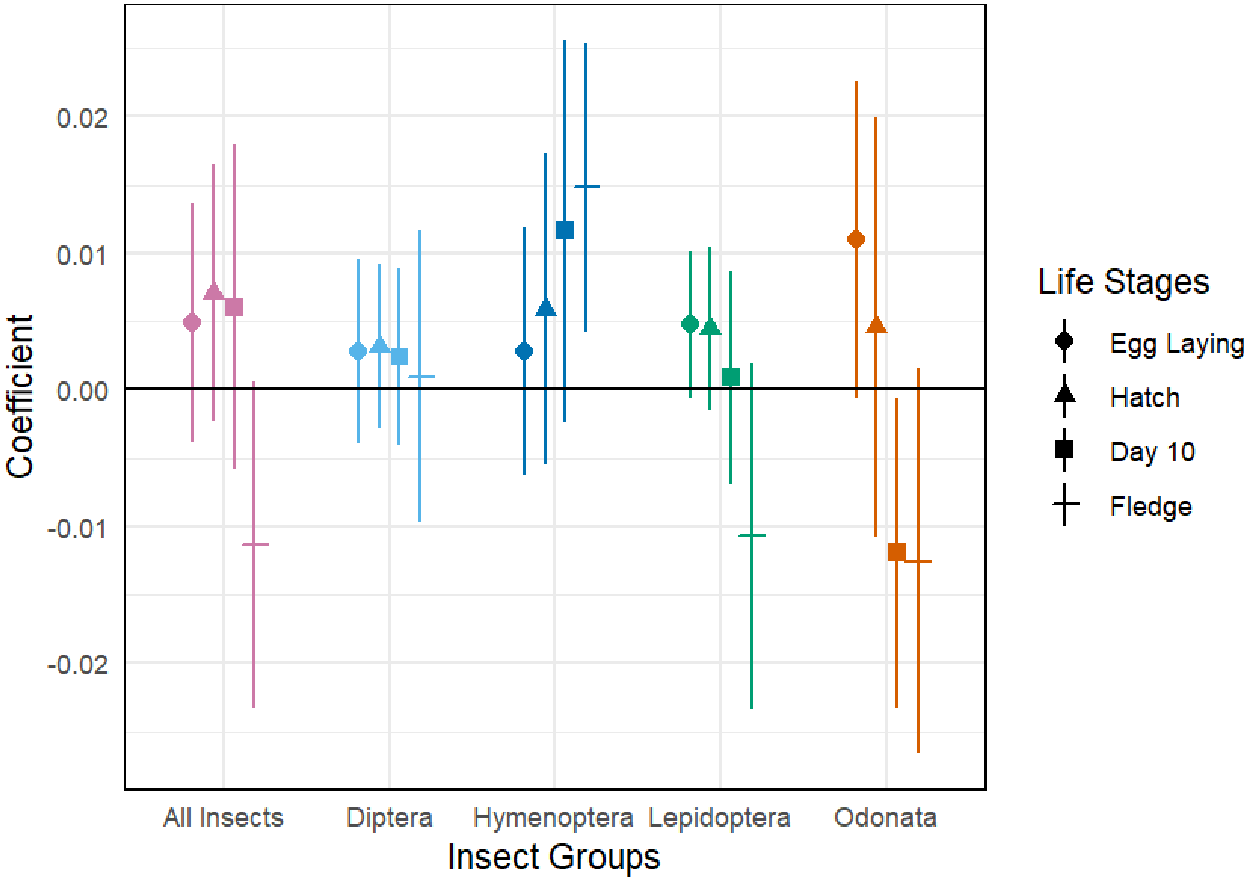

Figure 4. Coefficients from a generalized linear mixed model showing the relationship between the number of young fledged and the difference in dates between various purple martin life stages (first egg date, hatch date, date nestlings reach day 10 post-hatch of and fledge) and the

dates of insect peak availabilities. The shapes represent the coefficient estimates, whereas the whiskers represent the 95% confidence intervals. There is a significant relationship between the variables when the confidence intervals do not overlap with zero (accentuated by the black line). Values represent (absolute) differences in days between nesting stage and peak availability of each insect prey type. Negative coefficient values indicate that life stages occurring closer to peak insect prey dates result in a higher number of successful fledges, whereas positive coefficient value estimates indicate that life stages occurring further from peak insect prey dates results in a higher number (indicating these insect groups may not be important for fledge numbers).

Discussion

My findings show that timing nesting to align with key insect peaks positively influences reproductive success, including the time young spend in the nest, hatch and fledging success, and the total number of nestlings fledged (Figures 2, 3, and 4). This supports my prediction that matching the peak period of nestling growth (around day 10 post-hatch) with the highest availability of insect prey would increase the reproductive success of aerial insectivores. For example, a 27-day difference between the peak availability of a key prey (Odonates) and day 10 post hatch resulted in the number of fledged birds decreasing from approximately 4.31 individuals to 3.31. These findings provide evidence of the direct impact of the mismatch between prey availability and breeding timing on reproductive success, a relationship rarely demonstrated in songbirds. The proportion of fledged young was also found to increase when Odonates and Lepidopterans were timed with fledge dates, and timing fledge date closer to overall insect and Odonate peaks was found to significantly decrease the time birds spent in the nest.

Alignment between nesting stage and peak prey availability

While breeding represents a period of high energetic cost in the annual cycle, different stages of nesting may have varying energetic demands. For example, egg laying and the provisioning of early and later developmental stages can differ in their resource requirements. In songbirds, energetic demands are expected to peak during the period at which chick growth rates are highest, typically around day ten in purple martins (Allen et al., 1952; Poulin and Brigham, 2001). Based on earlier works with these birds (Dunoyer et al., 2024; Walsh, 1978), I had predicted that, if birds could flexibly time nesting to the peak availability of suitable prey, hatch dates would align more closely with smaller, soft-bodied prey (Dipterans and Lepidopterans). Older nestlings (having reached day ten of development) were predicted to be more aligned with larger prey, more chitinous prey, such as Odonates, while Hymenopterans were predicted to be aligned with fledge dates, due to their high abundance in adult purple martin diets (Dunoyer et al., 2024). My predictions for alignment with day 10 were supported, as peak overall insect availability aligned more closely with this very energetically demanding period, as compared to egg laying, hatch, or fledge dates. My predictions for how specific insect taxa may align with specific nestling life stages were less well supported. Softer-bodied and smaller insect (Diptera and Lepidoptera) peaks were more closely timed to day ten than to hatch date as originally predicted. However, given the spread of nest dates and median peak dates used in the analysis, a proportion of nests would still exhibit overlap between Dipteran peaks and hatch dates. Further, some other swallow species may also continue to feed Dipterans to older nestlings. In tree swallows, Dipterans were found to be very important in the diet of 12 day-old young, with the insects accounting for 16% of the total biomass fed to young (Mengelkoch et al., 2004). The smaller size of tree swallows compared to purple martins may account for Dipterans being important parts of older nestlings’ diets.

Surprisingly, Odonate peaks did not align most strongly with peak nestling energetic demand (around day 10) as predicted but instead aligned more closely with hatch dates. Many Odonates may be too large for younger nestlings to consume, with previous studies generally supporting their importance in older nestlings' diets (Dunoyer et al., 2024). This may reflect a degree of mismatch with insect prey phenology, considering the importance of Odonates to the number of young fledged that I found (further discussed below).

Fledge dates aligned well with the Hymenopteran peak, as predicted. This suggests that this insect order could serve as a crucial food source for nestlings when they fledge and learn to catch their own prey (Brown, 1978). This finding is also consistent with differences in diet between adults and nestlings, as adult purple martins were found to feed significantly more on Hymenopterans than the diet fed to nestlings (Dunoyer et al., 2024).

Impact on duration in nest

Young in the nest are under strong selection to fledge early to reduce the risk of predation (Kouba et al., 2015). This benefits parents by reducing the energy spent feeding and decreasing their exposure to nest predators (Michaud and Leonard, 2000; Turcotte-van de Rydt, 2022). According to Kouba et al. (2015), slow wing growth is the main factor delaying fledging, but providing ample food during energetically demanding periods has been shown to boost growth rates and shorten nest time. I had therefore predicted that timing day ten of development with insect peaks would shorten this time, as parents would have access to sufficient food sources to ensure a quick development and an early fledge. However, my results did not show a significant effect of alignment with day 10 on duration in the nest, but instead alignment with fledge dates, where fledge dates that were timed closer to peak insect availability were associated with shorter nest durations. This may reflect an overlap between peak prey in the very late stages of nesting affecting growth and subsequently duration in the nest. While I used day 10 as a proxy for peak nestling growth and energetic demand, chicks continue to develop rapidly and develop flight feathers during the whole late nesting period (day 10 to fledge at 26-32 days post hatch), thus energetic demand is expected to remain high throughout this period. Many studies support the 'threshold size model', in which nestlings leave the nest once they have reached a developmental threshold (Santema et al., 2011; Nilsson and Svensson, 1993; Michaud and Leonard, 2000). Fledge dates being closer to the overall insect peak may also reflect key periods of nest provisioning during late nesting, also overlapping with peak insect availability, therefore quickening the time needed for nestlings to reach a size threshold suitable for fledging. In my results, being 6.49 days away from the overall insect peak resulted in 27 days being spent in the nest, whereas being 35.58 days away from the peak resulted in 31 days being spent in the nest. Synchrony with the Odonate peak also increased the speed at which nestlings reached this threshold (Dunoyer et al., 2024).

A decrease of time spent in the nest when fledge dates were aligned with Odonate and overall insect peaks could also be indicative of factors influencing optimal time to fledge, where young are more likely to fledge during more favorable environmental conditions. For instance, Barn swallows (*Hirundo rustica*) can be opportunistic feeders that base their prey selection on availability rather than rely on consistent taxa across sites (Law et al., 2017). If applicable to purple martins, peak insect availability near fledge date may cue fledge itself, where fledging closer to the peak of overall insect availability would provide young with ideal environmental conditions as they learn to fly and feed themselves (Brown, 1978). Findings in Santema et al.

(2011) contradict this idea, however, as young blue tits' (*Cyanistes caeruleus*) tendency to fledge earlier in the day was not associated with a higher survival probability.

Impact on the proportion of hatched young that fledge and the number of young fledged

My results demonstrate, for the first time in a songbird, how misalignment with key insect prey during peak nest provisioning can directly impact the proportion of hatched young that fledge and the overall number of young that fledge. Previous work with resident songbirds has indicated a similar impact of mismatch between insect prey and nest timing (Reed et al., 2013; Verboven et al., 2001; Visser et al., 2006; Both et al., 2006). For instance, my Odonate results were comparable to those in Reed et al. (2013), one of the few papers to show direct links between phenology shifts and effects on population demography. The analysis of a 37-year dataset on great tits (*Parus major*) in the Netherlands revealed a decrease in offspring recruitment numbers associated with caterpillar phenology mismatch (Reed et al., 2013). The study also revealed a decrease in the probability of nestling recruitment associated with the mismatch (Reed et al., 2013), which my study supports through a decrease in successful fledge proportions when egg laying and hatch are timed with Lepidopterans, and an increase in proportions when fledge dates were timed with this same peak. Other studies focusing on great tits also demonstrated that fledging success and numbers increased in first clutches when birds bred closer to caterpillar peaks, rather than before or after them (Verboven et al., 2001; Visser et al., 2006).

There have been fewer studies on phenological mismatches, and particularly specific consequences for reproductive success, in migratory songbirds. In a correlational study (Both et al., 2006), populations of pied flycatchers in areas where the caterpillar peak date had advanced the most showed the steepest declines, suggesting that the impact of mismatch scales up from nest success to population patterns. However, direct impacts of misalignment on individual songbird reproductive success have not been investigated, leaving mechanisms for these population-level impacts unclear. My study fills this gap by directly examining that misalignment with key insect resources influences reproductive success in songbirds through decreases in fledge proportions and numbers and increases in time spent in the nest prior to fledging.

The two different measures of fledge success —proportion and number of fledglings— explored different aspects of how nest timing relative to peak prey availability influences reproductive success. I generally found that these two measures had the same directional effect, even if results were insignificant, such as when timing Odonates to day 10 significantly increased numbers and insignificantly increased proportions. However, in terms of significant results, timing day 10 with Odonates boosted the total quantity of fledglings, while aligning fledge dates with Odonates increased the proportion of fledged young, suggesting that later-stage feeding specifically improves offspring quality.

Relevance of timing to phenological mismatch and population decline

Phenotypic plasticity in migratory songbirds has been a much-investigated research topic (Smith and Fraser, 2024; Shave et al., 2019; Nussey et al., 2005) in part because these studies can indicate how birds may respond to a rapidly changing climate through behavioural plasticity. Purple martins, along with other bird species, show high plasticity in egg lay dates to local conditions, which are usually affected by temperature variation (Bonamour et al., 2019; Smith and Fraser, 2024; Shave et al., 2019; Nussey et al., 2005). Bonamour et al. (2019) mentions the use of temperature as a predictor of caterpillar peak abundance timing, with the blue tits

(*Cyanistes caeruleus*) in that study showing laying date variations throughout the French Mediterranean in response to temperature variations. Smith and Fraser (2024) note that the advancement of egg-laying with temperature resulted in the shortening of purple martins' arrival-breeding interval. Despite avian species' advancements with increasing temperatures, the rate of these advancements have not kept up with those of insect prey (Saalfeld et al., 2019; Visser and Gienapp, 2019; Kharouba et al., 2018), with Saalfeld et al. (2019) demonstrating that Arctic-breeding shorebirds experienced increased phenological mismatches with earlier snowmelt, the food available to young often being inadequate for their growth. Despite earlier nesting dates resulting in increased food availability for young, the advancement is thought to be constrained by shorebirds' plasticity in the start of migration (Saalfeld et al., 2019). One of the other few articles discussing the direct effects of phenological mismatches on great tit (*Parus major*) demography demonstrates that while mismatches have negative effects on offspring recruitment, the population growth was shown to be buffered through a more relaxed competition between individuals, as a result of fitness declines (Reed et al., 2013). My research provides new evidence of direct negative impacts on reproductive success brought about by phenological mismatches between purple martin breeding phenology and the emergence of prey resources, along with evidence of a potential mismatch, as timing fledge and day 10 with Odonate peak was found to increase the proportion and number of fledged, respectively. However, my analysis shows that birds timed hatch dates almost perfectly with Odonate peak, demonstrating late breeding relative to the optimal window suggested by my models.

It should be acknowledged that certain factors, although not the primary focus of my study, were still important considerations in the analysis. Age of parents, for instance, may affect a nest's fledge success, as older birds tend to arrive earlier at breeding sites, and therefore may have an increased ability to time themselves with peak dates (Morton and Derrickson, 1990). In addition, older birds tended to select higher cavities, decreasing the risk of nest predation as these cavities are more difficult to reach (Morton and Derrickson, 1990). Overall results showed that young adult breeding, particularly SY-SY pairings, resulted in lower successful fledge proportions and numbers. Year was controlled for as well, as climate change and irregular temporal fluctuations would lead to differences in environmental conditions. Different sites are also important to take into consideration, as birds in different locations may experience different conditions due to microhabitat variations (Both, 2010).

