DISSERTATION

RESPONSE OF ROOSTING AERIAL INSECTIVORES TO ONGOING CLIMATE CHANGE QUANTIFIED BY WEATHER SURVEILLANCE RADAR

Submitted by

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ABSTRACT

RESPONSE OF ROOSTING AERIAL INSECTIVORES TO ONGOING CLIMATE CHANGE QUANTIFIED BY WEATHER SURVEILLANCE RADAR

Aerial biotas encompass species that feed on airborne insects while in flight, including various bird species (e.g., swallows, martins, nightjars, and flycatchers), bats, and insects (e.g., dragonflies). This community inhabits aerial habitats and occupies a critical interface between terrestrial and aquatic ecosystems. Because these ecosystems provide essential food resources and habitats, aerial insectivores' responses to climate change are closely tied to shifts at these ecological boundaries. As climate change intensifies, these habitats are increasingly unpredictable due to long-term climate shifts and more frequent extreme weather events, like cold snaps. These environmental changes may have driven biological changes at varying levels across aerial trophic food webs, potentially leading to trophic mismatches—where the timing of consumer demand no longer aligns with the availability of their food resources. As a result, aerial insectivores are particularly vulnerable to these shifts, and many are experiencing acute population declines.

As key predators in the aerial trophic system, aerial insectivores help maintain ecosystem balance and health. They also provide ecosystem services, such as pest population control and the reduction of insect-borne diseases. Despite their ecological and agricultural importance, knowledge gaps remain regarding how aerial insectivores respond to environmental changes at a macrosystem scale—particularly regarding shifts in phenology and population dynamics.

Addressing this knowledge gap is crucial for understanding and mitigating the cascading effects of these changes on ecosystems. Therefore, there is a need to monitor changes in aerial insectivore populations and phenology. In North America, some aerial insectivore species form large roosting aggregations—sometimes numbering in tens of thousands—during certain life cycle stages. These roosts appear on Next Generation Weather Radars (NEXRAD) as expanding "angel rings," providing a unique opportunity to quantify their occurrence across broad spatial and temporal scales. To leverage this, I integrated decades of radar data with other remote sensing datasets and machine learning tools to quantify phenological and population changes and to investigate their drivers in two taxonomic groups of roosting aerial insectivores: swallows and bats.

My dissertation centers around the key question: How has the phenology and population of these aerial insectivores changed in response to changing climate? To address this, I first focused on roosting swallows in the Great Lakes region, primarily Tree Swallows and Purple Martins. Chapter 1 asks *How swallow roosting phenology changed over the past two decades?* Chapter 2 asks *Which aspects of climate change, during which periods, at what locations, impact swallow roosting phenology at the Great Lakes?* In Chapters 3 and 4, I shifted my focus to Mexican free-tailed bats in south-central Texas. Chapter 3 asks *Has phenology and population of Mexican free-tailed bats changed in this region?* Chapter 4 asks *Can I predict the intensity of nightly emergence events of Mexican free-tailed bats?* The goal of my work is to provide ecological evidence of these changes and uncover the underlying mechanisms, offering insights that can inform conservation policies and actions.

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CHAPTER ONE

QUANTIFYING LONG-TERM PHENOLOGICAL PATTERNS OF AERIAL INSECTIVORES ROOSTING IN THE GREAT LAKES REGION USING WEATHER SURVEILLANCE RADAR

Summary

Organisms have been shifting their timing of life history events (phenology) in response to changes in the emergence of resources induced by climate change. Yet understanding these patterns at large scales and across long time series is often challenging. Here I used the US weather surveillance radar network to collect data on the timing of communal swallow and martin roosts and evaluate the scale of phenological shifts and its potential association with temperature. The discrete morning departures of these aggregated aerial insectivores from ground-based roosting locations are detected by radars around sunrise. For the first time, I applied a machine learning algorithm to automatically detect and track these large-scale behaviors. I used 21 years of data from 12 weather surveillance radar stations in the Great Lakes region to quantify the phenology in roosting behavior of aerial insectivores at three spatial levels: local roost cluster, radar station, and across the Great Lakes region. I show that their peak roosting activity timing has advanced by 2.26 days per decade at the regional scale. Similar signals of advancement were found at the station scale, but not at the local roost cluster scale. Air temperature trends in the Great Lakes region during the active roosting period were predictive of later stages of roosting phenology trends (75% and 90% passage dates). Our study represents one of the longest-term broad-scale phenology examinations of avian aerial insectivore species responding to environmental change and provides a steppingstone for examining potential phenological mismatches across trophic levels at broad spatial scales.

Introduction

Anthropogenic climate change and its associated increasing temperature influence ecosystems at multiple scales (Inouye, 2022). Phenology is the study of recurring events in organisms' life cycles and their relationships with seasonal and interannual variations in climate (Schwartz, 2013). It is increasingly recognized that phenological changes are a common response to climate change (Menzel et al., 2006). Altered phenology has been documented in a variety of taxa across life stages, including changes in the timing of seasonal avian migration (Helm et al., 2019; Tryjanowski et al., 2002; Youngflesh et al., 2021), terrestrial vegetation green-up date or first bloom date (Cleland et al., 2007; Panchen et al., 2015; Schwartz, 2013), large herbivores' reproduction (Aikens et al., 2021; Kerby & Post, 2013; Post & Forchhammer, 2008), aquatic insect emergence (Everall et al., 2015), and many others. The phenology of key species across these taxa could serve as indicators of ecosystem viability (Gittings et al., 2019). Since phenology is consequential for population dynamics, demography, and community structure (Diez et al., 2012; Miller-Rushing et al., 2010), it is important to observe and quantify the potential shift, or lack thereof, of species' timing of annual events.

Avian aerial insectivore populations are experiencing acute declines, with species in North America experiencing a 31.8% population decline from 1970 to 2017 (Rosenberg et al., 2019). This decline is likely the result of multiple interacting drivers, including the large-scale decrease in abundance of food resources in the form of aerial insects (Conrad et al., 2006; Rioux Paquette et al., 2014; Stepanian et al., 2020), breeding and nonbreeding habitat loss (Herkert, 1994; Holmes & Sherry, 2001), and climate change imparting selection pressure on species with less flexible migration phenology (Spiller & Dettmers, 2019). These proximate threats broadly

influence aerial insectivores' annual cycle across breeding, migration, and nonbreeding seasons (Spiller & Dettmers, 2019).

While aerial insectivores' breeding biology is widely studied (Dunn & Winkler, 1999; Imlay et al., 2018; Neufeld et al., 2021; Saldanha et al., 2019), fewer studies focus on their unique post-breeding and pre-migratory period. Potentially due to less obvious and uniform migration patterns under less time constraints during this period, post-breeding phenology of migratory birds is still poorly understood (Gallinat et al., 2015; Haest et al., 2019; la Sorte et al., 2015). This study offers a unique angle on this understudied part of aerial insectivores' life history. After the breeding season, swallows and martins of all ages in North America transition to pre-migratory roosts in late June and July, some of which contain more than 100,000 birds (K. R. Russell & Gauthreaux, 1999). In the northern United States, summer roosts of aerial insectivore species are largely composed of Purple Martins (*Progne subis*), but also include Tree Swallows (*Tachycineta bicolor*), Barn Swallows (*Hirundo rustica*), Bank Swallows (*Riparia riparia*), and Cliff Swallows (*Petrochelidon pyrrhonota*) (Bent, 1963; Burney, 2002; Kelly et al., 2012; Kirby, 1978). Their communal roosting behaviors, where unrelated conspecifics and heterospecifics aggregate during the nocturnal resting period (Laughlin et al., 2014), present a unique means of examining the timing of a critical life-history stage when insectivores refuel to offset the energy demands of fall migration (Imlay & Taylor, 2020). Birds disperse from roost sites synchronously within one hour before dawn for daily foraging bouts over a large surrounding area and return to the roost 1-2 hours before sunset (Bridge et al., 2016; Brown et al., 2021). Roosts may persist on the landscape for 8-12 weeks, but as the season progresses, birds continue their southbound migration, with roosts all but disappearing in North America by

mid-October (Brown et al., 2021). This discrete roosting behavior can be captured on a macroscale using a remote sensing platform – weather surveillance radar (Laughlin et al., 2013).

