The impact of phenological mismatch between an aerial insectivore and prey abundance on nestling growth rates and fledge success

by

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Abstract:

Phenological mismatches between breeding birds and food availability are expected to increase with climate change and reduce reproductive success. This issue is particularly important for aerial insectivores, which rely on flying insects to feed their young. Purple Martins (*Progne subis*) are a declining aerial insectivore whose nestlings depend on parental provisioning during development. I examined how synchrony between Purple Martin nestling development and aerial insect abundance influenced growth and fledging success in southern Manitoba. These relationships were evaluated through the food limitation hypothesis, predicting that reduced insect availability slows nestling growth, and the predation exposure hypothesis, predicting that delayed development prolongs nest vulnerability. Nestling body weights, hatch to 19 days post-hatch, were measured every 1-3 days across four sites during the May-July breeding season. Aerial insect abundance was measured using transect surveys to calculate phenological mismatch with seasonal peaks and the number of days during the nestling period exceeding 30% of the seasonal maximum. I found that nestlings developing further from the seasonal insect peak, or those with fewer days above the 30% threshold, took longer to reach an adult-like body weight (+0.76 days per day of mismatch; +0.038 days per day below the threshold). Fledging success was higher in broods experiencing more days above the 30% threshold, with all nestlings that failed to fledge having zero days above the threshold. However, phenological mismatch with aerial insect abundance had little effect on short-term growth metrics. Overall, these results suggest that sustained periods of high insect abundance may be more important for nestling development and fledging success than short-term growth responses to food availability. Future work should examine the carry-over effects limited food availability may cause after fledging.

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Table of Contents:

Abstract ..... **i**

Acknowledgments ..... **ii**

List of Tables ..... **iv**

List of Figures: ..... **v**

Introduction **1**

Methods and Materials **5**

Study design 5

Experimental Protocol 6

Study System and Measured Variables 6

Nest Monitoring and Nestling Measurement Procedures 7

Quantification of Aerial Insect Phenology 9

Statistical Analysis 10

Estimation of Aerial Insect Abundance and Phenological Mismatch 10

Nestling Growth and Fledge Success Models 12

Results: **15**

Insect Phenology 15

Impact of Alignment with Aerial Insect Peaks on Growth 16

Impact of Days Above Sufficient Food Threshold on Growth 36

Discussion: **44**

Literature Cited: **58**

Supplemental Tables: **64**

Supplemental Figures **66**

List of Tables:

Table 1.....17

Table 2.....20

Table 3.....22

Table 4.....24

Table 5.....25

Table 6.....25

Table 7.....27

Table 8.....28

Table 9.....28

Table 10.....31

Table 11......34

Table 12.....36

Table 13.....38

Table 14.....40

Table 15.....43

Supplemental Table 1......64

List of Figures:

Figure 1 18

Figure 2 21

Figure 3 23

Figure 4 26

Figure 5 29

Figure 6 32

Figure 7 35

Figure 8 37

Figure 9 39

Figure 10 41

Figure 11 44

Supplemental Figure 1 66

Supplemental Figure 2 67

Supplemental Figure 3 68

Supplemental Figure 4 69

Supplemental Figure 5 70

Supplemental Figure 6 71

Supplemental Figure 7 72

Supplemental Figure 8 73

Supplemental Figure 9 74

Supplemental Figure 10. 75

Introduction:

The number and quality of offspring that survive to reproduce forms the basis of natural selection (Lack 1947; Magrath 1991). In birds, the growth and survival of nestlings represent a crucial component of reproductive success (Allen and Nice 1952; Fontaine et al. 2018). As only the young that successfully fledge and survive until entering the breeding population contribute to parental fitness, the nestling phase represents one of the most important life stages for birds (Walsh 1978; Kouba et al. 2015). Nestlings are especially vulnerable during this period because they cannot thermoregulate efficiently, have limited mobility, and rely completely on parental provisioning for food and protection (Mccarty and Winkler 1999; Kouba et al. 2015; Facey et al. 2020). For nestlings, the conditions faced while in the nest can carry over into the post-fledging period and beyond (Halliwell et al. 2023). Therefore, nest conditions can ultimately affect a young bird's survival during their first migration and their recruitment into the breeding population (Magrath 1991; Naef-Daenzer et al. 2001; Tarof et al. 2011; Jones et al. 2017; Freeman et al. 2020).

The nestling stage is a particularly vulnerable period as young birds often require intensive parental care (Allen and Nice 1952; Saino et al. 2012; Freeman et al. 2020). This is especially true for songbirds, as they have altricial young that are highly dependent on their parents (Allen and Nice 1952). A nestling's growth trajectory is influenced by the quality of parental care and external environmental conditions, such as weather and food availability (Walsh 1978; Kouba et al. 2015; Facey et al. 2020). As food availability fluctuates due to changing temperatures over the breeding season for many birds, the timing of reproduction is important (Kouba et al. 2015; Freeman et al. 2020). This is

especially true for aerial insectivores, such as swallows, which must time their egg laying and nesting stages to coincide with high levels of short-lived flying insects (Quinney et al. 1986). Phenological mismatches between the nestling's demand for food and insect availability can be detrimental (Quinney et al. 1986; Both et al. 2009b; Dunn et al. 2011). This trophic dependence has been implicated in population declines seen in aerial insectivore species across North America (Both et al. 2009b; Nebel et al. 2010). These declines may arise when repeated mismatches with food availability reduce nestling condition, lower post-fledging survival, and ultimately limit recruitment into the breeding population (Both and Visser 2001; McKinnon et al. 2012; Freeman et al. 2020). Mismatch is often measured by comparing the timing of nestling development with the seasonal peak in insect abundance, based on the assumption that nestlings perform best when these peaks overlap (Both et al. 2009b; McKinnon et al. 2012; Saalfeld et al. 2019). Alternatively, it can be quantified as the number of days during which insect abundance exceeds a threshold considered optimal for nestling growth, providing a measure of how long favourable feeding conditions are available (Mccarty and Winkler 1999; McKinnon et al. 2012; Saalfeld et al. 2019). However, few studies have directly examined how closely nestling growth trajectories actually coincide with local prey phenology and the impact that this phenological mismatch has on the reproductive success of aerial insectivores.

One such swallow species currently facing population declines is the Purple Martin (*Progne subis*) (Nebel et al. 2010; Sauer et al. 2013). Purple Martins are long-distance migrants that breed colonially across North America from spring to early fall (Allen and Nice 1952). In eastern North America, Purple Martins are almost entirely reliant on human-made bird houses (Brown et al. 2021). Upon arrival in spring, nests are

built and eggs laid (Brown et al. 2021). Once the eggs hatch, nestlings grow rapidly until 10-12 days old and typically fledge anytime between 26-30 days old (Brown et al. 2021). Purple Martins rely entirely on aerial insects to feed and raise their young, specifically insects in the orders Lepidoptera, Diptera, Odonata and Coleoptera (Dunoyer et al. 2024). Their short breeding window and reliance on continuous aerial foraging mean that even small shifts in seasonal insect emergence may affect their ability to meet nestling energy demands (Allen and Nice 1952; Williams et al. 2024). Food abundance is an important driver of nestling growth and overall developmental success in Purple Martins (Allen and Nice 1952). Previous studies on Purple Martins have shown that higher food availability is associated with increased wing chord length, a common metric of structural development in nestlings (Allen and Nice 1952; Williams et al. 2024). However, whether food abundance directly limits nestling weight has not been tested. It has also been noted that nestlings hatched earlier in the season exhibit better body condition as compared to those in later hatched nests (Williams et al. 2024). Parasites also play a key role in Purple Martin nestling success, especially in later hatched broods, which tend to experience higher levels of mites, fleas, and calliphorid fly larvae (Allen and Nice 1952). Overall, nestling success in Purple Martins is shaped by a complex interplay of factors which strongly influence growth and survival (Allen and Nice 1952; Tarof et al. 2011; Dunoyer et al. 2024; Williams et al. 2024).

Despite knowing these patterns of Purple Martin nestling success, less is known about how nestling growth rates, particularly their weights, are shaped by synchrony with local prey abundance (Tarof et al. 2011; Williams et al. 2024). This is important to understand as faster growth and higher nestling weights allow for earlier fledging, which lowers the risk of predation, reduces parental energetic costs, and improves survival

prospects after leaving the nest (Allen and Nice 1952; Freeman et al. 2020). When prey abundance is low, parents must expend more effort and time to provision nestlings, increasing the energetic cost per unit of food delivered and potentially affecting both parental condition and offspring survival after fledging (Walsh 1978; Cucco and Malacarne 1996; Mccarty and Winkler 1999). No study has specifically examined how the timing of Purple Martin nestling development relative to aerial insect availability influences growth trajectories from hatching to fledge. To address this gap, I will test two complementary hypotheses regarding the timing of Purple Martin nestling development in relation to aerial insect abundance. The food-limitation hypothesis proposes that nestling growth will be affected by the degree of mismatch between nestling development and local aerial insect abundance. I predict that broods with greater mismatch to local aerial insect abundance will experience reduced provisioning, leading to slower nestling growth rates and higher mortality due to starvation. I further predict that broods developing further from higher aerial insect abundance will reach key developmental milestones, including reaching adult-like body weight and fledging readiness, at older ages as a consequence of reduced growth and cumulative energetic constraints. The predation-exposure hypothesis proposes that nestling growth and survival are influenced by mismatch with insect abundance via changes in parental attendance, and that mismatch can also delay fledge timing. I predict that nestlings experiencing greater mismatch with aerial insect availability will be left unattended for longer periods as parents increase their foraging effort, which increases nestlings' vulnerability to predation; additionally, if suboptimal food availability delays the timing of fledging readiness, prolonged time in the nest may further extend exposure to nest predators. Addressing these research gaps and understanding how this mismatch affects Purple Martin nestling growth and survival will

provide insights into the drivers of Purple Martin nestling success and inform future conservation strategies.

Methods and Materials:

Study design

The focal species for this study is the Purple Martin (*Progne subis*). Fieldwork involved direct access to Purple Martin nestlings through routine monitoring of Purple Martin nestboxes during their nesting season.

Four field sites were included in this study, spaced throughout southern Manitoba. The Point Lands (PL) site, located on the University of Manitoba campus (49.813483, -97.126480), is adjacent to agricultural fields, mature deciduous trees, and the Red River, and contains two Purple Martin houses (14 nest cavities each). FortWhyte Alive (FWA; 49.820372, -97.224684) is situated near open plains, scattered deciduous and coniferous trees, and several human-made lakes, and hosts two Purple Martin houses (14 nest cavities each). Oak Hammock Marsh (OHM; 50.172847, -97.132762) lies within a wetland complex surrounded by deciduous and coniferous trees and agricultural lands, hosting two Purple Martin houses (14 nest cavities each). The final site, a private residence near Howden, Manitoba (CL; 49.734780, -97.130101), is located near the Red River and agricultural fields with nearby deciduous and coniferous tree cover. This location contains two Purple Martin houses. Each Purple Martin house can host up to 14 nests without additional gourds placed onto the house, and 18 nests with the addition of gourds (plastic nest boxes that hang beneath the main house, resembling the shape of squash gourds, an early nestbox type provided to martins by humans). The use of multiple

field sites allows for comparisons across habitat types, while standardised handling and measurement procedures ensured data consistency and reliability.

All research activities were conducted in compliance with the University of Manitoba's Animal Care Committee and in accordance with applicable permits approved by the committee (Animal Care Protocol Number AC11795). The permit ensures that all aspects of the study met ethical standards for animal handling and scientific research.

Experimental Protocol

Study System and Measured Variables

In this study individual Purple Martin (*Progne subis*) nestlings were treated as their own experimental unit. The following traits were measured for each individual nestling: body weight in grams, hatch date, developmental age (days since hatching), approximate fledge date, nest location (site, house number, cavity number), brood size (number of hatched nestlings per cavity), parental age, presence and type of ectoparasites. Surrounding insect abundance was also measured.

Parental age was determined through visual nest observations using binoculars or telescopes, with plumage characteristics being used to determine age categories (Purple Martin Conservation Association [PMCA], 2025). Each parent could fall into one of two categories: second year (SY) or after second year (ASY). Accordingly, each nest could have one of four parental combinations: ASY female with ASY male, ASY female with SY male, SY female with ASY male, or SY female with SY male. These observations were done prior to and during the period of time in which their broods were being weighed.

The presence and type of ectoparasites were determined through a brief visual inspection of feathers and skin. Ectoparasites were recorded under seven categories: mites, fleas, maggots, mites and fleas, mites and maggots, maggots and fleas, and all three present. Ectoparasites such as mites and fleas were not removed; however, Calliphoridae fly larvae (maggots) were removed from nestlings by hand if they were lightly attached and easily removable. If larvae were firmly embedded in the nestling's skin, they were not removed. Nest material was not replaced, meaning larvae not actively attached to a nestling also remained in the nest. The partial removal of parasites may have impacted results, as reductions in weight associated with ectoparasite load may appear less drastic than if all larvae had been left in place.

Nest Monitoring and Nestling Measurement Procedures

This study was conducted across four field sites (PL, FWA, OHM, CL). The target sample size was a minimum of 10–15 broods per site, with all nestlings in each brood measured; however, if fewer than 10 successful broods hatched at a site, all available broods were included. Within each brood, all nestlings were measured on the same day to control for diurnal variation in weight. Each site was visited every 2–3 days, with all active study nests measured during each visit. The aim was to obtain a minimum of seven weight measurements per nest over the course of the nestling period to provide a comprehensive measure of each nestling's weight gain and important developmental ages.

Nest monitoring and measurements were conducted every 1-3 days, or as weather permitted, and followed standardised procedures provided by the Purple Martin Conservation Association 'Project Martinwatch' (Purple Martin Conservation Association

[PMCA], 2025) to reduce disturbance and handling time. Purple Martin houses were lowered, and nest trays were temporarily removed. Nests, along with nestlings, were covered with a cloth bag to protect them from direct sunlight during handling. Hatch date was determined upon a nestling's first time being handled using size-accurate age photos provided by the PMCA. Aging was completed before day 3 for all nestlings to ensure that size-based differences were still reliable, since major weight variation had not yet developed enough to obscure age estimates. For three nestlings, age could not be confidently determined from the size-accurate age photos. In those cases, age was assigned using weight ranges: nestlings weighing 0–4 g were classified as newly hatched (day 0), 4–7 g as day 1, 7–10 g as day 2, and 10–15 g as day 3. Once aged, the nestlings' hatch date was calculated.

Prior to weighing nestlings, the scale used was tested using a coin of known weight to ensure its accuracy. The equipment was set up at the base of each Purple Martin house, allowing nestlings to be removed and weighed quickly before being returned to the nest. Nestlings were then gently removed by hand and placed into a clean baking cup for containment (Supplemental Figure 1). Body weight was measured using either a CS series CS200P portable digital scale (accurate to ±0.1 g) or a Smart Weigh ZIP300 digital scale (accurate to ±0.01 g). The scale used was determined at the time of weighing based on wind speeds, as the Smart Weigh ZIP300 digital scale could not provide accurate measurements under high wind speeds. To allow for temporary individual identification, the toenails of each nestling were marked with a small dab of non-toxic nail polish (brand Sinful Colors). After 12 days, nestlings received federally issued aluminium leg bands instead of nail polish for individual identification. Leg banding could not happen prior to 12 days of age, as a Purple Martin nestling's legs are too short and fat to accommodate

traditional leg bands without pinching, hence why nail polish was used for ID on all nestlings under 12 days old. Once all nestlings in a brood were weighed, the nest tray was returned to the cavity. During the time spent weighing a brood, the house was raised to avoid disrupting feeding at other cavities.

Nestlings were weighed until a maximum age of 19 days (Supplemental Figure 2) to minimise the risk of premature fledging as recommended by the PMCA due to the development of flight feathers. Once a single nestling within a brood reached 20 days of age, weighing of all nestlings in that brood ceased for the remainder of the study. This allowed the nestlings to fledge naturally, and not through stress related to being handled.

Fledge date was determined through routine site visits and monitoring of the nests, even after weighing ended. During a site visit, if there were fewer nestlings than recorded in the nest, they were recorded as fledged.

Quantification of Aerial Insect Phenology

Surrounding aerial insect abundance was quantified daily at the same site visit when nestlings were weighed using the methods outlined in Olson-Brissaud (2025). This was achieved through a 15-minute, 100-meter insect transect survey performed within a 250-meter distance of purple martin colonies. The same location was used for the transect each time it was performed, in areas with a high observed insect density. Transects were performed by two surveyors who walked at a constant speed of 0.4 km/h and reported all flying insects in their frontal view, with insects being identified to order. As acknowledged in Olson-Brissaud (2025), a bias towards larger insects may have occurred as they are easier to see further away during a transect. Sampling every 2–3 days provided a

dependable measure of prey availability across the nesting period, while still accounting for short-term shifts driven by weather.

Statistical Analysis

Estimation of Aerial Insect Abundance and Phenological Mismatch

The date of peak insect abundance was determined to assess its influence on Purple Martin nestling growth. The collected transect count data was fitted with quadratic models, similar to Saalfeld et al. (2019) and Olson-Brissaud (2025), with insect abundance as the response and date as the predictor. The predicted date of highest abundance from each model was identified as the peak date for each insect group. Peak dates were calculated for total insects, Diptera, Lepidoptera, Odonata, Coleoptera, and for combined groups representing early-season optimal prey (Diptera + Lepidoptera) and late-season optimal prey (Odonata + Coleoptera). These groupings reflect differences in prey suitability across nestling developmental stages: smaller, soft-bodied taxa such as Diptera and Lepidoptera are typically fed to younger nestlings, whereas larger bodied taxa such as Odonata and Coleoptera are more common in diets of older nestlings and fledglings (Dunoyer et al. 2024). Peak dates were found separately for OHM, while PL, FWA, and CL (hereafter referred to as the Southern sites) were combined to find a peak date as all three sites fall within overlapping foraging ranges and adults could easily access insects from any of those sites throughout the season (Lalla et al. 2022). The difference (in days) between the predicted insect peak date and each nestling's day 10 post-hatch was used to quantify the degree of phenological mismatch. Mixed-effects models were used to

evaluate whether synchrony between insect peaks and key nestling stages influenced growth, nestling period length, and survival.