Conclusion

Overall, this study demonstrates the positive effects of timing fledge with Lepidopterans and overall insect availability peaks, as well as timing day 10 and fledge with Odonate peaks, providing rare evidence of the direct effects of phenological mismatch in a migratory insectivore. The valuable insights into how the timing of breeding stages in purple martins is influenced by insect availability can inform conservation strategies aimed at mitigating the impacts of phenological mismatches caused by climate change. For instance, strategies such as phenological phase extensions (carried out through environmental manipulations or the introduction of new genetic variants exhibiting later phenological timings) could be used to extend insect prey phenology to be more closely timed with aerial insectivore reproduction (Olliff-Yang et al., 2020). Future research should focus on studying the mechanisms underlying the timing of breeding stages, such as carry-over effects from migration, individual quality, and the effects of parents' ages on breeding timing.

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Supplemental Material

Supplemental Table 1. Parameter estimates of linear mixed models describing the relationship of the difference in days between purple martin key life stages and (a) overall insect peak dates (n =506), (b) Lepidoptera peak dates (n =506), (c) Diptera peak dates (n =506), (d) Odonata peak dates (n =617) and (e) Hymenoptera peak dates (n =506). Age of male and female (second year – SY – or after second year – ASY –) were included as covariates. Year, site and Nest ID were added as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Total Insect Peak Difference ~ Life Stage + Age + (1|Year) + (1|Site) + (1|Nest ID)					
(Intercept)	31.84	3.01	25.93	37.74	**<0.001**
Day Ten	29.74	1.04	27.70	31.78	**<0.001**
Hatch	19.74	1.04	17.70	21.78	**<0.001**
Fledge	48.90	1.13	46.68	51.12	**<0.001**
ASY Male, SY Female	4.98	1.22	2.59	7.37	**<0.001**
SY Male, ASY Female	6.45	2.29	1.96	10.93	**0.005**
SY Male, SY Female	8.86	1.64	5.65	12.07	**<0.001**
Random Effects	**Variance**		**R2**		
Site	21.57		Marginal	0.728	
Year	7.70		Conditional	0.823	
Nest ID	9.77				
(b) Lepidoptera Peak Difference ~ Life Stage + Age + (1|Year) + (1|Site) + (1|Nest ID)					
(Intercept)	-31.84	3.01	-90.12	26.45	**<0.001**
Day Ten	29.74	1.04	27.70	31.78	**<0.001**
Hatch	19.74	1.04	17.70	21.78	**<0.001**
Fledge	48.90	1.13	46.68	51.12	**<0.001**
ASY Male, SY Female	4.98	1.22	2.59	7.37	**<0.001**
SY Male, ASY Female	6.45	2.29	1.96	10.93	**0.002**

SY Male, SY Female	8.86	1.64	5.65	12.07	**<0.001**
Random Effects	**Variance**		**R2**		
Site	186.54		Marginal	0.468	
Year	17.27		Conditional	0.818	
Nest ID	30.56				
(c) Diptera Peak Difference ~ Life Stage + Age + (1|Year) + (1|Site) + (1|Nest ID)					
(Intercept)	-26.78	10.93	-48.20	-5.35	**0.014**
Day Ten	29.74	1.08	27.62	31.86	**<0.001**
Hatch	19.74	1.08	17.62	21.86	**<0.001**
Fledge	48.94	1.18	46.63	51.24	**<0.001**
ASY Male, SY Female	-2.89	1.32	-5.47	-0.30	**0.028**
SY Male, ASY Female	0.83	2.41	-3.89	5.56	0.729
SY Male, SY Female	0.94	1.77	-2.53	4.41	0.596
Random Effects	**Variance**		**R2**		
Site	173.35		Marginal	0.375	
Year	224.49		Conditional	0.901	
Nest ID	16.19				
(d) Odonata Peak Difference ~ Life Stage + Age + (1|Year) + (1|Site) + (1|Nest ID)					
(Intercept)	-22.52	2.85	-28.11	-16.93	**<0.001**
Day Ten	29.78	0.67	28.46	31.10	**<0.001**
Hatch	19.78	0.67	18.46	21.10	**<0.001**
Fledge	49.10	0.80	47.53	50.68	**<0.001**
ASY Male, SY Female	2.21	0.83	0.57	3.85	**0.008**
SY Male, ASY Female	3.82	1.28	1.31	6.33	**0.003**
SY Male, SY Female	10.17	1.10	8.02	12.33	**<0.001**
Random Effects	**Variance**		**R2**		

Site	20.18		Marginal	0.780	
Year	9.78		Conditional	0.893	
Nest ID	11.00				
(e) Hymenoptera Peak Difference ~ Life Stage + Age + (1|Year) + (1|Site) + (1|Nest ID)					
(Intercept)	-59.82	5.75	-71.10	-48.55	**<0.001**
Day Ten	29.74	1.18	27.42	32.05	**<0.001**
Hatch	19.74	1.18	17.42	22.05	**<0.001**
Fledge	49.03	1.29	46.51	51.55	**<0.001**
ASY Male, SY Female	6.00	1.19	3.66	8.33	**<0.001**
SY Male, ASY Female	7.04	2.26	2.61	11.47	**0.002**
SY Male, SY Female	10.05	1.58	6.94	13.15	**<0.001**
Random Effects	**Variance**		**R2**		
Site	61.52		Marginal	0.597	
Year	50.32		Conditional	0.817	
Nest ID	0.00				

Supplemental Table 2. Parameter estimates of linear mixed models describing the relationship between the time taken to fledge from the nest and the absolute values of the difference in days between first egg-laying dates and (a) overall insect peak dates (n =104), (b) Lepidoptera peak dates (n =104), (c) Diptera peak dates (n =104), (d) Odonata peak dates (n =104) and (e) Hymenoptera peak dates (n =104). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Time to Fledge ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.40	0.06	3.27	3.52	**<0.001**
Egg Difference	<0.01	<0.01	<0.01	<0.01	0.837
ASY Male, SY Female	0.01	0.05	-0.10	0.11	0.897
SY Male, ASY Female	0.03	0.08	-0.14	0.19	0.753
SY Male, SY Female	-0.02	0.07	-0.17	0.13	0.781
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(b) Time to Fledge ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.38	0.05	3.29	3.47	**<0.001**
Egg Difference	<0.01	<0.01	<0.01	<0.01	0.939
ASY Male, SY Female	0.01	0.05	-0.10	0.11	0.866
SY Male, ASY Female	0.03	0.09	-0.14	0.20	0.737

SY Male, SY Female	-0.02	0.08	-0.17	0.13	0.827
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(c) Time to Fledge ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.43	0.04	3.35	3.51	**<0.001**
Egg Difference	<0.01	<0.01	<0.01	<0.01	0.136
ASY Male, SY Female	0.01	0.05	-0.09	0.11	0.864
SY Male, ASY Female	0.04	0.08	-0.13	0.20	0.644
SY Male, SY Female	-0.01	0.07	-0.16	0.13	0.876
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(d) Time to Fledge ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.42	0.06	3.30	3.54	**<0.001**
Egg Difference	<0.01	<0.01	-0.01	<0.01	0.510
ASY Male, SY Female	<0.01	0.05	-0.10	0.11	0.954
SY Male, ASY Female	0.02	0.08	-0.15	0.19	0.809
SY Male, SY Female	-0.03	0.08	-0.18	0.12	0.683
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	

Year	0.00		Conditional	N/A	
(e) Time to Fledge ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.45	0.14	3.18	3.72	**<0.001**
Egg Difference	<0.01	<0.01	-0.01	<0.01	0.631
ASY Male, SY Female	<0.01	0.05	-0.10	0.11	0.953
SY Male, ASY Female	0.03	0.08	-0.14	0.19	0.751
SY Male, SY Female	-0.03	0.08	-0.19	0.12	0.680
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	

Supplemental Table 3. Parameter estimates of linear mixed models describing the relationship between the time taken to fledge from the nest and the absolute values of the difference in days between hatch dates and (a) overall insect peak dates (n =104), (b) Lepidoptera peak dates (n =104), (c) Diptera peak dates (n =104), (d) Odonata peak dates (n =104) and (e) Hymenoptera peak dates (n =104). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Time to Fledge ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.39	0.04	3.31	3.47	**<0.001**
Hatch Difference	<0.01	<0.01	<0.01	<0.01	0.767
ASY Male, SY Female	0.01	0.05	-0.10	0.11	0.903
SY Male, ASY Female	0.02	0.09	-0.14	0.19	0.781
SY Male, SY Female	-0.02	0.07	-0.17	0.12	0.774
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(b) Time to Fledge ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.39	0.03	3.32	3.45	**<0.001**
Hatch Difference	<0.01	<0.01	<0.01	<0.01	0.823
ASY Male, SY Female	0.01	0.05	-0.10	0.11	0.908
SY Male, ASY Female	0.03	0.08	-0.14	0.19	0.761

SY Male, SY Female	-0.02	0.07	-0.17	0.13	0.786
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(c) Time to Fledge ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.40	0.03	3.34	3.46	**<0.001**
Hatch Difference	<0.01	<0.01	<0.01	<0.01	0.516
ASY Male, SY Female	0.01	0.05	-0.09	0.11	0.883
SY Male, ASY Female	0.03	0.08	-0.14	0.20	0.720
SY Male, SY Female	-0.01	0.07	-0.16	0.13	0.852
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(d) Time to Fledge ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.40	0.04	3.33	3.47	**<0.001**
Hatch Difference	<0.01	0.01	-0.01	0.01	0.521
ASY Male, SY Female	<0.01	0.05	-0.10	0.11	0.937
SY Male, ASY Female	0.03	0.08	-0.13	0.20	0.690
SY Male, SY Female	-0.01	0.07	-0.16	0.13	0.878
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	

Year	0.00		Conditional	N/A	
(e) Time to Fledge ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.44	0.12	3.21	3.67	**<0.001**
Hatch Difference	<0.01	<0.01	-0.01	<0.01	0.631
ASY Male, SY Female	<0.01	0.05	-0.10	0.11	0.944
SY Male, ASY Female	0.02	0.09	-0.15	0.19	0.804
SY Male, SY Female	-0.03	0.08	-0.19	0.12	0.689
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	

Supplemental Table 4. Parameter estimates of linear mixed models describing the relationship between the time taken to fledge from the nest and the absolute values of the difference in days between day 10 dates and (a) overall insect peak dates (n =104), (b) Lepidoptera peak dates (n =104), (c) Diptera peak dates (n =104), (d) Odonata peak dates (n =104) and (e) Hymenoptera peak dates (n =104). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Time to Fledge ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.39	0.04	3.32	3.46	**<0.001**
Day 10 Difference	<0.01	<0.01	<0.01	<0.01	0.874
ASY Male, SY Female	0.01	0.05	-0.10	0.11	0.899
SY Male, ASY Female	0.03	0.08	-0.14	0.19	0.759
SY Male, SY Female	-0.02	0.07	-0.16	0.13	0.798
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(b) Time to Fledge ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.39	0.03	3.33	3.46	**<0.001**
Day 10 Difference	<0.01	<0.01	<0.01	<0.01	0.627
ASY Male, SY Female	0.01	0.05	-0.10	0.11	0.901
SY Male, ASY Female	0.03	0.08	-0.14	0.19	0.726
SY Male, SY Female	-0.02	0.07	-0.16	0.13	0.827

Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(c) Time to Fledge ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.39	0.04	3.32	3.46	**<0.001**
Day 10 Difference	<0.01	<0.01	<0.01	<0.01	0.770
ASY Male, SY Female	0.01	0.05	-0.09	0.11	0.890
SY Male, ASY Female	0.03	0.08	-0.14	0.19	0.744
SY Male, SY Female	-0.02	0.07	-0.16	0.13	0.817
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(d) Time to Fledge ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.37	0.04	3.29	3.44	**<0.001**
Day 10 Difference	<0.01	<0.01	<0.01	0.01	0.449
ASY Male, SY Female	<0.01	0.05	-0.10	0.11	0.962
SY Male, ASY Female	0.01	0.09	-0.16	0.18	0.899
SY Male, SY Female	-0.04	0.08	-0.19	0.12	0.632
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(e) Time to Fledge ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					

(Intercept)	3.48	0.09	3.30	3.65	**<0.001**
Day 10 Difference	<0.01	<0.01	-0.01	<0.01	0.258
ASY Male, SY Female	<0.01	0.05	-0.10	0.10	0.996
SY Male, ASY Female	0.01	0.09	-0.16	0.18	0.891
SY Male, SY Female	-0.04	0.08	-0.19	0.11	0.602
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	

Supplemental Table 5. Parameter estimates of linear mixed models describing the relationship between the time taken to fledge from the nest and the absolute values of the difference in days between fledge dates and (a) overall insect peak dates (n =104), (b) Lepidoptera peak dates (n =104), (c) Diptera peak dates (n =104), (d) Odonata peak dates (n =104) and (e) Hymenoptera peak dates (n =104). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Time to Fledge ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.30	0.04	3.23	3.38	**<0.001**
Fledge Difference	<0.01	<0.01	<0.01	0.01	**0.016**
ASY Male, SY Female	<0.01	0.05	-0.10	0.10	0.977
SY Male, ASY Female	<0.01	0.08	-0.17	0.17	0.988
SY Male, SY Female	-0.05	0.07	-0.20	0.09	0.487
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(b) Time to Fledge ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.37	0.06	3.24	3.49	**<0.001**
Fledge Difference	<0.01	<0.01	<0.01	0.01	0.797
ASY Male, SY Female	0.01	0.05	-0.10	0.11	0.914
SY Male, ASY Female	0.02	0.09	-0.15	0.19	0.812
SY Male, SY Female	-0.02	0.08	-0.18	0.13	0.756

Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(c) Time to Fledge ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.32	0.04	3.24	3.39	**<0.001**
Fledge Difference	<0.01	<0.01	<0.01	<0.01	0.053
ASY Male, SY Female	0.02	0.05	-0.08	0.13	0.643
SY Male, ASY Female	0.05	0.08	-0.11	0.22	0.540
SY Male, SY Female	<0.01	0.07	-0.15	0.14	0.983
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(d) Time to Fledge ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	3.22	0.07	3.09	3.36	**<0.001**
Fledge Difference	0.01	<0.01	<0.01	0.01	**0.015**
ASY Male, SY Female	-0.01	0.05	-0.11	0.09	0.867
SY Male, ASY Female	-0.02	0.09	-0.19	0.15	0.810
SY Male, SY Female	-0.07	0.08	-0.22	0.08	0.371
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	
(e) Time to Fledge ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					