The use of next-generation weather surveillance radars (NEXRAD) in biological applications has contributed greatly to our understanding of many areas in ecology. Aeroecology, which is a field of study mostly concerning the movements and behaviors of airborne animals, namely birds, insects, and bats, has been greatly assisted by NEXRAD sensors. Those studies include examinations of avian nocturnal migration on a large spatial and temporal scale (Dokter et al., 2018; Horton et al., 2015, 2020; Nilsson et al., 2019), insect migration or abundance (Westbrook et al., 2014; Stepanian et al., 2020), bat emergence from caves and bridges (Haest et al., 2021; Horn & Kunz, 2008; Stepanian & Wainwright, 2018), stopover site and nesting site identification (Bigger et al., 2006; Bonter et al., 2009; Lafleur et al., 2016), as well as population and behavioral responses to human-introduced disturbances (Cabrera-Cruz et al., 2020; Horton et al., 2019; McLaren et al., 2018; Van Doren et al., 2017, 2021). While previous studies have leveraged this infrastructure for the study of roost identification (Bridge et al., 2016; Cheng et al., 2020; C. Chilson et al., 2019; Kelly & Pletschet, 2018; Laughlin et al., 2014; Russell & Gauthreaux, 1998), little has been done to quantify long-term phenology patterns of aerial insectivore roosting behaviors.

Temperature-associated shifts in life history timing have been reported in some insectivore species. For example, advances of lay dates in long-distance migratory Pied Flycatchers (*Ficedula hypoleuca*) were partly explained by ambient temperature on the breeding grounds (Helm et al., 2019), and warmer winter temperature on the breeding grounds predicted earlier breeding in Tree Swallows likely through insect availability (Imlay et al., 2018). While aerial insectivore phenology may be directly correlated to insect prey phenology (Shutler et al.,

2012), long-term measures of aerial insect distributions and their timing are still challenging to acquire. Therefore, air temperature may serve as a proxy for aerial insect phenology since growing degree days (GDD, a measure of heat accumulation) are tightly coupled with the timing of insect emergence (Everall et al., 2015).

The Great Lakes region is an important ecoregion for millions of en-route migratory birds (Diehl et al., 2003) and it is known that many insectivore species form pre-migratory roosts in this region, near water or crop fields (Bent, 1942; Bridge et al., 2016). The goal of this study was to use long-term radar data to quantify swallow and martin roosting phenology change and phenological plasticity in the Great Lakes region for the first time, as well as to explore the influence of air temperature on roosting timing.

Methods

Radar sites and system specification

The US **Nex**t-generation **Rad**ar (NEXRAD) network consists of 159 S-band radars and is operated by the National Oceanic and Atmospheric Administration (NOAA). Data collection from these remote sensors began in the early 1990s and has been consistent for many stations since the mid-1990s (Chilson et al., 2012; Stepanian et al., 2016; Figure 1.S1). NEXRAD radar products are archived and fully accessible via Amazon Web Services (https://s3.amazonaws.com/noaa-nexrad-level2/index.html). Not only is it a reliable tool for monitoring weather activity, but it also provides an opportunity to monitor animal airspace usage, including migration and dispersal (Kelly et al. 2012, Laughlin et al. 2013). From a radar perspective, swallows and martins show distinct morning exoduses as they emerge from nightly roosting locations, which appear as ring-shaped patterns expanding outwards from the initial roost locations. In the Great Lakes region, these "roost rings" populate radar imagery from late

June to late October (Laughlin et al., 2013). To quantify the timing of aerial insectivore roosting phenology, I extracted roost signals from radar imagery from 21 years of data (2000-2020) across 12 radar stations throughout the Great Lakes region (Figure 1.1). To capture the dispersal of insectivores emerging from roosts, I selected radar scans from 30 minutes before sunrise until 90 minutes after sunrise from June 1st to October 31st.

These 12 radar stations operate at S-band, with a wavelength of approximately 10.71 cm (ranges from 10.02 cm to 11.09 cm) and 2.7–3.0 GHz frequency. Airspace is sampled by the predetermined volume coverage patterns (VCPs), which vary in the number of beam sweeps and the amount of time needed to complete a volume scan ranging from 5 to 10 minutes. At each radar station, data are collected as the radar antenna scans 360 degrees at different elevation angles, ranging from as few as 5 unique elevational scans to as many as 15. The scans are organized into discrete azimuths and range gates. In 2008, the spatial resolution was increased from 1.0° azimuths and 1 km range gates (legacy resolution) to 0.5° azimuths and 250 m range gates (super-resolution). In 2013, the network was upgraded to dual-polarization, adding three more radar products (total measured differential phase, differential reflectivity, copolar correlation coefficient) to the original standard radar moments (radar reflectivity factor, radial velocity, spectrum width). Copolar correlation coefficient (ρ_{HV}) has proven useful in separating precipitation from biological scatters (Stepanian et al., 2016), as it was used in this capacity for this study when available. The beam samples the atmosphere at greater heights with increasing distance from the radar because radar beam geometry under the standard atmosphere refraction is assumed to be 4/3 of the earth's radius, as well as radar beam tilts usually start from 0.5° elevation angle. For this reason, I restricted our extractions to 150 km from each radar station (within a 300 km x 300 km square bounding box centered at the radar) to ensure roosts would be

visible within the radar beams. I acknowledge the influence of range on roost detections, specifically, roosts that are far away from or too close to the radar are likely to be underestimated or missed. However, detection bias introduced by the range effect would be stable across years, thus not broadly impacting the macro-phenology patterns that I am examining.

Automatic detection and validation through manual screening

Historically, it has been challenging to separate swallow and martin roost rings from non-biological information (e.g., precipitation) and other biological activities showing up on radar scans (e.g., insects, bats, and other birds). Without an automatic system, it is also prohibitive, particularly when manual detection is the only tool, to process large amounts of data covering a long time-series and large spatial extent. To tackle these challenges, we leveraged a deep-learning system introduced by Cheng et al. (2020) to automatically detect and track roosts in radar scans. This system consists of two modules: first, a single-frame detector was built on Faster R-CNN (Ren et al., 2017) to identify and localize the roosts per radar scan by predicting the probability that a roost of each candidate size exists near each reference position (45 reference anchors ranging from 16 x 16 to 512 x 512). Faster R-CNN is a widely deployed and highly cited region-based CNN (convolutional neural network) detector, which simultaneously classifies and localizes objects. Second, we used a tracking algorithm (Ren et al., 2017) to associate roost detections across temporally consecutive scans. The roost identification algorithm was trained on a manually annotated roost dataset collected in previous roost studies (Cheng et al., 2020; Laughlin et al., 2016), which consists of 88,972 radar scans with 63,691 labeled roosts. Following Cheng et al. (2020), we rendered 3 channels of radar products (reflectivity at 0.5° tilt, radial velocity at 0.5° tilt, and reflectivity at 1.5° tilt) as 600 x 600 pixels (1 pixel = 0.5 km) images in the "top-down" Cartesian-coordinate view and finetune a detector pretrained on a

large-scale natural image dataset (Russakovsky et al., 2015). The resulting system detections are given by a class probability and bounding box coordinates for each roost (Figure 1.1b). Lastly, to remove additional false positive detections, we used dual-polarization radar products to mitigate weather contamination and an existing wind turbine database (Hoen et al. 2018) to remove returns from those stationary ground-based targets. I refer the readers to Cheng et al. (2020) for more technical details.