In addition to finding dates of peak insect abundance, a threshold-based metric was calculated to quantify dates of moderate or high aerial insect abundance during the nestling period. For each site, the maximum observed insect abundance across the sampling season was identified, and a threshold value corresponding to 30% of this seasonal maximum was calculated. This threshold was chosen after exploratory analysis revealed that a small number of exceptionally high insect counts inflated the seasonal maximum, such that higher thresholds (e.g., 50% or 75%) resulted in few or no days exceeding the threshold. A 30% threshold was therefore used to capture periods of moderate-to-high insect availability that were more representative of conditions experienced across the nestling period. Because Oak Hammock Marsh (OHM) was analyzed separately for peak date estimation, threshold values were also determined independently for OHM. The Southern sites were combined prior to threshold calculation, and a single maximum abundance and corresponding 30% threshold were derived from pooled data, due to their overlapping foraging ranges. Each sampling date was then classified as either above or below the 30% threshold based on whether total insect count met or exceeded this value. For each nestling, the number of days above the 30% threshold was calculated by summing all sampling dates between, and including, hatch date and fledge date during which insect abundance exceeded the threshold. This variable was used as a representation of the number of days during the nestling period when food availability was at least 30% of the seasonal maximum.

Nestling Growth and Fledge Success Models

Nestling growth and survival (to fledge) was analysed using a series of linear mixed-effects models (LMMs) tailored to different developmental stages and hypotheses. Model 1 examined body weight trajectories for nestlings between day 2 and day 10, covering the period of rapid growth based on visual observations of the nestling's growth curves. Model 2 focused on body weight at day 10, a growth benchmark where rapid growth starts to slow down, also determined through visual observation of the nestling's growth curves. For both of these models, fixed effects included hatch date, brood size, parental age combination, ectoparasite presence and type, and synchrony with insect abundance, measured as the difference in days between peak total aerial insect abundance and each nestling's day 10. Random effects included site, nest ID, and individual nestling ID to account for repeated measures and non-independence within nests.

Model 3 tested whether nests farther off-peak experienced greater brood loss. A binomial generalized linear mixed-effects model (GLMM) modeled the proportion of fledged young missing or non-fledged young per brood as the response variable to test the predation–exposure hypothesis. Fixed effects included insect mismatch, calculated as the difference in days between peak total aerial insect abundance and day 10 of the missing/non-fledged nestlings, hatch date, brood size, parental age combination, and ectoparasite presence and type, while random effects included site and nest ID.

To assess the role of specific prey types, Model 4a examined nestlings early-stage growth (days 0–6) in relation to alignment with peaks of Diptera and Lepidoptera, the primary prey provisioned to young nestlings (Dunoyer et al. 2024). Separate LMMs were fitted to examine body weight trajectories for nestlings between day 0 and day 6. Model

4a.i evaluated synchrony between nestlings' day 3 and peak Diptera abundance, Model 4a.ii evaluated synchrony with peak Lepidoptera abundance, and Model 4a.iii evaluated synchrony with peak combined (Diptera + Lepidoptera) abundance. Alongside synchrony with insect peaks, fixed effects included hatch date, brood size, and parental age. Random effects included site, nest ID, and individual nestling ID. Model 4b analysed late-stage body weight trajectories (days 6–18) in relation to Coleoptera and Odonata, larger-bodied prey more relevant for older nestlings and fledglings (Dunoyer et al. 2024). Fixed and random effects were the same as in Model 4a; however, synchrony with insect peaks was measured as the difference in days between peak Coleopter abundance (Model 4b.i)**,** peak Odonata abundance (Model 4b.ii), and peak combined (Coleoptera + Odonata) (Model 4b.iii) abundance and each nestling's day 12, which falls at the midpoint of the 6–18 day older nestling stage.

Model 5 analyzed age at weight plateau, defined as the first age when a nestling reached ≥ 47.8 g. This weight represented the approximate adult weight, determined by calculating the average weight of the five lightest adult Purple Martins captured during the same field season (47 g, 47 g, 48 g, 48 g, and 49 g). The model included synchrony with insect abundance, measured as the difference in days between peak total aerial insect abundance and the day each nestling turned 10 days old, hatch date, brood size, parent age, and parasite presence and type as fixed effects. Random effects included site and cavity, to test whether mismatched broods reached peak weight later.

A secondary analysis explored additional aspects of nestling performance and survival. This analysis used a GLMM with the same fixed and random effects as the growth models, ensuring a consistent framework for evaluating ecological and life-history influences on nestling development. Using a Gamma GLMM with a log link, length of the

nestling period (days from hatch to fledge) was modelled as a continuous response to test whether hatch date influenced how long nestlings remained in the nest in Model 6.

To further evaluate the role of food availability on nestling growth, a second set of models was constructed using the threshold-based metric rather than peak mismatch. Model 7 examined body weight trajectories for nestlings between day 2 and day 10, similarly to model 1. Growth was calculated as the difference between day 10 and day 2 body mass. A LMM was fitted with growth as the response variable. Fixed effects included the number of days above the 30% threshold for each nestling, hatch date, brood size, parental age combination, and ectoparasite presence and type. Random effects included site and cavity.

Model 8 examined nestling body weight at day 10 in relation to the number of days during which aerial insect abundance exceeded the 30% threshold. A LMM was fitted with body weight at day 10 as the response variable and number of days above the 30% threshold, hatch date, brood size, parental age combination, and parasite presence and type as fixed effects. Site and cavity were included as random effects.

Model 9 tested whether the number of days during which aerial insect abundance exceeded the 30% threshold influenced brood loss and fledging success. A GLMM was fitted, modeling fledging success as a binomial response using the number of fledged versus non-fledged young per brood. Fixed effects included number of days above the 30% threshold, hatch date, brood size, parental age combination, and parasite presence and type. Site and cavity were included as random effects.

Model 10 analyzed age at weight plateau (≥ 47.8 g) in relation to the number of days during which aerial insect abundance exceeded the 30% threshold. A GLMM with a Gamma distribution and log link was used. Fixed effects included the number of days

above the 30% threshold, hatch date, brood size, parental age combination, and parasite presence and type. Cavity was included as a random effect to account for shared developmental environments within nests.

Analyses were conducted in R (version 4.4.2, RStudio version 2024.04.0+735). To facilitate interpretation, all models were validated through residual analyses.

Results:

Insect Phenology

Using quadratic models, peak dates in aerial insect abundance were identified for all insects and specific taxonomic group across the two foraging regions. The timing of insect prey peaks differed at the regional level. At the Southern sites, total insect abundance peaked on June 28 (Supplemental Figure 3), while the combined early-season prey group (Diptera + Lepidoptera) peaked one day later on June 29 (Supplemental Figure 4). Within this early-season group, Diptera peaked earlier (June 26) (Supplemental Figure 5) and Lepidoptera much later (July 18) (Supplemental Figure 6). Late-season prey (Odonata + Coleoptera) showed an earlier peak at the Southern sites (June 25) (Supplemental Figure 7), with Odonata peaking on June 25 as well (Supplemental Figure 9), and Coleoptera on June 26 (Supplemental Figure 8).

At OHM, insect phenology showed a similar ordering but consistently earlier peak timing. Total insects peaked on June 25 (Supplemental Figure 3), and the combined Diptera + Lepidoptera group peaked on June 23 (Supplemental Figure 4). Diptera peaked earliest (June 22) (Supplemental Figure 5), while Lepidoptera again showed a later summer peak (July 4) (Supplemental Figure 6). The combined Odonata + Coleoptera

group peaked on June 24 (Supplemental Figure 7), driven by aligned peaks in Odonata (June 24) (Supplemental Figure 9) and a slightly later Coleoptera peak (June 28) (Supplemental Figure 8).

The number of days during the nestling period in which aerial insect abundance exceeded 30% of the seasonal maximum varied across sites and broods, with individual nestlings experiencing between 0 and 7 days above this threshold. In general, some broods experienced consistently low insect availability, while others encountered more frequent periods of moderate to high abundance.

Impact of Alignment with Aerial Insect Peaks on Growth

For Model 1, a linear mixed-effects model was used to test whether nestling growth between days 2 and 10 was influenced by phenological mismatch with peak aerial insect abundance, along with hatch date, brood size, parental age, and ectoparasite presence (Table 1). Insect did not have a statistically significant relationship with growth (Figure 1). Hatch date and brood size also did not show statistically effects on growth. Neither parental age combinations nor the presence of mites significantly affected growth. Random-effect variances were small (Cavity = 10.73; Site = 0), indicating limited variation among nests or sites.

Table 1. Linear mixed-effects model results for nestling growth (between day 2 and 10) in Purple Martins, showing estimated effects of insect phenological mismatch, hatch date, brood size, parental age combination, and ectoparasite presence, with site and cavity included as random effects.

Model 1: Growth (day 10 – day 2)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	25.593	23.995	-55.110	106.297	1.067	0.371
Timing mismatch (days off peak)	-11.247	18.289	-75.513	53.019	-0.615	0.589
Hatch date	1.150	2.042	-5.554	7.854	0.563	0.615
Brood size	-1.586	1.797	-6.750	3.578	-0.883	0.431
Parent age: SY female + ASY male (vs ASY:ASY)	-1.133	3.987	-12.070	9.805	-0.284	0.790
Parent age: SY female + SY male (vs ASY:ASY)	1.460	12.908	-46.068	48.989	0.113	0.919
Parasites: mites present (vs none)	0.201	3.120	-6.273	6.675	0.064	0.949

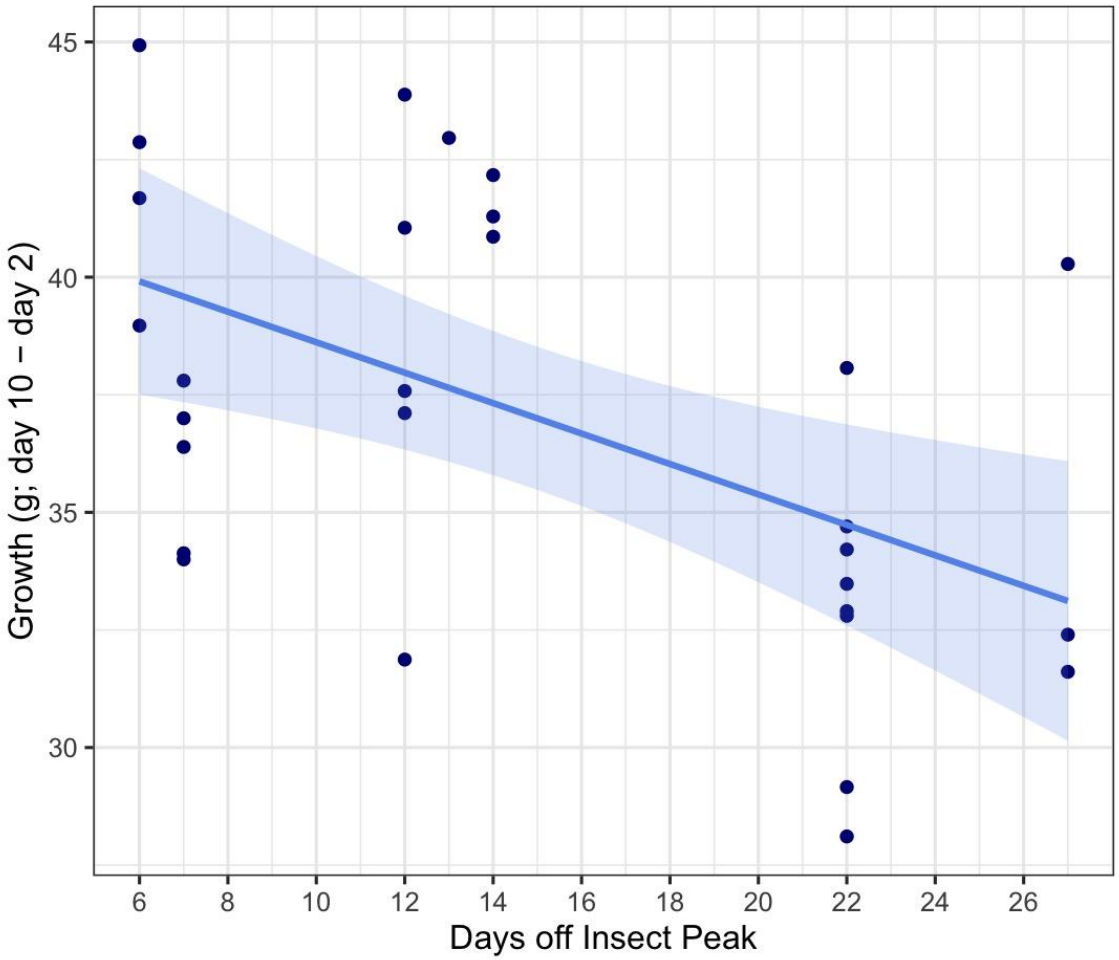

Figure 1. Relationship between Purple Martin nestling (n=29) growth (weight, in grams, gained from 2 days old to 10 days old) and the number of days between the date of peak aerial insect abundance and the date each nestling reached 10 days old at its respective site. Each point represents an individual nestling, and the solid line shows the fitted linear regression with 95% confidence intervals.

For Model 2, a linear mixed-effects model was used to test whether nestling body weight at day 10 was influenced by phenological mismatch with peak aerial insect abundance, along with hatch date, brood size, parental age, and ectoparasite presence (Table 2). The difference between peak insect abundance and each nestling's day 10 weight did not have a statistically significant effect per nestling (Figure 2). Hatch date also did not have a statistically significant effect. Brood size showed a strong significant negative effect, with each additional chick reducing the average weight by about 3.5g. Parental age showed weak evidence of explaining variation in nestling body weight at day 10, as none of the parental age combinations differed significantly from the ASY:ASY reference group. Ectoparasite presence was not significantly associated with day-10 weight overall. However, nestlings with mites tended to weigh less than unparasitized nestlings (−2.00 g ± 1.12), although this effect was not statistically significance. Random effects indicated that most variation occurred among cavities (variance = 10.81), with negligible site-level differences.

Table 2. Linear mixed-effects model results for nestling body weight at day 10 in Purple Martins, showing estimated effects of insect phenological mismatch, hatch date, brood size, parental age combination, and ectoparasite presence, with site and cavity included as random effects.

Model 2: Day-10 weight						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	6706.799	2819.660	744.403	12669.195	2.379	0.02980
Days above 30% aerial insect threshold	1.190	0.628	-0.085	2.465	1.896	0.06630
Hatch date	-0.328	0.139	-0.622	-0.035	-2.364	0.03060
Brood size	-2.617	0.921	-4.516	-0.719	-2.842	0.00889
Parent age: ASY female + SY male (vs ASY:ASY)	-3.115	2.520	-8.175	1.944	-1.236	0.22200
Parent age: unknown (vs ASY:ASY)	1.172	3.912	-6.637	8.982	0.300	0.76500
Parent age: SY female + ASY male (vs ASY:ASY)	1.655	1.414	-1.173	4.482	1.170	0.24700
Parent age: SY female + SY male (vs ASY:ASY)	8.165	2.858	2.469	13.861	2.857	0.00557
Parasites: mites present (vs none)	-1.568	1.100	-3.763	0.626	-1.425	0.15900
Parasites: fleas present (vs none)	-1.032	3.127	-7.279	5.215	-0.330	0.74200
Parasites: maggots present (vs none)	-2.861	4.297	-11.868	6.146	-0.666	0.51400
Parasites: mites + maggots present (vs none)	1.930	1.611	-1.287	5.146	1.198	0.23500
Parasites: mites + fleas present (vs none)	2.676	2.889	-3.114	8.467	0.926	0.35800
Parasites: maggots + fleas present (vs none)	-0.621	3.068	-6.771	5.529	-0.202	0.84000
Parasites: mite + maggots + fleas present (vs none)	-5.332	3.127	-11.579	0.915	-1.705	0.09300

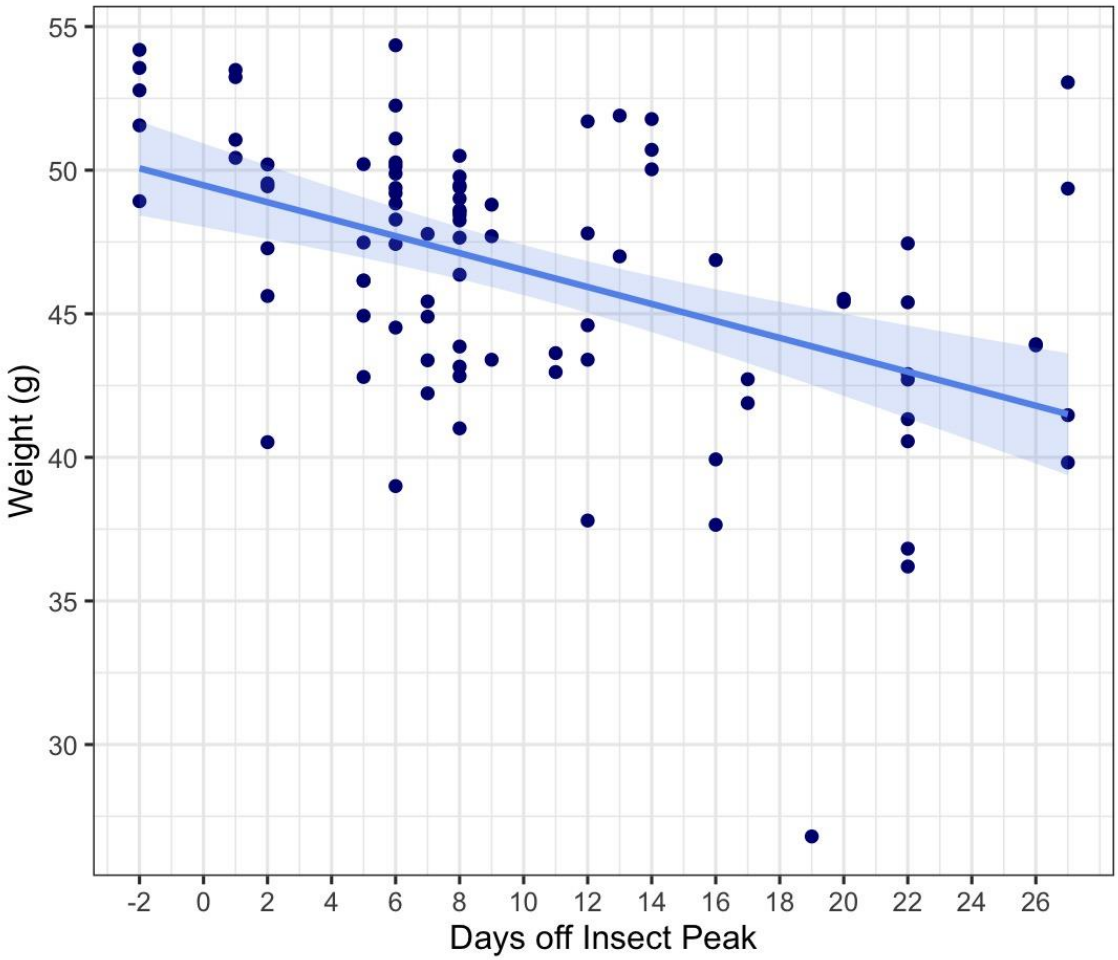

Figure 2. Relationship between Purple Martin nestling (n=91) weight (g) at 10 days old and the number of days between the date of peak aerial insect abundance and the date each nestling reached 10 days old at its respective site. Each point represents an individual nestling, and the solid line shows the fitted linear regression with 95% confidence intervals.