(Intercept)	3.46	0.05	3.37	3.55	**<0.001**
Fledge Difference	<0.01	<0.01	-0.01	<0.01	0.087
ASY Male, SY Female	<0.01	0.05	-0.10	0.10	0.985
SY Male, ASY Female	-0.01	0.09	-0.18	0.16	0.917
SY Male, SY Female	-0.03	0.07	-0.18	0.11	0.679
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	

Supplemental Table 6. Parameter estimates of linear mixed models describing the relationship between the proportion of successful fledges and the absolute values of the difference in days between first egg laying dates and (a) overall insect peak dates (n =134), (b) Lepidoptera peak dates (n =134), (c) Diptera peak dates (n =134), (d) Odonata peak dates (n =188) and (e) Hymenoptera peak dates (n =134). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Proportion Fledged ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.41	0.54	0.34	2.47	**0.010**
Egg Difference	<0.01	0.01	-0.01	0.02	0.625
ASY Male, SY Female	-0.39	0.25	-0.88	0.11	0.124
SY Male, ASY Female	0.09	0.51	-0.91	1.09	0.855
SY Male, SY Female	-1.02	0.31	-1.63	-0.41	**0.001**
Random Effects	**Variance**		**R2**		
Site	0.26		Marginal	0.078	
Year	0.34		Conditional	0.520	
(b) Proportion Fledged ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	0.99	0.51	-0.01	1.98	0.052
Egg Difference	0.02	0.01	<0.01	0.03	**0.049**
ASY Male, SY Female	-0.29	0.25	-0.78	0.21	0.257
SY Male, ASY Female	0.18	0.51	-0.82	1.18	0.726
SY Male, SY Female	-0.87	0.32	-1.49	-0.25	**0.006**

Random Effects	**Variance**		**R2**		
Site	0.17		Marginal	0.126	
Year	0.32		Conditional	0.501	
(c) Proportion Fledged ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.62	0.55	0.55	2.69	**0.003**
Egg Difference	<0.01	0.01	-0.02	0.02	0.822
ASY Male, SY Female	-0.41	0.25	-0.90	0.07	0.096
SY Male, ASY Female	0.08	0.51	-0.92	1.07	0.880
SY Male, SY Female	-1.06	0.30	-1.65	-0.46	**0.001**
Random Effects	**Variance**		**R2**		
Site	0.24		Marginal	0.077	
Year	0.36		Conditional	0.518	
(d) Proportion Fledged ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.40	0.53	0.37	2.44	**0.008**
Egg Difference	0.01	0.02	-0.02	0.04	0.504
ASY Male, SY Female	-0.20	0.24	-0.66	0.26	0.395
SY Male, ASY Female	0.12	0.39	-0.64	0.88	0.751
SY Male, SY Female	-0.71	0.28	-1.27	-0.15	**0.013**
Random Effects	**Variance**		**R2**		
Site	0.23		Marginal	0.048	
Year	0.30		Conditional	0.476	

(e) Proportion Fledged ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.61	0.76	0.11	3.11	**0.036**
Egg Difference	<0.01	0.01	-0.02	0.02	0.928
ASY Male, SY Female	-0.41	0.25	-0.91	0.08	0.104
SY Male, ASY Female	0.07	0.51	-0.92	1.07	0.885
SY Male, SY Female	-1.06	0.31	-1.68	-0.44	**0.001**
Random Effects	**Variance**		**R2**		
Site	0.23		Marginal	0.077	
Year	0.34		Conditional	0.507	

Supplemental Table 7. Parameter estimates of linear mixed models describing the relationship between the proportion of successful fledges and the absolute values of the difference in days between hatch dates and (a) overall insect peak dates (n =134), (b) Lepidoptera peak dates (n =134), (c) Diptera peak dates (n =134), (d) Odonata peak dates (n =188) and (e) Hymenoptera peak dates (n =134). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Proportion Fledged ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.39	0.48	0.44	2.33	**0.004**
Hatch Difference	0.01	0.01	-0.01	0.03	0.195
ASY Male, SY Female	-0.36	0.25	-0.85	0.13	0.148
SY Male, ASY Female	0.17	0.51	-0.84	1.18	0.741
SY Male, SY Female	-0.97	0.31	-1.58	-0.36	**0.002**
Random Effects	**Variance**		**R2**		
Site	0.28		Marginal	0.085	
Year	0.34		Conditional	0.532	
(b) Proportion Fledged ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.24	0.44	0.37	2.10	**0.005**
Hatch Difference	0.02	0.01	<0.01	0.04	**0.039**
ASY Male, SY Female	-0.30	0.25	-0.80	0.19	0.225
SY Male, ASY Female	0.11	0.51	-0.89	1.11	0.826

SY Male, SY Female	-0.97	0.31	-1.57	-0.37	**0.002**
Random Effects	**Variance**		**R2**		
Site	0.18		Marginal	0.138	
Year	0.29		Conditional	0.497	
(c) Proportion Fledged ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.46	0.46	0.57	2.36	**0.001**
Hatch Difference	0.01	0.01	-0.01	0.02	0.407
ASY Male, SY Female	-0.40	0.25	-0.88	0.09	0.106
SY Male, ASY Female	0.10	0.51	-0.90	1.10	0.848
SY Male, SY Female	-1.04	0.30	-1.64	-0.44	**0.001**
Random Effects	**Variance**		**R2**		
Site	0.23		Marginal	0.085	
Year	0.32		Conditional	0.506	
(d) Proportion Fledged ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.47	0.42	0.65	2.28	**<0.001**
Hatch Difference	0.02	0.02	-0.02	0.06	0.328
ASY Male, SY Female	-0.20	0.23	-0.66	0.26	0.401
SY Male, ASY Female	0.13	0.39	-0.63	0.88	0.745
SY Male, SY Female	-0.78	0.27	-1.32	-0.25	**0.004**
Random Effects	**Variance**		**R2**		
Site	0.18		Marginal	0.055	

Year	0.28		Conditional	0.447	
(e) Proportion Fledged ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.24	0.69	-0.11	2.59	0.072
Hatch Difference	0.01	0.01	-0.02	0.03	0.541
ASY Male, SY Female	-0.38	0.25	-0.87	0.11	0.132
SY Male, ASY Female	0.12	0.51	-0.88	1.12	0.817
SY Male, SY Female	-1.00	0.32	-1.62	-0.38	**0.002**
Random Effects	**Variance**		**R2**		
Site	0.29		Marginal	0.080	
Year	0.33		Conditional	0.528	

Supplemental Table 8. Parameter estimates of linear mixed models describing the relationship between the proportion of successful fledges and the absolute values of the difference in days between day 10 dates and (a) overall insect peak dates (n =134), (b) Lepidoptera peak dates (n =134), (c) Diptera peak dates (n =134), (d) Odonata peak dates (n =188) and (e) Hymenoptera peak dates (n =134). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Proportion Fledged ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.42	0.47	0.50	2.35	**0.003**
Day 10 Difference	0.02	0.01	-0.01	0.04	0.203
ASY Male, SY Female	-0.36	0.25	-0.85	0.13	0.146
SY Male, ASY Female	0.14	0.51	-0.86	1.15	0.778
SY Male, SY Female	-1.02	0.30	-1.62	-0.43	**0.001**
Random Effects	**Variance**		**R2**		
Site	0.23		Marginal	0.086	
Year	0.37		Conditional	0.524	
(b) Proportion Fledged ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.58	0.48	0.64	2.51	**0.001**
Day 10 Difference	<0.01	0.01	-0.02	0.02	0.873
ASY Male, SY Female	-0.41	0.25	-0.90	0.07	0.096
SY Male, ASY Female	0.08	0.51	-0.92	1.08	0.872
SY Male, SY Female	-1.05	0.30	-1.64	-0.45	**0.001**

Random Effects	**Variance**		**R2**		
Site	0.24		Marginal	0.076	
Year	0.34		Conditional	0.513	
(c) Proportion Fledged ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.44	0.47	0.53	2.36	**0.002**
Day 10 Difference	0.01	0.01	-0.01	0.02	0.269
ASY Male, SY Female	-0.39	0.25	-0.87	0.10	0.119
SY Male, ASY Female	0.11	0.51	-0.89	1.11	0.832
SY Male, SY Female	-1.04	0.30	-1.64	-0.45	**0.001**
Random Effects	**Variance**		**R2**		
Site	0.22		Marginal	0.084	
Year	0.36		Conditional	0.517	
(d) Proportion Fledged ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.82	0.42	1.00	2.64	**<0.001**
Day 10 Difference	-0.02	0.01	-0.05	<0.01	0.092
ASY Male, SY Female	-0.18	0.23	-0.64	0.28	0.443
SY Male, ASY Female	0.18	0.39	-0.59	0.94	0.649
SY Male, SY Female	-0.60	0.29	-1.16	-0.03	**0.038**
Random Effects	**Variance**		**R2**		
Site	0.23		Marginal	0.066	
Year	0.29		Conditional	0.482	
(e) Proportion Fledged ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					

(Intercept)	1.08	0.70	-0.28	2.45	0.120
Day 10 Difference	0.01	0.02	-0.02	0.05	0.375
ASY Male, SY Female	-0.37	0.25	-0.86	0.12	0.139
SY Male, ASY Female	0.15	0.51	-0.85	1.16	0.767
SY Male, SY Female	-0.96	0.32	-1.59	-0.34	**0.003**
Random Effects	**Variance**		**R2**		
Site	0.28		Marginal	0.084	
Year	0.33		Conditional	0.526	

Supplemental Table 9. Parameter estimates of linear mixed models describing the relationship between the proportion of successful fledges and the absolute values of the difference in days between fledge dates and (a) overall insect peak dates (n =104), (b) Lepidoptera peak dates (n =104), (c) Diptera peak dates (n =104), (d) Odonata peak dates (n =104) and (e) Hymenoptera peak dates (n =104). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Proportion Fledged ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.95	0.55	0.86	3.03	**<0.001**
Fledge Difference	-0.03	0.02	-0.06	<0.01	0.091
ASY Male, SY Female	0.42	0.33	-0.22	1.06	0.196
SY Male, ASY Female	0.38	0.51	-0.62	1.39	0.454
SY Male, SY Female	-0.14	0.46	-1.04	0.76	0.759
Random Effects	**Variance**		**R2**		
Site	0.44		Marginal	0.081	
Year	0.03		Conditional	0.471	
(b) Proportion Fledged ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	2.39	0.62	1.17	3.60	**<0.001**
Fledge Difference	-0.04	0.02	-0.08	-0.01	**0.006**
ASY Male, SY Female	0.47	0.33	-0.17	1.11	0.150
SY Male, ASY Female	0.52	0.52	-0.49	1.54	0.311
SY Male, SY Female	0.02	0.46	-0.88	0.93	0.959

Random Effects	**Variance**		**R2**		
Site	0.39		Marginal	0.107	
Year	0.18		Conditional	0.528	
(c) Proportion Fledged ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.06	0.59	-0.11	2.22	0.075
Fledge Difference	0.01	0.01	-0.02	0.03	0.448
ASY Male, SY Female	0.36	0.32	-0.28	1.00	0.267
SY Male, ASY Female	0.25	0.51	-0.75	1.24	0.626
SY Male, SY Female	-0.33	0.44	-1.19	0.53	0.447
Random Effects	**Variance**		**R2**		
Site	0.31		Marginal	0.035	
Year	0.22		Conditional	0.472	
(d) Proportion Fledged ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	2.41	0.66	1.12	3.70	**<0.001**
Fledge Difference	-0.04	0.02	-0.07	<0.01	**0.032**
ASY Male, SY Female	0.44	0.33	-0.20	1.08	0.176
SY Male, ASY Female	0.45	0.52	-0.56	1.46	0.382
SY Male, SY Female	-0.04	0.46	-0.94	0.87	0.939
Random Effects	**Variance**		**R2**		
Site	0.35		Marginal	0.086	
Year	0.08		Conditional	0.452	
(e) Proportion Fledged ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					

(Intercept)	0.52	0.43	-0.32	1.35	0.224
Fledge Difference	0.04	0.02	0.01	0.07	**0.009**
ASY Male, SY Female	0.41	0.32	-0.23	1.04	0.212
SY Male, ASY Female	0.47	0.51	-0.53	1.47	0.358
SY Male, SY Female	-0.09	0.46	-1.00	0.81	0.841
Random Effects	**Variance**		**R2**		
Site	0.18		Marginal	0.151	
Year	0.03		Conditional	0.359	

Supplemental Table 10. Parameter estimates of linear mixed models describing the relationship between the number of successful fledges and the absolute values of the difference in days between first egg laying dates and (a) overall insect peak dates (n =134), (b) Lepidoptera peak dates (n =134), (c) Diptera peak dates (n =134), (d) Odonata peak dates (n =188) and (e) Hymenoptera peak dates (n =134). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Number Fledged ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.20	0.17	0.86	1.53	**<0.001**
Egg Difference	<0.01	<0.01	<0.01	0.01	0.269
ASY Male, SY Female	-0.20	0.13	-0.46	0.06	0.127
SY Male, ASY Female	-0.13	0.25	-0.62	0.35	0.591
SY Male, SY Female	-0.37	0.19	-0.75	0.00	**0.050**
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(b) Number Fledged ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.20	0.12	0.96	1.45	**<0.001**
Egg Difference	<0.01	<0.01	-0.01	<0.01	0.077
ASY Male, SY Female	-0.17	0.13	-0.43	0.09	0.204
SY Male, ASY Female	-0.08	0.25	-0.57	0.42	0.762
SY Male, SY Female	-0.34	0.19	-0.71	0.04	0.080

Random Effects		**R2**			
Site		Marginal	N/A		
Year		Conditional	N/A		
(c) Number Fledged ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.31	0.12	1.08	1.54	<0.001
Egg Difference	0.00	0.00	-0.01	0.00	0.585
ASY Male, SY Female	-0.22	0.13	-0.48	0.03	0.087
SY Male, ASY Female	-0.17	0.25	-0.66	0.33	0.504
SY Male, SY Female	-0.42	0.19	-0.79	-0.05	0.026
Random Effects		**R2**			
Site		Marginal	N/A		
Year		Conditional	N/A		
(d) Number Fledged ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.12	0.16	0.81	1.43	**<0.001**
Egg Difference	0.01	0.01	<0.01	0.02	0.064
ASY Male, SY Female	-0.14	0.12	-0.37	0.09	0.235
SY Male, ASY Female	-0.03	0.17	-0.36	0.30	0.874
SY Male, SY Female	-0.26	0.16	-0.57	0.05	0.100
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(e) Number Fledged ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					

(Intercept)	1.18	0.30	0.59	1.78	**<0.001**
Egg Difference	<0.01	<0.01	-0.01	0.01	0.542
ASY Male, SY Female	-0.21	0.13	-0.46	0.05	0.117
SY Male, ASY Female	-0.14	0.25	-0.63	0.34	0.563
SY Male, SY Female	-0.39	0.19	-0.76	-0.02	**0.041**
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	