While the automated detector accurately identified the location of most roosts, it was also prone to some errors introduced by non-biological targets or unknown noises. To ensure confidence in our detections, we (YD, MCB, and VS) manually screened all detections to remove false positives, including contamination from precipitation and anomalous propagation, and we worked to ensure that bounding boxes appropriately estimated the boundaries of the roosts. A rigorous screening protocol was developed to ensure consistency among three screeners. During the screening, days with more than 50% of the radar domain contaminated by precipitation or anomalous propagation were discarded. Different labels were created for detections of roosts, non-roosts, weather-contaminated roosts, anomalous propagation roosts, unknown-noise roosts (roosts with strong scattered undefined signals in the background), and bad tracks. Bad tracks were defined as detection tracks that failed to follow the typical roost emergence and disappearance pattern, stopped early, jumped to track another roost or other objects, continued tracking when roosts already disappeared, or captured bounding boxes that were too large or too small. This extensive screening effort will help improve the roost detection algorithm performance in the future, as well as provide us with information of potential noises introduced by the environment and radar system.

After the screening process, I tested if the number of roost detections differed before and after super-resolution and dual-polarization upgrades. I calculated the mean number of unique roost tracks detected within each radar station across all years before and after the upgrades, then I conducted paired sample Wilcoxon tests (non-parametric due to non-normal distributions) in R. I did not find significant differences between pre-upgrade and post-upgrade roost detections for super-resolution and dual-polarization upgrades (Figure 1.S2).

Radar data processing

To estimate the number of swallows and martins within each roost, we extracted the raw reflectivity factor values from Level II weather radar data and translated it into the number of birds (Chilson et al., 2012; Diehl et al., 2003; Dokter et al., 2011; Gauthreaux & Belser, 1998; Nebuloni et al., 2008). Specifically, we converted the radar reflectivity factor Z (dBZ) to radar reflectivity η (cm²/km³) in the linear scale, which is directly related to the density of bioscatterers, using

$$\eta\,[dB] = Z\,[dBZ] + \beta$$

$$\eta\,[dB] = 10 * \log_{10}(\eta\,[cm^2/km^3]/\eta_0)$$

where $\beta = 10\log_{10}(10^3\pi^5|K_m|^2/\lambda^4)$ with $|K_m|^2 = 0.93$ for liquid water, $\eta_0 = 1$ cm^2/km^3 and $\lambda = 10.71\ cm$ (typical value for WSR-88D S-band; wavelength of these 12 radars ranges from 10.02 cm to 11.09 cm).

Purple Martins are the largest species in the *Hirundinidae* family in North America, so we used its radar cross section (RCS) to produce conservative estimates of the number of birds. Assuming all birds are uniformly distributed within the radar sampling volume and using a radar cross section (RCS) for Purple Martins of 16.2 cm^2 according to the linear relationship between bird mass and radar cross section (Horton et al., 2019):

$$log_{10}(cross\text{-}section) = 0.670 * \log_{10}(bodymass)$$

and mean purple martin mass of 51 g (Dunning, 2007), we calculated a number density D_{bio} and number of birds per roost N_{bio} for each roost detection at each tilt using

$$D_{bio} = \eta / \sigma$$

$$N_{bio} = D_{bio} * V_{rad}$$

where V_{rad} is the volume of a voxel, a sampling unit in a three-dimensional cone cut by two parallel planes 250 m apart. We calculated the volume of each voxel of the radar sampling volume by assuming a 1° symmetric circular conical beam width for legacy-resolution scans (before the 2007-2008 Super Resolution upgrade), and an elliptical conical shape of 1° vertical beam width and 0.5° horizontal beam width for super-resolution scans (Torres et al. 2007). Lastly, we summarized the cumulative number of birds below the height of 5000 m by adding up the averaged bird counts in each standardized elevation angle bin (1-degree interval). All radar data processing was done in Python (version 3.9.4) using *PyArt* and *pywsrlib* packages and R (version 4.0.2).

Quantifying phenological trends

I explored phenological trends at three spatial levels: persistent local roost clusters, radar stations, and the Great Lakes region. Roost clusters were generated by a mean shift clustering algorithm (Pedregosa et al., 2011) using our roost track detections, which calculated density-based clusters while maintaining a minimum shape (Belotti et al., in review). First detection points included in the same cluster represent a region consistently used by swallows and martins to roost in a local region, thus defined as a roost cluster. I defined persistent roosts as those that had roosting activity in 90% or more of available years (i.e., > 18 years). I excluded station-years or roost-years that had fewer than ten days with roost detections from the analysis. Following the

manual screening, I filtered for detections labeled as *swallow roosts* and excluded detections with all other labels (e.g., *bad track*, *weather contamination*, etc.). To calculate the daily bird count for each station-year, I derived the mean number of birds for each roost track, then summed up all the birds from all roosts detected in a day within a station. I excluded the days from the analysis if there was more than 50% weather contamination in the radar scanning area, intense anomalous propagation, or the sampling period of the day was less than 100 minutes. Days without any detections and not excluded from the analysis were filled as true zeros.

To estimate potential changes in different roosting phenology stages at persistent roost cluster and radar station scales, I first used a generalized additive model (GAM) fit to each station-year and roost-year to model the roosting activity throughout a roosting season, using R package *mgcv* (Wood & Wood, 2015). I constructed GAMs with daily bird counts as the response variable and day of year (DOY) as the independent variable with the smoothing parameter (k) set to 5 using a quasi-Poisson correction for overdispersion, with *thin plate regression splines (tp)* smooth term and *REML* smoothing parameter estimation method. I used this model construction to predict counts throughout the season. From these predicted counts, I calculated the 10^{th}, 25^{th}, 50^{th}, 75^{th}, and 90^{th} percentile dates and mean dates as phenology estimates since I want to capture the phenological trend at different stages of roosting. Each percentile date is the first date by which a certain percent of the cumulative bird count has been reached. I also included the mean date since estimating trends using the mean date is often most accurate, as well as robust to variation in sample sizes (Moussus et al., 2010). The mean date is calculated as the mean passage date weighted by the bird counts at each date over the whole sampling period of a year. To extract each phenology estimate at the Great Lakes region level, I calculated weighted passage dates using station-level phenology estimates weighted by log-

transformed cumulative passage in each year. Taking year as an independent sampling unit, I tested for long-term trends for phenology using a linear regression model at all three different scales. To compare the long-term phenology trends to the results found in other literature (Horton et al., 2020), I conducted a non-parametric Wilcoxon test (small sample size and not normally distributed) for paired samples to assess if the phenology trends are significantly different across the Great Lakes region.

The distributions of peak roosting activity dates across stations were tested for normality using the Shapiro-Wilk test. Since the hypothesis of normality was not met for all the stations, I used non-parametric tests (Kruskal–Wallis test and Fligner-Killeen test of homogeneity of variances) to test for differences in means and variances of the peak roosting activity timing across stations.

Air temperature as an indicator of phenology change

To examine the association between air temperature and aerial insectivore roosting phenology, I used air temperature 2 m above ground (°C) gridded at 32 km from NCEP North American Regional Reanalysis (NARR) data archive (https://psl.noaa.gov/data/gridded/data.narr.html), which is available from 1979 to the present and measured 8 times daily. I calculated the daily mean temperature for the entire study region and within the 150 km buffer area around each station during the active roosting months (July 1st to September 30th). Seasonal means of mean temperatures were then calculated for each year and each station. To quantify the trend in surface air temperature, I used a linear regression with year and radar ID as fixed effects for region-level analysis and year as fixed effect for station-level analysis. To test if surface air temperature was predictive of roosting phenology interannual variations, I fit linear regressions for each station and the whole region using all six phenology

estimates to relate roosting phenology to air temperature. To examine the relationship between trends in temperature and roosting phenology, I conducted linear regression analysis at the station level. All analyses were conducted in R (version 4.0.2).

