THESIS

PROVISIONING AND NEST SUCCESS OF AN AERIAL INSECTIVORE AT A HIGH ELEVATION BREEDING SITE

Submitted by

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ABSTRACT

PROVISIONING AND NEST SUCCESS OF AN AERIAL INSECTIVORE AT A HIGH ELEVATION BREEDING SITE

Tree Swallows (*Tachycineta bicolor*) are a model organism in ornithology. However, few studies have been conducted in the western portion of their breeding range, particularly at high elevation. High elevation habitats, like Colorado State University's Mountain Campus, are impacted by climate change. Tree Swallows in these ecosystems face threats due to recent population declines and climate-related changes. These challenges could impact the species' survival in these areas, and for my Master's thesis I investigated two aspects of provisioning behavior, namely weather conditions and insect abundance.

My first chapter focused on how daily weather conditions influenced female Tree Swallow's rates of nest visitation and food provisioning. Using radio-frequency identification technology, I compared visitation rates to hourly weather conditions. I found that poor weather, including cooler temperatures and precipitation events, was negatively correlated with the number of visits made to the nest, which subsequently influenced the growth and development of nestlings.

In Chapter 2, I addressed the question of how weather affected food availability. Tree Swallows rely on flying insects as their main food source, and inclement weather is known to decrease insect availability in the airspace. To investigate if lowered female provisioning effort matched periods of food unavailability, I deployed a mobile radar unit – the BirdScan MR1 – to quantify insect abundance. I then compared insect activity to nest visitation rates and found that females made significantly more visits to their nestlings when insects were more abundant.

Additionally, I found that insect activity was significantly influenced by weather conditions, demonstrating that weather may be used as a proxy for insect abundance at sites where direct monitoring of insects is not possible.

Put together, the results of my first and second chapters deepen our understanding of how female Tree Swallows navigate the complexities of aerial conditions – both biotic and abiotic – to forage and provision for their growing nestlings in an ever-changing high elevation environment. As the effects of climate change become more pronounced, high elevation habitats are likely to undergo rapid changes. Consequently, insight into the relationship between weather and food availability becomes increasingly important.

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Chapter 1 – Tree Swallow (*Tachycineta bicolor*) nest visitation is negatively correlated with cold and rainy conditions at a high elevation

SUMMARY

High-elevation montane areas are characterized by dynamic weather patterns and are impacted by climate change. Hence, studies of aeroecology in these regions can offer important insights about how insectivorous birds respond to rapidly changing atmospheric conditions. I investigated aerial insectivore provisioning in Tree Swallows (*Tachycineta bicolor*) in relation to weather conditions at a high elevation breeding site at Colorado State University's Mountain Campus. During the 2022 and 2023 breeding seasons, I used radio-frequency identification (RFID) technology to monitor nest provisioning rates and to investigate how adult foraging effort impacts nestling growth. I measured parental effort and modeled individual nest box visitation rates in response to changing atmospheric conditions. I predicted that cold, windy, and rainy conditions would reduce aerial insect abundance, leading to lower provisioning rates in Tree Swallows, and our nest monitoring revealed that low temperatures, precipitation, and elevated wind speed all had a significant negative impact on parental provisioning effort, which translated into negative effects on nestling growth metrics. These results demonstrate how reproduction in aerial insectivores is often coupled with atmospheric conditions. My results also reinforce the concept of the airspace as a habitat that is linked to the broader landscape through the activities of insects, aerial insectivores, and other volant species.

INTRODUCTION

Provisioning nestlings is one of the most energetically taxing activities for most birds, and it is intimately tied to fitness, especially for aerial insectivores (Winkler and Allen 1996; Imlay, et al. 2017; Twining, et al. 2018). In an ever-changing environment, parents must negotiate a tradeoff between the nutritional demands of their rapidly developing offspring and self-maintenance. Aerial insectivores forage on the wing and rely on the availability of aerial insects, which is heavily influenced by prevailing weather conditions and can change quickly (Hallmann et al. 2017; Hussell and Quinney, 2008; Shipley, et al. 2020). Cooler temperatures and precipitation negatively affect aerial insect abundance (Cox, et al. 2020; Winkler, et al. 2013). This lowered availability of insects is often insufficient to meet energetic demands, resulting in reduced chick survival following poor weather conditions (Shipley, et al. 2020; Winkler, et al. 2013), likely augmented by increased metabolic demands to maintain body temperature (McCarty 1995; Winkler, et al. 2013). Short term changes in food supply are expected to occur more frequently as weather conditions become increasingly variable due to climate change (Cox, et al. 2019; Cox, et al. 2020).

Avian aerial insectivores, including Tree Swallows, are experiencing serious population declines (Bourret, et al. 2015; Nebel, et al. 2010). Between 1970 and 2017, aerial insectivores declined by an estimated 31.8% across North America (Rosenberg, et al 2019). Tree Swallow abundances based on eBird data from 2007 to 2022 show abundance declines ranging between 20% to 50% across most of the breeding range (Fink, et al. 2022). Changes in prey abundance is among the most important potential causes for Tree Swallow declines (Cox, et al. 2019; Spiller and Dettmers 2019).

As aerial insectivores, Tree Swallows (*Tachycineta bicolor*) constitute an intricate link between aerial and terrestrial ecosystems. Because of their frequent reliance on ephemeral food resources, Tree Swallows are viewed as biological indicators, especially in their preferred riparian habitats (McCarty 2002; Jones 2003). Due to their widespread distribution and use of man-made nest boxes (Robertson and Rendell, 1990; Gómez et al. 2014), Tree Swallows are intensively studied in North America (Jones 2003). A Web-of-Science literature review (using the keywords "Tree Swallows and foraging", "Tree Swallows and breeding success", and "Tree Swallows and elevation") yielded 175 peer-reviewed articles. However, approximately two thirds of these studies took place in either New York, Ontario, or Quebec. Only 6 were located west of 94th west meridian in the United States (See Figure 1) and only study was of a high elevation breeding population (Winkler, et al. 2020).

The relationships between weather and food availability become more impactful in understudied high elevation regions, where daily atmospheric conditions fluctuate frequently and rapidly (Martin 2001; Bears, et al. 2009). Studies located in high elevation areas may provide insight into behavioral and physiological strategies that promote survival in inherently challenging environmental conditions (Boyle, et al. 2015). In songbirds breeding at high elevations, smaller clutches are common (Boyle, et al. 2015), which, for Dark-eyed Juncos, translated to a shift to a high-survivorship strategy with reduced fecundity as opposed to the high-reproduction strategy common at lower elevations (Bears, et al. 2009). A study by Johnson, et al. (2018) compared breeding characteristics from two populations of Tree Swallows breeding at different elevations in Wyoming's Bighorn Mountains. They demonstrated that the population at the higher elevation not only laid smaller clutches, but also had significantly smaller egg sizes by volume, likely due to the energetic constraints that come with breeding at high elevations (Johnson, et al. 2018). These studies indicate that high-elevation breeding populations present opportunities to study classic life history trade-offs faced broadly by aerial insectivores. Moreover, some of the most pronounced impacts of climate change, including increased seasonal temperatures and variability, extreme precipitation events, and rapid changes in atmospheric conditions, are manifested at high altitudes (Freeman, et al. 2018).

As the climate shifts, so does Tree Swallow breeding phenology (Bourret, et al. 2015; Dunn, et al. 2011; Imlay, et al. 2018; Shipley, et al. 2022). Emerging studies show breeding is advancing between 2.8 and 4.2 days per decade (Dunn and Winkler 1999; Bourett, et al. 2015; Shipley, et al. 2022), resulting in increased risk of exposure to inclement weather events that often result in increased chick mortality (Cox, et al. 2020; Dunn, et al. 2011; Shipley, et al. 2020). Reduced offspring survival has been identified as one of the likely causes for population declines, and poor weather conditions during nestling development appear to be a key driver (Cox, et al. 2020). Increased frequency of cold snaps and precipitation leads to highly variable food availability – a scenario that can leave nestlings lacking the energy they require for thermoregulation, growth, and development. Using a long-term nest box monitoring dataset from 1975 to 2017, Cox et al. (2019) showed that overall nestling body mass was lower than historically seen, possibly driven by climate change and the resulting shifts in prey availability. Even when nestlings survive such challenging conditions, poor body condition may negatively impact their post-fledging survival (Naef-Daenzer and Grüebler 2016). In some areas, rainfall events have been increasing over the past few decades, potentially explaining documented Tree Swallow population declines (Cox, et al. 2019). Consequently, understanding the complex interactions between phenology, weather, and food availability is vitally important.

In this study I investigated how nestling provisioning rate is affected by prevailing atmospheric conditions and how this is linked to Tree Swallow nestling growth. I used radio-frequency identification (RFID) technology (Bonter and Bridge 2011; Lendvai, et al. 2015;

Sonnenberg, et al. 2019; Turner, et al. 2020) for data collection for each breeding pair of swallows at a high-altitude montane site. Once eggs have hatched, 95% to 98% of nest box visits constitute parental provisioning trips, and food load size remains consistent throughout time and across nests (McCarty 2001). Thus, the frequency of nest visits is a reliable index for quantification of foraging and provisioning effort (Cox, et al. 2019; Iserbyt et al. 2018). I correlated this provisioning data with data on local weather (temperature, precipitation, and wind speed) and nestling development to investigate relationships among weather, foraging behavior, and nestling success.

I predicted that females would avoid provisioning under suboptimal weather conditions and instead maximize effort when conditions were favorable. Schifferli, et al. (2014) showed that Barn Swallows (*Hirundo rustica*), avoid foraging in poor conditions and instead buffer against the loss of food intake by maximizing foraging effort when insects are abundant. Consequently, I expected that hourly female provisioning effort would be negatively correlated with cool temperatures, increased precipitation, and strong winds. Since nestling success depends on meeting considerable energetic demands, I also predicted that nestling growth and development would be positively correlated with the number of provisioning visits. Ultimately, I sought to verify that nestling growth and survival are linked to atmospheric conditions through parental foraging and provisioning behavior.

METHODS

Data collection

To obtain data on Tree Swallow behavior in a high elevation portion of their breeding range, I deployed and monitored 166 nest boxes at Colorado State University's Mountain Campus (40.5705° N, 105.5913° W, 2743m elevation) during the breeding seasons in 2022 and 2023. This site also houses a weather instrumentation station at the same elevation, located about 200 meters from the nearest nest boxes. This station records data including air temperature, precipitation, and wind speed at five-minute intervals. From May through July, the data for these weather variables were used to assess if atmospheric conditions influenced adult provisioning effort at the nest box.