Supplemental Table 11. Parameter estimates of linear mixed models describing the relationship between the number of successful fledges and the absolute values of the difference in days between hatch dates and (a) overall insect peak dates (n =134), (b) Lepidoptera peak dates (n =134), (c) Diptera peak dates (n =134), (d) Odonata peak dates (n =188) and (e) Hymenoptera peak dates (n =134). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Number Fledged ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.26	0.11	1.05	1.47	**<0.001**
Hatch Difference	0.01	<0.01	<0.01	0.02	0.139
ASY Male, SY Female	-0.19	0.13	-0.45	0.06	0.139
SY Male, ASY Female	-0.10	0.25	-0.59	0.40	0.705
SY Male, SY Female	-0.36	0.19	-0.74	0.01	0.057
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(b) Number Fledged ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.29	0.09	1.11	1.48	**<0.001**
Hatch Difference	<0.01	<0.01	<0.01	0.01	0.138
ASY Male, SY Female	-0.18	0.13	-0.44	0.08	0.169
SY Male, ASY Female	-0.11	0.25	-0.60	0.38	0.652
SY Male, SY Female	-0.38	0.19	-0.75	-0.01	**0.047**

Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(c) Number Fledged ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.31	0.09	1.14	1.49	**<0.001**
Hatch Difference	<0.01	<0.01	<0.01	0.01	0.301
ASY Male, SY Female	-0.22	0.13	-0.47	0.04	0.095
SY Male, ASY Female	-0.16	0.25	-0.65	0.33	0.524
SY Male, SY Female	-0.42	0.19	-0.78	-0.05	**0.026**
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(d) Number Fledged ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.35	0.09	1.18	1.52	**<0.001**
Hatch Difference	<0.01	0.01	-0.01	0.02	0.557
ASY Male, SY Female	-0.16	0.12	-0.39	0.07	0.179
SY Male, ASY Female	-0.05	0.17	-0.38	0.28	0.773
SY Male, SY Female	-0.34	0.16	-0.64	-0.03	**0.030**
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(e) Number Fledged ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					

(Intercept)	1.10	0.27	0.57	1.63	**<0.001**
Hatch Difference	0.01	0.01	-0.01	0.02	0.308
ASY Male, SY Female	-0.20	0.13	-0.46	0.06	0.131
SY Male, ASY Female	-0.12	0.25	-0.61	0.38	0.645
SY Male, SY Female	-0.37	0.19	-0.75	0.00	0.053
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	

Supplemental Table 12. Parameter estimates of linear mixed models describing the relationship between the number of successful fledges and the absolute values of the difference in days between day 10 dates and (a) overall insect peak dates (n =134), (b) Lepidoptera peak dates (n =134), (c) Diptera peak dates (n =134), (d) Odonata peak dates (n =188) and (e) Hymenoptera peak dates (n =134). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Number Fledged ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.31	0.10	1.11	1.51	**<0.001**
Day 10 Difference	0.01	0.01	-0.01	0.02	0.317
ASY Male, SY Female	-0.20	0.13	-0.46	0.06	0.137
SY Male, ASY Female	-0.12	0.25	-0.61	0.37	0.630
SY Male, SY Female	-0.39	0.19	-0.76	-0.02	**0.038**
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(b) Number Fledged ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.35	0.10	1.16	1.54	**<0.001**
Day 10 Difference	<0.01	<0.01	-0.01	0.01	0.824
ASY Male, SY Female	-0.22	0.13	-0.47	0.04	0.098
SY Male, ASY Female	-0.15	0.25	-0.64	0.34	0.550
SY Male, SY Female	-0.41	0.19	-0.78	-0.04	**0.029**

Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(c) Number Fledged ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.33	0.10	1.14	1.52	**<0.001**
Day 10 Difference	<0.01	<0.01	<0.01	0.01	0.462
ASY Male, SY Female	-0.21	0.13	-0.47	0.04	0.103
SY Male, ASY Female	-0.15	0.25	-0.64	0.34	0.550
SY Male, SY Female	-0.41	0.19	-0.78	-0.04	**0.028**
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(d) Number Fledged ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.46	0.08	1.31	1.62	**<0.001**
Day 10 Difference	-0.01	0.01	-0.02	<0.01	**0.039**
ASY Male, SY Female	-0.14	0.12	-0.37	0.09	0.223
SY Male, ASY Female	-0.01	0.17	-0.35	0.32	0.932
SY Male, SY Female	-0.23	0.16	-0.54	0.09	0.155
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(e) Number Fledged ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					

(Intercept)	0.94	0.27	0.42	1.47	**<0.001**
Day 10 Difference	0.01	0.01	<0.01	0.03	0.104
ASY Male, SY Female	-0.19	0.13	-0.45	0.07	0.155
SY Male, ASY Female	-0.08	0.25	-0.57	0.42	0.764
SY Male, SY Female	-0.34	0.19	-0.72	0.04	0.080
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	

Supplemental Table 13. Parameter estimates of linear mixed models describing the relationship between the number of successful fledges and the absolute values of the difference in days between fledge dates and (a) overall insect peak dates (n =104), (b) Lepidoptera peak dates (n =104), (c) Diptera peak dates (n =104), (d) Odonata peak dates (n =104) and (e) Hymenoptera peak dates (n =104). Age of male and female (third year or after third year) were included as covariates, and year and site as random effects.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Number Fledged ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.58	0.14	1.31	1.85	**<0.001**
Fledge Difference	-0.01	0.01	-0.02	<0.01	0.063
ASY Male, SY Female	-0.01	0.15	-0.30	0.28	0.957
SY Male, ASY Female	-0.03	0.26	-0.54	0.48	0.897
SY Male, SY Female	-0.14	0.23	-0.59	0.30	0.532
Random Effects	**Variance**		**R2**		
Site	0.01		Marginal	N/A	
Year	0.00		Conditional	N/A	
(b) Number Fledged ~ Lepidoptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.60	0.18	1.25	1.94	**<0.001**
Fledge Difference	-0.01	0.01	-0.02	<0.01	0.097
ASY Male, SY Female	-0.01	0.15	-0.30	0.28	0.942
SY Male, ASY Female	-0.01	0.26	-0.52	0.50	0.958
SY Male, SY Female	-0.12	0.23	-0.57	0.33	0.597

Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(c) Number Fledged ~ Diptera Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.31	0.18	0.95	1.68	**<0.001**
Fledge Difference	<0.01	0.01	-0.01	0.01	0.858
ASY Male, SY Female	-0.04	0.15	-0.34	0.25	0.764
SY Male, ASY Female	-0.13	0.26	-0.63	0.38	0.624
SY Male, SY Female	-0.22	0.22	-0.66	0.22	0.318
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.01		Conditional	N/A	
(d) Number Fledged ~ Odonata Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	1.71	0.24	1.25	2.17	**<0.001**
Fledge Difference	-0.01	0.01	-0.03	<0.01	0.081
ASY Male, SY Female	0.00	0.15	-0.30	0.29	0.989
SY Male, ASY Female	-0.01	0.26	-0.53	0.51	0.974
SY Male, SY Female	-0.11	0.23	-0.57	0.34	0.624
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	0.052	
Year	0.00		Conditional	0.082	
(e) Number Fledged ~ Hymenoptera Insect Peak Difference + Age + (1|year) + (1|site)					

(Intercept)	1.05	0.13	0.80	1.31	**<0.001**
Fledge Difference	0.01	0.01	<0.01	0.03	**0.006**
ASY Male, SY Female	-0.03	0.15	-0.31	0.26	0.861
SY Male, ASY Female	0.01	0.26	-0.49	0.51	0.977
SY Male, SY Female	-0.20	0.22	-0.64	0.23	0.356
Random Effects	**Variance**		**R2**		
Site	0.00		Marginal	N/A	
Year	0.00		Conditional	N/A	

CHAPTER 3: Microhabitat phenology differs more widely than avian nesting phenology: implications for phenological mismatch

Abstract

As climate change drives rapid environmental changes, phenological mismatches are likely to occur between species of different trophic levels. In migratory avian species, phenotypic plasticity may allow birds to adjust their migratory and breeding cues to synchronise with the timing of resource availability, although the degree of this response remains unclear in many systems. In particular, little is known about whether migratory passerines can synchronize their breeding with microhabitat (at the colony level) resource phenology. I investigated microhabitat and breeding phenology differences between four purple martin (*Progne subis*) colony sites in southern Manitoba. I first compared microhabitat phenology between sites by analyzing the dates of peak insect prey availability and green-up. I then determined migration arrival (settlement) and egg-laying dates, modeling the latter, to assess variation between colony sites. Finally, I compared the timing of purple martin settlement and egg-laying with microhabitat variation to see if environmental phenology differences were reflected in avian timing.

I found that microhabitat phenology varied widely within year between sites where green-up (leaf emergence dates) differed 1-20 days and the availability of peak insect prey differed by 1-49 days, suggesting that birds should adjust timing at a microhabitat scale to be aligned with peak resource availability. However, variability in avian timing between sites varied less than environmental phenology, as settlement timing varied by 1-6 days between sites (with the exception of one outlier), and no significant differences were found between sites in the timing of egg laying (median first egg dates varied by 1-15 days within year between sites). Comparing and modeling settlement and egg laying relative to timing with environmental conditions

revealed significant differences between sites, showing wide disparities in how birds time their arrival and breeding with the timing of ecological conditions. My results suggest the potential for phenological mismatches in key resources that purple martins require for breeding. These interactions could help us predict potential causes of purple martin population declines, with future research focusing on the phenological responses of trees and insects to better understand the potential impact of microscale mismatches between resource availability and avian timing.

Introduction

Climate change is driving rapid shifts in environmental phenology that sometimes occur too quickly for species to adapt, as change throughout their evolutionary history typically happened more gradually (Sih et al., 2011; Visser and Gienapp, 2019). To adapt to these new conditions, organisms must adjust their phenology. However, due to the varying mechanisms underlying different species' timing, these shifts may occur at uneven rates (Visser and Gienapp, 2019). This could result in a phenological mismatch between species of different trophic levels, causing a disturbance in both mutualistic and antagonistic interactions (Visser and Gienapp, 2019; Renner and Zohner, 2018). For instance, a great tit (*Parus major*) population in the Netherlands experienced a mismatch between its annual breeding time and caterpillar peak abundance due to caterpillars' rapid development under warmer conditions, resulting in directional selection for earlier egg laying (Reed et al., 2013). Furthermore, in a study by Kharouba et al. (2018), a mismatch occurred between red alders (*Alnus rubra*) and western tent caterpillars (*Malacosoma californicum pluviale*) when the caterpillars experienced an advancement in their larval emergence timing while red alder timing remained the same. Such mismatches have the potential to reduce fitness in organisms, as activities such as reproduction are very energetically demanding, and are required to take place during periods of high resource abundance (Visser and Gienapp, 2019).

Phenotypic plasticity, defined as an organism's ability to exhibit different characteristics in response to environmental variations, may help minimize these fitness reductions (Xue and Leibler, 2018; Oostra et al., 2018; Bonamour et al., 2019; Chevin et al., 2010). It enables organisms to respond to predictable cycles of changing ecological conditions, such as the changing of seasons, which impose selective pressures on their life histories (Oostra et al., 2018). This behavioural plasticity can be crucial, as environmental factors also vary within a species' range, requiring the ability to flexibly adjust to habitat differences (Cogoni et al., 2015; Kalisz, 1986; Rytteri, 2021). For example, phenotypic plasticity allows animals to finely tune their responses to various environmental timings across microhabitats (Tamian et al., 2022). In Columbian ground squirrels (*Urocitellus columbianus*), emergence timing was found to fluctuate over time and was found to be highly dependent on the differing environmental conditions experienced across four neighbouring meadows, such as the timing of snowmelt (Tamian et al., 2022). Similarly, in blue tits (*Cyanistes caeruleus*), individuals inhabiting different habitats in the French Mediterranean were found to significantly differ in their responses to temperature, the environmental cue used to predict caterpillar abundance, in turn influencing laying dates (Bonamour et al., 2019).

In addition to synchronizing their phenology with food abundance at their breeding sites, migratory bird species must also ensure that their migration timing aligns with the emergence of key resources (Visser et al., 2004). For long-distance migrants, this can pose as a challenge, as the cues used at wintering grounds may become unreliable indicators of conditions at breeding grounds, especially as climate change affects regions around the globe differently (Visser et al., 2004; Jones and Creswell, 2009; Horton et al., 2019). Timing breeding with insect availability, for instance, may become a challenge for insectivorous birds. Failure to sufficiently synchronise with this key resource may reduce the fitness of young, lowering their chances of successfully fledging and prolonging the time spent in the nest as they wait for their wings to fully develop (Chapter 2; Kouba et al., 2015). Both et al.'s (2006) study on pied flycatchers (*Ficedula hypoleuca*) in the Netherlands demonstrates that while the birds were able to advance their laying dates to match food peaks, their failure to advance their migratory arrival limited their ability to sufficiently synchronise with the advancement of spring, resulting in a 90% population decline in areas with earlier food peaks. For certain species, fresh tree leaves also serve as an important resource for nest building. These leaves have been shown to positively affect European starling nestlings (*Sturnus vulgaris*) by mediating immune responses through their impact on reducing parasite loads in the nest (Gwinner et al., 2000; Williams et al., 2020).

One species that may be vulnerable to these mismatches is the purple martin (*Progne subis*), a long-distance aerial insectivore experiencing population declines across much of its northern breeding range (Jervis et al., 2019)**.** This species feeds on flying insects and lines its nest with tree leaves, meaning it must have the ability to time its migration arrival and timing of breeding with the emergence of these two resources to ensure its reproductive success. Previous studies have shown that martins exhibit flexibility in their breeding time, with Shave et al. (2019) showing that birds time their egg-laying with temperature, as their laying dates were found to advance with warmer springs. Smith and Fraser (2024) further demonstrate that purple martins flexibly adjust their nesting timing once they arrive at their breeding grounds, shortening their arrival-breeding interval with warmer temperatures by laying eggs earlier. However, it remains unclear as to whether this plasticity to temperature translates to birds being able to align their breeding to the timing of key resource emergence during peak energetic demand. In Chapter 2, I demonstrated that while birds are overall able to time themselves with key prey resources, being a little outside of the optimal timing window (in terms of alignment with resources) is enough to negatively affect fitness and reproductive success.

Migratory birds, such as swallows, are expected to adjust their foraging behaviour to environmental variation. As central-place foragers during the breeding season, martins may only travel an average of 2.94 km from their breeding sites (Lalla et al. 2021), therefore any microhabitat site differences in environmental phenology would reflect the food resources birds capture with their local movements. Comparing the timing of resource emergence and breeding across microhabitats would therefore provide valuable insight into this species' ability to adapt to changing environmental conditions.