Results

Descriptions of aerial insectivore roosting phenology

I sampled 3192 mornings for 12 radar stations across the Great Lakes Region from 2000 to 2020. In total, I processed and screened 940,641 radar scans, within which I obtained 67,273 detections of roosts, grouped into 16,222 tracks (non-duplicated) by the machine learning algorithm. Across this period, 85.32% of the total tracks were identified as swallow and martin roosts (non-contaminated and well tracked). Each station-year had a mean of 60.4 unique roost tracks detected (SD = 43.2). Some martin roosts were discarded in the analysis due to anomalous propagation (0.6%), imperfect tracking (3.8%), unknown noise (7.3%), and weather contamination (2.9%). After filtering out the years with roost detections on fewer than 10 days, I excluded radar station KMQT (located at Marquette, Michigan) from the analysis since it did not meet this criterion.

Swallow and martin roosting activity (mean daily bird count across all stations and years) increased from early August [10% passage date: 212 ± 7.78 (±SD) DOY; 25% passage date: 220 ± 5.89 (±SD) DOY], peaked in mid-August [50% passage date: 227 ± 5.69 (±SD) DOY; mean date: 227 ± 4.66 (±SD) DOY], and then declined in late August [75% passage date: 234 ± 6.21 (±SD) DOY; 90% passage date: 240 ± 7.20 (±SD) DOY] in the Great Lakes region (Figure 1.2a-b). Means in peak roosting activity dates did not differ across stations (Figure 1.2c, Kruskal-Wallis test: chi-squared = 9.2065, df = 10, *p*-value = 0.5126), however, variances in peak roosting activity dates differed across stations (Figure 1.2c, Fligner-Killeen test of homogeneity

of variances: chi-squared = 19.802, df = 10, *p*-value = 0.03118). To examine the pair-wise correlations between 50th percentile passage date at each station, I calculated Pearson's correlation coefficients. I found that the timing of events was positively correlated with each other at the majority of the stations, and all significant ($p < 0.05$) correlations were positive (Figure 1.3; Figure 1.S3).

Changes in phenology at three different spatial scales

At the regional scale, I found that across 21 years, swallows and martins formed pre-migratory roosts in the Great Lakes region approximately 2.26 ± 2.23 days earlier per decade (coefficient ± 95% CI, $p = 0.047$) for peak roosting activity date (Figure 1.4). Similar advances were shown in the mean date metrics (coefficient ± 95% CI = -2.23 ± 2.00 d decade^{-1}, $p = 0.030$), 75% passage date metrics (coefficient ± 95% CI = -3.10 ± 2.51 d decade^{-1}, $p = 0.018$) and 90% passage date metrics (coefficient ± 95% CI = -4.09 ± 3.67 d decade^{-1}, $p = 0.031$). However, I did not see significant trends for the 10% and 25% dates. Our phenology trends were significantly different between this study and a previous study on nocturnal avian migration (Horton et al., 2020) across the Great Lakes region (Wilcoxon test for paired samples, *p*-value < 0.05, V-statistic = 9, n = 11). At the station scale, I found significant advancements in peak roosting activity dates in 3 out of 11 stations, with the rate of change varying between -8.2 to -4.5 d decade^{-1} ($p < 0.05$). At the local persistent roost scale, I did not find any significant phenological shifts for peak roosting activity date (n = 16).

Association between air temperature changes and phenological changes

Air temperature at 2 m above ground level during the active roosting months (July to September) increased over the past two decades at the Great Lakes region (estimate ± 95% CI =

0.58 ± 0.18 °C decade^{-1}; p-value < 0.001) and warmed up significantly at 41.7% of the stations (5 out of 12 stations), varying between 0.67 to 0.80 °C decade^{-1} (p-value < 0.05).

I compared phenology metrics to mean air temperature at station and regional scales, using the 10th, 25th, 50th, 75th, and 90th percentile passage dates and mean date to capture all the phases of the roosting behavior. At the region scale, the daily mean temperature was not a significant predictor for any of the phenological estimators (10% passage date: slope = -0.010, p = 0.944; 25% passage date: slope = -0.108, p = 0.789; 50% passage date: slope = -0.501, p = 0.283; mean date: slope = -0.172, p = 0.692; 75% passage date: slope = -0.214, p = 0.737; 90% passage date: slope = 0.253, p = 0.765). At the station scale, the daily mean temperature was also not predictive of roost phenology. Since I did not detect a significant phenology trend at the persistent roost scale, I did not explore the effect of air temperature on phenology at the roost scale.

However, I found that temperature trends positively correlated with the trends in roosting phenology 75% passage dates (coefficient ± 95% CI = 0.030 ± 0.024, p-value = 0.0197, F(9) = 8.015) and 90% passage dates (coefficient ± 95% CI = 0.022 ± 0.018, p-value = 0.0208, F(9) = 7.826), but were not correlated with our other phenological estimators, for example 50% passage dates (p-value = 0.267, F(9) = 1.399).

Discussion

Migration and pre-migratory roosts are essential periods in swallow and martin life histories, and using remote sensing, paired with new machine learning techniques, I show that this critical phenophase has been shifting earlier throughout the past two decades. Specifically, our results indicate that their peak roosting phenology has advanced by 2.26 ± 2.23 days per decade (coefficient ± 95% CI) across the Great Lakes region. Air temperature trends in the same

region during the active roosting period were predictive of later stages of roosting phenology trends (75% and 90% passage dates). There was also great within-season synchrony of peak timing of roosting across the stations, which suggests phenology is paced by a region-wide environmental cue not fully described by temperature alone. This study represents the first long-term broad-scale examination of aerial insectivore species' phenology during the non-breeding season and the first ecological application using roost detection by a deep-learning approach at scale.

Our finding of advancing phenology is consistent with other large-scale studies on migratory birds in North America and Europe. In a recent study on nocturnal avian migration using weather surveillance radar data, peak autumn migration timing advanced 0.52 ± 0.12 days decade^{-1} at the eastern flyway of the contiguous United States (Horton et al., 2020). However, the magnitudes of advancement were significantly different between our measures from the Great Lakes region and those of Horton et al. (2020). Differences may not be surprising in this comparison, particularly because our measures exclusively characterize aerial insectivores, whereas the other study focused on measures from all nocturnal migrant species (likely hundreds of species). Given that I showed more rapid advancements using similar technology, it may suggest that aerial insectivores display greater sensitivity to changes in aerial insect prey composition under climate change (Clark & Hobson, 2022; Twining et al., 2018, 2022). In addition, using citizen science data (i.e., eBird), Youngflesh et al. (2021) found that Tree Swallows, Barn Swallows, and Cliff Swallows arrived earlier in spring during periods with earlier vegetation green-up, with the first two species having non-zero overlapping 95% credible intervals. In another large-scale phenological study in the UK, projected median shifts in phenology based on more than 10,000 terrestrial and aquatic phenological datasets over 20 years

suggest that birds will advance their seasonal timing 2-4 days by the 2050s (Thackeray et al., 2016). Additionally, evidence from mist-netting data on autumn avian migration in Europe (Haest et al., 2019; Tøttrup et al., 2006) showed interspecific variations in phenology trends, with species showing earlier departure (-1.8 days decade^{-1}) and earlier mean autumn passage date (-0.01 to -1.86 days year^{-1}). Apart from evidence on shifts in migration timing, the breeding phenology in various aerial insectivores is also shifting earlier. Cliff, Barn, and Tree Swallows in southeast Canada (New Brunswick and Nova Scotia) initiated clutches 8.1, 9.9, and 10.4 days earlier from 2006-2016 compared to 1962-1972, which is equivalent to 1.8, 2.2, and 2.3 days earlier decade^{-1} (Imlay et al., 2018). In another long-term study, Tree Swallows have advanced their egg-laying date 4.2 days decade^{-1} in southern Quebec, Canada (Bourret et al., 2015).