Beginning in early May, I visited all nest boxes weekly to monitor nest initiation. Upon nest completion, visit frequency increased to three times per week to track egg laying activity. At approximately day 10 of incubation, females were captured by hand from the nest box and fitted with an aluminum federal bird band as well as a lightweight (~0.1g) passive integrated transponder (PIT) tag attached to a plastic leg band. For each banded female, I also measured, bill length (mm), tarsus length (mm), wing chord (mm), and mass (g).

Nest boxes are an optimal location for the deployment of RFID antenna and readers given the high level of fidelity that adults exhibit during the breeding season (Bridge, et al. 2019; Iserbyt, et al. 2018). The day following capture, an RFID antenna was secured around the entrance to the nest box and attached to an RFID reader similar to the model described in Bridge, et al. 2019. Each time a tagged adult passes through the nest box entrance, the reader recorded the adult's ID and time of day. RFID antennas were programmed to cycle between searching for a signal for 100 milliseconds and a 200-millisecond period in a low-power sleep mode. Adult Tree Swallows commonly perch in the entrance of the nest box while feeding their nestlings. Although the RFID readers were programmed to wait 8 seconds between recording repeated detections of the same PIT tag, I often collected long series of continuous PIT tag detections when a female perched at the nest box entrance, potentially leading to an overestimation of provisioning trips. To address this issue, multiple detections within a two-minute window were interpreted as a single provisioning visit, which mirrors the time threshold used in other RFID-based studies on provisioning rates of Tree Swallows (Taff, et al. 2019; Injaian, et al. 2021). Provisioning trips often occur faster than two-minute intervals, so my provisioning rate is likely a conservative estimate.

Following RFID implementation, each nest box was visited every two days to monitor the initiation of hatching activity. To track nestling development, I recorded measurements of bill length (mm), tarsus length (mm), wing length (mm), and mass (g) at 3-, 6-, and 10-days post-hatching. No visits were conducted between day 10 and day 18 post-hatching to reduce the risk of premature fledging. Starting at day 18, nest boxes were checked every other day for fledging and any nestling mortalities.

Data analysis

All analyses were conducted in R (v4.1.2; R Core Team 2022). After testing pairwise correlations between predictor variables of temperature, wind speed, precipitation, and proportion of the day, I found that all correlation coefficients fell between -0.24 and 0.41, and thus I maintained all variables in my analyses. To assess if atmospheric conditions influenced female provisioning effort, hourly averages of the weather variables collected on-site were computed and compared to the hourly visitation rates at nest boxes. I used the "mgcv" package (Wood, 2017) to build a generalized additive mixed model (GAMM) using a Poisson error distribution with the response variable as the number of female visits per hour. To determine which predictors predominantly influenced provisioning rate, I used the MuMIn package (Bartoń 2023) to run all possible model combinations without interactions. My predictors included splines for wind speed (m/s), temperature (°C), the proportion of day as fixed effects, and precipitation as a binary factor (raining or not) linear fixed effect. Additionally, observation date and female band number were included as random effects. The proportion of the day was determined by calculating the number of hours after local sunrise divided by the total number of daylight hours per day (sunset minus sunrise). This metric was used to account for changing daylength through the season, with 0 reflecting times at sunrise, 0.5 at mid-day, and 1.0 at sunset. I constrained smoothers for average hourly temperature and wind speed to three knots and proportion of day to seven knots to reduce overfitting and improve the predictive abilities of these variables. I selected the top model based on Akaike's Information Criterion (AIC_c) and model weight.

To test for a relationship between nestling development and female provisioning effort, I compared nestling measurements at day 10 post-hatching to visitation rates. Mass, bill length, wing length, and tarsus length were all highly positively correlated (values between 0.53 and 0.85), so I chose to use mass (g) to represent body condition. I modeled nestling mass as a function of the total number of female provisioning trips in a season and total number of chicks in the nest as fixed effects using a generalized linear model. I used box-year as a random effect to account for multiple nestling measurements from the same nest box. I implemented the mixed model using lme4 (Bates, et al. 2015) and lmerTest (Kuznetsova, et al. 2017) and built confidence intervals using the merTools package (Knowles, 2023).

RESULTS

Provisioning and breeding metrics

I tagged 19 females in 2022 and 22 females in 2023 for a total sample size of 41 females across both years. Of the females from 2023, 14 were recaptures that had been banded in 2022, and of these, 9 were females that had been tracked in 2022 with PIT tags (Figure 1.2). I recorded 210,297 PIT tag detections in 2022 and 341,440 in 2023, resulting in a total of 551,737 PIT tag detections across both years. After filtering out successive readings within a 120-second timeframe, I ended with 50,866 provisioning trips in 2022 and 61,865 in 2023, resulting in a total of 112,731 distinct provisioning trips across both years. I calculated a mean provisioning rate of 7.45 visits per hour (σ = 1.42) across females in 2022 and a rate of 7.68 in 2023 (σ = 0.75).

Hatching success for RFID-monitored boxes in 2022 was 87.2% (σ = 21.1%) and 87.3% in 2023 (σ = 16.9%), and the combined hatching success rate for both years was 87.3% (σ = 18.7%). Fledging success was 80.7% for 2022 (σ = 32.4%) and 90.4% (σ = 23.7%) for 2023, giving a combined fledging success rate of 85.9% (σ = 28.1%) across both years of the study.

Of the 166 nest boxes, 35 were active in 2022, and 40 were active in 2023. The total hatching success rate (regardless of RFID monitoring) was 54.9% (σ = 45.6%) in 2022 and 72.9% (σ = 34.4%) in 2023, and the combined total hatching success was 63.9% (σ = 40%). 22 out of 35 boxes in 2022 and 30 out of 40 boxes in 2023 successfully hatched at least one nestling. Of those that hatched, fledging success was 83.3% in 2022 (σ = 30.8%) and 86.6% in 2023 (σ = 27.9%), resulting in a total combined fledging success rate of 85.0% (σ = 29.3%) across both years of the study.

Atmospheric conditions versus provisioning effort

The top model examining provisioning counts and atmospheric conditions included all predictors and had a model weight of 0.998. This GAMM explained 44.2% of the deviance in my data and had an R^2 of 0.41 (see Table 1 for full model results). My model indicated significant effects of temperature, precipitation, wind, and proportion of the day on female provisioning rate. Regarding hourly temperature, the hourly provisioning rate increased with temperature and peaked at approximately 18°C before beginning to decline (Figure 3A). Hourly wind speed also had a negative relationship with the number of provisioning trips, with more pronounced reductions in provisioning during especially high winds (Figure 3B). The presence of precipitation decreased the average number of female provisioning trips by approximately 1.5 visits per hour (Figure 3C). Examination of provisioning activity across the proportion of the day indicated a pattern wherein visits increased each morning, at which point they roughly plateaued throughout the middle of the day, peaking again before sunset (Figure 3D). Finally, both random effects of band number and date were significant predictors in my final model.

Nestling development and provisioning effort

Nestling mass at day 10 post-hatching had a significantly positive relationship with the total number of female provisioning visits to the nest box (slope = 0.002, 95% CI = (0.0001 to 0.003), $p > 0.038$, df = 37.257, Figure 4). I also found that the total number of nestlings in the nest had a significant negative relationship with the nestling growth index (slope = -0.939 ± 95% CI = (-1.747 to -0.130), $p = 0.031$, df = 38.651, Figure 4). The conditional R^2 value for our model was 0.79, and the marginal R^2 value representing fixed effects was 0.12.

DISCUSSION

Provisioning for nestlings is one of the most energetically taxing activities and is directly linked to adult fitness (Winkler and Allen 1996). Suboptimal weather conditions can quickly influence the availability of aerial insect food resources (Hallmann et al. 2017; Hussell and Quinney, 2008; Winkler, et al. 2013). My results indicate that weather conditions have a significant impact on female provisioning behaviors at a high elevation, where suboptimal weather conditions occur at relatively high frequency.

Previous findings demonstrate that cooler temperatures negatively affect aerial insect activity (Cox, et al. 2020; Winkler, et al. 2013). Consequently, I hypothesized that warmer temperatures would be associated with increased foraging effort. My findings show that higher average hourly temperatures lead to increased female provisioning visits until approximately 18°C, at which point the rate of visits begins to level off. An increased availability of aerial insects in warmer temperatures likely drives increased female activity, and cool temperatures present a limitation to Tree Swallow activity. The fitness consequences of low temperatures appear to be widespread, as a continental-scale study found that Tree Swallows – along with 16 other North American bird species – have sensitivity to cold temperatures that negatively impact reproduction (Taff and Shipley, accepted 2023). The ecological group that most consistently displayed sensitivity to low temperatures during reproduction was aerial insectivores, suggesting a similar mechanism may be driving reduced fitness.

Cooler temperatures often accompany precipitation events, both of which are thought to decrease short-term insect abundance (Winkler, et al. 2013). My finding of a negative relationship between precipitation and provisioning visits may also be a result of lower insect availability under cool temperatures as well. Barn Swallow (*Hirundo rustica*) parents forego foraging during precipitation events and presumably concentrate foraging effort during time periods where insects are more readily available (Schifferli et al. 2014). The Tree Swallows in my study possibly followed a similar strategy, or alternatively they maintained foraging effort during precipitation events but simply had a reduced success rate leading to reduced provisioning.

While Tree Swallows have been shown to use wind assistance for efficient gliding (Blake 1948), I predicted that calmer conditions would aid foraging. My results indicate that lower wind speeds do not have a strong effect on female activity, but winds stronger than 3 m/s tend to decrease provisioning visits. This decline in female activity under strong winds may indicate that insects avoid high wind speeds. Strong winds may cause more flight turbulence for both taxa, adding energetic costs to Tree Swallow foraging as well as difficulty in capturing insects on the wing.

In addition to shaping food availability and provisioning behavior, weather conditions have a strong impact on embryonic development (Olson, et al. 2006), and cold snaps can disrupt incubation and result in lowered hatching success. This could explain the low hatching rate (54.9%) at the Mountain Campus in 2022, especially given the low temperatures that occurred in early June that year. For example, on June 1, 2022, the average temperature was only 2.75°C, compared to an average temperature of 7.28°C on June 1, 2023. As breeding phenology shifts earlier into the spring (Dunn and Winkler 1999; Bourett, et al. 2015), encounters with cold temperatures may become more common (Cox, et al. 2020; Shipley, et al. 2020). Furthermore, weather extremes are predicted to occur more frequently across the globe (Rummukainen 2012), whereby exposure to cold snaps may be a threat that Tree Swallows will face not only at high elevations, but across the full extent of their breeding range.