Using the purple martin (*Progne subis*) as a model species, I aimed to investigate whether they experienced microhabitat timing differences at the colony level, and if so, whether the timing of nesting was consistent with the variations. I therefore aimed to test the hypothesis that migratory songbird breeding timing is flexible to fine scale, local environmental conditions, such as the timing of insect availability and leaf availability at breeding sites. Aerial insects are the major prey for both adult and nestling purple martins during the breeding season, while leaves are used to line nests before egg laying, possibly to provide additional moisture and act as a chemical deterrent to nest parasites (Gwinner et al., 2000; Williams et al., 2020). I predicted that both leaf and insect emergence would vary between microhabitats (breeding colonies). I also predicted that settlement and egg laying dates would differ by site and be consistent with the timing of resource availability.

The ongoing decline in migratory songbird populations, which is believed to be partly driven by climate change, lends urgency to understanding the factors that influence reproductive timing, and whether birds are able to time themselves with resources to avoid the detrimental effects of a phenological mismatch (Fraser et al., 2019; Chapter 2). Doing so will provide new insight into the plasticity of migratory songbirds to changing conditions by determining whether purple martins are able to fine-tune to microhabitat differences.

Methods

Study sites

The four purple martin (*Progne subis*) breeding colonies used in the study were located near Winnipeg, in Manitoba, Canada. These sites include a private backyard south of Winnipeg (49.74°N, 97.13°W), FortWhyte Alive (FWA), a wildlife preserve and recreation area in Winnipeg (49.82°N, 97.23°W), Oak Hammock Marsh (OHM), a marsh located north of Winnipeg (50.17°N, 97.13°W), and Pointlands (PL), located on the University of Manitoba campus (49.81°N, 97.13°W). All four sites were located between 2.94-48.86 km apart from each other, which ensured a distinct separation of microhabitats between colonies. The purple martin's preference for nesting in man-made houses, which are easy to manipulate, makes it an ideal model species for this project. Each site contained two houses, except for the private residence, which had three houses, equipped with 14 nest compartments per house, with 3-4 cavities stacked vertically facing four different directions.

Migration arrival and settlement dates

Each spring, the purple martin travels between 7,000 km to 12, 000 km from its wintering grounds in South America to breeding grounds in North America (Turcotte-van de Rydt et al., 2023). To determine the arrival date of purple martins, which was approximated by the settlement date at a given site, I visited breeding colonies every 2-3 days starting from the first week of May during the years 2023 and 2024. Through visual observations, I tracked the arrival of new individuals, counting the number of birds present at the colony each day, and noting the band numbers, ages, and sexes of the birds as they guarded cavity entrances.

Nest monitoring

All nest data collection adhered to guidelines provided by the Purple Martin Conservation Association' 'Project Martinwatch' (Purple Martin Conservation Association [PMCA], 2017). Throughout the years 2021, 2023 and 2024, purple martin houses were visited every 2-3 days to record the number of eggs and the dates of egg laying. As female purple martins typically lay one egg per day, first egg dates, which were used as a measure of nest timing in this study, were determined by subtracting the number of eggs present in the nest from the nest-check date. All data collection procedures followed the guideline of the University of Manitoba's Animal Care Committee, which approved the methods used in this experiment (Animal Care Protocol Number F23-001-1).

Insect monitoring

Insect availabilities were measured every other day from 8:00 to 16:00 from the start of May to mid-August, in 2021, 2023 and 2024 through transect surveys located within a 250 m distance of purple martin colonies. Transects were 100 m in length and were completed in 15 minutes, with surveyors walking at a constant speed of 0.4 km/h. Two surveyors conducted transects: one was responsible for counting and identifying all flying insects within their frontal view, while the other recorded the data, noting the number of insects observed from each order. All flying insects observed were identified to order, with the exception of data recorded in 2017, when only Odonate dates were recorded. Since there was no distance limit for counting insect, these methods come with the caveat that larger insects may be seen at a farther distance than their smaller counterparts, potentially creating a sampling bias towards bigger insects. Transects were conducted only once upon visiting each site on any given day, and the same locations were used each time (within 150 meters of purple martin houses, in areas with a high observed insect density). As these methods reflect prey availability to birds on a specific day rather than the overall abundance over the summer, weather effects were not directly controlled for. The reasoning is that weather impacts would already influence insect availability on any given day and therefore are captured in the data. Furthermore, since prey is sampled every 1-3 days, this sampling frequency provides a reliable index of prey availability over the nesting period, accounting for short-term weather fluctuations.

Green-up monitoring

The timing of green-up was determined by monitoring the phenology of tree leaf out. Tree leaves were monitored throughout the season by non-systematically selecting fixe trees within 150 meters of the purple martin nestboxes in 2023 and 2024. The trees selected were chosen to represent a variety of species, reflecting the range of trees accessible to the purple martins at each site. During every field site visit, a new tree branch was non-systematically selected from each tree, ensuring that a different branch was sampled each time. The percentage of leaves at various development stages, as outlined in Ribeiro et al. (2021), was estimated from that branch and recorded. Leaves were scored into categories along a development spectrum of stage 1 to 6, where V1 represents a budding leaf, while V6 indicates a fully matured leaf. With this method comes the caveat that lower branches on the tree must be selected in order to properly view and evaluate and categorize the leaves, as leaves located at different heights of tree crowns were found to vary in timing of unfolding and senescence, in part caused by differences in structural and chemical traits (Zahnd et al., 2023; Niinemets et al., 2014; Pons and Anten, 2004).

Statistical methods

Site differences in microhabitat timing: insect peaks

To determine peak insect availability dates, quadratic models were fitted to the transect data, using similar methods outlined in Saalfeld et al. (2019). The response variable in each of those models was the number of insects observed, whereas the independent variable was the date converted to Julian date. The peak date was then determined by calculating the maximum value of each model's predictions. This method was repeated for all four study sites during 2023 and 2024, three of those sites during 2021, and three during 2024 (Table 2).

Site differences in microhabitat timing: green-up

To compare the timing of leaf emergence between sites, I recorded the dates of first emergence for the leaf development stages V4, V5, and V6. The selection of these three stages was based on previous observations, where I counted leaf types in 12 different nests and found that purple martins lined their nests with these specific stages. Therefore, the first availability of these leaf stages in the environment would reflect their availability to Martins for lining their nests, with dates being used in further analysis (Table 3).

Site differences in avian timing: arrival-settlement dates

The settlement date was defined as the day when the first ten birds had arrived at a breeding colony and exhibited evidence of cavity use, such as entering and exiting the cavity or guarding the entrance. Settlement at these cavities was confirmed if sites where birds were seen entering or exiting a cavity were used for nest building and egg laying later in the season, with dates being compared in further analysis (Table 4).

Site differences in avian timing: first egg dates

To determine whether there were significant differences in egg laying dates between sites, I fitted a Poisson generalized linear model using R (version 4.4.1) and RStudio (version 2024.09.0+375, R Core Team, 2024). The Poisson family was specifically chosen due to the use of non-negative discrete count data. In this model, egg laying date (converted to Julian date) served as the response variable, and site as the independent variable, with year being included as a fixed effect (Table 5). While an interaction term between egg laying and year was originally assessed in the model, a post hoc ANOVA performed to assess its significance revealed that it did not enhance the model’s performance. The interaction was therefore excluded from the model.

Comparing timing of microhabitat and avian phenology

To examine whether differences in settlement timing between sites are reflected by differences in insect peak timing, I subtracted the dates of occurrence of local environmental conditions (emergence of V5 leaves, emergence of V6 leaves, and insect peaks) from settlement dates, and compared the differences (Table 6).

In addition, I calculated differences between egg laying dates and the timings of the same environmental conditions and generated nine Kruskal-Wallis tests, followed by Dunn's post hoc tests, to compare calculated values between sites within-year. Green-up data were not collected in 2021, so comparisons for that year included only one insect peak model (Supplemental Table 14). The remaining eight models compared egg laying differences with insect peak, V4 emergence, V5 emergence and V6 emergence during the years 2023 (Supplemental Table 15-18) and 2024 (Supplemental Table 19-22).

Results

Site differences in microhabitat timing: insects

Overall, peak insect availability differed widely among colony sites over the three years of the study, varying between 0 and 49 days. Peak insect availability also varied widely within year between the study sites. For example, in 2021, peak insect availability varied across sites by 9-45 days. The earliest peak was June 29th (Julian date of 180) at OHM, and the latest was August 13th (Julian date of 225) at FWA, occurring at the very end of the field season. In 2023, the peak dates varied by 5-18 days, with OHM having the earliest peak on June 25th (Julian date of 176), and the private field site peaking at the latest date of July 13th (Julian date of 194). In 2024, the dates varied by 1-15 days. The earliest peak occurred on July 11th (Julian date of 193) at FWA, while the latest occurred on July 26th (Julian date of 208) at PL (Table 2, Figure 5).

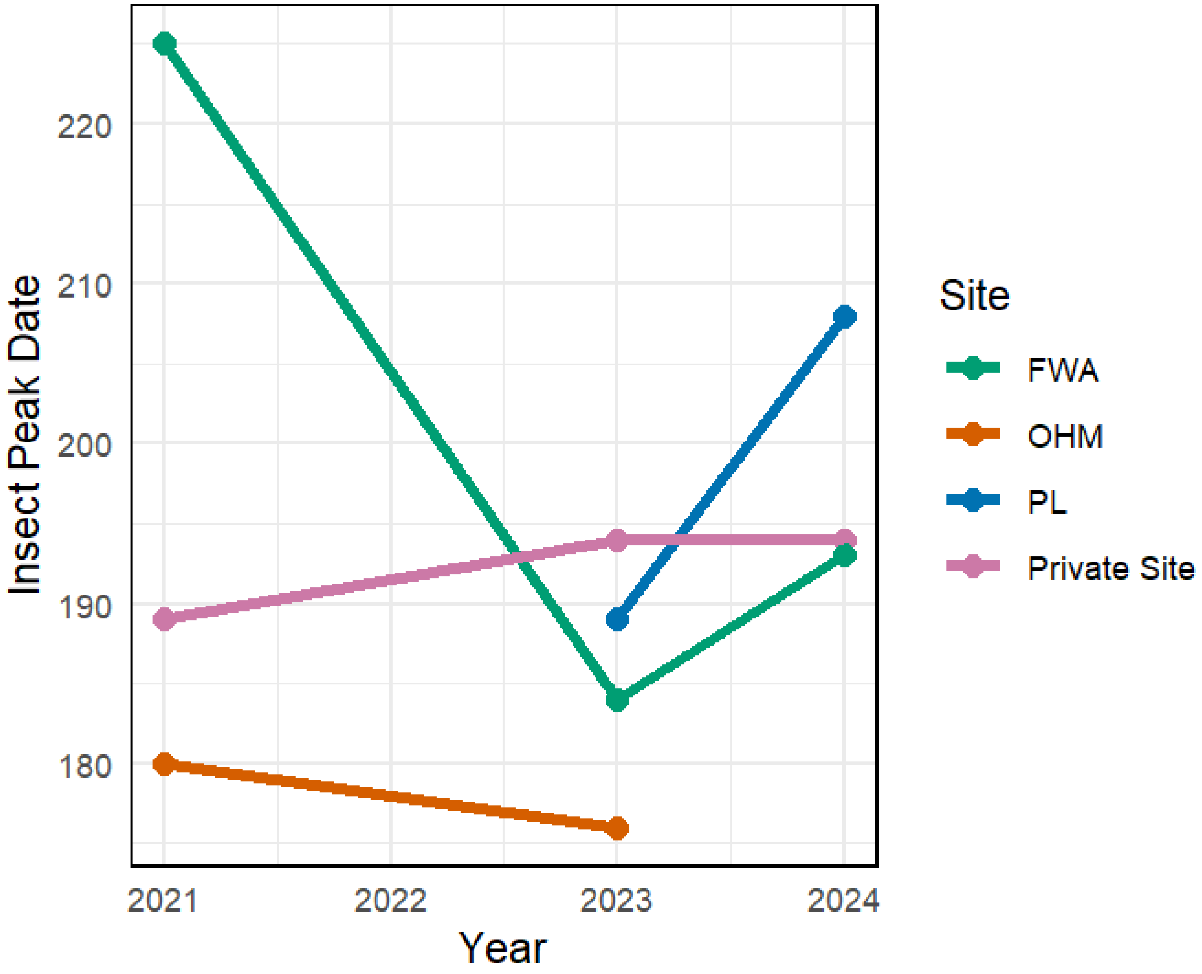

Figure 5. Line plot demonstrating the variation of insect peak availability dates across four field sites and three separate years. While dates were found to vary throughout sites, this variation was not consistent throughout years. Insect peak availability dates were converted to Julian dates

Table 2. Summary of peak insect availability dates at four field sites across three separate years.

		Estimated Peak Insect Date	
Site	**Year**	**Calendar Date**	**Julian Date**
Private Site	2021	07-08	189
	2023	07-13	194
	2024	07-12	194
FWA	2021	08-13	225

	2023	07-03	184
	2024	07-11	193
OHM	2021	06-29	180
	2023	06-25	176
PL	2023	07-08	189
	2024	07-26	208

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Site differences in microhabitat timing: green-up

In contrast to peak insect prey availability, the phenology of green-up did not vary as widely between sites. Across two years of sampling, the first emergence of leaves used by martins varied by 0-20 days for stage V4, 0-13 days for stage V5, and 1-20 days for stage V6 (Table 3, Figure 6).

In 2023, leaf emergence dates varied by 1-11 days for stage V4, 0-2 days for stage V5 and 2-14 days for stage V6. The earliest date of emergence of stage V4 leaves occurred at FWA on May 18th (Julian date 138), while the latest occurred on May 29th (Julian date 149) at the private field site. Stage V5 leaves first emerged on May 18th (Julian date 138) at both the private site and FWA at the earliest, and May 20th (Julian date 140) at the latest at PL. Stage V6 leaves first emerged on May 18th (Julian date 138) at FWA, and June 1st (Julian date 152) at OHM. In 2024, leaf emergence dates varied by 1-9 days for stage V4, 0-11 days for stage V5, and 5-20 days for stage V6. The earliest V4 emergence occurred on May 8th (Julian date 129) at PL, whereas the latest was on May 17th (Julian date 138) at OHM. The earliest stage V5 occurrence was at FWA on May 6th (Julian date 127), and the latest at OHM on May 17th (Julian date 138).

The earliest emergence of stage V6 was at FWA on May 14th (Julian date 135), and the latest at OHM on June 3rd (Julian date 155) (Table 3, Figure 6).