For Model 3, a generalized linear mixed-effects model (Binomial distribution and log link) was used to test whether fledging success (the proportion of young fledged per brood) was associated with insect mismatch, hatch date, brood size, parental age, or parasite presence (Table 3). The proportion of fledged young did not have a statistically significantly effect regarding the timing of peak insect abundance relative to brood timing (Figure 3) or regarding hatch date, brood size, or any parental age combination, which also showed no statistically significant differences in post-hoc comparisons. The presence of parasites also had no measurable effect on fledging proportion. Site and cavity variances were estimated at zero, indicating little variation among sites or cavity.

Table 3. Binomial generalized linear mixed-effects model results for fledging success in Purple Martins, showing estimated effects of insect phenological mismatch, hatch date, brood size, parental age combination, and ectoparasite presence, with site and cavity included as random effects.

Model 3: Fledging success (binomial GLMM)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	1704.024	7002.872	-12021.354	15429.401	0.243	0.808
Timing mismatch (days off peak)	0.062	0.346	-0.616	0.739	0.178	0.859
Hatch date	-0.084	0.346	-0.761	0.594	-0.243	0.808
Brood size	0.217	0.408	-0.582	1.016	0.532	0.595
Parent age: ASY female + SY male (vs ASY:ASY)	-1.201	1.346	-3.840	1.438	-0.892	0.373
Parent age: unknown (vs ASY:ASY)	23.992	570103.326	-1117357.995	1117405.978	0.000	1.000
Parent age: SY female + ASY male (vs ASY:ASY)	-1.146	0.790	-2.695	0.403	-1.450	0.147
Parent age: SY female + SY male (vs ASY:ASY)	-1.010	1.306	-3.570	1.549	-0.774	0.439
Parasites: mites present (vs none)	-0.812	0.818	-2.417	0.792	-0.993	0.321

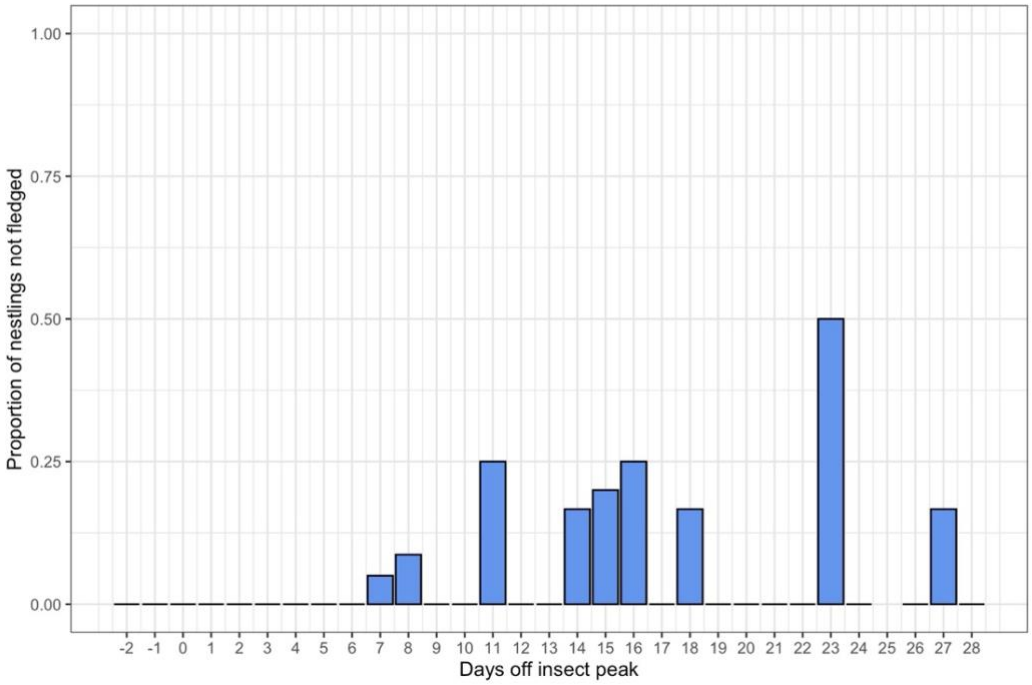

Figure 3. Proportion of Purple Martin nestlings that failed to fledge in relation to the number of days between the date of peak aerial insect abundance and the date each nestling reached 10 days old at its respective site. Bars represent the proportion of nestlings at each day off peak aerial insect abundance that did not fledge.

For Model 4a, three mixed-effects models (Models 4ai-iii) were performed to test whether early nestling growth (day-0 to day-6 weight gain) was influenced by mismatch with peak Diptera (Table 4), Lepidoptera (Table 5), or their combined abundance (Table 6) (Figure 4), while accounting for hatch date, brood size, and parental age. Parasites were not included in these analyses because none were detected on nestlings in this age range. Across all three insect-specific models, nestling growth showed no statistically significant relationship with insect timing mismatch, whether calculated using the combined Diptera–Lepidoptera peak (Figure 4a), the Diptera peak (Figure 4b), or the Lepidoptera peak (Figure 4c). Brood size consistently showed a weak, non-statistically significant effect. Hatch date showed a non-statistically significant effect in the combined-peak model, in the Lepidoptera model, and in the Diptera model with later-hatching broods exhibiting

slower early growth. Parental-age combinations had no measurable influence on nestling early growth, with no parental age category differing significantly from the ASY:ASY reference group in the Diptera, Lepidoptera, or combined prey models. Random effects were the same across all three models, with moderate variation among cavities (variance = 3.20) and sites (variance = 1.29) and most remaining variation occurring at the nestling level.

Table 4. Linear mixed-effects model results for early nestling growth (between day 0 and 6) in Purple Martins, evaluating the effects of synchrony with peak Diptera abundance, hatch date, brood size, and parental age combination, with site and cavity included as random effects.

Model 4a.i: Early growth vs Diptera peak (day 6 – day 0)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	4918.276	10778.557	-27003.110	36839.663	0.456	0.6750
Timing mismatch vs Diptera peak (days)	0.053	0.555	-1.468	1.573	0.095	0.9290
Hatch date	-0.241	0.532	-1.817	1.334	-0.454	0.6770
Brood size	-1.160	0.596	-2.405	0.085	-1.946	0.0662
Parent age: unknown (vs ASY:ASY)	2.055	2.330	-3.077	7.187	0.882	0.3970
Parent age: SY female + ASY male (vs ASY:ASY)	1.112	1.385	-2.021	4.245	0.803	0.4430

Table 5. Linear mixed-effects model results for early nestling growth (between day 0 and 6) in Purple Martins, evaluating the effects of synchrony with peak Lepidoptera abundance, hatch date, brood size, and parental age combination, with site and cavity included as random effects.

Model 4a.ii: Early growth vs Lepidoptera peak (day 6 – day 0)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	4156.145	3341.446	-4922.558	13234.848	1.244	0.2780
Timing mismatch vs Lepidoptera peak (days)	0.015	0.159	-0.422	0.452	0.095	0.9290
Hatch date	-0.204	0.165	-0.651	0.244	-1.236	0.2810
Brood size	-1.160	0.596	-2.406	0.085	-1.946	0.0661
Parent age: unknown (vs ASY:ASY)	2.055	2.331	-3.079	7.190	0.882	0.3970
Parent age: SY female + ASY male (vs ASY:ASY)	1.112	1.385	-2.024	4.248	0.803	0.4430

Table 6. Linear mixed-effects model results for early nestling growth (between day 0 and 6) in Purple Martins, evaluating the effects of synchrony with combined peak Diptera and Lepidoptera abundance, hatch date, brood size, and parental age combination, with site and cavity included as random effects.

Model 4a.iii: Early growth vs Combined DL peak (day 6 – day 0)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	4561.779	7153.366	-16371.532	25495.090	0.638	0.5630
Timing mismatch vs combined Diptera+Lepidoptera peak (days)	0.035	0.370	-0.960	1.030	0.095	0.9290
Hatch date	-0.224	0.353	-1.257	0.809	-0.634	0.5650
Brood size	-1.160	0.596	-2.406	0.085	-1.946	0.0661
Parent age: unknown (vs ASY:ASY)	2.055	2.331	-3.073	7.184	0.882	0.3970
Parent age: SY female + ASY male (vs ASY:ASY)	1.112	1.385	-2.026	4.250	0.803	0.4430

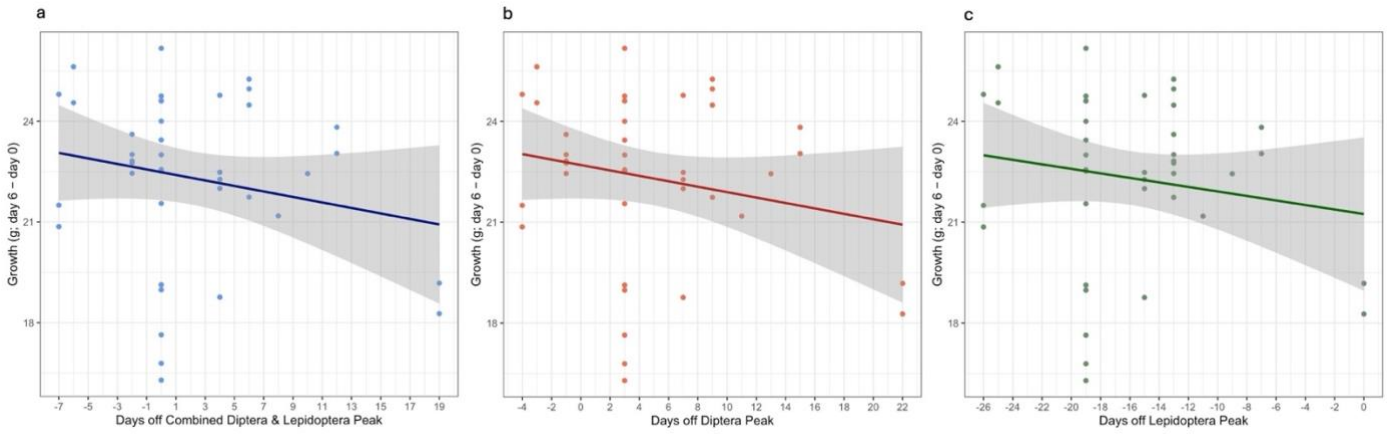

Figure 4. Relationships between Purple Martin nestling (n=40) early growth (weight, in grams, gained from hatch date (0 days old) to 6 days old) and the number of days between the date of aerial insect abundances and the date each nestling reached 3 days old at its respective site. Each point represents an individual nestling, and solid lines show fitted linear regressions with 95% confidence intervals (grey shading). (a) Growth in relation to the number of days between day 3 and the combined Diptera and Lepidoptera peak at each site. (b) Growth in relation to the number of days between day 3 and the Diptera peak at each site (c) Growth in relation to the number of days between day 3 and the Lepidoptera peak at each site.

For Model 4b, three mixed-effects models (Models 4bi-iii) were performed to test whether late-season nestling growth (day-6 to day-18 weight gain) was influenced by mismatch with peak Coleoptera (Table 7), Odonata (Table 8), or their combined abundance (Table 9) (Figure 5), while accounting for brood size, parental age, and parasite presence. Hatch date was excluded from all three models because it was completely collinear with the timing mismatch variables, making the terms statistically indistinguishable. Across all three insect-specific models, nestling growth showed no statistically significant relationship with insect timing mismatch, whether calculated using the combined Coleoptera–Odonata peak (Figure 5a), the Coleoptera peak (Figure 5c), or the Odonata peak (Figure 5b). Brood size consistently showed a non-statistically significant negative effect. Parasite presence also had no measurable effect on nestling growth. Parental-age combinations similarly showed no influence on growth, with no

parental age category differing significantly from the ASY:ASY reference group in the Coleoptera, Odonata, or combined prey models. Random effects were identical across all analyses, indicating moderate variance among cavities (variance = 12.64) and lower but notable variance among sites (variance = 2.67).

Table 7. Linear mixed-effects model results for older nestling growth (between day 6 and 18) in Purple Martins, evaluating the effects of synchrony with peak Coleoptera abundance, hatch date, brood size, and parental age combination, with site and cavity included as random effects.

Model 4b.i: Late growth vs Coleoptera peak (day 18 – day 6)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	39.567	7.008	23.746	55.388	5.646	0.0003
Timing mismatch vs Coleoptera peak (days)	-0.246	0.341	-1.020	0.528	-0.722	0.4890
Brood size	-1.643	1.402	-4.841	1.556	-1.172	0.2730
Parent age: ASY female + SY male (vs ASY:ASY)	3.428	5.843	-10.040	16.896	0.587	0.5740
Parent age: unknown (vs ASY:ASY)	-6.056	4.993	-17.113	5.001	-1.213	0.2520
Parent age: SY female + ASY male (vs ASY:ASY)	1.162	3.296	-6.779	9.102	0.352	0.7360
Parasites: mites present (vs none)	-0.454	1.682	-3.958	3.051	-0.270	0.7900

Table 8. Linear mixed-effects model results for older nestling growth (between day 6 and 18) in Purple Martins, evaluating the effects of synchrony with peak Odonata abundance, hatch date, brood size, and parental age combination, with site and cavity included as random effects.

Model 4b.ii: Late growth vs Odonata peak (day 18 – day 6)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	42.519	10.152	19.371	65.667	4.188	0.00262
Timing mismatch vs Odonata peak (days)	-0.246	0.341	-1.020	0.528	-0.722	0.48900
Brood size	-1.643	1.402	-4.841	1.556	-1.172	0.27300
Parent age: ASY female + SY male (vs ASY:ASY)	3.428	5.843	-10.040	16.896	0.587	0.57400
Parent age: unknown (vs ASY:ASY)	-6.056	4.993	-17.113	5.001	-1.213	0.25200
Parent age: SY female + ASY male (vs ASY:ASY)	1.162	3.296	-6.779	9.102	0.352	0.73600
Parasites: mites present (vs none)	-0.454	1.682	-3.958	3.051	-0.270	0.79000

Table 9. Linear mixed-effects model results for older nestling growth (between day 6 and 18) in Purple Martins, evaluating the effects of synchrony with combined peak Coleoptera and Odonata abundance, hatch date, brood size, and parental age combination, with site and cavity included as random effects.

Model 4b.iii: Late growth vs Combined OC peak (day 18 – day 6)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	41.781	9.298	20.612	62.950	4.494	0.00167
Timing mismatch vs combined Odonata+Coleoptera peak (days)	-0.246	0.341	-1.020	0.528	-0.722	0.48900
Brood size	-1.643	1.402	-4.841	1.556	-1.172	0.27300
Parent age: ASY female + SY male (vs ASY:ASY)	3.428	5.843	-10.040	16.896	0.587	0.57400
Parent age: unknown (vs ASY:ASY)	-6.056	4.993	-17.113	5.001	-1.213	0.25200
Parent age: SY female + ASY male (vs ASY:ASY)	1.162	3.296	-6.779	9.102	0.352	0.73600
Parasites: mites present (vs none)	-0.454	1.682	-3.958	3.051	-0.270	0.79000

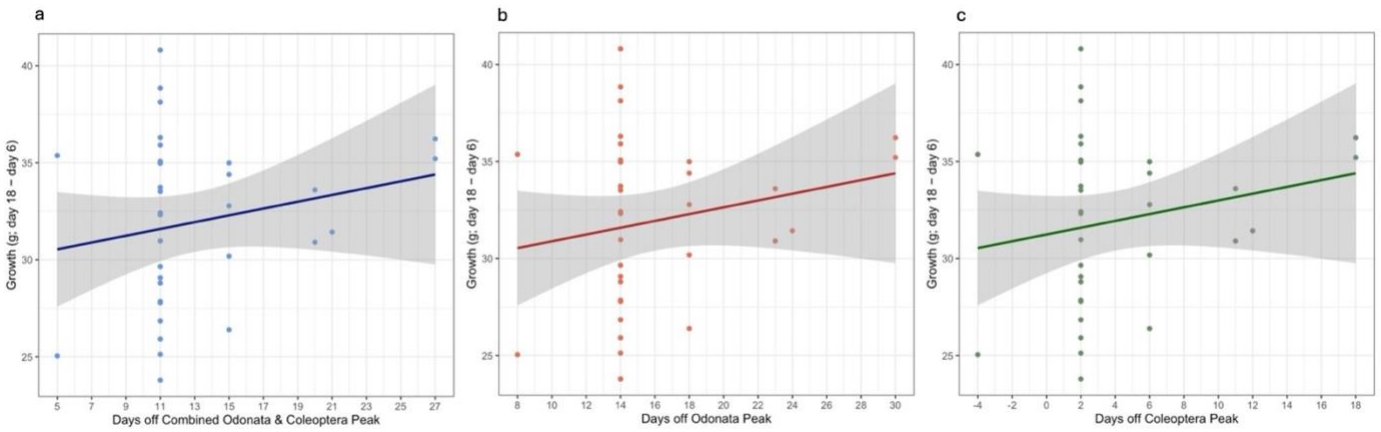

Figure 5. Relationships between Purple Martin nestling (n = 33) late-season growth (weight, in grams, gained from day 6 to day 18) and the number of days between the predicted dates of late-season aerial insect abundance and the date each nestling reached 12 days old at its respective site. Each point represents an individual nestling, and solid lines show fitted linear regressions with 95% confidence intervals (grey shading). (a) Growth in relation to the number of days between day 12 and the combined Odonata and Coleoptera peak at each site. (b) Growth in relation to the number of days between day 12 and the Odonata peak at each site. (c) Growth in relation to the number of days between day 12 and the Coleoptera peak at each site.

For Model 5, a linear mixed-effects model was used to test whether the age at which nestlings reached lower-level adult weight was influenced by the timing mismatch with peak aerial insect abundance, hatch date, brood size, parental age, and parasite presence (Table 10). Timing mismatch with peak insect abundance had a statistically significant effect on the age at which an adult-like weight was reached (Figure 6), indicating that broods further from the seasonal food peak required more days to reach adult-like weight. Hatch date also showed a statistically significant trend, as well as brood size. Parental age combination had a strong influence on the timing at which nestlings reached minimum adult-like weight, with all parental age categories differing significantly from the ASY:ASY reference group. In each case, nestlings raised by younger parental combinations reached adult-like weight at younger ages, with the largest advancement observed for broods raised by second-year females and second-year males. Ectoparasite presence was strongly associated with delayed age at which nestlings reached an adult-like weight. Relative to non-parasitized nestlings, individuals with mites or fleas reached 47.8g at significantly older ages. Nestlings with multiple parasite types experienced even greater delays, particularly those with mites and maggots, mites and fleas, maggots and fleas, and all three combined. In contrast, maggots alone were not statistically significantly associated with the timing of reaching adult-like mass. Random effects indicated some variation among cavities (variance = 1.53) and no site-level differences.