I found that my nestling mass at ten days post-hatching was significantly positively associated with the number of female provisioning visits. Additionally, the total number of nestlings in a nest was a significant negative predictor. Based on this result, it seems likely that nestlings with fewer siblings are able to grow larger due to the lessened competition for provisioned food, and intra-nest competition may play a larger role in inhibiting growth compared to external factors. Increased nestling competition points to possible selection for smaller clutch sizes, which have previously been documented in montane habitats (Boyle, et al. 2015). With smaller clutches, difficulty provisioning due to variability in insect abundance may be offset by fewer nestlings to feed (Boyle, et al. 2015). As largescale weather patterns become more variable under climate change (Rummukainen 2012), food availability may become more uncertain across the breeding range. Subsequently, selection for smaller clutches may proliferate across lower elevation regions and begin to negatively impact Tree Swallow populations across their range.

Utilizing long-term data sets to investigate clutch sizes in lower elevation populations could indicate if any trend in clutch size already exists.

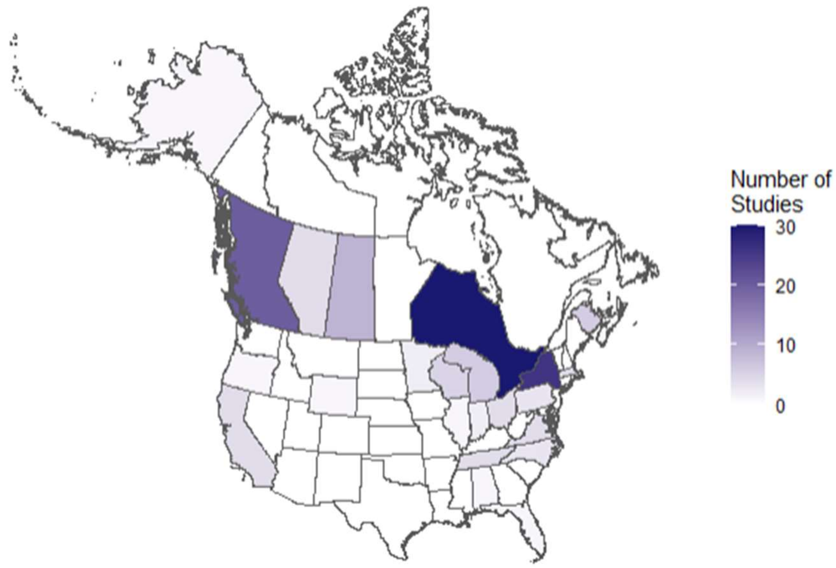
Nestling development is intimately tied to food availability, which in turn is influenced by weather conditions (Hallmann et al. 2017; Hussell and Quinney, 2008; Shipley, et al. 2020). The way individuals change their foraging behaviors in response to shifts in food availability greatly impacts nestling success, and an inability to overcome severe weather conditions often leads to high rates of nestling mortality. For example, Figure 5 depicts daily visit counts for two unique females – from Box 120 and Box 158 – in the 2022 season. While recorded visits drop suddenly for both females in early July, the female at Box 120 quickly returned to normal foraging behavior and successfully fledged all nestlings. In contrast, the female at Box 158 had few visits recorded for multiple days. Although visitation rates eventually rose again, this nest experienced complete mortality just a few days later. This disruption in provisioning activity was likely caused by inclement weather, as average temperatures fell between 14 and 15℃, accompanied by precipitation. The female from Box 120 was possibly more experienced and thus better able to cope with an unexpected drop in food availability. Previous analyses have shown that parents demonstrate different sensitivity in how they respond to inclement weather events and the associated reductions in insect activity, and that intermediate aged chicks (day 7-12 post hatch) are the most negatively impacted by such weather events (Shipley 2018). If instances of severe and inclement weather become more frequent, the failure at box 158 could foreshadow more widespread unsuccessful nesting attempts (Cox, et al. 2020; Dunn, et al. 2011; Shipley, et al. 2020).

This study assumes that atmospheric conditions are predictive of aerial insect prey. Direct quantification of insect activity can be accomplished by traditional trap sampling or through implementation of more recent radar technology (Chapman, et al. 2003, Chapman, et al. 2011;

Montgomery, et al. 2021). Investigating this link is the next step in furthering our understanding of the intricacies of dynamic high-elevation airspace habitat. Furthermore, this connection may forecast aerial insectivore responses to continued widespread declines in flying insect abundance (Hallmann, e al. 2017) across all elevational gradients, a scenario likely to worsen as instances of extreme weather become commonplace on a global scale (Rummukainen 2012).

My findings begin to tease apart the mechanisms that drive individual female foraging behavior. While the relationships I found are like those expected at lower elevations, Tree Swallows at my mountainous breeding site must balance the energetic costs associated with foraging against their nestlings' success in rapidly shifting conditions, conferring additional challenges to the classic theory of optimal foraging. Weather conditions in high elevation regions are predicted to become even more variable under climate change (Freeman, et al. 2018), and Tree Swallows will likely need to shift their behaviors to forage and breed successfully under such conditions if they are to persist in high elevation portions of their traditional breeding range. With population declines impacting this species, gaining a holistic understanding of Tree Swallow behavior across their entire breeding range, including understudied areas of high elevation, is needed. Long-term monitoring of this population at the forefront of climate-related threats may lend insights into how phenology shapes individual fitness – from spring arrival to fledging success.

The impacts of climate change ripple through many aspects of Tree Swallow fitness. Broad-level warming trends have been linked to shifts in breeding phenology, subsequently exposing Tree Swallows to a higher risk of breeding disruption due to cold snaps and other inclement weather events. Such conditions negatively influence food availability, conferring additional challenges to nestling growth and survival (Cox, et al. 2019; Shipley, et al. 2020). My results demonstrate how nestlings that experienced lower levels of provisioning had smaller body sizes. This reduction in size may signify a poor body condition, which may reduce post-fledging survival and recruitment into the breeding population (Cox, et al. 2019). With so many potential drivers of population declines, Tree Swallows face death by a thousand cuts. Understanding the suite of threats to their survival is key in mitigating further declines, not only for Tree Swallows, but across the entire guild of aerial insectivores.



State/Province	Relevant Studies
Ontario	30
New York	26
Quebec	20
British Columbia	20
Multiple Locations	12
Saskatchewan	9
New Brunswick	6
Michigan	6
Wisconsin	5
Ohio	4
California	4
Virginia	4
Tennessee	4
Massachusetts	4
Alberta	4
Pennsylvania	3
North Carolina	3
Minnesota	2
Indiana	2
Florida	1
Alaska	1
Alabama	1
Illinois	1
Nova Scotia	1
Oregon	1
Wyoming	1

Figure 1.1 Locations of Tree Swallow breeding studies from a literature review. Results from the Web of Science database show that the vast majority of Tree Swallow studies focused on foraging and breeding success have occurred in the north and east portions of their breeding range.

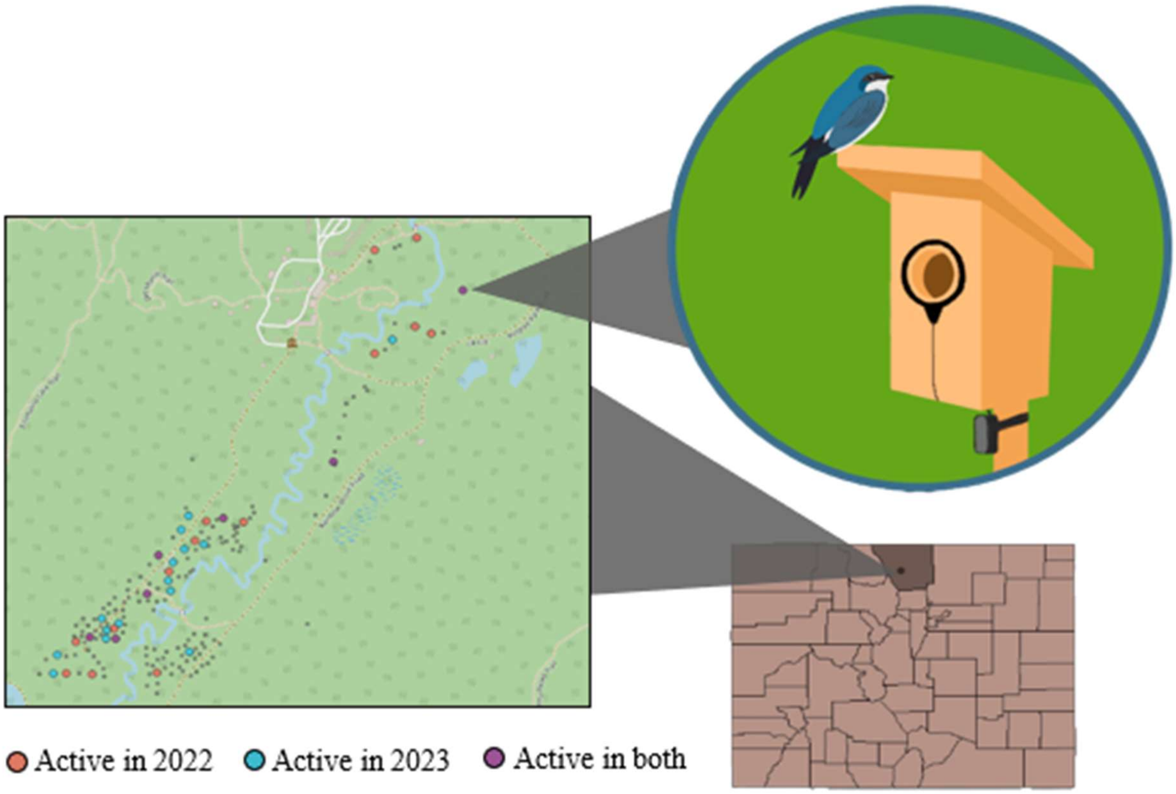


Figure 1.2 A map of RFID-monitored nest boxes at Colorado State University's Mountain Campus. Each nest box location point is colored blue if it was active in 2022, red if active in 2023, or purple if active during both breeding seasons.