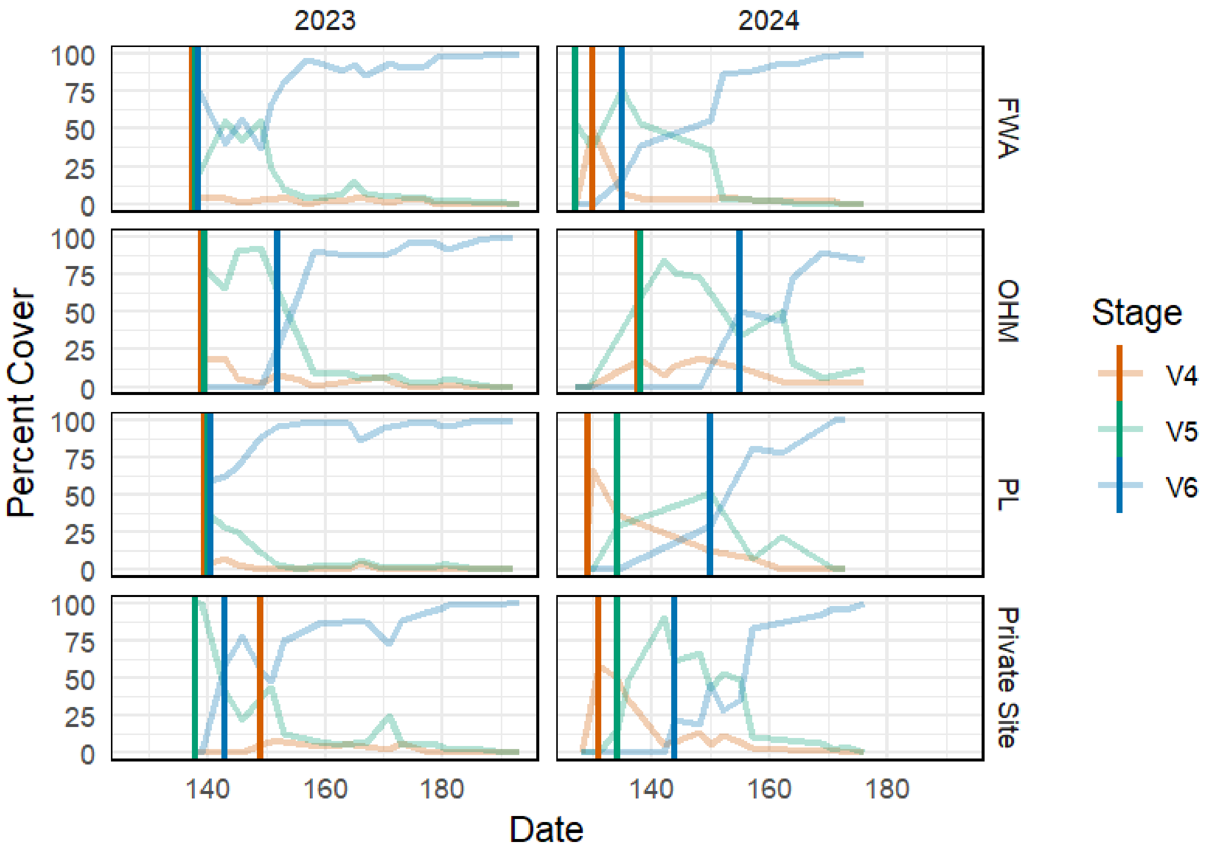

Figure 6. Line graph demonstrating the progression of three leaf development stages (V4, V5 and V6, in which stage V6 represents a fully matured leaf) at four field sites throughout the years 2023 and 2024. The dates of first emergence of each development stage were accentuated by orange (V4), green (V5) and blue (V6) vertical lines.

Table 3. Summary of first emergence dates of three leaf development stages (V4, V5 and V6, with V6 representing a fully matured leaf) at four field sites across two years.

		Date of first V4 emergence		**Date of first V5 emergence**		**Date of first V6 emergence**	
Site	**Year**	**Calendar**	**Julian**	**Calendar**	**Julian**	**Calendar**	**Julian**
	2023	05-29	149	05-18	138	05-23	143

Private Site	2024	05-10	131	05-13	134	05-23	144
FWA	2023	05-18	138	05-18	138	05-18	138
	2024	05-09	130	05-06	127	05-14	135
OHM	2023	05-19	139	05-19	139	06-01	152
	2024	05-17	138	05-17	138	06-03	155
PL	2023	05-20	140	05-20	140	05-20	140
	2024	05-08	129	05-13	134	05-29	150

Site differences in avian timing: arrival-settlement dates

For the most part, settlement dates did not vary throughout sites, with the exception of PL in 2023, which increased the settlement variation across years from 1-6 days to 1-33 days. As houses had only been installed at this location in 2021, the late date can be treated as an outlier, as it may reflect occupancy by birds that were outcompeted in other areas for nest cavities.

The earliest settlement date in 2023 occurred on May 5th (Julian date 125) at the private site, with FWA and OHM following 5 and 6 days later, respectively. The settlement date at PL occurred on June 1st (Julian date 152), 27 days after that of the private site. In 2024, dates varied by 1-3 days, the earliest date occurring at OHM on May 6th (Julian date 126), and the latest at FWA, on May 9th (Julian date 129) (Table 4).

Table 4. Summary of settlement dates, defined by the date at which the ten first purple martins arrived at each of four field sites across two years.

		Settlement Date	
Site	**Year**	**Calendar**	**Julian**
	2023	05-05	125

Private Site	2024	05-07	127
FWA	2023	05-10	130
	2024	05-09	129
OHM	2023	05-11	131
	2024	05-06	126
PL	2023	06-01	152
	2024	05-08	128

Site differences in avian timing: first egg dates

Contrary to my prediction, there were no significant differences between egg laying dates at the different field sites (*p* > 0.05, Table 5, Figure 7). However, as predicted from past studies (Pärn et al., 2011; Liebezeit et al., 2014; Gordo et al., 2007; Visser and Gienapp, 2019; Reed et al., 2013), the model demonstrated significant differences between years, with purple martin having laid their eggs significantly earlier (-0.04 ± 0.02) in ~~the year~~ 2023 compared to other years (*p* = 0.028).

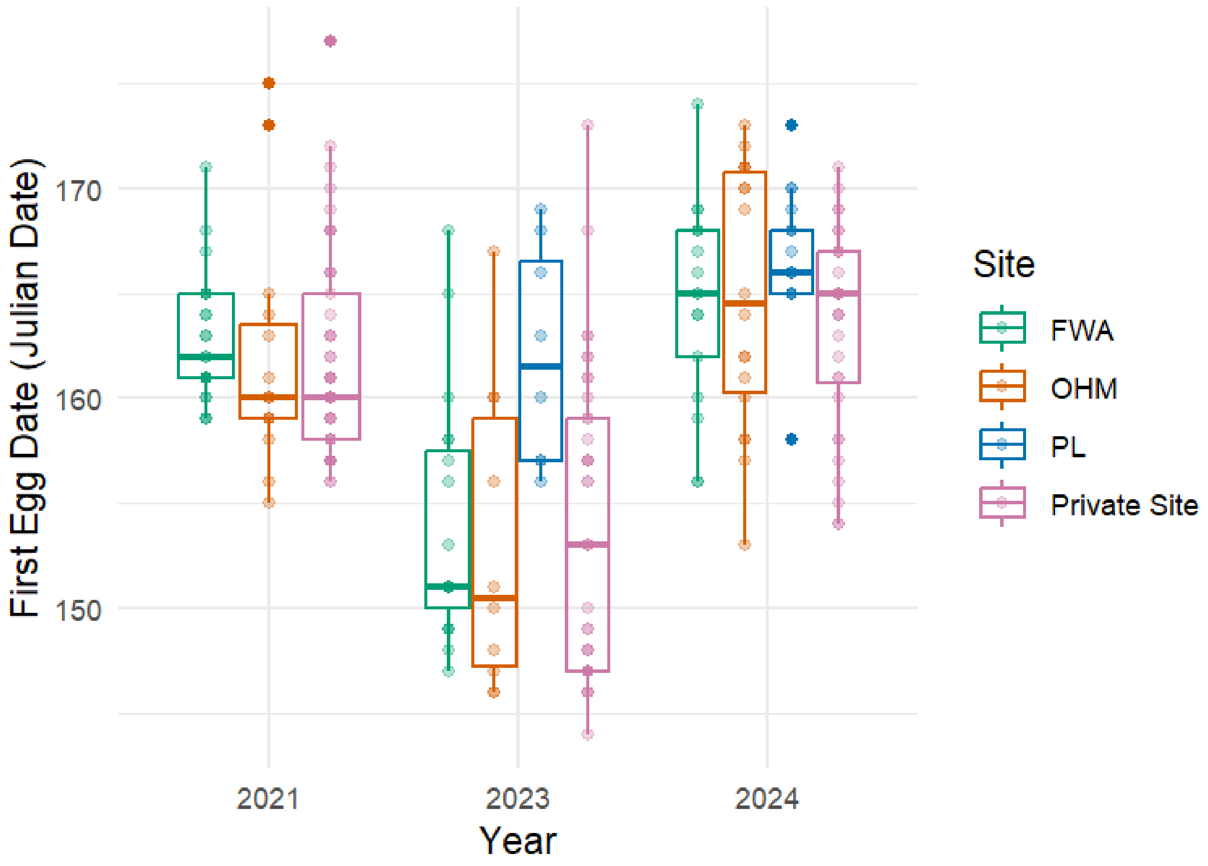

Figure 7. Boxplot comparing first egg laying dates between four different field sites over three different years. Egg laying dates were converted to Julian dates. Data were collected over the years 2021, 2023 and 2024. In 2023, PL demonstrated a later average egg date relative to other field sites, but the difference was not enough to be significant in its associated generalized linear model (*p* > 0.05).

Table 5. Parameter estimates of general linear model showing the difference in date of first egg laid (n = 139) between sites (n = 4). Year and age of parents (second year or after second year) were included as covariates. No significant differences were found between sites, but there were significant differences found between years.

Fixed Effects	**Estimate**	**SE**	**Lower 95% confidence interval**	**Upper 95% confidence interval**	**P-value**
(a) Number Fledged ~ Total Insect Peak Difference + Age + (1|year) + (1|site)					
(Intercept)	5.09	0.01	5.07	15.02	**<0.001**
Site PL	0.00	0.02	-0.03	-0.07	0.183

Site OHM	0.03	0.02	-0.01	0.00	0.901
Private Site	0.00	0.01	-0.03	-0.06	0.701
Year 2023	-0.05	0.01	-0.08	-0.20	**<0.001**
Year 2024	0.01	0.01	-0.02	-0.02	0.452
R2	0.446				

Comparing timing of microhabitat and avian phenology

Settlement timing

Overall, the timings of settlement relative to insect peak varied greatly across sites, showing inconsistencies in how purple martins align their arrival with the subsequent timing of conditions. Across both years, settlement differences varied by 1 to 24 days with V4 emergence, 2 to 13 days with V5 emergence, 6 to 29 days with V6 emergence, and 35 to 80 days with insect peak.

In 2023, differences between sites varied by 37-69 days with insect peaks, with the private site showing the greatest difference whereas PL showed the smallest one. The timing difference for V4 leaves varied by 8-24 days, with OHM and FWA showing the smallest differences, and the private site showing the greatest one. The difference in timing between settlement and V5 leaf emergence was greatest at the private site by 13 days, and smallest at both FWA and OHM by 8 days. For timing with V6 emergence, OHM showed the greatest difference at 21 days, whereas FWA showed the smallest at 8 days of difference (Table 6).

In 2024, insect peak differences between sites were found to be largest at PL with an 80-day difference, and smallest at FWA with a difference of 64 days. V4 emergence differences varied from 1 day at FWA, and 12 days at OHM. The V5 emergence difference with settlement was greatest at OHM at 12 days, and smallest at FWA by 2 days. For the V6 emergence difference, OHM had the greatest one at 29 days, and FWA had the smallest one at 6 days (Table 6).

Table 6. Summary of the difference in days between settlement dates and four microhabitat timings (V4 leaf emergence, V5 leaf emergence, V6 leaf emergence and insect peak date) across two years and between four sites (with the exception of insect peak data at OHM in 2024). Negative values indicate that settlement dates occurred before microhabitat dates, whereas positive values indicate a later occurrence of settlement dates.

Site	Year	V4 Difference	V5 Difference	V6 Difference	Insect Peak Difference
Private Site	2023	-24	-13	-18	-69
	2024	-4	-7	-17	-67
FWA	2023	-8	-8	-8	-54
	2024	-1	2	-6	-64
OHM	2023	-8	-8	-21	-45
	2024	-12	-12	-29	n/a
PL	2023	12	12	12	-37
	2024	-1	-6	-22	-80

Egg laying timing

There were significant differences in egg laying and insect peak date differences across the three sites in all three years of the study (Kruskal-Wallis test, $p < 0.05$). Specifically, the post-hoc analysis showed significant differences in 2021 between FWA and OHM (Z = 7.58, *adjusted* $p < 0.001$), FWA and the Private Site (Z = 6.08, *adjusted* $p < 0.001$), and OHM and the Private Site (Z = -3.33, *adjusted* $p = 0.001$, Supplemental Table 14, Figure 8).

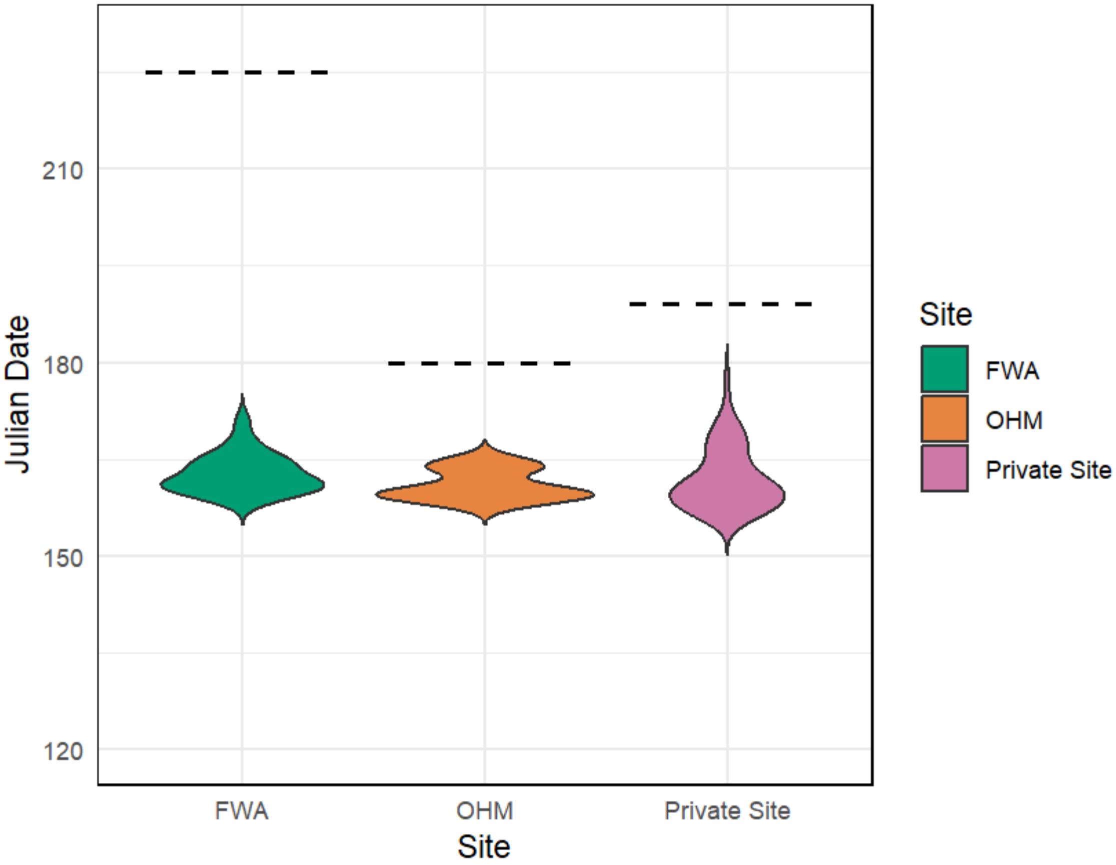

Figure 8. Violin plot showing the range and density of egg laying dates per site in 2021. Dashed Horizontal lines demonstrate the dates of insect peaks.