At the regional scale, I observed that 90% passage dates showed the strongest advances compared to weaker 75% passage date, and even weaker 50% passage date, potentially due to the pressure to avoid harsher environmental conditions in the latter part of the season, including cold snaps, depleting food resources, and low water availability (Horton et al., 2020; La Sorte et al., 2015; Xu & Si, 2019). Early parts of the season (10% and 25% passage date) did not show a significant trend, which could have resulted from nonuniform arrivals composed of different age groups, individuals coming from different breeding grounds, different sexes, or individuals traveling at different rates (Neufeld et al., 2021). This suggests that climate change may be impacting aerial insectivore phenology unevenly across different periods of their roosting stage, potentially leading to a shortened pre-migratory roosting season.

Climate change affects aerial insectivores differently depending on life history stage, and these differences may be due to diet diversity (Winkler et al., 2002). Specifically, during egg-laying and chick-rearing periods, when food supply is most important, aerial insectivore species

with diverse prey availability may be more resilient to mis-timing and less affected by climate change. Purple martins have been shown to exploit a variety of food sources during their breeding season, including 56 prey species (79% ants and 1.5% dragonflies), as shown in a foraging study at Lake Texoma, Oklahoma (Helms et al., 2016). Adding to this, a 20-year dataset has shown that Purple Martins lay eggs earlier in warmer springs and produce more fledglings (Shave et al., 2019). While the initiation of long-distance migration is often regarded as less flexible, our study shows that swallows and martins do display phenotypic plasticity and that this occurs after arrival to their breeding grounds. Their ability to adapt to seasonal variation, and by extension climate change, may apply to other periods of the non-breeding season as evidenced by phenological response to temperature change across the Great Lakes region.

One limitation of this study is our inability to separate an apparent second wave of roosting emergence in late September and October from the main August emergence. The second wave here is defined as a roost emergence event that continues for a few days after the first wave has stopped for at least 5 days. Out of 12 radar stations examined, only some years in KGRB station (Green Bay, Wisconsin) and KIWX station (Fort Wayne, Indiana) had secondary waves after mid-September. Without ground-truth observations, I was not able to confirm the species identity of the second wave of roosting species. Late summer roosts in September could be a mixture of Purple Martins, Tree Swallows, and other swallow species (Burney 2002, Kelly & Pletschet, 2018; Laughlin et al., 2013). I compared roost locations with previous studies (Bridge et al., 2016; Kelly & Pletschet, 2018) and plotted the known swallow roost species identity (Figure 1.S4). Out of 104 roost clusters, 33 roost clusters (39.80% of the number of birds quantified by radar) in our paper overlapped with roost locations documented in previous literature and are considered as known species ID roosts. Out of 33 known roosts, 30 roost

clusters were Purple Martin roosts (89.83% of the number of known ID birds), and 3 roost clusters belonged to a mix of Tree Swallows and Bank Swallows (10.17% of the number of known ID birds). While I cannot ascertain species identities of all roosts used in this study, evidence suggests that Purple Martins are the dominant signal in this study, with a lesser contribution from Tree Swallows and Bank Swallows. Future research at a contiguous United States spatial scale needs to be cautious about swallow species separation.

This study provides the first quantification of the phenological trend in aerial insectivore roosting behavior and explores potential associations of phenology change with air temperature by leveraging the increasing accessibility of long-term weather surveillance radar data and advanced machine learning methods applicable to aeroecology studies. Discovering mechanisms behind phenological change remains a priority for aerial insectivore conservation, and future research that explores long-term phenology records of various species of prey in relation to insectivore phenology at different scales is still urgently needed. Our study shows phenotypic plasticity in these long-distance hemispheric migrants at different spatial scales, providing insights into the ability of aerial insectivores to respond to global change. It provides a steppingstone for understanding the impact of climate change on this group of rapidly declining species and for examining the phenology mismatch in trophic interactions at even broad spatial scales in future studies.