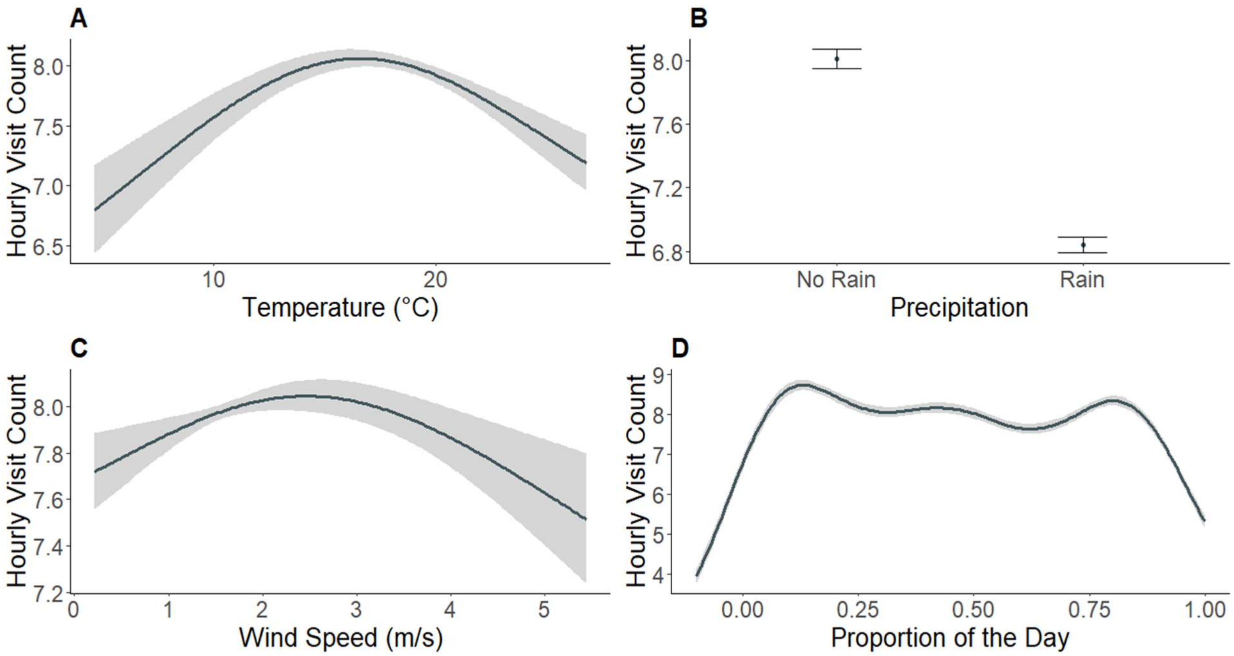


Figure 1.3 GAMM model fits for significant weather and temporal predictors. Predictions were made holding the other model predictors constant at their median values and varying the predictor of interests across the range of the 1st and 99th quantile of observed values. A) Average hourly temperature had a significant relationship with the hourly count of female provisioning trips, peaking around 18°C. B) Precipitation had a negative correlation with the number of hourly female provisioning visits. C) Average hourly wind speed had a significant relationship with hourly female provisioning trips, generally declining as wind speeds increased. D) Proportion of the day had a significant correlation with hourly female provisioning visits with activity generally increasing in the morning and decreasing after a second peak in the evening. Note, measures less than 0 reflect measures prior to sunrise.

Table 1.1 Output of results from the GAMM model. Precipitation and barometric pressure were included as linear fixed effects. Temperature, precipitation, wind speed, and proportion of day were included as thin plate regression splines. Female band number and observation date were included as random effects. Asterisks denote variables that are significant. "Band no." represents female band number, and "Obs. Date" represents observation date.

	Parametric coefficients			**Smooth terms**		**All**
	Estimate	SE	z-value	edf	Chi-square	*p*-value
Deviance explained: 44.2% **R-squared: 0.41**						
Precipitation	-0.16	0.02	-9.34	-	-	0.0001*
Temperature	-	-	-	1.99	69.06	< 0.0001*
Wind speed	-	-	-	1.892	8.555	0.0009*
Proportion of day	-	-	-	5.98	1478.95	< 0.0001*
Random effect: **Band no., Obs. date**	-	-	-	705.93	4021.09	< 0.0001*

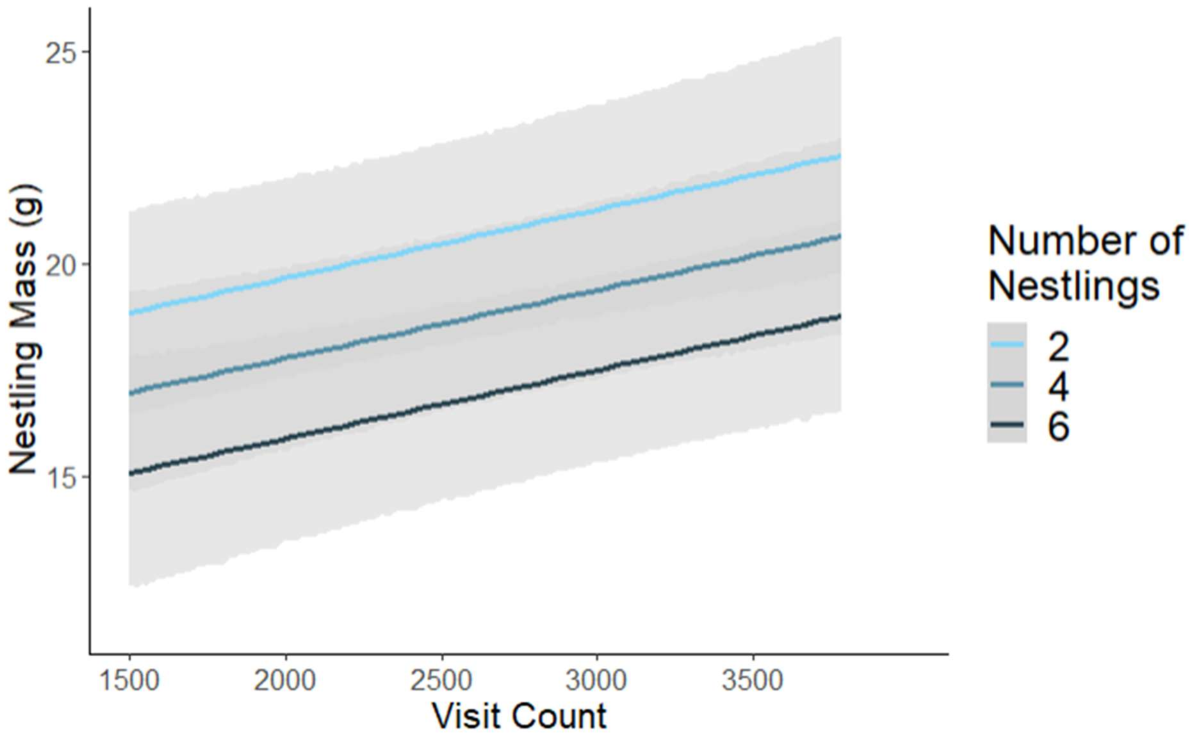


Figure 1.4 Linear regression fits for nestling mass at day 10 post-hatching. The total count of female provisioning visits in a season was found to have a significant positive effect (p = 0.038) on nestling mass. The number of nestlings in the nest had a significant negative effect (p = 0.031) on nestling mass at 10 days old post-hatching.

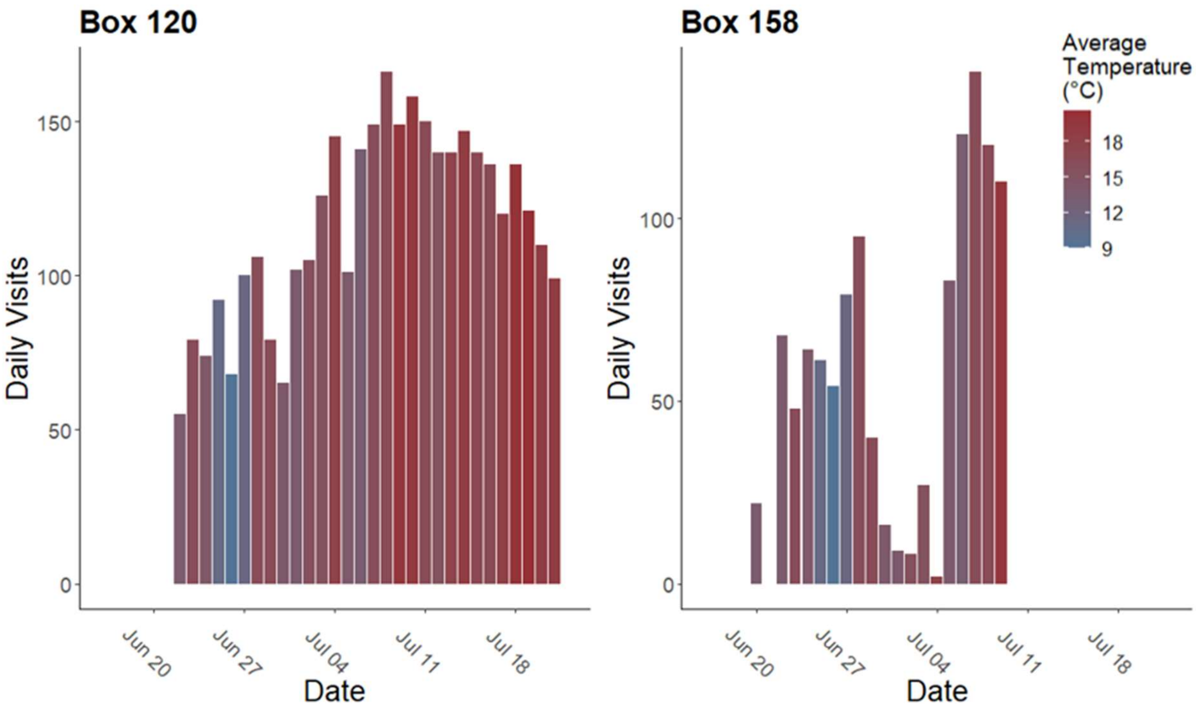


Figure 1.5 Histograms showing daily counts of female visits for two nest boxes active in 2022. The number of daily female visits tended to increase after eggs hatched. At Box 120, visits were much more consistent and frequent than at Box 158. By the end of the season, Box 120 had successfully fledged all 5 nestlings, and Box 158 saw mortalities for all 6 nestlings.