In 2023, the post-hoc analysis examining insect dates showed significant differences between FWA and the Private Site (Z = -3.95, *adjusted p* < 0.001), OHM and the Private Site (Z = -5.21, *adjusted p* < 0.001), and PL and the Private Site (Z = -3.98, *adjusted p* < 0.001, Supplemental Table 15). No significant differences were found otherwise between the rest of the sites. Timing differences of V4 leaves were significantly different between FWA and the private site (Z = 4.59, *adjusted p* < 0.001), OHM and the private site (Z = 2.73, *adjusted p* = 0.019) and PL and the private site (Z = 4.83, *adjusted p* < 0.001, Supplemental Table 16), with the other comparisons showing insignificant results. The Kruskal-Wallis test showed no significant differences in egg laying and V5 emergence date differences (*p* = 0.06075, Supplemental Table

17). However, Dunn's post-hoc test revealed significant differences between OHM and PL (Z = -2.52, *adjusted p* = 0.035), as well as between PL and the Private Site (Z = 2.44, *adjusted p* = 0.044, Supplemental Table 17). No significant differences were found between the other site comparisons. Dunn's post-hoc test revealed significant differences in V6 emergence between FWA and OHM (Z = 3.32, *adjusted p* = 0.003), OHM and PL (Z = -4.28, *adjusted p* < 0.001), FWA and the Private Site (Z = 2.44, *adjusted p* = 0.044), and PL and the Private Site (Z = 3.64, *adjusted p* < 0.001, Table 18, Figure 9).

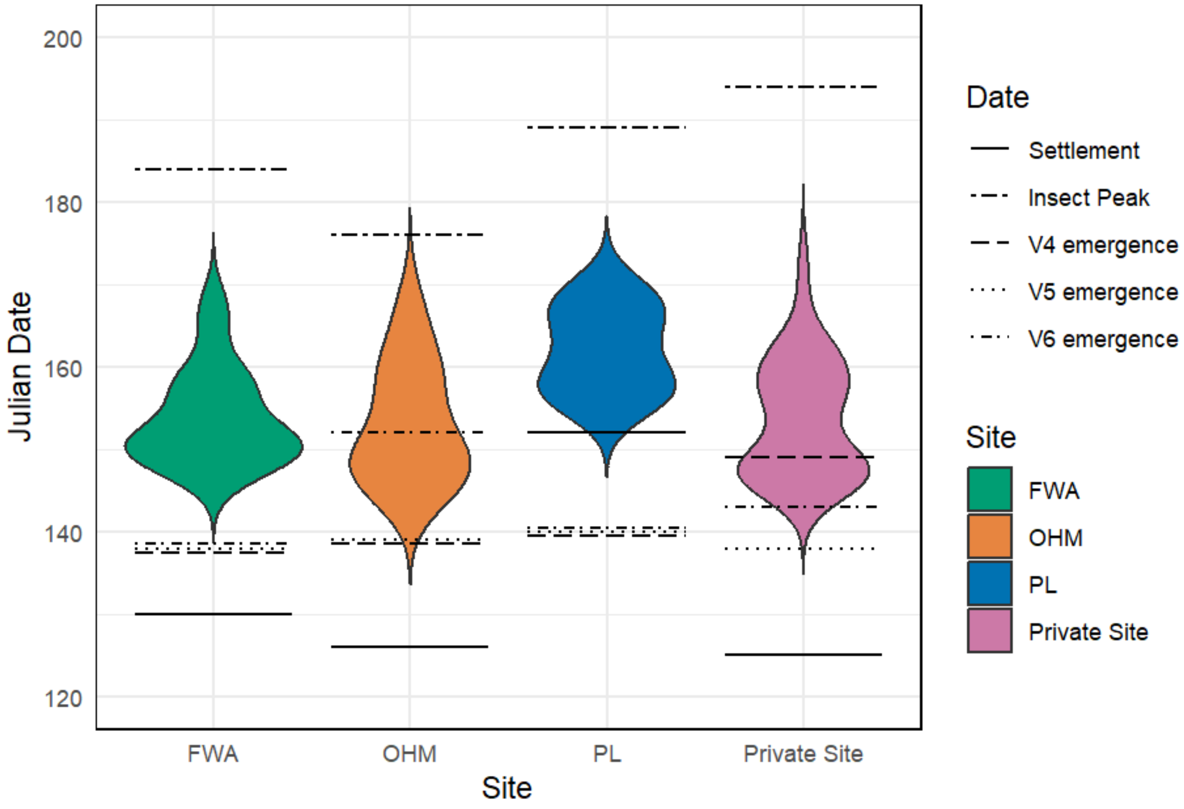

Figure 9. Violin plot showing the range and density of egg laying dates per site in 2023. Horizontal lines demonstrate the dates of settlement, V4 emergence, V5 emergence, V6 emergence and insect peaks.

In 2024, the post-hoc test examining insect dates revealed significant differences between FWA and PL (Z = -5.52, adjusted p < 0.001) and PL and the Private Site (Z = 4.99, adjusted p <

0.001). No significant differences were found between FWA and the Private Site (Z = -1.32, adjusted p = 0.282, Table 19, Figure 10). Timing differences of V4 leaves were significantly different between FWA and OHM (Z = -3.67, *adjusted p* < 0.001), OHM and PL (Z = -5.58, *adjusted p* <0.001), OHM and the private site (Z = -2.69, *adjusted p* = 0.022), and PL and the private site (Z = 3.65, *adjusted p* < 0.001, Table 20), with the other site showing insignificant results. Significant differences in egg laying and V5 emergence date were found (p < 0.001), with Dunn's post-hoc test revealing differences between FWA and OHM (Z = 4.81, *adjusted p* < 0.001), FWA and the Private Site (Z = 4.61, *adjusted p* < 0.001), and OHM and PL (Z = -2.62, *adjusted p* = 0.026, Table 21). Finally, significant differences in egg laying and V6 emergence date differences occurred across sites (p < 0.001), with the post-hoc revealing significant differences between FWA and OHM (Z = 7.04, *adjusted p* < 0.001), FWA and PL (Z = 4.81, *adjusted p* < 0.001), FWA and the Private Site (Z = 3.86, *adjusted p* < 0.001), and OHM and the Private Site (Z = -4.15, *adjusted p* < 0.001, Table 22, Figure 10).

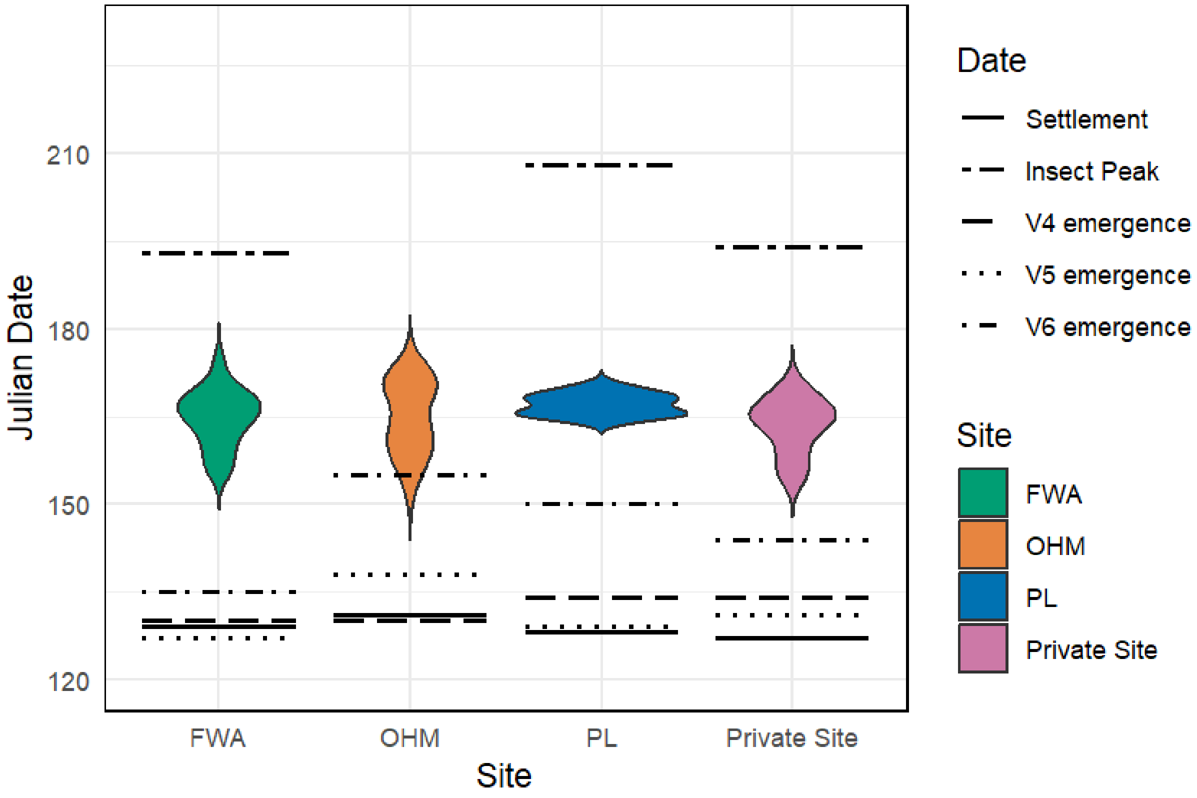

Figure 10. Violin plot showing the range and density of egg laying dates per site in 2024. Horizontal lines demonstrate the dates of settlement, V5 emergence, V6 emergence and insect peaks.

Discussion

My results reveal that while the timing of peak insect availability varies widely across sites within a year, and there is some variability in green-up, avian timing (settlement and egg-laying dates) did not exhibit similar variation. My models further showed that the birds were found to differ in their timing relative to that of the environmental conditions across sites. These findings did not align with my prediction that purple martin egg laying and settlement would be consistent with microhabitat differences, suggesting that the birds were not aligned in their timing at the microhabitat scale.

My results suggest that the differences in insect timing between microhabitats at the different study areas around the Winnipeg region varied enough that birds may need to adjust the timing of their settlement and egg laying accordingly to prevent a phenological mismatch. These study areas were all located near waterbodies of varying characteristics, including a retention pond at the private site, a shallow marsh at OHM, a lake at FWA and the fast-moving Red River at PL. In southern Germany, Salvarina et al. (2017) observed that the timing of aquatic insect abundance varied, with the emergence peak of flying arthropods at three nearby lakes fluctuating across seasons. This variation could be explained by differences in water temperature, as waterbodies of different sizes and depths are known to exhibit temperature variations (Pujoni et al., 2019). If insect activity is closely tied to water temperature, then the varying thermal conditions across sites—created by the different waterbody types—could help explain the observed differences in peak insect availability timing at a smaller spatial scale (approximately 49 km).

While green-up also varied between sites, the variation was much smaller than for insects. The earliest leaf stage used in purple martin nests was available well in advance of nest lining for all sites, suggesting that the birds align well with this resource (Figures 9-10). Other studies of plant spring phenology were consistent with these findings, with Naithani et al. (2013), which showed that trees in a forested area in central Pennsylvania showed differences in budbreak and leaf maturation at a fine-scale (over 7.9 ha). Results also contrasted with those found in a study by Cole and Sheldon (2017), which found spatial differences in phenology in UK trees.

Surprisingly, given the large differences in peak insect availability, my model comparing egg dates between sites showed no significant differences, suggesting that martins do not adjust their timing to match differences in conditions between microhabitats. Despite previous studies showing purple martins aligning their breeding with temperature, often used as a proxy for the timing of insects, (Smith and Fraser, 2024; Shave et al., 2019; Bonamour et al., 2019; Nussey et al., 2005), my results suggest that birds lack the ability to fine-tune the timing of their egg-laying to the peak availability of key resources (i.e. insect prey) at a microhabitat scale. This is further shown by my comparisons of how birds at different sites aligned with environmental variability, demonstrating broad ranges in degrees of alignment between egg-laying and microhabitat conditions (particularly insect peaks) across sites. It is likely that insect timing may be driven by additional factors, as when Salvarina et al., (2017) demonstrated that water temperature drove the timing of peaks. We can therefore infer that phenotypic plasticity to temperature may not always translate well to birds' adjustment to the timing of peak resources, which is influenced by other ecological factors. While purple martins in this study failed to align with microhabitat conditions, a previous study focusing on blue tits (*Cyanistes caeruleus*), showed laying date variations throughout the French Mediterranean, including between sites in Corsica, located approximately 40 km – 50 km from each other (Bonamour et al., 2019). As blue tits are mostly sedentary, with northern populations migrating short distances in spring and autumn, this could suggest that the purple martin's long-distance migrations may further impact its ability to sufficiently fine tune its timing to microhabitat variations.

It should be noted that sampling of leaves in this study began when tree leaves had already started emerging, which could have led to inaccurate emergence dates for earlier leaf development stages—such as when I recorded certain V4 emergence dates occurring after or simultaneously with V5 and V6 leaves. Future studies should start sampling before or during the early stages of leaf development, when leaves are budding. Although not the primary focus of my study, other factors in my models were still important. The significant difference between years, for instance, shows that purple martin egg laying dates are affected by the yearly variation of conditions at breeding sites, something repeatedly seen in past studies (Pärn et al., 2011; Liebezeit et al., 2014; Gordo et al., 2007; Visser and Gienapp, 2019; Reed et al., 2013; Shave et al., 2019).

Conclusion

Overall, the results of this study indicate that while microhabitats in Winnipeg, Manitoba exhibit timing differences in insect peaks, purple martin egg laying did not vary by site to match, showing wide ranges of alignment between sites. Contrary to past studies showing that martins' plasticity to temperature to time egg laying, these results suggest that the birds may not be as fine-tuned to specific sites as needed to avoid phenological mismatches with resources, potentially resulting in decreases in reproductive success (Chapter 2). By providing evidence suggesting that the use of temperature as a timing cue (shown in past studies to predict insect emergence) does not translate well to timing with microhabitat differences, my findings have provided more needed insight into martins' phenotypic plasticity, in turn providing important information for their conservation. The next research steps would be to further investigate the cues aerial insectivores use to time their breeding, as well as quantify the prevalence of mismatches within their populations.