Table 10. Linear mixed-effects model results for the age at which Purple Martin nestlings reached minimum adult-like body mass (≥ 47.8 g), evaluating the effects of insect phenological mismatch, hatch date, brood size, parental age combination, and ectoparasite presence, with site and cavity included as random effects.

Model 5: Age at minimum adult weight (≥ 47.8 g)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	13095.045	2987.804	7200.889	18989.200	4.383	1.95e-05
Timing mismatch (days off peak)	0.764	0.153	0.462	1.066	4.985	1.41e-06
Hatch date	-0.646	0.147	-0.937	-0.355	-4.381	1.96e-05
Brood size	0.892	0.167	0.562	1.223	5.335	2.83e-07
Parent age: ASY female + SY male (vs ASY:ASY)	0.134	0.691	-1.230	1.498	0.194	8.46e-01
Parent age: unknown (vs ASY:ASY)	1.036	0.814	-0.569	2.641	1.273	2.05e-01
Parent age: SY female + ASY male (vs ASY:ASY)	-0.248	0.344	-0.928	0.432	-0.719	4.73e-01
Parent age: SY female + SY male (vs ASY:ASY)	-3.504	1.051	-5.622	-1.387	-3.335	1.73e-03
Parasites: mites present (vs none)	1.965	0.342	1.290	2.639	5.749	3.66e-08
Parasites: fleas present (vs none)	3.845	1.764	0.361	7.328	2.180	3.07e-02
Parasites: maggots present (vs none)	0.683	0.761	-0.819	2.186	0.897	3.71e-01
Parasites: mites + maggots present (vs none)	1.645	0.397	0.861	2.428	4.142	5.22e-05
Parasites: mites + fleas present (vs none)	2.352	0.593	1.180	3.524	3.963	1.11e-04
Parasites: maggots + fleas present (vs none)	3.621	1.344	0.952	6.291	2.695	8.39e-03
Parasites: mite + maggots + fleas present (vs none)	4.456	1.049	2.387	6.525	4.249	3.39e-05

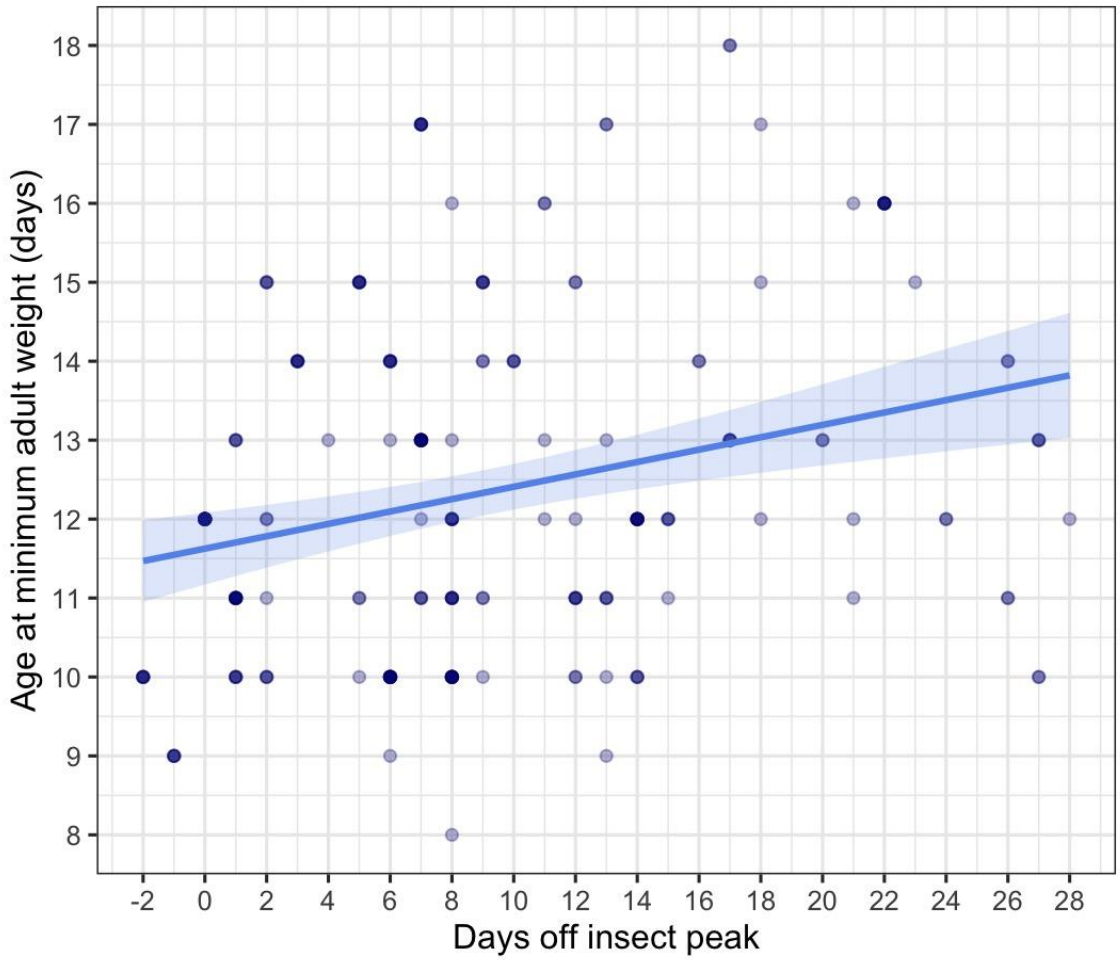

Figure 6. Relationship between the age in days at which Purple Martin nestlings (n = 202) reached minimum adult weight (47.8 g) and the number of days between the date of peak aerial insect abundance and the date each nestling reached 10 days old at its respective site. The solid line shows the fitted linear regression with 95% confidence intervals. Point shading represents the number of nestlings sharing the same age at adult-like weight and days off peak (darker = more).

For Model 6, a generalized linear mixed-effects model with a Gamma error distribution and log link was used to test whether nestling period length (days from hatching to fledging) was influenced by phenological mismatch with peak insect abundance, hatch date, brood size, parental age, or ectoparasite presence (Table 11). Nestling period was not statistically significantly associated with the timing of peak insect abundance relative to brood timing (Figure 7) or hatch date. However, brood size had a strong negative effect, indicating that larger broods fledged earlier on average. Several parental age combinations were also found to be statistically significant; compared to ASY:ASY pairs, nestlings from SY:SY pairs had significantly longer nestling periods, while mixed-age combinations (ASY:SY and SY:ASY) showed smaller but significant positive effects. Parasite effects were generally weak, though the presence of maggots was associated with statistically significantly longer nestling periods. Other parasite types showed no measurable influence. Random effects for site (variance = 0.0013) and cavity (variance = 0.015) explained minimal variation, suggesting that most differences in nestling duration arose from brood-level rather than spatial effects.

Table 11. Gamma generalized linear mixed-effects model results for the length of the nestling period (days from hatch to fledge), evaluating the effects of insect phenological mismatch, hatch date, brood size, parental age combination, and ectoparasite presence, with site and cavity included as random effects.

Model 6: Nestling period length (days)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	3.295	0.030	3.237	3.354	110.413	0.00e+00
Timing mismatch (days off peak)	-0.178	0.104	-0.382	0.027	-1.703	8.86e-02
Hatch date	0.164	0.105	-0.042	0.370	1.558	1.19e-01
Brood size	-0.030	0.002	-0.034	-0.025	-12.767	2.50e-37
Parent age: ASY female + SY male (vs ASY:ASY)	0.053	0.012	0.029	0.076	4.368	1.26e-05
Parent age: unknown (vs ASY:ASY)	0.233	0.012	0.210	0.256	19.720	1.44e-86
Parent age: SY female + ASY male (vs ASY:ASY)	0.026	0.006	0.015	0.037	4.686	2.78e-06
Parent age: SY female + SY male (vs ASY:ASY)	0.462	0.015	0.433	0.491	31.460	3.09e-217
Parasites: mites present (vs none)	-0.003	0.003	-0.009	0.002	-1.157	2.47e-01
Parasites: fleas present (vs none)	0.015	0.018	-0.020	0.050	0.835	4.04e-01
Parasites: maggots present (vs none)	0.032	0.014	0.004	0.060	2.270	2.32e-02
Parasites: mites + maggots present (vs none)	-0.011	0.006	-0.022	0.000	-1.955	5.06e-02
Parasites: mites + fleas present (vs none)	0.005	0.010	-0.015	0.026	0.522	6.02e-01
Parasites: maggots + fleas present (vs none)	0.005	0.019	-0.032	0.043	0.273	7.85e-01
Parasites: mite + maggots + fleas present (vs none)	0.005	0.013	-0.021	0.031	0.387	6.99e-01

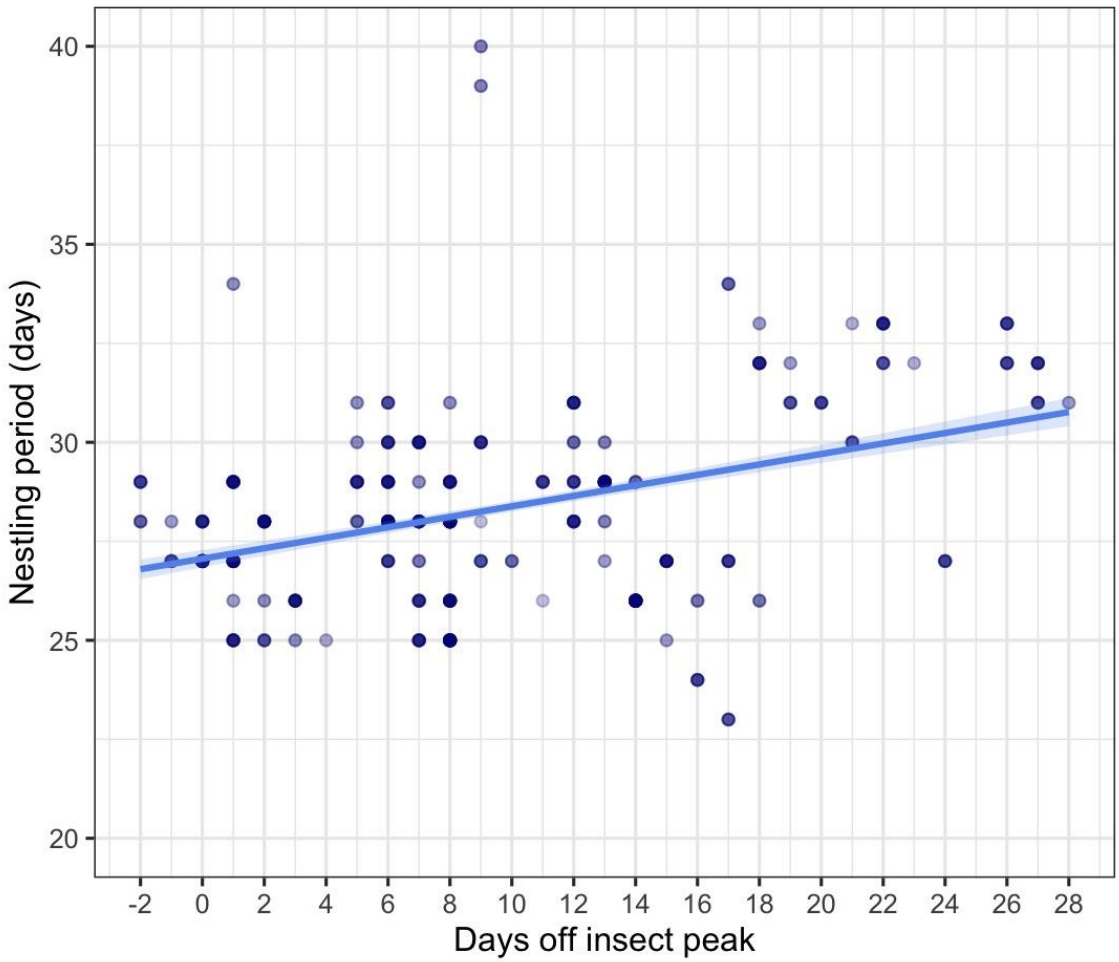

Figure 7. Relationship between the duration of the nestling period (days) in Purple Martin nestlings (n = 202) and the number of days between the date of peak aerial insect abundance and the date each nestling reached 10 days old at its respective site. The solid line shows the fitted linear regression with 95% confidence intervals. Point shading represents the number of nestlings sharing the same nestling period length and days off peak.

Impact of Days Above Sufficient Food Threshold on Growth

For model 7, a linear mixed-effects model was used to test whether nestling growth was influenced by the number of days during days 0-19 of the nestling phase when aerial insect abundance was over 30% of peak abundance, hatch date, brood size, parental age, and parasite presence (Table 12). Days above the 30% insect threshold did not have a statistically significant relationship with growth (Figure 8). Hatch date and brood size showed no statistically significant effects on growth either. Growth did not differ among parental-age pairings, and the presence of parasites had no detectable effect. Random-effect variances were modest (Cavity = 6.41; Site = 0.09), indicating limited variation among nests and minimal variation among sites.

Table 12. Linear mixed-effects model results for Purple Martin nestling growth (day 2–10) in relation to days above the 30% aerial insect abundance threshold, hatch date, brood size, parental age combination, and ectoparasite presence, with site and cavity included as random effects.

Model 8: Growth (day 10-day 2)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	-577.024	8636.995	-30691.501	29537.453	-0.067	0.952
Days above 30% aerial insect threshold	2.225	1.348	-2.533	6.983	1.651	0.213
Hatch date	0.030	0.426	-1.455	1.515	0.071	0.949
Brood size	-0.951	1.554	-5.397	3.495	-0.612	0.576
Parent age: SY female + ASY male (vs ASY:ASY)	1.049	3.326	-8.055	10.152	0.315	0.768
Parent age: SY female + SY male (vs ASY:ASY)	3.302	7.925	-22.878	29.481	0.417	0.707
Parasites: mites present (vs none)	0.259	2.776	-5.640	6.159	0.093	0.927

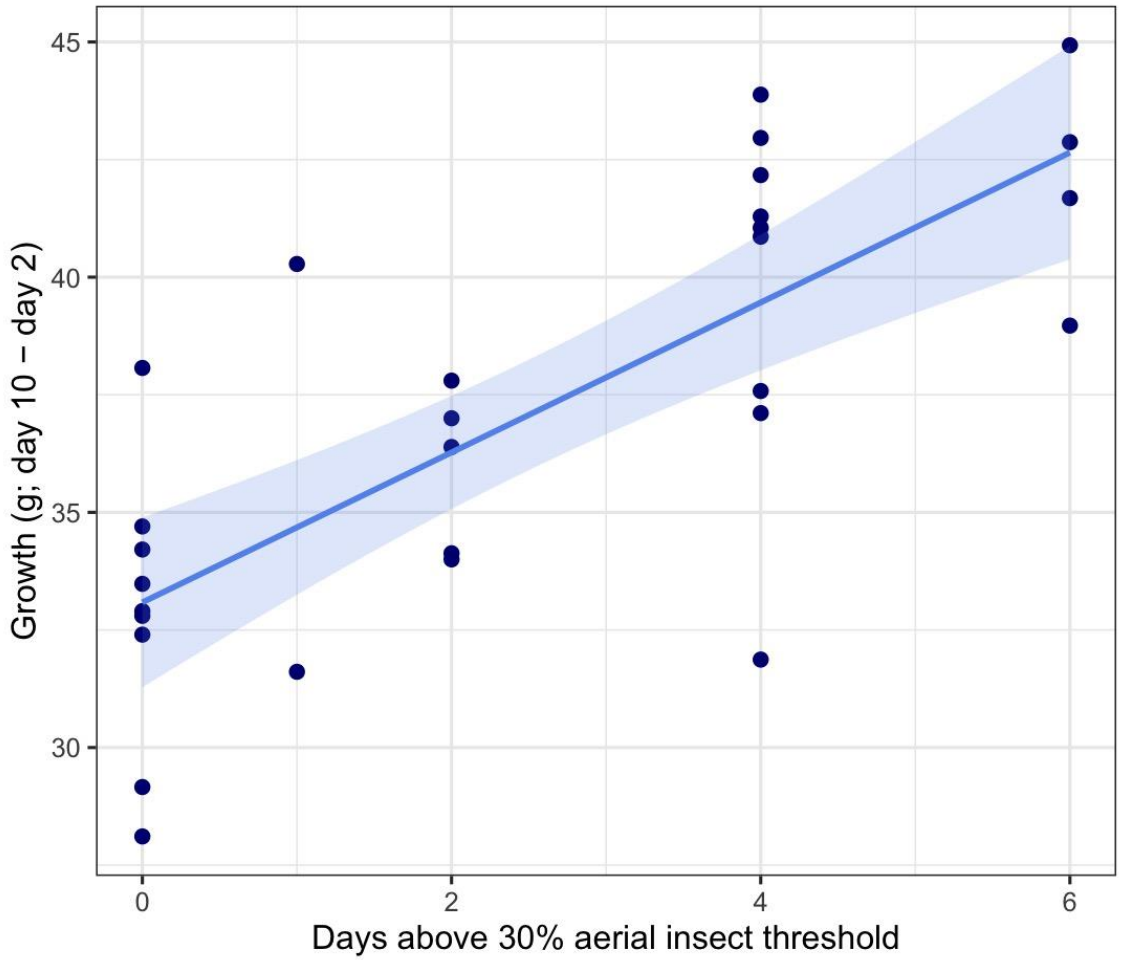

Figure 8. Relationship between Purple Martin nestling (n=29) growth (weight, in grams, gained from 2 days old to 10 days old) and the number of days above 30% of peak aerial insect abundance at its respective site. Each point represents an individual nestling, and the solid line shows the fitted linear regression with 95% confidence intervals.

For model 8, a linear mixed-effects model was used to examine whether nestling weight at day 10 was influenced by the number of days above 30% of peak aerial insect abundance, hatch date, brood size, parental age, and parasite presence (Table 13). Weight showed no statistically significant relationship with days above 30% peak insect abundance (Figure 9). Later hatch dates were associated with significantly lower nestling weight, and larger broods had significantly lower nestling weight as well. Parental age had mixed effects: only chicks from SY:SY parents were significantly heavier. Parasites had

no statistically significant effect on nestling weight (all $p > 0.05$). Random-effect variance was mostly attributable to cavities (11.74), with negligible site-level variation.