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Chapter 2 – Radar revelations: insect availability is correlated with weather and parental provisioning in breeding Tree Swallows (*Tachycineta bicolor*)

SUMMARY

Airspace habitat is essential foraging space for Tree Swallows (*Tachycineta bicolor*), which rely on flying insects as their main source of food. However, insect availability can diminish rapidly with inclement weather conditions. Such conditions are common in high elevation areas – an understudied portion of the Tree Swallow's breeding range. To explore the relationship between food availability and high elevation weather conditions as related to female provisioning and nestling growth, I deployed a mobile radar unit to collect insect abundance data during the 2022 and 2023 summer breeding seasons at a high elevation site in Colorado's Rocky Mountains. I monitored 166 nest boxes to observe nestling success, and I used radio-frequency identification (RFID) technology to track female provisioning behavior. I found that temperature, wind speed, precipitation, and proportion of the day all correlated with insect traffic rate, and the strength of these relationships suggest weather conditions serve as a good proxy of airborne insect activity. Furthermore, weather conditions and aerial insect abundance all influenced female provisioning rates, emphasizing how the complexity of conditions and resources in airspace landscapes affect aerial insectivore fitness. My results demonstrate the severity of potential threats to aerial insectivores due to climate change via increased weather extremes, especially in high elevation portions of their range.

INTRODUCTION

Airspaces are vast habitats, critically overlooked, but essential for trillions of insects, bats, and birds – needed for foraging, migration, and provisioning of young (Diehl 2013; Diehl, et al. 2017). Because food resources found in airspaces are both highly clumped and variable, weather patterns can cause rapid shifts in food availability (Cox, et al. 2020; Dunn, et al. 2011).

Airspaces are characteristically dynamic, changing on temporal scales ranging from minutes to hours. Airspaces are also affected by long-term directional changes such as anthropogenic activity and climate change. Temperature, wind speed and direction, precipitation, and thunderstorms, all integrally intertwined, uniquely shape the habitat and distribution of aerial organisms (Cox, et al. 2020; Diehl 2013). Rapid daily shifts from clear skies to thunderstorms are especially apparent in high elevation regions within the Rocky Mountains. Unfortunately, species from high elevation regions experience some of the strongest consequences of climate change (Freeman, et al. 2018), and these regions represent critically understudied portions of some species' ranges (Martin 2001; Bears, et al. 2009). High elevation habitats serve as model environments for understanding natural and anthropogenic pressures faced broadly by aerial insectivores. This guild is experiencing dramatic population declines (Bourret, et al. 2015; Nebel, et al. 2010; Rosenberg, et al 2019). While a combination of many factors likely contributes to these losses, declines in aerial insects – the main source of prey – is one of the main contributors (Cox, et al. 2019; Spiller and Dettmers 2019).

One commonly studied aerial insectivore, the Tree Swallow (*Tachycineta bicolor*), spends most of its time foraging and provisioning young during the breeding season (McCarty and Winkler 1999). Airspace conditions are important for foraging, and provisioning for growing nestlings represents a challenge integral to individual fitness (Winkler and Allen 1996; Imlay, et al. 2017). The dynamic nature of airspace habitat leads to rapid temporal fluctuations in flying insects (Cox, et al. 2019, Shipley, et al. 2020), and Tree Swallows must cope with periods of food unavailability while balancing their own energetic demands with the nutritional needs of their developing nestlings. This short-term unavailability of insect prey is especially prevalent during periods with cold temperatures and precipitation (Hallmann et al. 2017; Hussell and Quinney, 2008; Shipley, et al. 2020). Such inclement weather conditions make it difficult for nestlings to access the energy needed not only to grow, but also to thermoregulate, often causing higher rates of mortality during cold and rainy spells (McCarty 1995, Shipley, et al. 2020; Winkler, et al. 2013). High elevation regions undergo stormy conditions on a frequent basis, creating a formidable environment for breeding Tree Swallows.

Few studies of breeding Tree Swallows have been conducted in high elevation habitats, and most research is focused in the northeastern portion of their range (Winkler, et al. 2020). This gap in knowledge is particularly concerning given the challenges that organisms in high elevation areas routinely face. Organisms in these habitats must overcome risks brought on by extreme weather conditions, a challenge likely to be compounded by the effects of climate change (Freeman, et al. 2018). Not only must organisms adapt to lessened food availability resulting from shorter growing seasons, but they must also navigate survival under the rapid fluctuations in weather conditions that occur on a daily basis (Martin 2001; Bears, et al. 2009). For some avian species, adapting to these harsh environmental conditions has led to changes in life history strategies, including smaller clutch sizes (Boyle, et al. 2015; Johnson, et al. 2018) and increased survivorship (Bears, et al. 2009). However, largescale shifts in weather patterns are expected to bring even more variation and weather extremes into high elevation areas (Martin and Wiebe 2004), potentially pushing some species beyond their limit of survival. With steep declines already seen in the availability of flying insects (Hallmann, et al. 2017, Lukach, et al. 2022), the interconnection of weather conditions and insect abundance is critical in understanding Tree Swallow provisioning behavior in this unique portion of their range.

Obtaining data on insect abundance has classically relied on in-field methods such of trapping, acoustic monitoring, or visual observations (Montgomery, et al. 2021). More recently, automatic monitoring using radar has become an option to supplement or replace these field-intensive sampling methods (Chapman, et al. 2003, J. Roffey 2009; Noskav, et al. 2021; Lukach, et al. 2022). Radar technology has advanced from broad-scale detections to those on a finer spatial and temporal scale, particularly with the use of the BirdScan MR1 (Shi, et al. 2021). The BirdScan MR1 is a portable, vertical-looking pulsed radar created specifically for the purpose of biomonitoring. While the BirdScan is most often used to study bird and bat movements (Zaugg, et al. 2008; Schmidt, et al. 2017; Tschanz, et al. 2020; Werber, et al. 2023), its ability to record wing flapping patterns allows for the detection of insect activity, and a traffic rate can be calculated across different flight altitudes. Although fine taxonomic classifications are not possible with the BirdScan, its automatic quantification of insect activity in a localized area proves useful for minimizing the effort required to collect data on overall aerial insect abundance across longer timeframes (Shi, et al. 2021).

Radar is not the only technological advancement that has enhanced automated data collection in the field. Traditionally, collecting data on avian provisioning rates involved direct observations of visits to nest boxes, limiting the scope of these projects due to the time and effort required in the field. However, automated data collection of nest box visits is now possible, particularly when implementing radio-frequency identification (RFID) technology (Bonter and Bridge 2011; Lendvai, et al. 2015; Turner, et al. 2020). Tree Swallows exhibit a high level of fidelity to their nest boxes while breeding, allowing for convenient deployment of an RFID reader and antenna at the nest box to collect data on visitation and provisioning behaviors (Bridge, et al. 2019; Iserbyt et al. 2018). The number of recorded visits made to the nest box can be used as a metric of provisioning effort by an individual tagged with a passive integrated transmitter (PIT) tag (Cox, et al. 2019; Iserbyt et al. 2018), as up to 98% of visits to nestlings are for the purpose of provisioning (McCarty 2001). Pairing this automated quantification of provisioning effort with environmental data allows for a holistic understanding of foraging behavior.

This study focused on pairing radar-collected insect abundance data with RFID-collected data on female provisioning rates. I coupled these data with weather data collected on site to gather further insight into the direct link between insect availability and provisioning behavior, with the aim of building a more complete understanding of airspace use as related to foraging. I predicted that females would dedicate more time to foraging when insects were more readily available in the airspace. Consequently, I expected to see higher provisioning rates with higher levels of insect abundance. Additionally, I predicted that the BirdScan MR1 would detect low numbers of insects during poor weather conditions such as cold temperatures, precipitation, and strong winds. Previous studies have shown that inclement weather negatively influences insect availability (Cox, et al. 2020). Validating this relationship with radar-collected data would lend more confidence to using weather conditions as a proxy for insect abundance when insect sampling was not possible at a site.

METHODS

Study site

A system of 166 nest boxes was monitored in the 2022 and 2023 summer breeding seasons at Colorado State University's Mountain Campus (40.5705° N, 105.5913° W, 2743m elevation) to collect data on female provisioning behavior, nestling development, and insect abundance. I deployed the BirdScan MR1 onsite (Figure 2.1A) to ensure measures of insect activity were broadly representative of Tree Swallow foraging areas within the valley where nest boxes were located. Weather instrumentation located approximately 200 meters from the nest boxes collected data every five minutes on temperature, precipitation, and wind speed.

Field methods

I deployed the BirdScan MR1 at a site within a 1-kilometer distance from all nest boxes in the Mountain Campus valley. I originally planned to collect data on insect abundance from mid-June through the end of July in both years, however, I encountered technical difficulties in July of 2022 which prevented data collection past July 9. For this reason, my data spans the dates of June 14 to July 9 during 2022. In 2023, radar sampling was continuous from June 14 to July 29. I recorded insect detections as a measurement of traffic rate – a calculation of the number of insects passing every hour. Rather than measuring true insect abundance, traffic rates measure the number of insects passing overhead. I used this measurement as an index of insect activity that represented food availability for Tree Swallows each hour. While insect traffic rate allows insects moving through the radar beam to be double-counted, the occurrence of double-counts is much less than that of double-counts that would occur if stationary insects were sampled. Therefore, while not error-free, insect traffic rate serves as a better indication of food availability than insect abundance as measured by the BirdScan.

I monitored the 166 nest boxes from early May through early August to check for nest building activity and increased visits to twice each week once a complete nest was present. I tracked egg laying, and once a full clutch was present, I captured females inside the nest box as they incubated their eggs. I then banded females with an aluminum federal band and attached a PIT tag to their other leg. Although not used in this study, I recorded measurements of mass, bill length, wing chord length, and tarsus length before releasing each female.

Following female capture, I deployed RFID units on active nest boxes. The RFID readers were programmed following the protocol outlined in Bridge, et al. 2019. Antennas searched for a signal for 100 milliseconds and cycled into a sleep mode for 200 milliseconds to conserve power. I programmed readers to wait 8 seconds between consecutive detections before recording a new visit from the same PIT tag. However, consecutive PIT tag readings often result when Tree Swallows perch at the entrance of their nest box. To account for these strings of continuous readings and prevent overestimating the number of female nest box visits, I filtered out successive readings that occurred within a 2-minute window. This approach was used in other Tree Swallow studies utilizing RFID (Taff, et al. 2019; Injaian, et al. 2021).