Figures and Tables

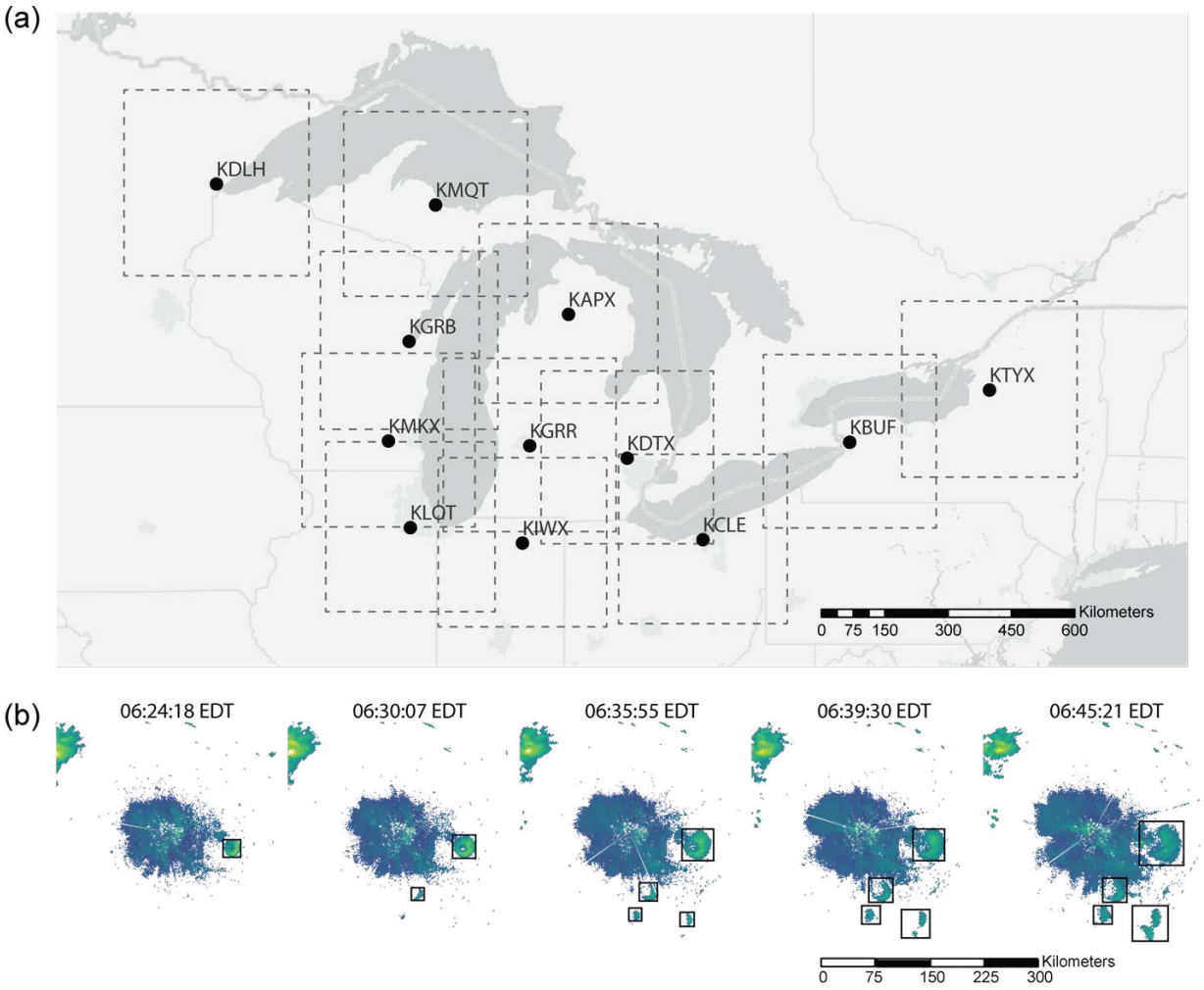

Figure 1.1. (a) Location of 12 radar stations across the Great Lakes Region. The square buffer around each site indicates a 300 km x 300 km detection range. Four-letter radar station names represent the following locations: KDLH = Duluth, Minnesota; KMQT = Marquette, Michigan; KGRB = Green Bay, Wisconsin; KMKX = Milwaukee, Wisconsin; KLOT = Chicago, Illinois; KIWX = Fort Wayne, Indiana; KGRR = Grand Rapids, Michigan; KAPX = Gaylord, Michigan; KDTX = Detroit, Michigan; KCLE = Cleveland, Ohio; KBUF = Buffalo, New York; KTYX = Fort Drum, New York. Map lines delineate study areas and do not necessarily depict accepted national boundaries. (b) Five successive radar reflectivity images (6:24 AM, 6:30 AM, 6:35 AM, 6:39 AM, 6:45 AM) from KDTX station on the morning of August 18, 2005, showing detection bounding boxes around each roost.

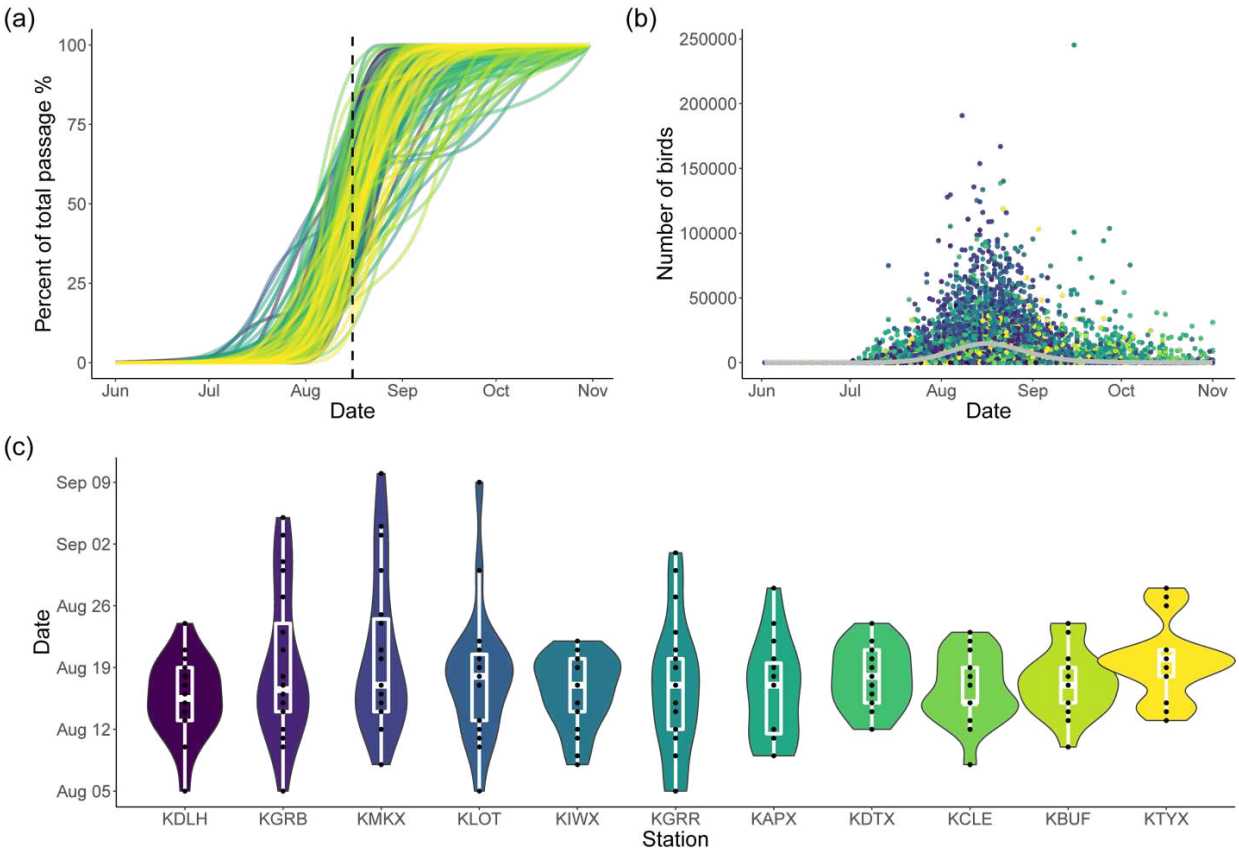

Figure 1.2. (a) Seasonally cumulative roosting activity for 11 radar stations in the Great Lakes region from 2000 to 2020. Each curve represents a unique station-year. The averaged peak roosting activity date (August 16th) is shown with a dotted vertical line. Color corresponds to the radar station as shown in Figure 1.2c. (b) Scatter plot of raw daily sum of the number of birds from all station years, showing the general pattern of roosting activity in the Great Lakes region over 21 years. The fitted line is derived from a generalized additive model (GAM). Color corresponds to the radar station, as shown in Figure 1.2c. (c) Violin plot of peak roosting activity dates (50% passage) in each radar station from 2000 to 2020. Radar stations are sequenced in order along the southern coastline of the Great Lakes (west to east).