Table 13. Linear mixed-effects model results for nestling body weight at day 10 in Purple Martins, in relation to days above the 30% aerial insect abundance threshold, hatch date, brood size, parental age combination, and ectoparasite presence, with site and cavity included as random effects.

Model 9: Day-10 weight						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	6706.799	2819.660	744.403	12669.195	2.379	0.02980
Days above 30% aerial insect threshold	1.190	0.628	-0.085	2.465	1.896	0.06630
Hatch date	-0.328	0.139	-0.622	-0.035	-2.364	0.03060
Brood size	-2.617	0.921	-4.516	-0.719	-2.842	0.00889
Parent age: ASY female + SY male (vs ASY:ASY)	-3.115	2.520	-8.175	1.944	-1.236	0.22200
Parent age: unknown (vs ASY:ASY)	1.172	3.912	-6.637	8.982	0.300	0.76500
Parent age: SY female + ASY male (vs ASY:ASY)	1.655	1.414	-1.173	4.482	1.170	0.24700
Parent age: SY female + SY male (vs ASY:ASY)	8.165	2.858	2.469	13.861	2.857	0.00557
Parasites: mites present (vs none)	-1.568	1.100	-3.763	0.626	-1.425	0.15900
Parasites: fleas present (vs none)	-1.032	3.127	-7.279	5.215	-0.330	0.74200
Parasites: maggots present (vs none)	-2.861	4.297	-11.868	6.146	-0.666	0.51400
Parasites: mites + maggots present (vs none)	1.930	1.611	-1.287	5.146	1.198	0.23500
Parasites: mites + fleas present (vs none)	2.676	2.889	-3.114	8.467	0.926	0.35800
Parasites: maggots + fleas present (vs none)	-0.621	3.068	-6.771	5.529	-0.202	0.84000
Parasites: mite + maggots + fleas present (vs none)	-5.332	3.127	-11.579	0.915	-1.705	0.09300

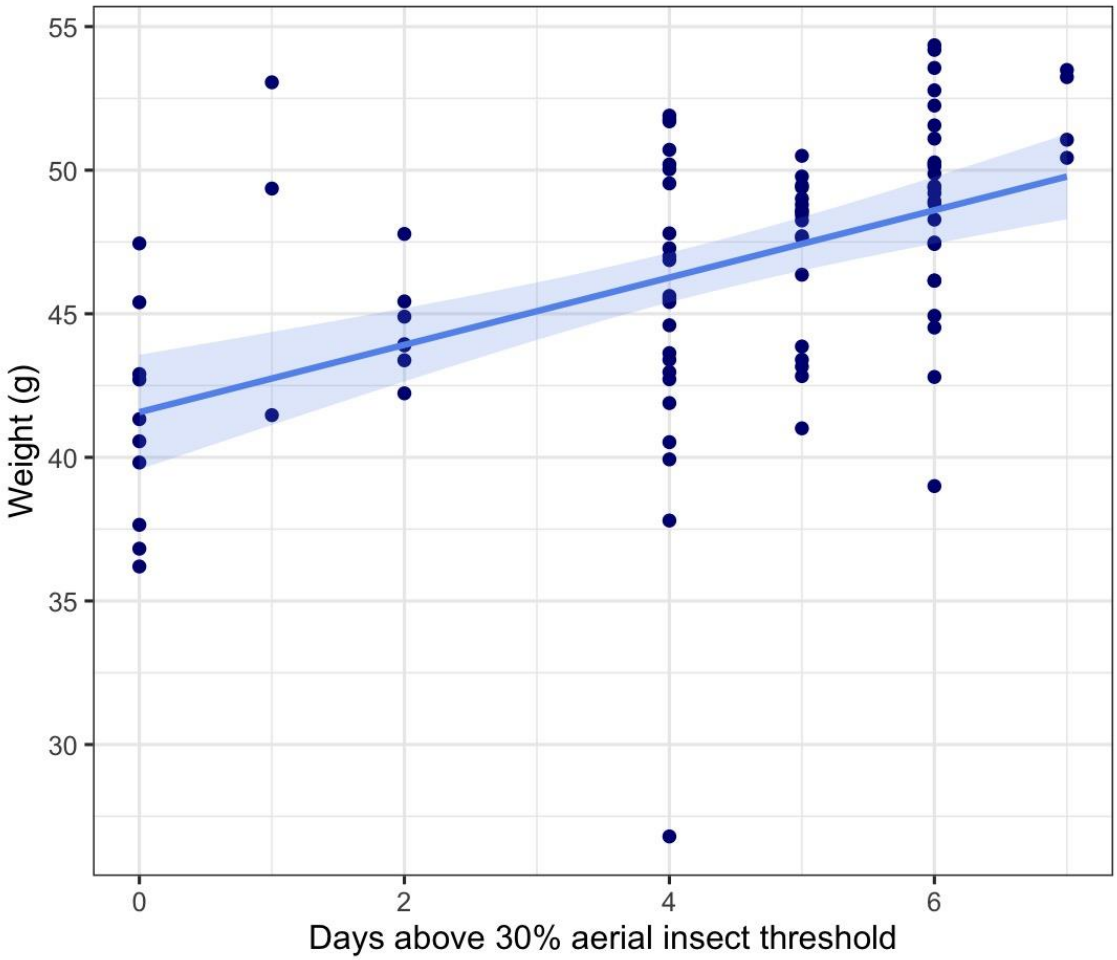

Figure 9. Relationship between Purple Martin nestling (n=91) weight (g) at 10 days old and the number of days above 30% of peak aerial insect abundance at its respective site. Each point represents an individual nestling, and the solid line shows the fitted linear regression with 95% confidence intervals.

For model 9, a generalized linear mixed-effects model (binomial, logit link) was used to test whether the proportion of fledged young was influenced by the number of days above 30% peak aerial insect abundance, hatch date, brood size, parental age, and parasite presence (Table 14). When no days exceeded 30% of peak insect abundance, the likelihood that all nestlings fledged decreased significantly (Figure 10). Hatch date and brood size had no statistically significant effects on fledging success. Parental age combinations had no statistical significant influence. The presence of mites had no

statistically significant effect on fledging. Random-effect variance was zero at both cavity and site levels, indicating minimal variation among nests or locations.

Table 14. Binomial generalized linear mixed-effects model results for fledging success in Purple Martins in relation to days above the 30% aerial insect abundance threshold, hatch date, brood size, parental age combination, and ectoparasite presence, with site and cavity included as random effects.

Model 10: Fledging success (binomial GLMM)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	-2301.526	1700.312	-5634.075	1031.024	-1.354	0.1760
Days above 30% aerial insect threshold	0.935	0.364	0.222	1.648	2.571	0.0101
Hatch date	0.113	0.084	-0.051	0.278	1.354	0.1760
Brood size	0.765	0.521	-0.256	1.787	1.468	0.1420
Parent age: ASY female + SY male (vs ASY:ASY)	-1.112	1.329	-3.718	1.493	-0.837	0.4030
Parent age: unknown (vs ASY:ASY)	22.731	1114937.543	-2185214.699	2185260.160	0.000	1.0000
Parent age: SY female + ASY male (vs ASY:ASY)	-0.533	0.839	-2.176	1.111	-0.635	0.5250
Parent age: SY female + SY male (vs ASY:ASY)	0.522	1.325	-2.074	3.118	0.394	0.6940
Parasites: mites present (vs none)	-1.735	0.980	-3.657	0.186	-1.770	0.0767

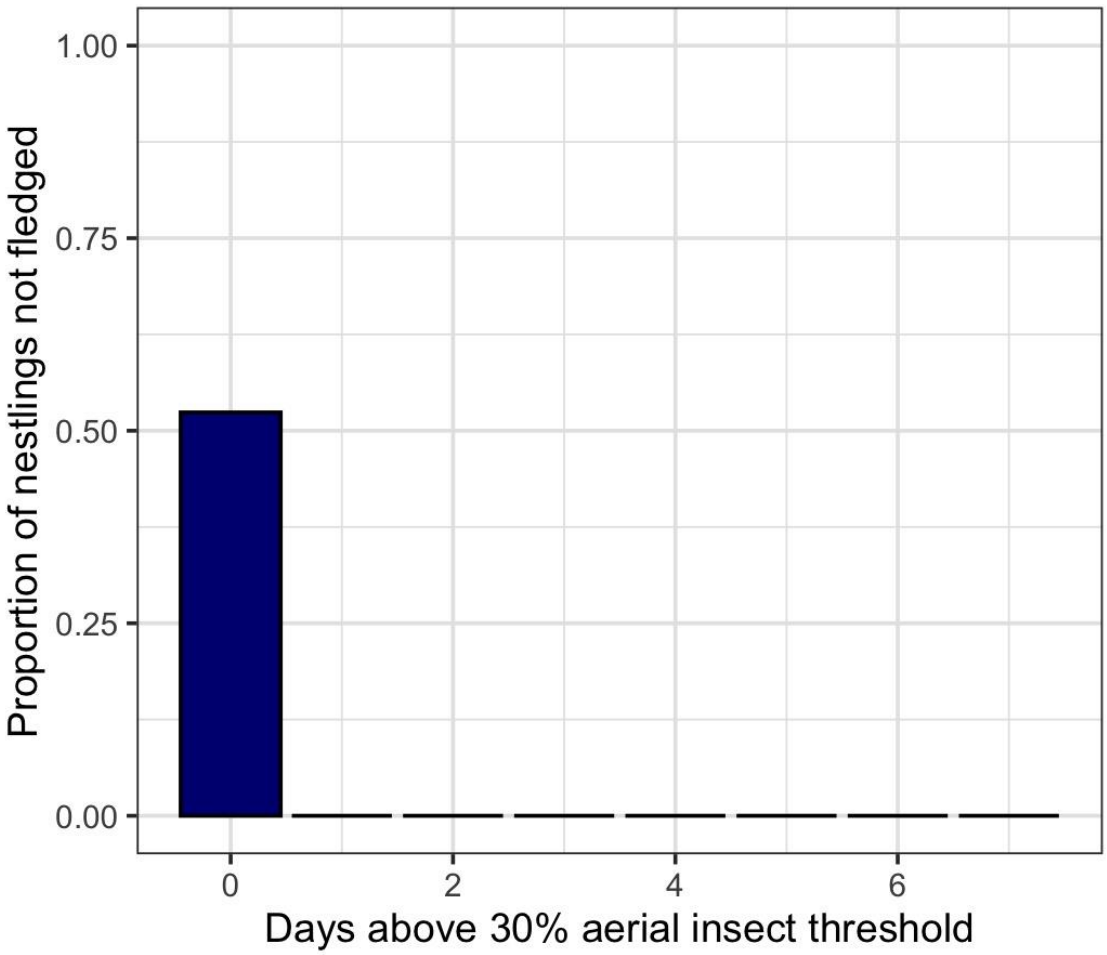

Figure 10. Proportion of Purple Martin nestlings that failed to fledge in relation to the number of days above 30% of peak aerial insect abundance at its respective site. Bars represent the proportion of nestlings at each day above 30% of peak aerial insect abundance that did not fledge.

For model 10, a generalized linear mixed-effects model with a Gamma distribution and log link was used to test whether the age at which nestlings reached lower-level adult-like weight (≥ 47.8 g) was influenced by days above 30% peak aerial insect abundance, hatch date, brood size, parental age, and parasite presence (Table 15). More days above 30% peak aerial insect abundance significantly reduced the age at which nestling reached an adult-like weight (Figure 11). Hatch date showed no statistically significant trend, while larger broods significantly delayed the age at which adult-like weight was achieved.

Parental age effects were mostly not statistically significant, except nestlings from SY:SY parents which reached adult-like weight earlier. Parasite presence had a consistent cumulative effect on plateau age. Parasites significantly delayed the age at which nestlings reached adult-like weight. Mite infestations lead to adult-like weights being reached at older ages, as did flea infestations and maggot infestations. Co-infestations increased these delays, with maggot and mite combinations, mite and flea combinations, maggot and flea combinations, and infestations with all three parasite types all significantly postponing the age at which nestlings reached adult-like weight. Random-effect variance was small at the cavity level (0.00468), indicating minimal nest-to-nest variation.

Table 15. Gamma generalized linear mixed-effects model results for the age at which Purple Martin nestlings reached minimum adult-like body mass (≥ 47.8 g), in relation to days above the 30% aerial insect abundance threshold, hatch date, brood size, parental age combination, and ectoparasite presence, with site and cavity included as random effects.

Model 11: Age at minimum adult weight (≥ 47.8 g) (gamma GLMM)						
Fixed effect	Estimate	SE	CI low	CI high	Test stat	p
Intercept	2.422	0.035	2.354	2.490	69.884	0.00e+00
Days above 30% aerial insect threshold	-0.038	0.016	-0.070	-0.006	-2.329	1.99e-02
Hatch date	0.035	0.019	-0.002	0.072	1.848	6.46e-02
Brood size	0.081	0.014	0.054	0.108	5.920	3.21e-09
Parent age: ASY female + SY male (vs ASY:ASY)	0.074	0.054	-0.031	0.180	1.387	1.65e-01
Parent age: unknown (vs ASY:ASY)	0.092	0.067	-0.039	0.222	1.379	1.68e-01
Parent age: SY female + ASY male (vs ASY:ASY)	-0.013	0.029	-0.070	0.044	-0.456	6.48e-01
Parent age: SY female + SY male (vs ASY:ASY)	-0.254	0.091	-0.432	-0.076	-2.794	5.21e-03
Parasites: mites present (vs none)	0.160	0.028	0.105	0.215	5.688	1.29e-08
Parasites: fleas present (vs none)	0.343	0.143	0.063	0.623	2.403	1.63e-02
Parasites: maggots present (vs none)	0.166	0.057	0.055	0.276	2.926	3.43e-03
Parasites: mites + maggots present (vs none)	0.151	0.032	0.088	0.214	4.703	2.56e-06
Parasites: mites + fleas present (vs none)	0.209	0.049	0.113	0.304	4.288	1.80e-05
Parasites: maggots + fleas present (vs none)	0.329	0.112	0.110	0.547	2.947	3.21e-03
Parasites: mite + maggots + fleas present (vs none)	0.348	0.085	0.181	0.515	4.075	4.61e-05

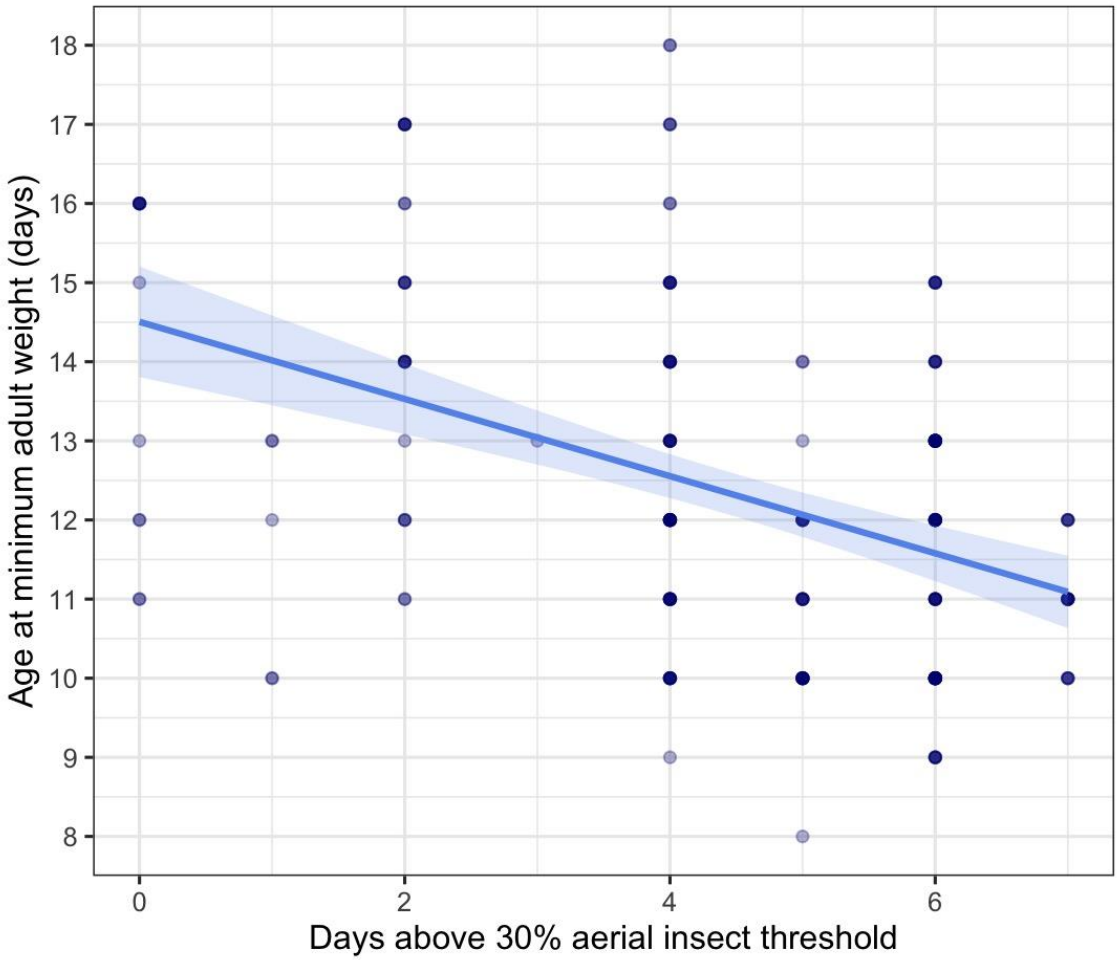

Figure 11. Relationship between the age in days at which Purple Martin nestlings (n = 202) reached minimum adult weight (47.8 g) and the number of above 30% of peak aerial insect abundance at its respective site. The solid line shows the fitted linear regression with 95% confidence intervals. Point shading represents the number of nestlings sharing the same age at adult-like weight and days above 30% of peak aerial insect abundance.