Data analysis: atmospheric conditions and insect activity

To assess if weather conditions were predictive of flying insect activity, I compared hourly insect traffic rates collected by the BirdScan MR1 to hourly weather conditions on site. I created a generalized additive mixed model (GAMM) using the package “mgcv” (Wood, 2017) in R (v4.1.2; R Core Team 2022) using insect traffic rate (the number of insects detected in a horizontal km each hour) as my response variable. To find which variables predicted insect activity, I used the package MuMIn (Bartoń 2023) to run all possible combinations of predictors and selected the top model based on Akaike’s Information Criterion (AIC_c) and model weight. Given the skewed distribution of my data, I performed a square root transformation on insect traffic rate prior to analysis. I tested fixed effects of proportion of the day, temperature (°C), and wind speed (m/s) as splines. I constrained the smoothing terms to 7 knots for proportion of the day, and 3 knots for temperature and wind speed to preserve generalizability of the model fit. I included precipitation as a binary factor (raining or not) as a linear fixed effect in addition to observation date as a random effect. I accounted for changes in day length across the season by incorporating a daily calculation of proportion of the day, which I calculated by dividing the number of hours after local sunrise by the total number of hours of daylight. Based on this calculation, proportions ranged from 0 to 1 with 0 corresponding to sunrise and 1 corresponding to sunset.

Data analysis: insects, weather, and female provisioning rates

To investigate how aerial insect availability influenced female provisioning activity, I constructed a GAMM using hourly provisioning visits under a Poisson error distribution as my response variable. I modeled insect traffic rate and proportion of the day as fixed effect splines and constrained smoothers to 10 knots and 7 knots respectively. I included observation date and female band number as random effects. By excluding all weather predictors from the model, I examined directly how food availability shaped provisioning behaviors.

To compare the influence of insect availability to that of weather conditions regarding hourly female provisioning effort, I modeled provisioning rates as a function of insect traffic rate in addition to weather predictors. I tested all variables for correlation and found temperature had a positive correlation of 0.72 with insect traffic rate (Figure 2.2). I excluded temperature from my model, which included insect traffic rate, wind speed (m/s), and proportion of the day as fixed effects modeled as splines. Smoothers were constrained to 10 knots for insect traffic rate, 3 knots for wind speed, and 7 knots for proportion of the day. I included precipitation as a binary factor (raining or not) linear fixed effect in addition to observation date and female band number as random effects.

RESULTS

RFID monitoring

I monitored 19 total nest boxes with RFID during the 2022 breeding season and 22 boxes during the 2023 breeding season. Of these, 14 females were banded from the previous year, 9 of which had been RFID-monitored during the 2022 season. Thus, my total sample size over the two-year span of this study was 41 females. Before filtering out continuous PIT tag readings, I recorded a total of 551,737 detections – 210,297 in 2022 and 341,440 in 2023. After filtering out successive readings within a two-minute window, I had 112,731 total detections recorded – 50,866 in 2022, and 61,865 in 2023. The average provisioning rate for females was 7.45 visits per hour ($\sigma = 1.42$) in 2022, and 7.68 visits per hour ($\sigma = 0.75$) in 2023.

Insect abundance measurements

I detected a total of 4,329,033 insects across 24 unique sampling days in 2022 and 9,375,468 insects across 46 sampling days in 2023, resulting in a combined total of 13,704,501 insects recorded across 70 days spanning both years of the study. The average daily insect traffic rate was 12,066 insects per km for 2022 ($\sigma = 7{,}734$) and 12,844 insects per km for 2023 ($\sigma = 7{,}500$). Insects were detected between 25 and 825 m above ground level. I found 32.72% of insect activity occurred between 75 and 125 m above ground level, with a daily average traffic rate of 4,148 ($\sigma = 3{,}467$) at this flight altitude.

Atmospheric conditions and insect activity

The top model examining insect traffic rate as a function of weather conditions included all predictors and had a weight of 0.986. This model explained 73.4% of the overall deviance in my data and had an R^2 of 0.72 (see Table 2.1 for full model results). Each predictor had a significant correlation with insect activity. Increasing temperature had a positive correlation with insect activity (Figure 2.1B). High wind speed and presence of precipitation were negatively correlated with insect activity (Figure 2.1C and 2.1D respectively). Finally, insect activity across the proportion of the day indicated increasing activity throughout the morning and decreasing activity throughout the afternoon, followed by a slight increase near sunset (Figure 2.1E).

Insects, weather, and female provisioning rates

My generalized additive mixed model GAMM including only insect traffic rate and proportion of the day as fixed effect predictors explained 37.5% of the overall deviance in female provisioning visitation rates and had an R^2 of 0.35 (see Table 2.2 for full model results). Increasing insect traffic rate was positively correlated with female provisioning activity, with visitation rate eventually plateauing at high levels of insect activity (Figure 2.3A). The proportion of the day was also a significant predictor, with visits increasing in the morning, plateauing throughout midday, and peaking a second time before decreasing at sunset (Figure 2.3B).

My GAMM examining female provisioning rates as a function of insect traffic rate, precipitation, wind speed, and proportion of the day explained 38.1% of the deviance in my data and had an R^2 of 0.36 (see Table 2.3 for full model results). Apart from insect traffic rate, all predictors had a significant correlation with female visitation rates. The presence of precipitation had a negative correlation with female visitation rates, with approximately 1.5 fewer visits occurring during hours with precipitation. Wind speed had a generally negative relationship with provisioning rate, and steeper declines were seen in stronger winds. Across the proportion of the day, female visits increased throughout the morning, plateaued throughout midday, and peaked again before decreasing near sunset.

DISCUSSION

Airspaces are characteristically ephemeral environments, and rapid shifts in weather conditions are linked to fluctuations in airborne food resources (Diehl 2013; Diehl, et al. 2017). For avian aerial insectivores, navigating this landscape to successfully provision nestlings is a critical aspect of adult fitness (Winkler and Allen 1996; Twining, et al. 2018) which becomes an even greater challenge at high elevations. My results support the high dependency of aerial insect abundance on clear weather conditions, and I show that the availability of insect prey is an important driver of Tree Swallow provisioning effort.

Aerial insect activity is highly weather dependent (Taylor 1963; Hallmann et al. 2017; Hussell and Quinney, 2008; Shipley, et al. 2020). With over 70% of the deviance in insect traffic rate being explained by my model, my results corroborate these previously documented relationships and lend support for the use of radar-collected insect traffic rates as a metric of aerial insect activity. Furthermore, the strength of the relationship between weather conditions and insect activity demonstrates that weather conditions can serve as a proxy of insect abundance. This could be especially useful in instances where collecting insect abundance data on-site is not feasible.

My data showed extreme variability in the intensity of insect traffic rates across the breeding season (Figure 2.4), with 27,000 more insects detected on average on high activity days compared to days with low activity. At the Mountain Campus, I found insect activity was generally higher in July compared to dates in June. With phenology shifts advancing Tree Swallow breeding as much as 4.2 days earlier each decade (Dunn and Winkler 1999; Bourett, et al. 2015; Shipley, et al. 2022), this indicates increased potential for early breeders to experience periods of low food availability. Furthermore, weather conditions earlier in the spring are much more variable, conferring increased chances of cold snaps that negatively influence food availability as well as nestling survival (Shipley, et al. 2020). For example, on June 24, 2023, the average daily insect traffic rate was only 1,600 ($\sigma = 2{,}647$) – one of the lowest daily averages recorded in our 2023 data. The average daytime temperature was only 12.37°C on this day. In contrast, I recorded an average daily insect traffic rate of 26,786 ($\sigma = 8{,}260$) on July 12 – one of the highest rates 2023. The average daytime temperature on July 12 was 20.01°C, a value common later in the breeding season and much more conducive to aerial insect activity (Figure 2.5).

Temperature has long been known to influence aerial insect activity (Taylor 1963), and my results support previous findings that aerial insect activity diminishes with cooler temperatures (Cox, et al. 2020; Winkler, et al. 2013). I found that insect traffic rate was positively correlated with average hourly temperature. I would expect that airspace foraging conditions would be optimal for Tree Swallows under warmer temperatures as their ability to detect and capture insect prey should increase. However, an upper threshold possibly exists in which increased insect movement could decrease catchability (Poulsen, 1995), making foraging conditions more difficult for avian aerial predators.

Across June and July, we recorded 47.5% of days with precipitation at our field site during the 2023 season, whereas only 37.5% of days had precipitation occur during 2022. Precipitation events are predicted to increase in frequency under climate change (Cox, et al. 2020), which could exacerbate decreases in insect availability resulting from largescale declines in aerial insect abundance (Hallmann, et al. 2017). While I did not record high instances of nestling mortality in 2023 compared to 2022, these temporary food shortages likely have a negative impact on nestling development, which may have carry-over effects on post-fledging survival (Cox, et al. 2020; Shipley, et al. 2020).

By modeling Tree Swallow provisioning effort as a function of insect activity, I sought to quantify how the food availability influenced provisioning behavior. My model including only insect traffic rate and proportion of the day as fixed effect predictors showed a significant positive relationship between insect activity and female provisioning effort, lending evidence to support my initial prediction. It is worth noting that the full model, which included two additional variables, only explained 0.6% more of the deviance in provisioning rates compared to the model without weather predictors. Therefore, it appears that food availability is a main driver of provisioning activity, but these relationships are difficult to untangle given the intimate ties between insect activity and weather conditions. It seems likely that Tree Swallows are maximizing their provisioning effort when insects are more readily available in the airspace. This strategy would yield higher rates of insect prey for the energy invested, and providing nestlings with high levels of food input might serve as a buffer against short periods of suboptimal weather conditions when food is not readily available (Schifferli, et al. 2014).

While radar-collected data reduces the effort required in the field, they have some limitations. First, I cannot determine from my taxon-level insect data if the species being detected constitute species that are preyed upon by Tree Swallows. Furthermore, my insect data span flight heights from 25 to 1,475 m above ground – a range that is likely much broader than that used for foraging. Refining my insect data to altitudes used most frequently by Tree Swallows might result in a stronger relationship between insect activity and foraging effort. Finally, the BirdScan has a limited horizontal range in which it detects insect activity. Female Tree Swallow home ranges can be as large as 2-3 km during the breeding season (Winkler, et al. 2020) – whereas the BirdScan's beam at 250m above ground level is about 500m wide. We used the BirdScan to characterize foraging opportunities across all breeding female Tree Swallow home ranges, which is an area much larger than sampled by the radar. Lastly, if females are traveling outside of the field site to forage, my insect sampling may not be indicative of food availability, thereby weakening the relationship between insect traffic rate and foraging activity. Implementing other technologies such as radio telemetry (Bil, et al. 2023) or altitude loggers (Helms, et al. 2016; Shipley, et al. 2018) to track airspace use of Tree Swallows could help fill these gaps in the future.