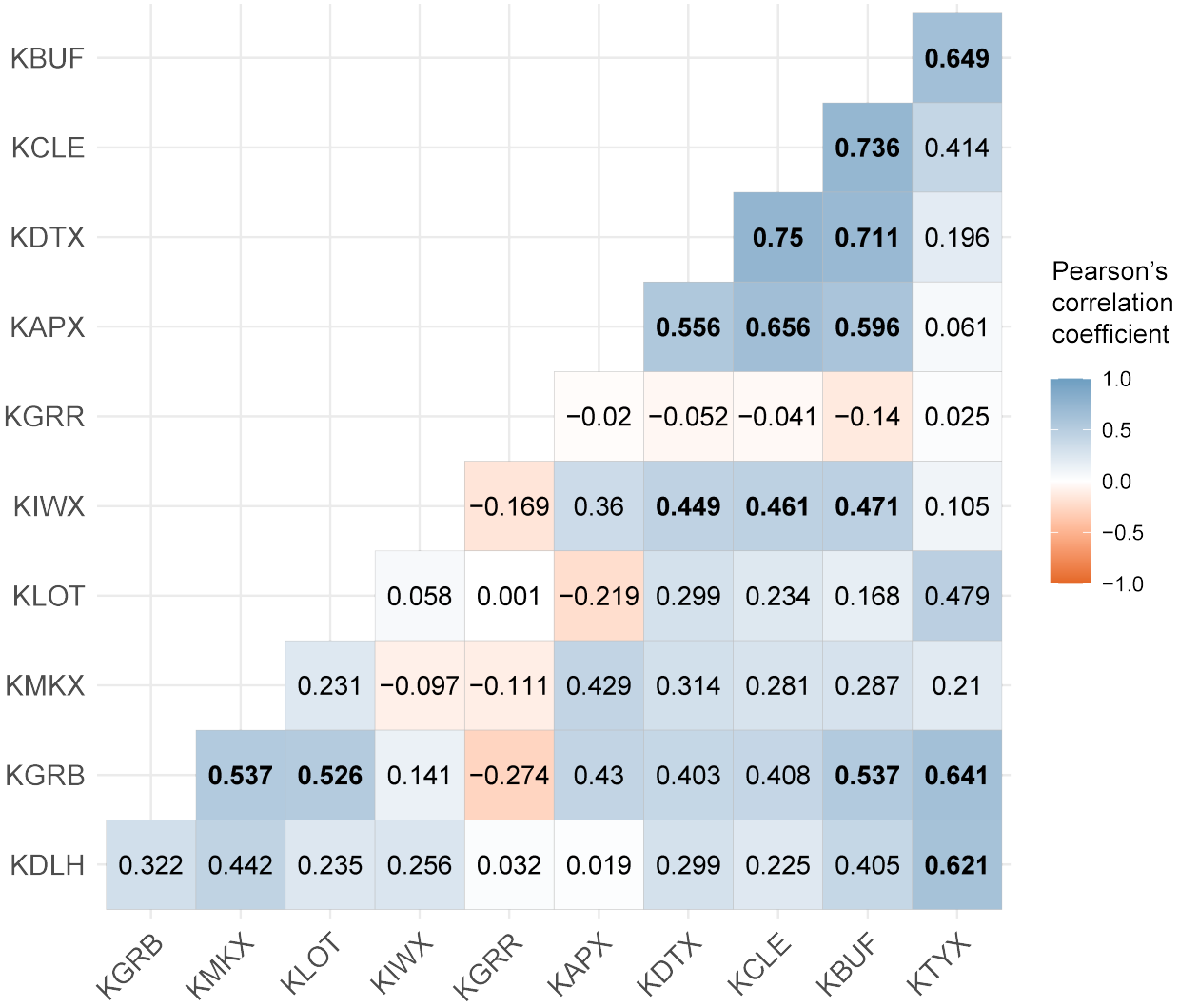

Figure 1.3. Pearson's correlation coefficient plot between yearly peak roosting activity dates at 11 radar stations. Colors indicate positive (blue) and negative (red) correlations. The value in each grid cell indicates Pearson's correlation coefficient for the station pair. Significant correlations ($p < 0.05$) are denoted by bold font. Radar stations are sequenced in order along the southern coastline of the Great Lakes (west to east).

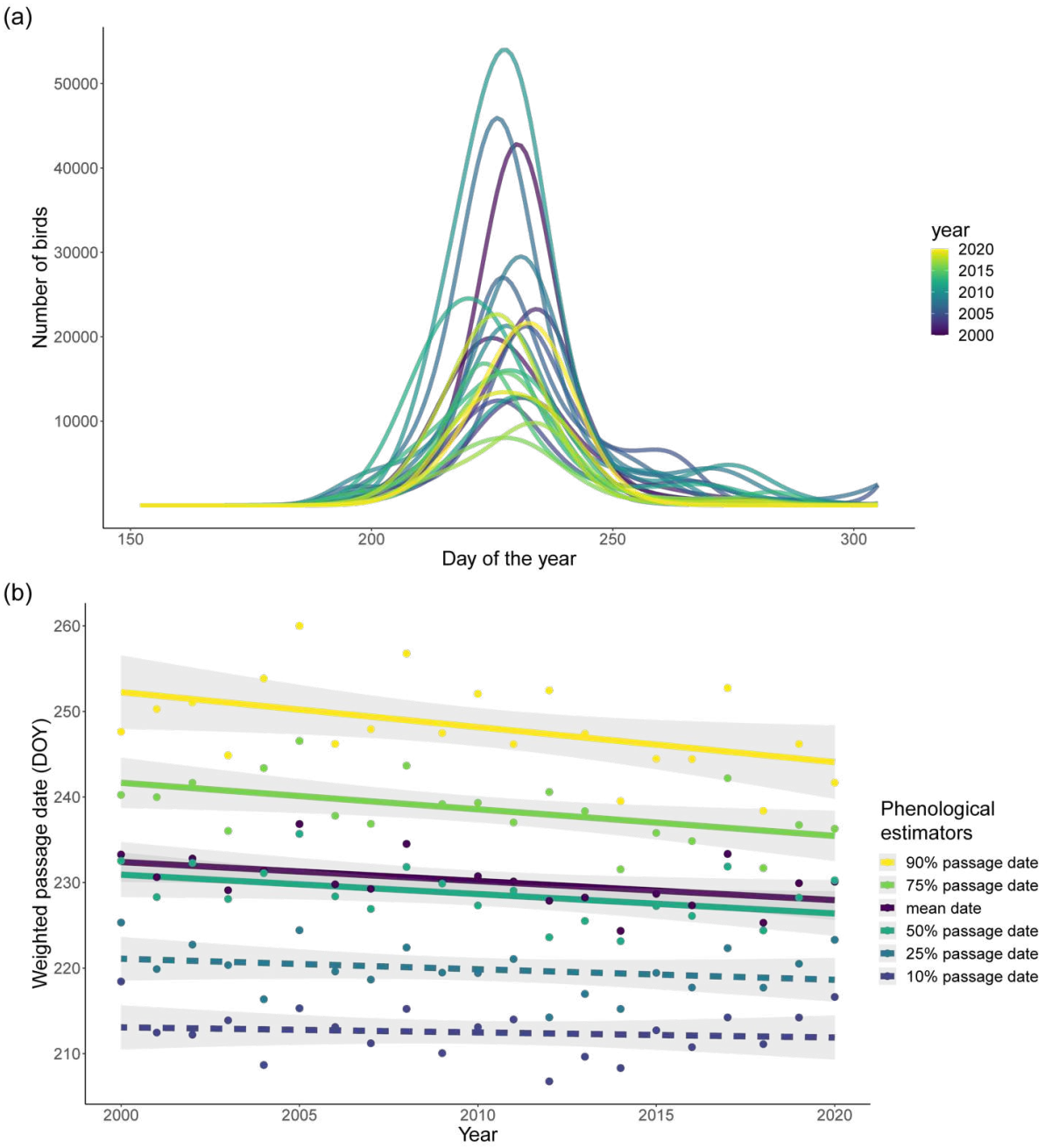

Figure 1.4. (a) Aerial insectivores' yearly roosting activity intensity (the number of birds) characterized at the Great Lakes region scale. The fitted lines are from a GAM fit to the whole region for each year. (b) Regional weighted passage dates (90%, 75%, mean, 50%, 25%, 10%) versus year. Each point represents a regional passage date in one year using station-level phenology estimates weighted by log-transformed cumulative passage in each station. Fitted line and 95% confidence interval are derived from a linear regression for each phenological estimator. Solid lines represent significant (p<0.05) regressions, and dotted lines represent non-significant regressions (p≥0.05).

REFERENCES

Aikens, E. O., Dwinnell, S. P. H., LaSharr, T. N., Jakopak, R. P., Fralick, G. L., Randall, J., Kaiser, R., Thonhoff, M., Kauffman, M. J., & Monteith, K. L. (2021). Migration distance and maternal resource allocation determine timing of birth in a large herbivore. *Ecology*, *102*(6), e03334. https://doi.org/10.1002/ecy.3334

Belotti, M. C. T. D., Deng, Y., Zhao, W., Simmons, V. F., Cheng, Z., Perez, G., Tielens, E., Maji, S., Sheldon, D., Kelly, J. F., Horton, K. G. Long-term analysis of persistence and size of swallow and martin roosts in the US Great Lakes. Manuscript in review.