Discussion:

Phenological mismatch between the timing of nestling development and seasonal peaks in prey abundance has been widely studied as a mechanism linking climate-driven shifts in food phenology to variation in reproductive success and offspring performance in many birds (Both et al. 2009b; Dunn et al. 2011). Such mismatches can influence multiple aspects of development, from growth rates and body condition to survival and the timing

of key developmental milestones. This study examined how phenological mismatch, alongside other secondary factors such as brood size, parasite type and presence, parental age, and hatch date influence nestling development in Purple Martins. Mismatch with peak aerial insect abundance significantly delayed the age at which nestlings reached an adult-like weight by approximately 0.76 days per day of mismatch, such that a nestling 15 days off peak abundance would be approximately 11 days delayed in reaching an adult-like weight. The number of days above the 30% aerial insect threshold also significantly influenced developmental timing, with more days above the threshold reducing the age at which adult-like weight was reached by approximately 0.038 days per additional day above 30% abundance. These delays suggests that developmental timing reflects seasonal food conditions more clearly than short-term growth measurements do. Fledge success appeared to be significantly more dependent on the number of days with sufficient food supply and not how far off peak abundance they were. In contrast, phenological mismatch with peak aerial insect abundance and limited exposure to days above the 30% threshold had weak or inconsistent effects on nestling growth at younger ages, day-10 body weight, fledging success, and nestling period.

Mismatch with peak aerial insect abundance, as well as the number of days above the sufficient aerial insect abundance threshold (30% of peak abundance), had a clear effect on the longer-term timing of nestling Purple Martin development. These results seem to partially support the food-limitation hypothesis, testing whether nestling development would be affected by mismatch with local aerial insect abundance. Nestlings that developed further from the seasonal aerial insect peak, or which had fewer days above the 30% threshold, reached an adult-like weight later than nestlings that developed closer to the peak or with more days above the threshold. Notably, this delay occurred

despite mismatch having no consistent negative effect on short-term growth metrics such as early growth rate or day-10 body weight. Accordingly, while we did not observe strong evidence for starvation due to reduced provisioning as was predicted under the food-limitation hypothesis, the delay in reaching adult-like weight suggests partial support for the prediction that mismatch imposes cumulative energetic constraints. This suggests that phenological mismatch influenced the timing of developmental milestones rather than causing major reductions in nestling weight. Delays in nestlings reaching key developmental thresholds may therefore have fitness consequences even when short-term growth appears resilient (Hegyi and Török 2007). Compensatory growth can mask early physiological constraints (Hegyi and Török 2007) yet still lead to delays in reaching key life stages, and several species show reduced juvenile survival when development is delayed (Naef-Daenzer et al. 2001; Saino et al. 2012). Similar patterns occur in migratory birds where delayed timing of key developmental stages or poor body conditions at the time of fledging lowers first-year survival of these juvenile birds, including purple martins specifically (Tarof et al. 2011; Williams et al. 2024). Delays in reaching adult-like weight may similarly increase exposure to nest-related risks and reduce flexibility at fledging, particularly if environmental conditions deteriorate late in the nestling period (Raja-aho et al. 2017; Freeman et al. 2020). This delay is also consistent with the predation-exposure hypothesis, which predicts that mismatch may increase predation vulnerability by prolonging the nestling period. For migratory species, if nestlings successfully fledge, such delays may carry over to influence post-fledging survival and recruitment, even when short-term growth or body mass appears relatively unaffected (Raja-aho et al. 2017; Freeman et al. 2020).

In this context, nestling metrics such as growth between day-2 and day-10 post-hatch in Purple Martins may fail to capture biologically meaningful delays in development, as nestlings at this age are typically not yet at an adult-like weight and are not yet capable of fledging. The timing of reaching adult-like weight may therefore be a more meaningful measure of the relationship between phenological mismatch and fitness outcomes, since nestlings that develop closer to the insect peak may be in a better position to fledge rapidly if conditions deteriorate, such as the loss of a parent or the presence of a predator at the nest. In Purple Martins, nest failure can occur when nestlings cannot fledge to escape in the presence of a predator (Allen and Nice 1952). For Purple Martins in Manitoba predation of nestlings typically occurs by nocturnal predators such as Great-Horned Owls (*Bubo virginianus*) or by hawks and falcons who prey on nestlings and adults, with the loss of a parent also increasing the risk of premature death for altricial nestlings (Allen and Nice 1952; Ray 2014). Under such scenarios, reaching a fledge-ready state earlier may reduce the exposure time to nest-related predation risks, an advantage that would not necessarily be detected by metrics such as the number of young fledged. Although parental attendance (i.e. time at the nest) was not directly measured in this study, the developmental delays observed here are consistent with the idea that mismatched broods may be exposed to greater nest-based risk, both by remaining in the nest longer and by experiencing reduced parental attendance as foraging demands increase. If such advantages operate over longer timescales, selection may continue to favour nestlings that align more closely with their seasonal food peak or whose nestling period aligns with more days above a sufficient aerial insect abundance threshold, even if these benefits are subtle. These parallels suggest that while Purple Martins may be able to offset short-term variation in food availability, they cannot fully avoid the cumulative

developmental costs when nestlings develop further away from the seasonal aerial insect peak or experience fewer days of sufficient prey availability.

In line with this cumulative effect, longer exposure to sufficient aerial insect availability also played an important role in shaping fledging success. Consistent with the food-limitation hypothesis, where it was predicted that reduced access to sufficient prey would increase mortality, the number of days during the nestling period when aerial insect abundance exceeded 30% of peak abundance significantly increased the likelihood that a nestling would fledge successfully. Notably, all nestlings that failed to fledge experienced zero days above this threshold, underscoring the potential importance of longer access to sufficient aerial insect levels. This finding suggests that fledging success in Purple Martins may depend less on precise synchrony with peak aerial insect abundance and more on whether nestlings experience a sufficiently long window of moderate-to-high prey availability. Even if nestlings are several days off the aerial insect peak, they may still be able to fledge successfully, as long as aerial insect availability remains above a sufficient threshold. Similar threshold-based patterns have been documented in other systems. Saalfeld et al. (2019) showed that shorebird chicks only achieved average growth when invertebrate biomass exceeded a defined sufficiency level during critical developmental windows, and reduced growth in early life is closely tied to lower survival probabilities. Similarly, McKinnon et al. (2012) identified an “ideal” hatch window based on a high-food threshold and found that chicks hatching outside this period exhibited reduced growth rates, a pattern likely to carry fitness costs beyond early development. Together, these studies suggest that surpassing biologically meaningful food thresholds may be essential not only for growth but for successful fledging and recruitment, as poor growth means that successful fledging is unlikely. Previous work on Purple Martins in

Manitoba found that greater mismatch between a nestlings peak energetic demand (day 10 post-hatch) and peak Odonate abundance significantly reduced the number of fledged young, with a 27-day mismatch lowering average fledging output by approximately one nestling per brood (Olson-Brissaud 2025). These results somewhat contrast the finding in this study, that fledge success was not significantly related to mismatch with peak aerial insect abundance but was related to days over the sufficient aerial insect threshold. One possible explanation as to why these results somewhat conflict is that in previous Manitoba studies, aerial insect abundance may have declined more gradually after the seasonal peak, whereas during the summer of this study smoke from nearby wildfires may have sharply reduced insect activity more sporadically than in previous seasons. Had insect abundance declined more similarly to past years, peak mismatch might also have shown significant effects on fledging alongside days above the threshold. Additionally, Olson-Brissaud (2025) quantified mismatch relative to peak Odonate abundance specifically, whereas this study considered total aerial insect abundance; differences in focal prey taxa may therefore contribute to the differing patterns observed. Overall, these results suggest stronger support for cumulative energetic constraints than for acute starvation, while remaining broadly consistent with both the food-limitation and predation-exposure hypotheses. Rather than operating through immediate growth suppression, phenological mismatch in this system appears to influence developmental timing and survival through delayed readiness and prolonged exposure to nest-based risks.

While mismatch from peak aerial insect abundance or days above the sufficient aerial insect availability threshold shows significance in both fledge success and reaching an adult-like weight, its effects on short-term growth appear less consistent. Similarly, mismatch with individual aerial insect groups was not significantly related to growth

metrics. The generally weak effects of phenological mismatch on nestling growth found in this study suggest that several ecological and behavioural factors may buffer or reduce the detectability of mismatch effects when growth is assessed using short-term, weight-based metrics. Purple Martins are highly mobile aerial foragers and may partially buffer nestlings against reduced prey availability by increasing foraging effort or switching prey types, thereby maintaining nestling weight even when development occurs away from peak aerial insect abundance (Allen and Nice 1952; Imlay et al. 2017; Dunoyer et al. 2024). In addition, insect availability varies day to day, so nestlings may be greatly mismatched with peak prey availability yet still experience enough days above the sufficient aerial insect threshold, allowing moderate mismatches to fall within a functional range of prey availability (Dunn et al. 2011; Imlay et al. 2017). However, simply exceeding this threshold does not guarantee that all energetic demands are met, so even moderate mismatches can impose cumulative constraints, which may obscure short-term growth responses when using threshold as a predictor. In contrast, the significant delay in reaching adult-like weight suggests that phenological mismatch may instead impose cumulative energetic constraints that only emerge later on in nestling development. This interpretation aligns with site-specific findings reported for purple martins by Olson-Brissaud (2025), where stronger phenological mismatch was associated with reduced fledging success. Together, these findings suggest that mismatch effects in this system may operate less through acute starvation, as predicted under the food-limitation hypothesis, and more through delayed developmental readiness and reduced tolerance to suboptimal food conditions. Such mechanisms could explain why fledging success declines under mismatch even when early growth metrics remain relatively stable, potentially reflecting increased parental foraging effort, reduced nest attendance, or

cumulative energetic constraints. These mechanisms are not fully captured by short-term growth or body weight metrics and highlight that factors beyond just aerial insect availability may play a central role in shaping nestling development.

One such factor, besides aerial insect availability, that affects Purple Martin nestling development is brood size, as it was one of the strongest predictors across models. Larger broods weighed less at growth benchmarks, grew slower, and took longer to reach adult-like weight. These results align with widespread evidence of resource distribution and competition in aerial insectivore nestlings (Walsh 1978; Cucco and Malacarne 1996; Teglhøj 2017). It has been found that Purple Martin parents do not consistently compensate for larger brood sizes by increasing the biomass of food delivered per feeding trip, based on analyses of the mean mass of prey items collected during provisioning visits (Walsh 1978). Instead, Walsh (1978) noted that parents may increase provisioning effort through more frequent feeding trips as brood size increases. However, when food availability is low, this behavioural response may be insufficient to offset reduced prey availability, resulting in increased competition among nestlings (Walsh 1978), a pattern consistent with the slower growth rates observed in this study for nestlings from larger broods. Previous work on House Martins (*Delichon urbica*) and Barn Swallows (*Hirundo rustica*) have also shown a link between brood size and reduced or slower nestling growth (Bryant 1975; Mainwaring et al. 2009). Brood size also strongly influenced the nestling period. Larger broods fledged earlier on average, a pattern seen in other cavity nesters and one that has been interpreted as competition-driven acceleration or parental forcing (Mainwaring et al. 2009; Kouba et al. 2015). However, in some species, such as the Pallid Swift, larger broods took longer to fledge (Cucco and Malacarne 1996). This contrast shows that the relationship between brood size and

fledging time may be species-specific. In Purple Martins, nestlings may fledge prematurely when broods are crowded because strong competition for limited resources pushes them to leave the nest earlier, even though their slower growth would normally predict later fledging.

In addition to brood size, hatch date was a significant predictor in a subset of models, specifically those examining early body mass (days 0–6) relative to peaks in Diptera and Lepidoptera abundance. However, hatch date was not consistently significant across all models and appeared to capture finer-scale variation among nestlings. Hatch date likely integrates several underlying processes, including seasonal changes in prey availability and variation in parental quality. Earlier breeders are often higher-quality individuals that arrive sooner and may provision more effectively (Morton and Derrickson 1990; Tarof et al. 2011). Additionally, the timing of a brood relative to the seasonal insect peak differs in effect, as food availability increases leading up to the peak but declines afterwards, meaning broods before the peak experience improving foraging conditions while those after face progressively reduced prey abundance. The significance of hatch date in early growth models therefore suggests that both parental quality and seasonal dynamics shape initial provisioning conditions, particularly in relation to taxon-specific insect peaks. Early-season broods may benefit from more favourable prey phenology during the first days post-hatch, when growth rates are highly sensitive to resource availability. In contrast, its effect in the age-at-adult-like-weight model conflicted with the mismatch metric, indicating potential overlap between seasonal timing and phenological alignment. This suggests that hatch date may partly capture broader seasonal environmental variation that is not fully explained by peak-based mismatch measures alone. Together, these results indicate that hatch date influences early developmental

processes, but its effects are context-dependent and do not uniformly translate into differences in fledging success.

In addition to seasonal effects, variation in parental age also shaped reproductive outcomes, although its effects in this study did not fully align with the typical expectation that After Second Year (ASY) birds outperform Second Year (SY) breeders. In Purple Martins, ASY adults generally arrive earlier, secure higher-quality nesting cavities, provision at higher rates, and produce fledglings in better body condition, whereas SY-SY pairings are often associated with reduced fledging success and lower offspring condition (Williams et al. 2024; Olson-Brissaud 2025). However, in this study, SY-SY pairs occasionally performed as well as or better than mixed-age or ASY pairs. However, it is important to note that in this study SY-SY pairs were relatively rare, with most nestling having parents of mixed-age (one ASY and one SY) or ASY-ASY pairs, which could have skewed the observed patterns. It is possible that due to the limited SY-SY pairs observed in this study, quality filtering among younger breeders occurred, where SY individuals that successfully bred may have represented a particularly high-quality subset. Environmental variability in aerial insect availability may have reduced the typical advantage of early ASY arrival and high-quality cavity selection. These results suggest that parental age effects can be context-dependent and sensitive to both environmental conditions and the relative abundance of different age-class pairings.

In addition to parental characteristics, parasite presence also had measurable effects on Purple Martin nestling development in this study, consistent with findings in other cavity-nesting aerial insectivores. Parasites, including mites, fleas, and blowfly larvae, may have created developmental costs by depleting nestlings' nutritional resources and diverting nestlings' energy toward costly immune responses. In our dataset,

parasitized nestlings experienced delays of 2-4.5 days in reaching adult-like weight, and maggot infestations prolonged the nestling period significantly, indicating that both growth rate and developmental timing can be affected by parasite presence. These results align with previous work done on Barn Swallows, House Sparrows, and House Wrens showing that parasites can reduce nestling weight and slow overall development, sometimes forcing earlier fledging in poor condition or delaying fledging due to slowed growth (Moller 1990; Weddle 2000; Mainwaring et al. 2009; Dugas and Border 2022). The severity of these effects is likely influenced by environmental context, including food availability and seasonal timing. High-quality or abundant prey can allow parents to buffer nestlings against the costs of parasitism through increased provisioning, whereas late-season broods or those experiencing limited food may be more vulnerable to parasite effects (Allen and Nice 1952; Moller 1990; Stansberry et al. 2025). In this study, parasite presence was not significantly associated with phenological mismatch with peak insect abundance, hatch date, or brood size, suggesting that infestation patterns were largely independent of these temporal or demographic factors. Nonetheless, parasite exposure still had measurable effects on nestling development in many models, indicating that even when occurrence is not linked to degree of mismatch, parasites can influence growth and developmental outcomes in Purple Martin nestlings. Brood size may also interact with parasitism, as competition for limited food can amplify the energetic costs of parasite exposure, contributing to slower growth and delayed developmental milestones, even when parasite occurrence is independent of mismatch, hatch date, or brood size (Allen and Nice 1952; Stierhoff et al. 2024; Stansberry et al. 2025). Behavioural or physiological strategies, such as nest lining with green leaves as a natural repellent, growth plasticity prioritizing feather development as barn swallows do, or selective parental investment in

higher-quality nestlings, may mitigate some effects but cannot fully eliminate the cumulative stress imposed by parasites (Gwinner et al. 2000; Mainwaring et al. 2009; Williams et al. 2020). Overall, these findings highlight that parasites act as a significant secondary factor influencing nestling development in Purple Martins, affecting both the timing of reaching adult-like weight and the duration of the nestling period, and may compound the energetic constraints imposed by suboptimal food availability, ultimately influencing fledging success.

Overall, the results of this study suggest that phenological mismatch in Purple Martins may influence nestling development primarily through cumulative developmental effects rather than through immediate reductions in nestling growth. Although early growth metrics often appeared resilient to variation in insect availability, mismatch with peak aerial insect abundance and reduced exposure to days above the sufficient aerial insect abundance threshold delayed the timing at which nestlings reached adult-like weight and increased the likelihood of fledging failure. These findings provide partial support for the food-limitation hypothesis, not necessarily through acute starvation or strong reductions in body mass, but through subtle energetic constraints that accumulate across the nestling period and delay developmental readiness. In addition, delayed development may also increase exposure to nest-related risks, which is consistent with elements of the predation-exposure hypothesis. Together, these patterns suggest that phenological mismatch may affect nestling success in this system through multiple interacting pathways, including cumulative energetic limitation and prolonged exposure to environmental risks during the nestling stage.

More broadly, these findings contribute to a growing body of work demonstrating that the effects of phenological mismatch are often expressed through subtle changes in

offspring development rather than immediate reproductive failure (Mccarty and Winkler 1999; Tarof et al. 2011; Raja-aho et al. 2017; Olson-Brissaud 2025). In aerial insectivore systems in particular, variation in insect abundance across the breeding season can influence nestling growth trajectories, the timing of developmental milestones, and the condition of fledglings at departure (Quinney et al. 1986; Williams et al. 2024; Olson-Brissaud 2025). Previous work has showed how phenological mismatch can affect fledging success of Purple Martins in Manitoba (Olson-Brissaud 2025), and in this study I showed how that may have occurred through delayed developmental timing and reduced exposure to days above the sufficient aerial insect abundance threshold. These developmental differences may carry important downstream consequences, as fledgling size and condition can influence post fledging survival, recruitment, and ultimately population dynamics (Tarof et al. 2011; Williams et al. 2024). As a result, even modest delays in development associated with breeding outside the seasonal resource peak may have lasting effects that extend beyond the nesting period. Understanding these dynamics is especially important in the context of ongoing climate change, which is altering the timing and magnitude of resource availability across many ecosystems (Both and Visser 2001; Both et al. 2009b; Pérez et al. 2016; Saalfeld et al. 2019). Shifts in insect phenology may increasingly throw off the timing of breeding for many aerial insectivore species from the seasonal peaks in food abundance that historically supported successful reproduction (Both and Visser 2001; Saino et al. 2012; Olson-Brissaud 2025). At larger scales, such mismatches have been linked to population declines, as species that fail to advance breeding in step with their prey experience reduced reproductive success over time (Both et al. 2009a). By linking variation in insect availability to nestling growth and

developmental timing, this study helps clarify the mechanisms through which phenological mismatch may contribute to the widespread population declines observed in aerial insectivores, where underlying drivers remain poorly understood (Both et al. 2009b; Nebel et al. 2010). The developmental delays observed in this study highlight how conditions experienced during the nestling period may carry over into reduced post-fledging survival and, ultimately, contribute to population declines through decreased recruitment (Naef-Daenzer et al. 2001; Both and Visser 2001; Tarof et al. 2011; Freeman et al. 2020). Future research could build on these findings by tracking fledglings from broods that experienced different degrees of phenological mismatch to determine whether early developmental differences persist into migration, survival, and eventual recruitment to the breeding population. Integrating this knowledge with continued research on aerial insect availability, parental provisioning behaviour, and nestling development will be critical for predicting how changing seasonal dynamics may shape the future of these declining bird populations.