As the effects of climate change introduce even greater weather variability into already extreme montane habitats (Freeman, et al. 2018), Tree Swallows will likely be pushed to their limits to survive in high elevation areas of their breeding range. However, these challenges likely extend beyond high elevation habitats for several species of aerial insectivores. Recent reductions in the availability of airborne insects (Hallmann, et al. 2017), a necessary component of adult fitness, have already been recognized as a likely driver of the pronounced population declines in many species of aerial insectivores (Cox, et al. 2019; Spiller and Dettmers 2019). Airborne insect availability may become more uncertain under increased weather extremes, creating hardships for Tree Swallows and many other organisms that rely on aerial insects as a food resource (Imlay, et al. 2018). My results indicate that even temporary instances of reduced food availability correlate with lessened provisioning, translating into lower measurements of nestling mass. Although I documented a fledging success rate of 85% ($\sigma = 29\%$) during this study, this does not necessarily correlate with fledgling survival after leaving the nest. Fledglings face high rates mortality, and smaller body sizes could have negative carry-over effects that further decrease fledgling survival (Cox, et al. 2019). Reductions in fledgling survival and recruitment may be yet another factor contributing to Tree Swallow population declines on a broader scale.

My direct quantification of insect abundance lends a more complete understanding of the intricate interplay of weather, food availability, and provisioning behavior in a high elevation system. With predictions indicating widespread increases in extreme weather events (Rummukainen 2012), the challenging conditions currently unique to montane systems may become commonplace across the entirety of the breeding range. The Mountain Campus serves as a model environment, representing a habitat at the frontier of threats brought on by climate change. My results may serve as a forecast of how multiple aerial insectivore populations will likely respond to novel atmospheric conditions and subsequent reductions in food availability across a broad range of habitats.

Aerial activity of both birds and insects is challenging to quantify. I combined multiple technologies – radar and RFID – to better understand the intricate connections between taxa across the seemingly invisible habitats that surround us — airspaces. My previous investigation shows a strong connection between Tree Swallow provisioning rates, growth rates, and atmospheric conditions (Chapter 1), and now, through this study, I make the connection between atmospheric conditions and prey availability — a missing link in our understanding. The organisms that rely on airspace habitats must contend with the risks and challenges associated with novel and extreme conditions. Aerial insectivores constitute critical links in the ecosystems that they inhabit, and it is essential that we continue studies in these regions to help predict the challenges they will face more broadly in a rapidly changing world.

Table 2.1 Model results for GAMM comparing insect traffic rate to weather conditions. Temperature, wind speed, precipitation, and proportion of the day were included as fixed effects. Observation date was included as a random effect. Asterisks denote significant predictors.

	Parametric coefficients			**Smooth terms**		**All**
	Estimate	SE	*t*-value	edf	*F*	*p*-value
Deviance explained: 73.4% **R-squared: 0.72**						
Temperature	-	-	-	1.94	137.15	<0.0001*
Wind speed	-	-	-	1.00	82.97	<0.0001*
Precipitation	-16.01	5.38	-2.98	-	-	0.03*
Proportion of day	-	-	-	5.75	42.43	<0.0001*
Random effect: Observation date	-	-	-	61.23	7.78	<0.0001*

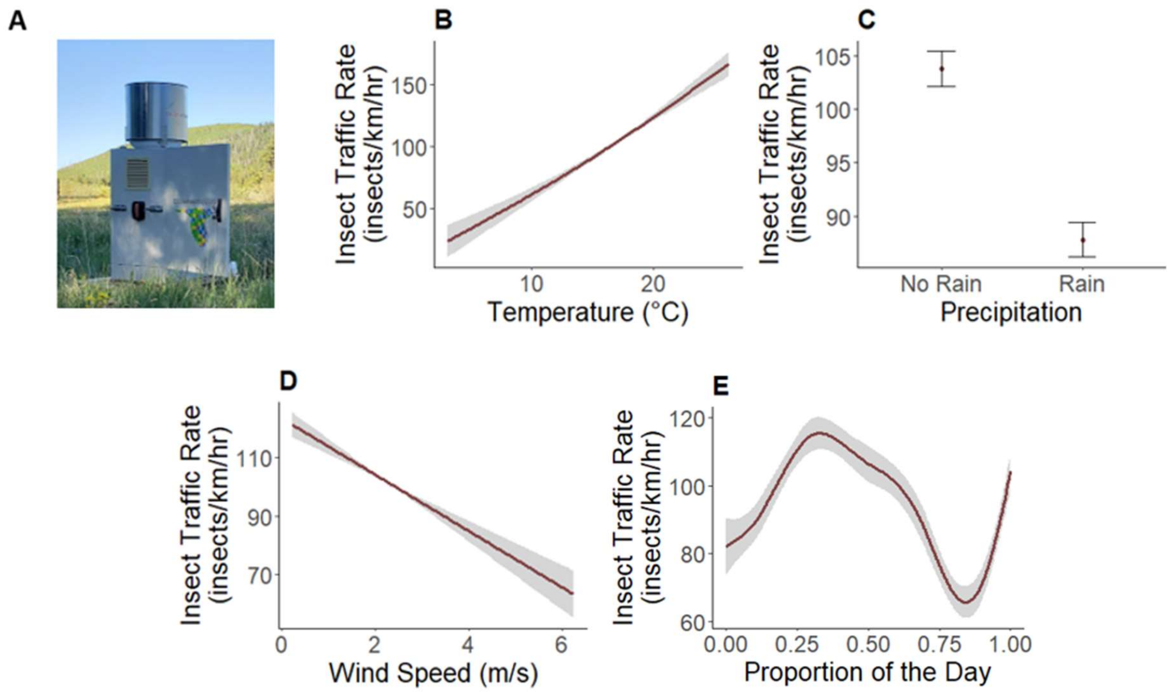

Figure 2.1 GAMM fits for significant weather and temporal predictors of insect traffic rate. Predictor values ranged between their 1st and 99th quantile of observed values, and other model predictors were held constant at their median observed values. A) Insect data was collected by the BirdScan MR1, deployed at CSU's Mountain Campus. B) Average hourly temperature had a significant positive relationship with insect traffic rate. C) Precipitation had a significant negative effect on hourly insect traffic rate. D) Average hourly wind speed had a significant negative relationship with insect traffic rate. E) Proportion of the day had a significant effect on insect traffic rate, with activity generally increasing throughout the morning, decreasing in the afternoon, and slightly increasing near sunset.

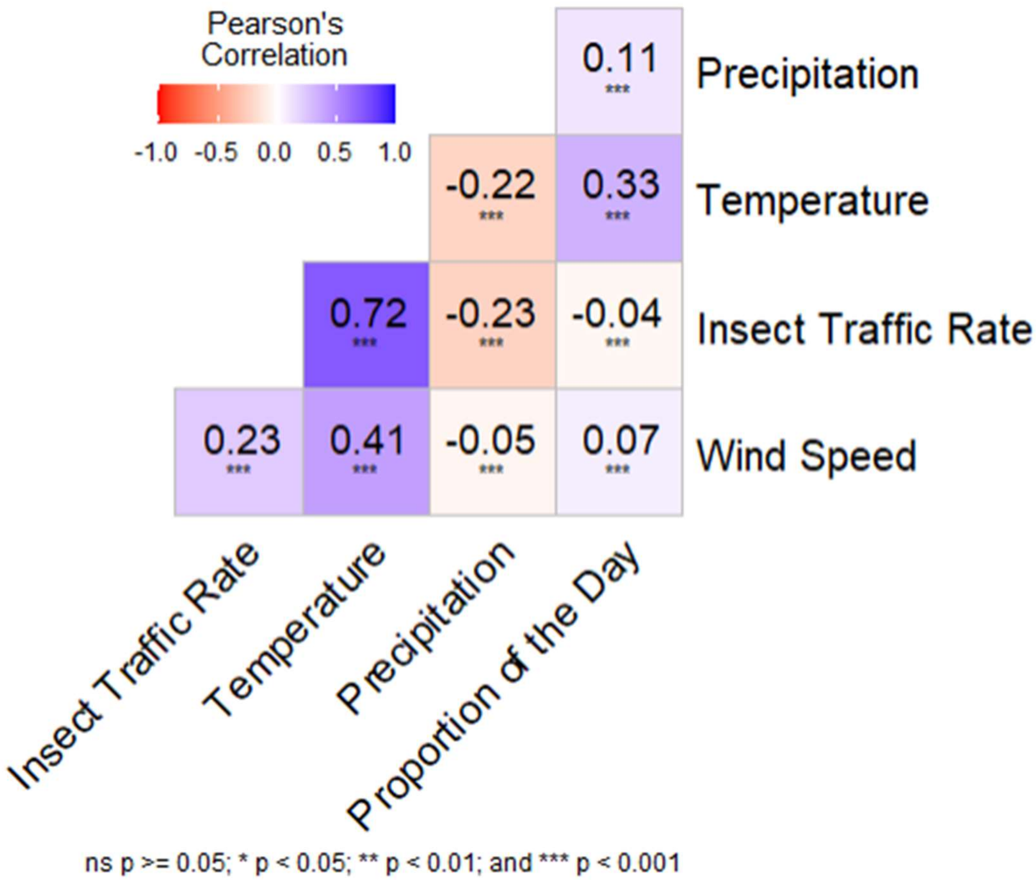

Figure 2.2 Pearson's correlation coefficient plot for weather and insect activity predictors. Most predictors did not have very strong correlations. However, insect traffic rate had a strong positive correlation with average hourly temperature.

Table 2.2 Output of GAMM of insect activity predicting female provisioning visits. Insect traffic rate and proportion of the day were modeled as splines. Observation date and female band number were included as random effects. "Band no." represents female band number, and "Obs. Date" represents observation date.

	edf	Chi-square	*p*-value
Deviance explained: 37.5% **R-squared: 0.35**			
Insect traffic rate	2.36	15.00	0.002*
Proportion of day	5.96	965.00	<0.0001*
Random effect: Band no., obs. date	453.01	1936.00	<0.0001*

Table 2.3 Output of GAMM predictions of female provisioning visits as a function of insect availability and weather conditions. The best model included insect traffic rate, wind speed, precipitation, and proportion of the day. Observation date and female band number were included as random effects.