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Supplemental Material

Supplemental Table 14. Kruskal-Wallis test parameters, followed by a Dunn's post-hoc test parameters, comparing the difference in days between egg laying and insect peak dates at three field sites in 2021. P-values were adjusted using the Bonferroni correction method.

Kruskal-Wallis Test	**Chi-Squared**	**Degrees of Freedom**	**P Value**
Egg laying and insect peak date difference by site	64.56	2	**>0.001**
Dunn's Post Hoc Test	**Z-Value**	**P-Value**	**Adjusted P-Value**
FWA - OHM	7.58	**>0.001**	**>0.001**
FWA - Private Site	6.08	**>0.001**	**>0.001**
OHM - Private Site	-3.33	**>0.001**	**0.001**

Supplemental Table 15. Kruskal-Wallis test parameters, followed by a Dunn's post-hoc test parameters, comparing the difference in days between egg laying and insect peak dates at four field sites in 2023. P-values were adjusted using the Bonferroni correction method.

Kruskal-Wallis Test	**Chi-Squared**	**Degrees of Freedom**	**P Value**
Egg laying and insect peak date difference by site	41.29	3	**>0.001**
Dunn's Post Hoc Test	**Z-Value**	**P-Value**	**Adjusted P-Value**
FWA - OHM	1.90	**0.029**	0.172
FWA - PL	1.05	0.147	0.884
OHM - PL	-0.63	0.263	1.000
FWA - Private Site	-3.95	**>0.001**	**>0.001**
OHM - Private Site	-5.21	**>0.001**	**>0.001**
PL - Private Site	-3.98	**>0.001**	**>0.001**

Supplemental Table 16. Kruskal-Wallis test parameters, followed by a Dunn's post-hoc test parameters, comparing the difference in days between egg laying and V4 leaf emergence dates at four field sites in 2023. P-values were adjusted using the Bonferroni correction method.

Kruskal-Wallis Test	Chi-Squared	Degrees of Freedom	P Value
Egg laying and V4 emergence date difference by site	37.32	3	<0.001
Dunn's Post Hoc Test	**Z-Value**	**P-Value**	**Adjusted P-Value**
FWA - OHM	0.81	0.210	1.000
FWA - PL	-1.40	0.081	0.485
OHM - PL	-1.91	0.028	0.169
FWA - Private Site	4.59	<0.001	<0.001
OHM - Private Site	2.73	0.003	0.019
PL - Private Site	4.83	<0.001	<0.001

Supplemental Table 17. Kruskal-Wallis test parameters, followed by a Dunn's post-hoc test parameters, comparing the difference in days between egg laying and V5 leaf emergence dates at four field sites in 2023. P-values were adjusted using the Bonferroni correction method.

Kruskal-Wallis Test	Chi-Squared	Degrees of Freedom	P Value
Egg laying and V5 emergence date difference by site	7.38	3	0.061
Dunn's Post Hoc Test	**Z-Value**	**P-Value**	**Adjusted P-Value**
FWA - OHM	1.04	0.150	0.901
FWA - PL	-1.87	**0.031**	0.183
OHM - PL	-2.52	**0.006**	**0.035**
FWA - Private Site	0.55	0.290	1.000

OHM - Private Site	-0.71	0.239	1.000
PL - Private Site	2.44	**0.007**	**0.044**

Supplemental Table 18. Kruskal-Wallis test parameters, followed by a Dunn's post-hoc test parameters, comparing the difference in days between egg laying and V6 leaf emergence dates at four field sites in 2023. P-values were adjusted using the Bonferroni correction method.

Kruskal-Wallis Test	**Chi-Squared**	**Degrees of Freedom**	**P Value**
Egg laying and V6 emergence date difference by site	24.29	3	**>0.001**
Dunn's Post Hoc Test	**Z-Value**	**P-Value**	**Adjusted P-Value**
FWA - OHM	3.32	**>0.001**	**0.003**
FWA - PL	-1.73	**0.042**	0.249
OHM - PL	-4.28	**>0.001**	**>0.001**
FWA - Private Site	2.44	**0.007**	**0.044**
OHM - Private Site	-1.75	**0.04**	0.242
PL - Private Site	3.64	**>0.001**	**>0.001**

Supplemental Table 19. Kruskal-Wallis test parameters, followed by a Dunn's post-hoc test parameters, comparing the difference in days between egg laying and insect peak dates at three field sites in 2024. P-values were adjusted using the Bonferroni correction method.

Kruskal-Wallis Test	**Chi-Squared**	**Degrees of Freedom**	**P Value**
Egg laying and insect peak date difference by site	35.4344	2	**>0.001**

Dunn's Post Hoc Test	Z-Value	P-Value	Adjusted P-Value
FWA - PL	-5.516087	**>0.001**	**>0.001**
FWA - Private Site	-1.315699	0.094	0.282
PL - Private Site	4.988401	**>0.001**	**>0.001**

Supplemental Table 20. Kruskal-Wallis test parameters, followed by a Dunn's post-hoc test parameters, comparing the difference in days between egg laying and V4 leaf emergence dates at four field sites in 2024. P-values were adjusted using the Bonferroni correction method.

Kruskal-Wallis Test	Chi-Squared	Degrees of Freedom	P Value
Egg laying and V4 emergence date difference by site	33.44	3	<0.001
Dunn's Post Hoc Test	**Z-Value**	**P-Value**	**Adjusted P-Value**
FWA - OHM	3.67	<0.001	<0.001
FWA - PL	-1.89	0.030	0.177
OHM - PL	-5.58	<0.001	<0.001
FWA - Private Site	1.50	0.067	0.404
OHM - Private Site	-2.69	0.004	0.022
PL - Private Site	3.65	<0.001	<0.001

Supplemental Table 21. Kruskal-Wallis test parameters, followed by a Dunn's post-hoc test parameters, comparing the difference in days between egg laying and V5 leaf emergence dates at four field sites in 2024. P-values were adjusted using the Bonferroni correction method.

Kruskal-Wallis Test	Chi-Squared	Degrees of Freedom	P Value

Egg laying and V5 emergence date difference by site	29.87	3	**>0.001**
Dunn's Post Hoc Test	**Z-Value**	**P-Value**	**Adjusted P-Value**
FWA - OHM	4.81	**>0.001**	**>0.001**
FWA - PL	2.16	0.016	0.093
OHM - PL	-2.62	**0.004**	**0.026**
FWA - Private Site	4.61	**>0.001**	**>0.001**
OHM - Private Site	-0.82	0.206	1.000
PL - Private Site	2.15	**0.016**	0.096

Supplemental Table 22. Kruskal-Wallis test parameters, followed by a Dunn's post-hoc test parameters, comparing the difference in days between egg laying and V6 leaf emergence dates at four field sites in 2024. P-values were adjusted using the Bonferroni correction method.

Kruskal-Wallis Test	**Chi-Squared**	**Degrees of Freedom**	**P Value**
Egg laying and V6 emergence date difference by site	52.44	3	**>0.001**
Dunn's Post Hoc Test	**Z-Value**	**P-Value**	**Adjusted P-Value**
FWA - OHM	7.04	**>0.001**	**>0.001**
FWA - PL	4.81	**>0.001**	**>0.001**
OHM - PL	-2.16	**0.015**	0.093
FWA - Private Site	3.86	**>0.001**	**>0.001**
OHM - Private Site	-4.15	**>0.001**	**>0.001**
PL - Private Site	-1.64	0.051	0.304

CHAPTER 4: Overall discussion

The effects of mistiming with key prey resources on purple martin reproduction

In Chapter 2, I contributed to the few studies showing evidence of the direct effects of phenological mismatches with food resources on the reproductive success of migratory aerial insectivores. To do so, I conducted insect transects every other day from the start of May to the middle of August, providing a large dataset of insect availabilities throughout the summer, and allowing me to estimate a peak date. Alongside those transects, I visited purple martin (*Progne subis*) nesting cavities at four different colony sites, where I collected nestling data such as clutch sizes and the number of successful fledges (Purple Martin Conservation Association [PMCA], 2017). My most exciting results showed evidence of positive effects on reproductive success associated with timing of nestling stages (most notably day ten of development and fledge) closely to food resource peaks. For instance, timing fledge with the overall insect peak was found to significantly reduce the amount of time young spent in the nest prior to fledging, suggesting that the increased availability of insects during that stage may provide nestlings with the necessary resources for their final developmental needs before fledging. These results were consistent with those of the few other studies directly testing the effects of mismatch with peak resource availability, showing a decrease in reproductive output and fitness with greater distance from peak (Saalfeld et al., 2019; Reed et al., 2013).

In addition, I found evidence of a potential phenotypic mismatch. My models showed that timing later nestling stages with the peak of Odonate availability – a key food resource for purple martin nestlings (Dunoyer et al., 2024) – increased both fledge proportions (i.e. the number of hatched young that fledged) and the total number fledged. When comparing the actual breeding timing observed in the colony with that of the peak, Odonates were almost perfectly aligned with median hatches, suggesting that birds are timed relatively later than the ideal life stage suggested by the model, day 10. This is furthered by the fact that Odonates' relatively larger sizes compared to other insects samples may be too big for small nestlings to consume. These findings provide additional evidence, alongside many other studies, that the advancement of insect phenology is occurring at a rate much faster than that of the birds that feed on them (Saalfeld et al., 2019; Visser and Gienapp, 2019; Kharouba et al., 2018).

Microhabitat variations and arrival-breeding timing

In Chapter 3, I compared the timing differences in microhabitat conditions and avian arrival and breeding between four field sites in Winnipeg, Manitoba, Canada. To do so, I used the same insect transect data and nest data as in Chapter 2. In addition, I repeatedly sampled tree leaves throughout the spring, allowing me to keep track of their development – as a proxy to green-up – until the tree canopy reached full maturity. I found that the phenology of insect peaks varied greatly between field sites, leaf emergence varied less, whereas settlement and egg-laying varied very little. The timing of insects between sites varied similarly to that of a previous study also studying flying arthropods (Salvarina et al., 2017), whereas the green-up results were only similar to those found in González-Rodríguez et al. (2011), but otherwise differed from those of other studies showing spatial differences in vegetation phenology throughout habitats (Naithani et al., 2013; Cole and Sheldon, 2017; Wei at al., 2024).

These results suggest that purple martins do not adjust the timing of their egg laying to match the high variability in the peak availability of insect prey found at different sites. Furthermore, when comparing differences in days between the timing of egg laying, insect peaks and leaf out, I found that there were significant differences across field sites, showing wide disparities in how purple martins aligned themselves to the timing of microhabitat conditions. While previous studies have demonstrated evidence of martins, as well as other birds, advancing their breeding with temperature changes (Smith and Fraser, 2024; Shave et al., 2019; Bonamour et al., 2019), my results suggest that martins' plasticity to temperature is not translatable to their synchrony (or lack thereof) to peak resources at the scale of their foraging and nesting areas at specific breeding sites.

Environmental constraints on plasticity to timing

Together, these findings suggest that purple martins, along with other migratory insectivores, may face significant challenges during breeding as climate change continues to drive rapid environmental changes (Visser and Gienapp, 2019). The rate at which insect prey advance their emergence dates—driven by different mechanisms underlying their phenology—has consistently outpaced the timing adjustments of avian species (Saalfeld et al., 2019; Visser and Gienapp, 2019; Kharouba et al., 2018). While many birds have shown the ability to flexibly advance their nesting and laying dates in response to temperature (Bonamour et al., 2019; Smith and Fraser, 2024; Shave et al., 2019; Nussey et al., 2005), migratory species are more limited in how much they can adjust. The cues birds rely on at their wintering sites to time their spring migrations, such as photoperiod (Jones and Creswell, 2009), may become less reliable as climate change affects the regions of the globe in various ways, resulting in cues that no longer align with the optimal timing for birds to reach their breeding grounds (Visser et al., 2004; Horton et al., 2019). Additionally, migrating earlier poses the risk of traveling in unfavorable conditions (Norris et al., 2004). If birds continue migrating at their usual time but attempt to advance their laying dates, this could shorten their arrival-breeding interval, reducing the time available to recover from migration before settling into nesting sites (Smith and Fraser, 2024). My results show that the alignment of breeding timing with temperature—often used as a predictor of insect timing— also does not directly translate to alignment with the varying resource peaks across different microhabitats. While few studies have demonstrated a direct effect of phenotypic mismatch on fitness and reproductive success (Bonamour et al., 2019; Reed et al., 2013), my findings suggest that the misalignment with key resources, caused by environmental constraints on migratory species, could negatively impact their reproductive success.

Study Limitations

The insect transect method used to quantify insect availability throughout the purple martin breeding season comes with the caveat that larger insects may be easier to observe at a distance, therefore biasing the collection of data towards bigger organisms (i.e. dragonflies and butterflies), as smaller organisms would need to be within closer proximity of surveyors to be observed and recorded.

Furthermore, the sampling of trees was done too late in the season, with as the leaf stages observed in purple martin nests had already emerged on certain trees prior to sampling. Future research studying leaf development in the field should aim to sample them much earlier prior to the arrival of the purple martins.

Conservation applications of findings

The findings of this study highlight the importance of habitat management in conserving purple martins due to the increasing challenges they face from phenological mismatches with their food resources (Visser and Gienapp, 2019). As climate change alters the timing of insect availability, it is crucial to enhance the protection of habitats that support large populations of aerial insect species, such as wetlands. This is especially important as insect populations are declining, with a reduction of over 70% in abundance in Europe since the mid-1960s (Møller, 2020). Given this trend, future research should focus on understanding the magnitude and shape of insect population peaks, in addition to their timing. Currently, I am contributing data to a North American-wide insect population study aiming to track changes in insect abundance throughout North America, with initial trends showing similar decreases to those observed in Europe.

Significance and conclusion

This study provides critical insights into the effects of phenological mismatches between migratory insectivores and their food resources, contributing to limited songbird research that directly links these mismatches to reproductive success (Reed et al., 2013, Saalfeld et al., 2019). In Chapter 2, by examining the timing of purple martin (*Progne subis*) nesting stages in relation to insect availabilities, I found that the synchronization of breeding, especially day ten of development and fledge timing with peak food resources such as Odonates, significantly improved reproductive success. In Chapter 3, my results revealed a lack of flexibility in purple martins' ability to adjust their breeding timing in response to variations in microhabitat conditions. Despite previous studies showing a strong association between temperature and advanced laying dates (Bonamour et al., 2019; Smith and Fraser, 2024; Shave et al., 2019; Nussey et al., 2005), my results suggest that plasticity to temperature, despite being considered a predictor of insect timing (Bonamour et al., 2019), does not translate to bird’s adjustment to peak resource timing. These insights are crucial for conservation efforts, as they demonstrate the need for habitat management strategies protecting healthy aerial insect populations, which could potentially help mitigate the negative impacts of phenological mismatches.

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