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Supplemental Tables:

Supplemental Table 1. Summary of models used to test hypotheses regarding Purple Martin nestling growth, developmental timing, and survival. For each model, the response variable, model type, fixed effects, and random effects are shown.

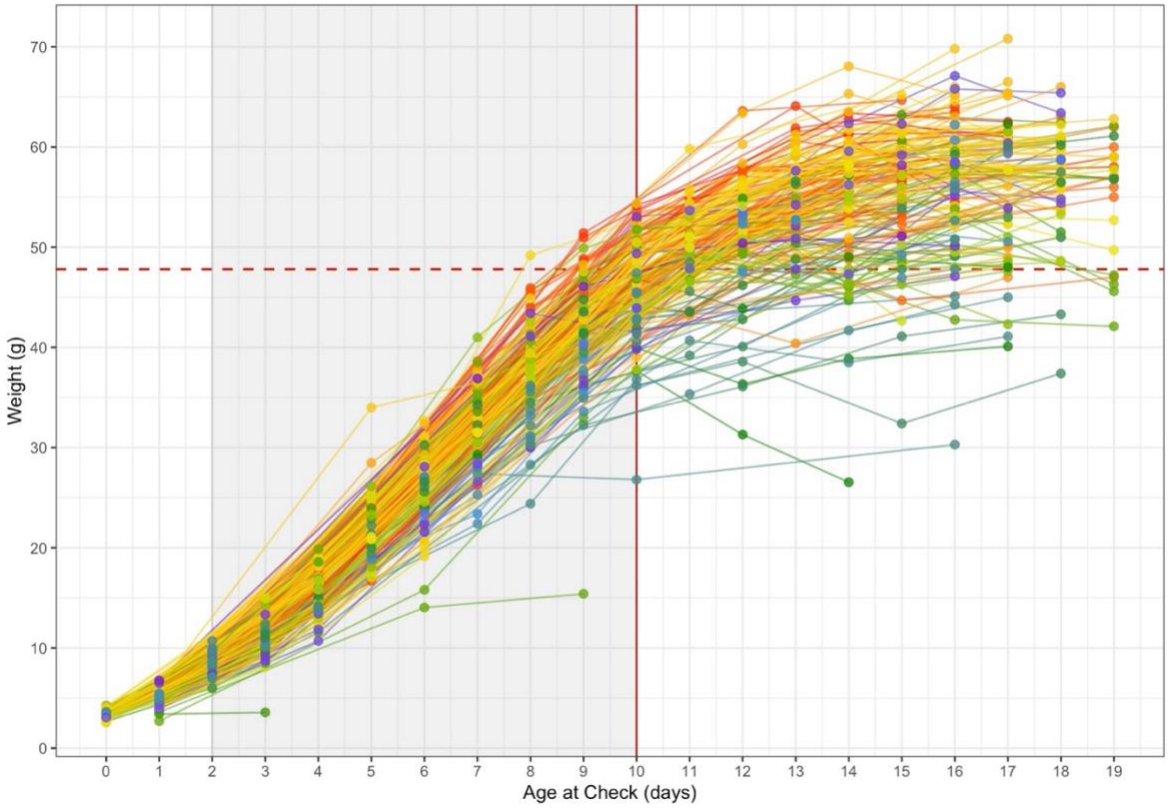
Model	Response Variable	Model Type	Fixed Effects	Random Effects
1	Nestling body weight trajectories (days 2–10)	LMM	Insect mismatch, hatch date, brood size, parental age combination, ectoparasite presence/type	Site, Nest ID, Nestling ID
2	Body weight at day 10	LMM	Insect mismatch, hatch date, brood size, parental age combination, ectoparasite presence/type	Site, Nest ID, Nestling ID
3	Proportion non-fledged young per brood	Binomial GLMM	Insect mismatch, hatch date, brood size, parental age combination, ectoparasite presence/type	Site, Nest ID
4a.i	Early growth (days 0–6)	LMM	Synchrony with Diptera peak, hatch date, brood size, parental age	Site, Nest ID, Nestling ID
4a.ii	Early growth (days 0–6)	LMM	Synchrony with Lepidoptera peak, hatch date, brood size, parental age	Site, Nest ID, Nestling ID
4a.iii	Early growth (days 0–6)	LMM	Synchrony with Diptera + Lepidoptera peak, hatch date, brood size, parental age	Site, Nest ID, Nestling ID
4b.i	Late growth (days 6–18)	LMM	Synchrony with Coleoptera peak, hatch date, brood size, parental age	Site, Nest ID, Nestling ID
4b.ii	Late growth (days 6–18)	LMM	Synchrony with Odonata peak, hatch date, brood size, parental age	Site, Nest ID, Nestling ID

4b.iii	Late growth (days 6–18)	LMM	Synchrony with Coleoptera + Odonata peak, hatch date, brood size, parental age	Site, Nest ID, Nestling ID
5	Age at adult like weight (≥47.8 g)	LMM	Insect mismatch, hatch date, brood size, parental age, ectoparasite presence/type	Site, Nest ID
6	Nestling period length (hatch to fledge)	Gamma GLMM	Insect mismatch, hatch date, brood size, parental age, ectoparasite presence/type	Site, Nest ID
7	Growth (day 10 – day 2 mass)	LMM	Days above 30% insect threshold, hatch date, brood size, parental age combination, ectoparasite presence/type	Site, Nest ID
8	Body weight at day 10	LMM	Days above 30% threshold, hatch date, brood size, parental age combination, ectoparasite presence/type	Site, Nest ID
9	Proportion non-fledged young per brood	Binomial GLMM	Days above 30% threshold, hatch date, brood size, parental age combination, ectoparasite presence/type	Site, Nest ID
10	Age at adult like weight (≥47.8 g)	Gamma GLMM	Days above 30% threshold, hatch date, brood size, parental age combination, ectoparasite presence/type	Nest ID

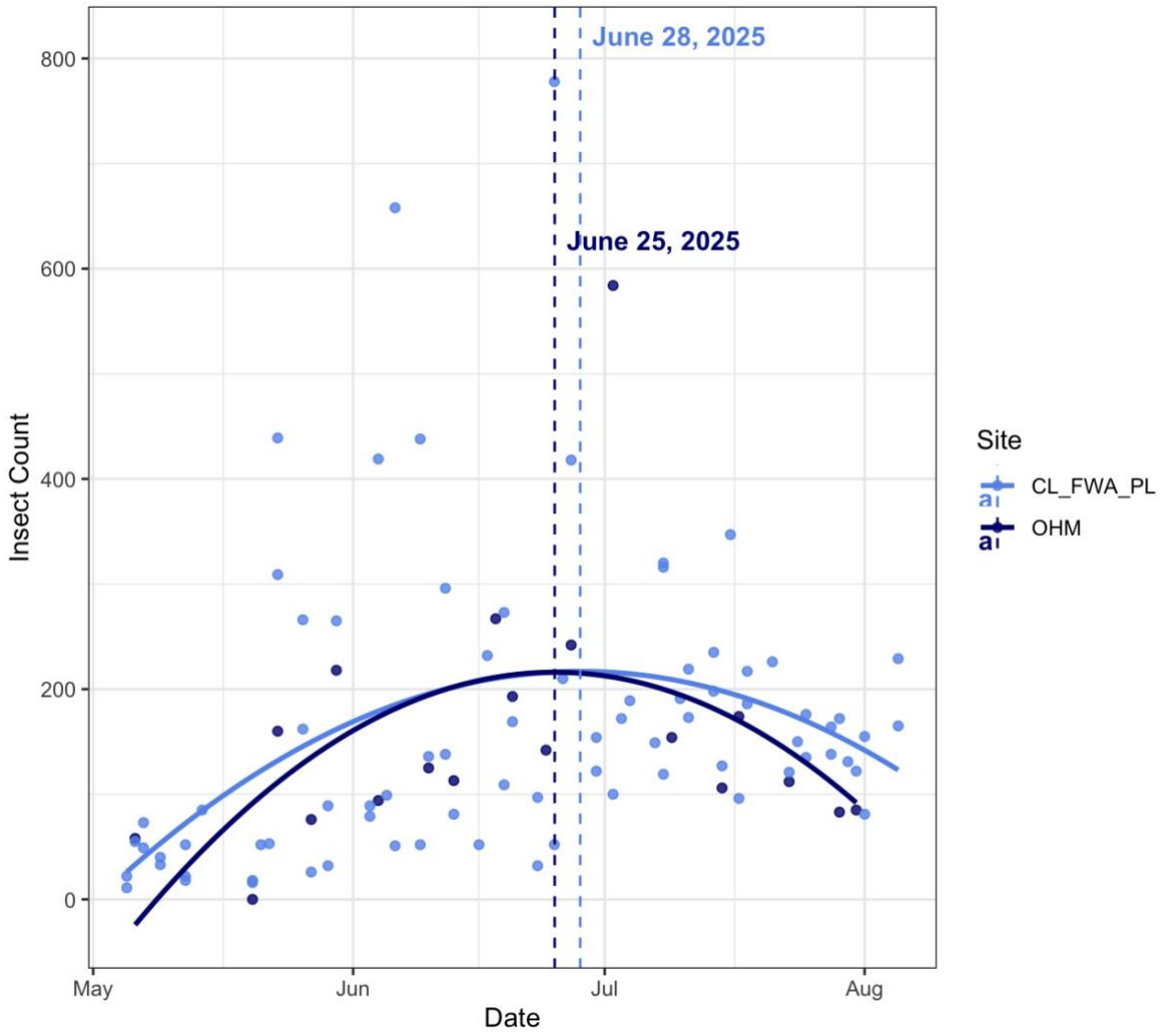
Supplemental Figures:



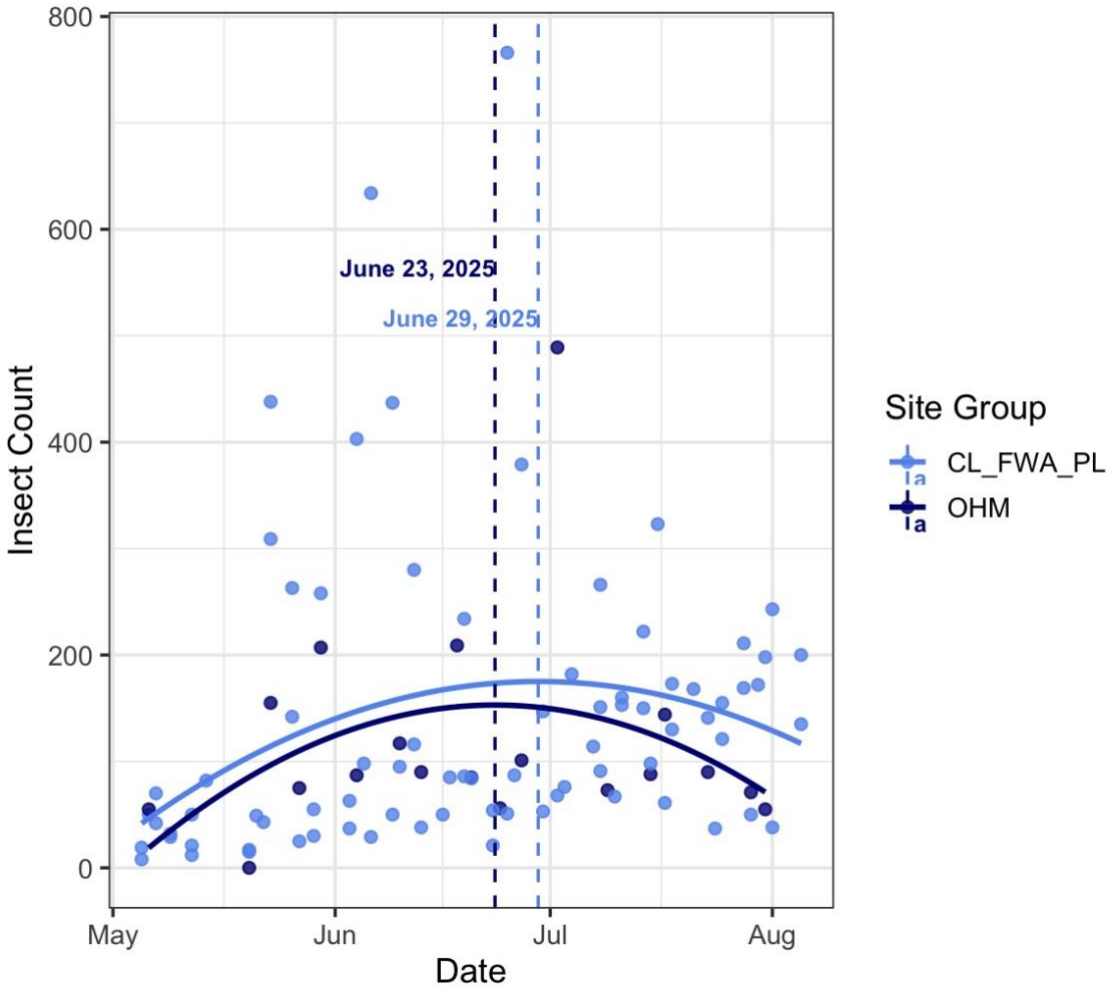
Supplemental Figure 1. Purple Martin nestling (~15 days post-hatch) being weighed on a Smart Weigh ZIP300 digital scale (accurate to ±0.01 g), placed in a clean baking cup for containment.



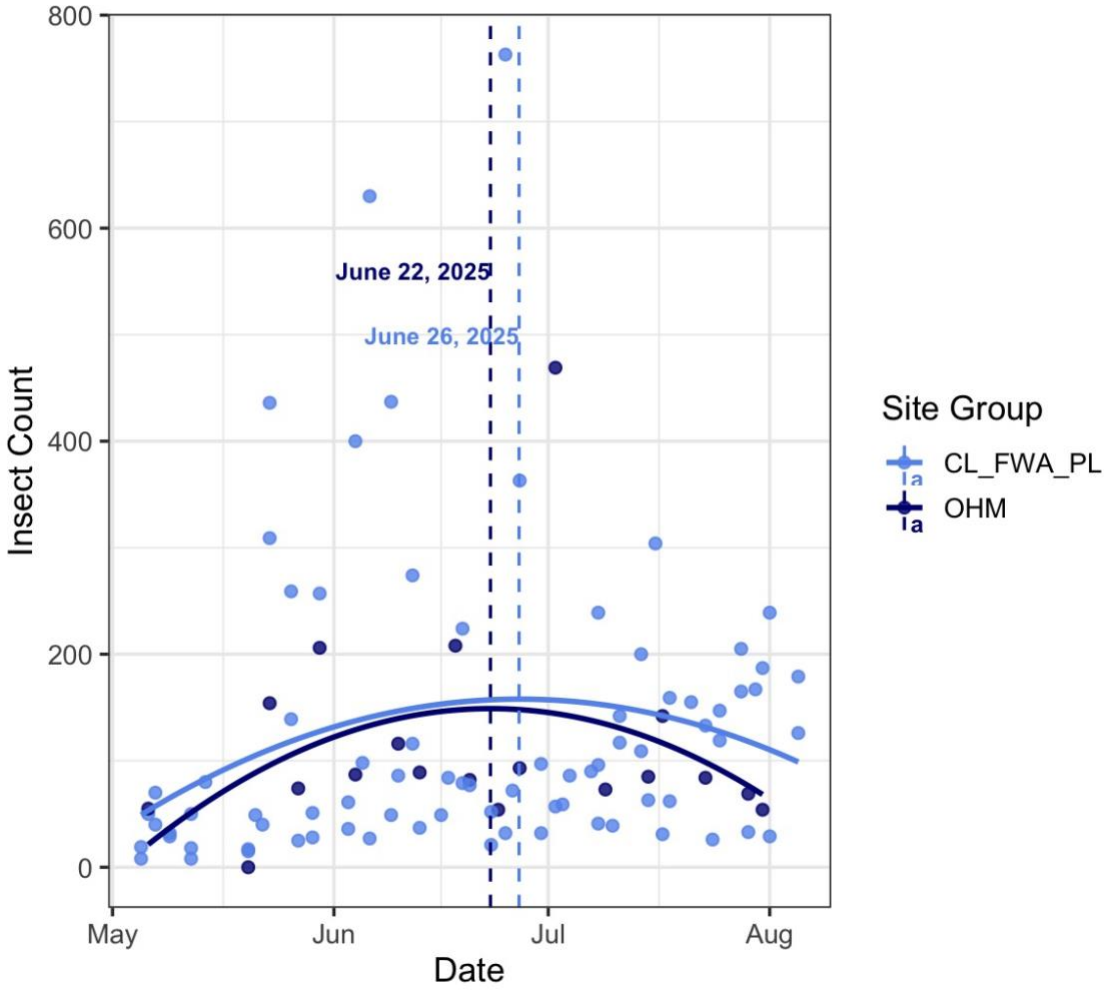
Supplemental Figure 2. Growth curves of all nestling (n=219) weights (g) from 0-19 days old, coloured by relative hatch date (order follows the rainbow sequence, red = early season, purple = late season). Solid red vertical line shows day 10 post-hatch (nestlings peak energetic demand). Red dashed horizontal line shows minimum adult weight (47.8g). Light grey box shows nestlings period of rapid growth (weight gain between ages of 2 and 10 days post-hatch).