	Parametric coefficients			**Smooth terms**		**All**
	Estimate	SE	*z*-value	edf	Chi-square	*p*-value
Deviance explained: 38.1% **R-squared: 0.36**						
Insect traffic rate	-	-	-	1.94	2.64	0.39
Wind speed	-	-	-	1.79	5.39	0.04*
Precipitation	-0.14	0.02	-7.33	-	-	<0.0001*
Proportion of day	-	-	-	5.96	983.00	<0.0001*
Random effect: Band no., obs. date	-	-	-	452.97	1924.63	<0.0001*

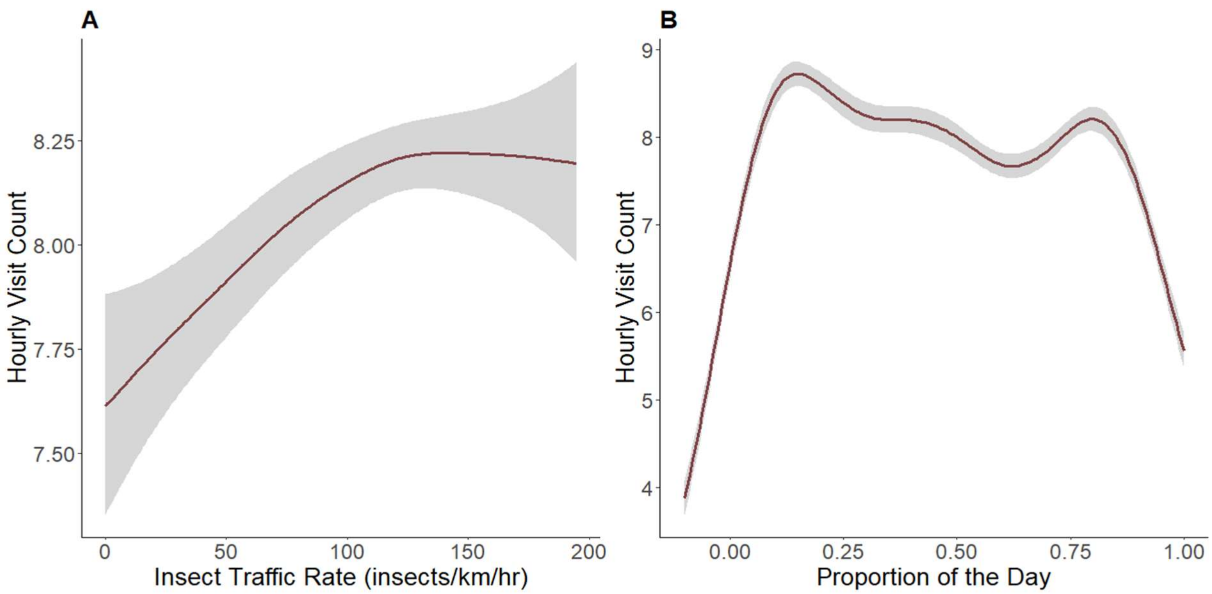

Figure 2.3 GAMM fits for female provisioning visits as a function of insect activity and proportion of the day. A) Hourly visits significantly increased with insect traffic rate before plateauing at high levels of insect availability. B) Provisioning visits increased throughout the morning, plateaued throughout the day, and peaked a second time just before sunrise.

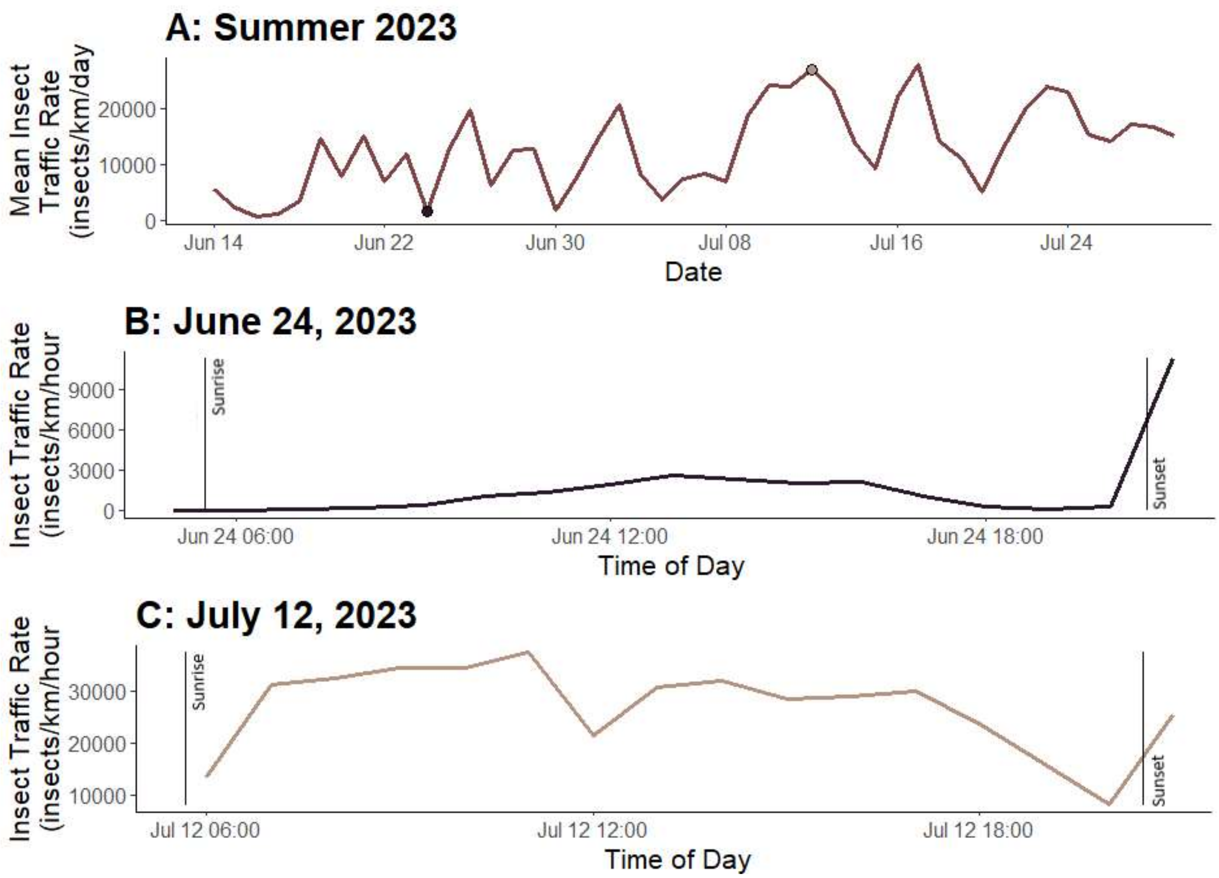

Figure 2.4 Seasonal variation in insect traffic rate. A) Insect activity varied greatly between June 14 and July 29, 2023. B) On June 24, average temperatures were cooler, and the average daily insect traffic rate was one of the lowest values recorded during 2023. C) On July 12, average temperatures were high, and insect traffic rate was one of the highest values recorded during 2023.

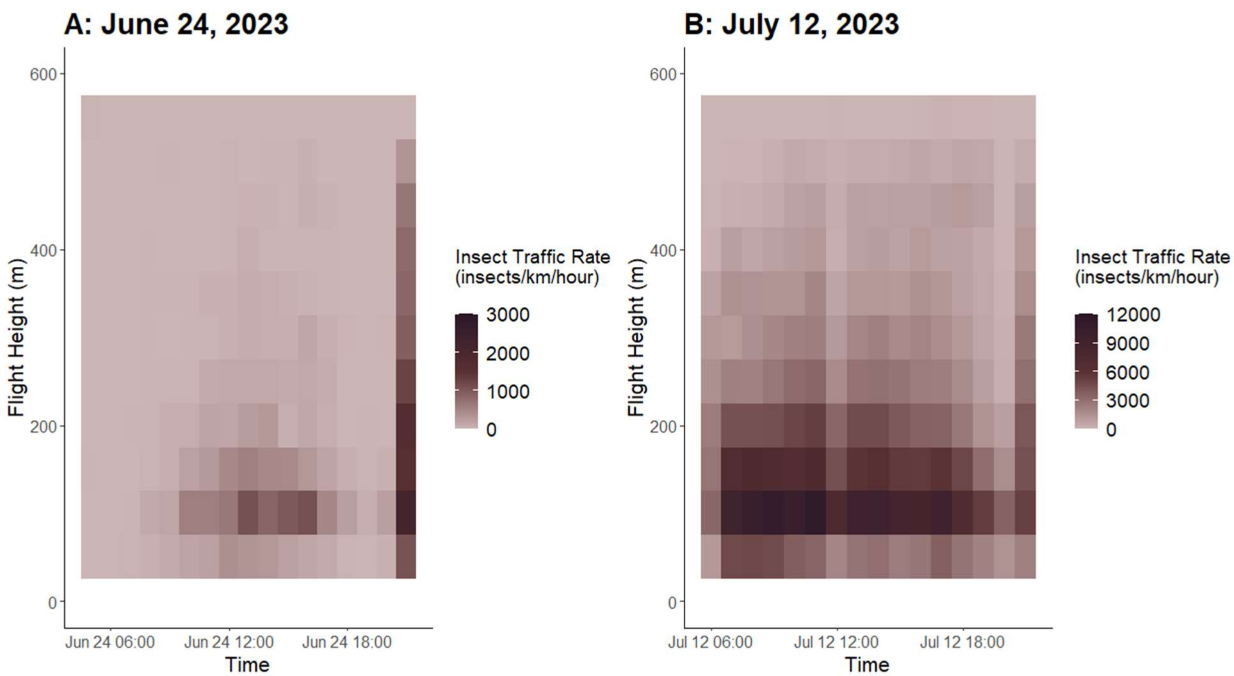

Figure 2.5 Insect traffic rate across high and low activity days. Insect density decreased as flight height increased. Insect activity varied greatly throughout the summer. A) June 24, 2023 had a low average daytime temperature of 12.37℃ and saw minimal insect activity. B) July 12, 2023 was a warm and clear day with an average daytime temperature of 20.01℃ and very high levels of insect activity. Note that the color scales denoting the intensity of insect activity differ between plots.

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