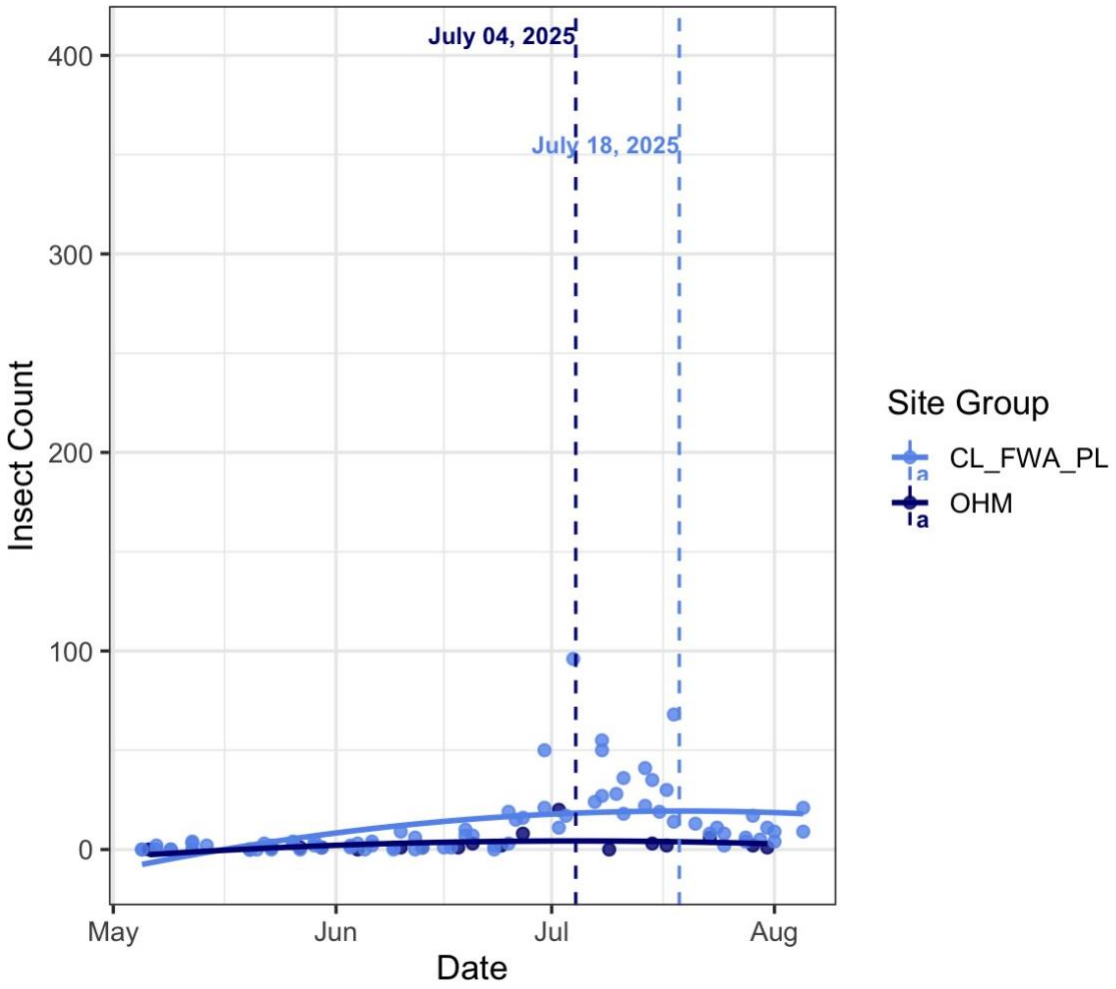
Supplemental Figure 3. Aerial insect counts over the breeding season with a quadratic fit. Vertical lines indicate dates of peak abundance. Light blue points represent the Southern sites (CL, FWA, and PL), and dark blue points represent Oak Hammock Marsh (OHM).



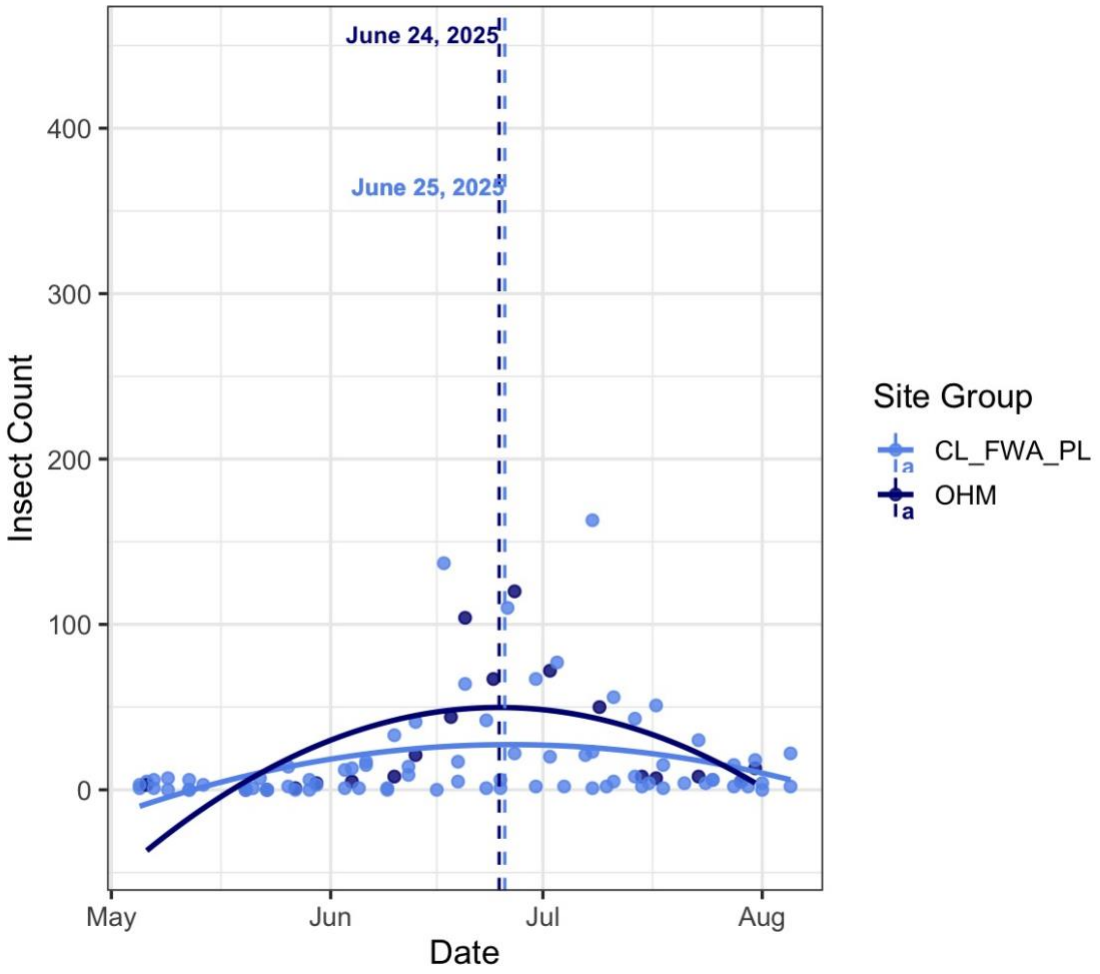
Supplemental Figure 4. Combined Diptera and Lepidoptera counts over the breeding season with a quadratic fit. Vertical lines indicate dates of peak abundance. Light blue points represent the Southern sites (CL, FWA, and PL), and dark blue points represent Oak Hammock Marsh (OHM).



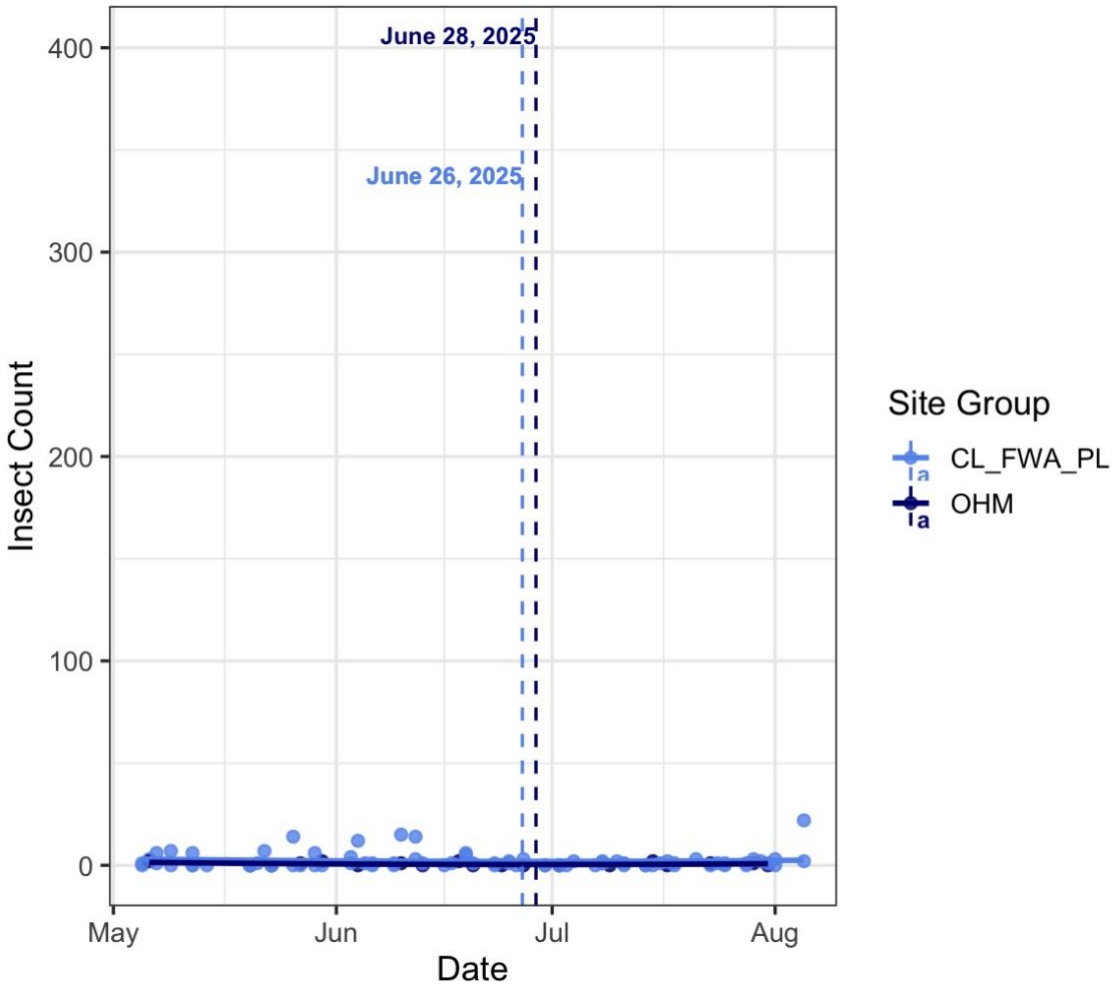
Supplemental Figure 5. Diptera counts over the breeding season with a quadratic fit. Vertical lines indicate dates of peak abundance. Light blue points represent the Southern sites (CL, FWA, and PL), and dark blue points represent Oak Hammock Marsh (OHM).



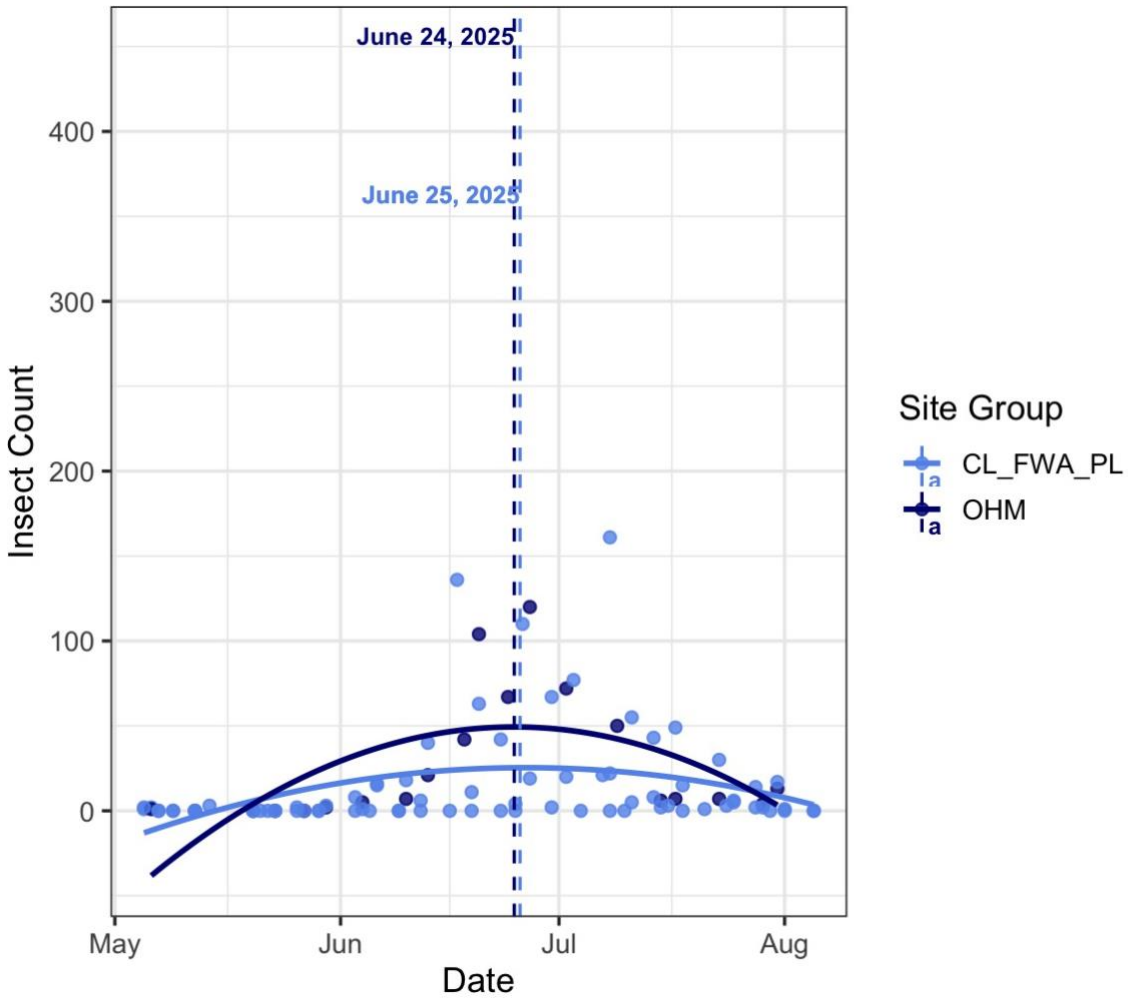
Supplemental Figure 6. Lepidoptera counts over the breeding season with a quadratic fit. Vertical lines indicate dates of peak abundance. Light blue points represent the Southern sites (CL, FWA, and PL), and dark blue points represent Oak Hammock Marsh (OHM).



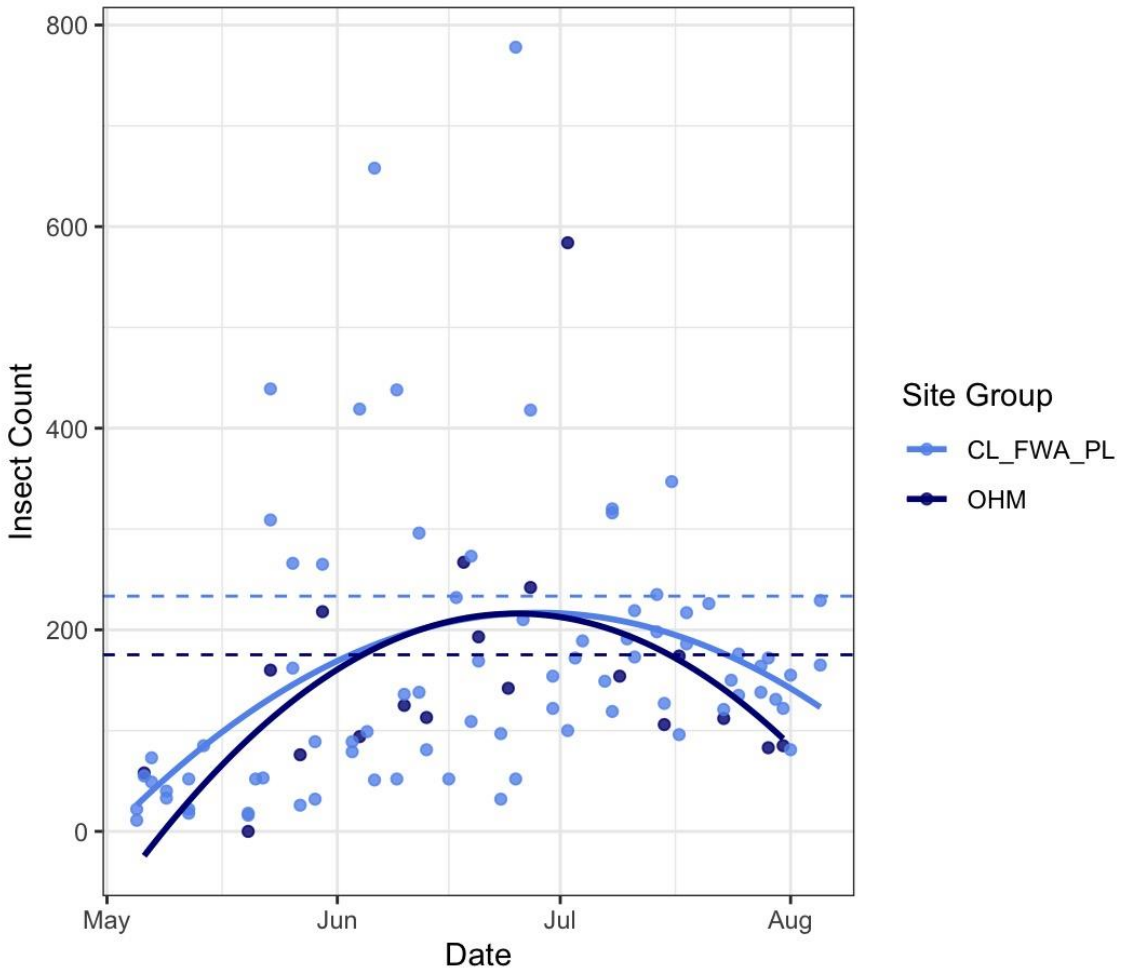
Supplemental Figure 7. Combined Coleoptera and Odonata counts over the breeding season with a quadratic fit. Vertical lines indicate dates of peak abundance. Light blue points represent the Southern sites (CL, FWA, and PL), and dark blue points represent Oak Hammock Marsh (OHM).



Supplemental Figure 8. Coleoptera counts over the breeding season with a quadratic fit. Vertical lines indicate dates of peak abundance. Light blue points represent the Southern sites (CL, FWA, and PL), and dark blue points represent Oak Hammock Marsh (OHM).



Supplemental Figure 9. Odonata counts over the breeding season with a quadratic fit. Vertical lines indicate dates of peak abundance. Light blue points represent the Southern sites (CL, FWA, and PL), and dark blue points represent Oak Hammock Marsh (OHM).



Supplemental Figure 10. Aerial insect counts over the breeding season with a quadratic fit. Horizontal lines indicate 30% of peak aerial insect abundance. Light blue points represent the Southern sites (CL, FWA, and PL), and dark blue points represent Oak Hammock Marsh (OHM).