Bent, A. C. (1942). Life histories of North American flycatchers, larks, swallows, and their allies. Order Passeriformes (Families Cotingidae, Tyrannidae, Alaudidae, and Hirundinidae). *Bulletin of the United States National Museum*, *179*. https://doi.org/10.5479/si.03629236.179.i

Bigger, D., Peery, M. Z., Chinnici, S., & Courtney, S. P. (2006). Efficacy of audiovisual and radar surveys for studying marbled murrelets in inland habitats. *Journal of Wildlife Management*, *70*(2), 505–516. https://doi.org/10.2193/0022-541x(2006)70[505:eoaars]2.0.co;2

Bonter, D. N., Gauthreaux Jr, S. A., & Donovan, T. M. (2009). Characteristics of important stopover locations for migrating birds: remote sensing with radar in the great lakes basin. *Conservation Biology*, *23*(2), 440–448. https://doi.org/10.1111/j.1523-1739.2008.01085.x

Bourret, A., Bélisle, M., Pelletier, F., & Garant, D. (2015). Multidimensional environmental influences on timing of breeding in a tree swallow population facing climate change. *Evolutionary Applications*, *8*(10), 933–944. https://doi.org/10.1111/eva.12315

Bridge, E. S., Pletschet, S. M., Fagin, T., Chilson, P. B., Horton, K. G., Broadfoot, K. R., & Kelly, J. F. (2016). Persistence and habitat associations of Purple Martin roosts quantified via weather surveillance radar. *Landscape Ecology*, *31*(1), 43–53. https://doi.org/10.1007/s10980-015-0279-0

Brown, C. R., D. A. Airola, and S. Tarof. (2021). Purple Martin (Progne subis), version 2.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.

Burney, C. W. (2002). *A study of Swallow Roosts Found in the Eastern United States* [Master's Thesis]. Cornell University.

Cabrera-Cruz, S. A., Cohen, E. B., Smolinsky, J. A., & Buler, J. J. (2020). Artificial light at night is related to broad-scale stopover distributions of nocturnally migrating landbirds along the Yucatan Peninsula, Mexico. *Remote Sensing*, *12*(3), 395. https://doi.org/10.3390/rs12030395

Cheng, Z., Gabriel, S., Bhambhani, P., Sheldon, D., Maji, S., Laughlin, A., & Winkler, D. (2020). Detecting and tracking communal bird roosts in weather radar data. *Proceedings of the AAAI Conference on Artificial Intelligence*, *34*(01), 378–385. http://arxiv.org/abs/2004.12819

Chilson, C., Avery, K., McGovern, A., Bridge, E., Sheldon, D., & Kelly, J. (2019). Automated detection of bird roosts using NEXRAD radar data and Convolutional Neural Networks. *Remote Sensing in Ecology and Conservation*, *5*(1), 20–32. https://doi.org/10.1002/rse2.92

Chilson, P. B., Frick, W. F., Stepanian, P. M., Shipley, J. R., Kunz, T. H., & Kelly, J. F. (2012). Estimating animal densities in the aerosphere using weather radar: To Z or not to Z? *Ecosphere*, *3*(8), 1–19. https://doi.org/10.1890/es12-00027.1

Clark, R., & Hobson, K. (2022). Climate change: Aerial insectivores struggle to keep pace with earlier pulses of nutritious aquatic foods. *Current Biology*, *32*(6), R267–R269. https://doi.org/10.1016/J.CUB.2022.01.076

Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., & Schwartz, M. D. (2007). Shifting plant phenology in response to global change. *Trends in Ecology and Evolution*, *22*(7), 357–365. https://doi.org/10.1016/j.tree.2007.04.003

Conrad, K. F., Warren, M. S., Fox, R., Parsons, M. S., & Woiwod, I. P. (2006). Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, *132*(3), 279–291. https://doi.org/10.1016/j.biocon.2006.04.020

Diehl, R. H., Larkin, R. P., & Black, J. E. (2003). Radar observations of bird migration over the Great Lakes. *The Auk*, *120*(2), 278–290. https://doi.org/10.2307/4090180

Diez, J. M., Ibáñez, I., Miller-Rushing, A. J., Mazer, S. J., Crimmins, T. M., Crimmins, M. A., Bertelsen, C. D., & Inouye, D. W. (2012). Forecasting phenology: From species variability to community patterns. *Ecology Letters*, *15*(6), 545–553. https://doi.org/10.1111/j.1461-0248.2012.01765.x

Dokter, A. M., Farnsworth, A., Fink, D., Ruiz-Gutierrez, V., Hochachka, W. M., la Sorte, F. A., Robinson, O. J., Rosenberg, K. v., & Kelling, S. (2018). Seasonal abundance and survival of North America's migratory avifauna determined by weather radar. *Nature Ecology and Evolution*, *2*(10), 1603–1609. https://doi.org/10.1038/s41559-018-0666-4

Dokter, A. M., Liechti, F., Stark, H., Delobbe, L., Tabary, P., & Holleman, I. (2011). Bird migration flight altitudes studied by a network of operational weather radars. *Journal of the Royal Society Interface*, *8*(54), 30–43. https://doi.org/10.1098/rsif.2010.0116

Dunn, P. O., & Winkler, D. W. (1999). Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society B: Biological Sciences*, *266*(1437), 2487–2490. https://doi.org/10.1098/RSPB.1999.0950

Dunning, J. B. (2007). *CRC handbook of avian body masses.* CRC press.

Everall, N. C., Johnson, M. F., Wilby, R. L., & Bennett, C. J. (2015). Detecting phenology change in the mayfly Ephemera danica: Responses to spatial and temporal water temperature variations. *Ecological Entomology*, *40*(2), 95–105. https://doi.org/10.1111/een.12164

Gallinat, A. S., Primack, R. B., & Wagner, D. L. (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution*, *30*(3), 169–176. https://doi.org/10.1016/j.tree.2015.01.004

Gauthreaux, S. A., & Belser, C. G. (1998). Displays of bird movements on the WSR-88D: Patterns and quantification. *Weather and Forecasting*, *13*(2), 453–464. https://doi.org/10.1175/1520-0434(1998)013<0453:DOBMOT>2.0.CO;2

Gittings, J. A., Raitsos, D. E., Kheireddine, M., Racault, M. F., Claustre, H., & Hoteit, I. (2019). Evaluating tropical phytoplankton phenology metrics using contemporary tools. *Scientific Reports*, *9*(1), 1-9. https://doi.org/10.1038/s41598-018-37370-4

Haest, B., Hüppop, O., van de Pol, M., & Bairlein, F. (2019). Autumn bird migration phenology: A potpourri of wind, precipitation and temperature effects. *Global Change Biology*, *25*(12), 4064–4080. https://doi.org/10.1111/gcb.14746

Haest, B., Stepanian, P. M., Wainwright, C. E., Liechti, F., & Bauer, S. (2021). Climatic drivers of (changes in) bat migration phenology at Bracken Cave (USA). *Global Change Biology*, *27*(4), 768–780. https://doi.org/10.1111/gcb.15433

Helm, B., Van Doren, B. M., Hoffmann, D., & Hoffmann, U. (2019). Evolutionary response to climate change in migratory pied flycatchers. *Current Biology*, *29*(21), 3714-3719. https://doi.org/10.1016/j.cub.2019.08.072

Helms, J. A., Godfrey, A. P., Ames, T., & Bridge, E. S. (2016). Predator foraging altitudes reveal the structure of aerial insect communities. *Scientific Reports*, *6*(1), 1–10. https://doi.org/10.1038/srep28670

Herkert, J. R. (1994). The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications*, *4*(3), 461–471. https://doi.org/10.2307/1941950

Hoen, B.D., Diffendorfer, J.E., Rand, J.T., Kramer, L.A., Garrity, C.P., and Hunt, H.E. (2018). United States Wind Turbine Database (v4.3, January 14, 2022): U.S. Geological Survey, American Clean Power Association, and Lawrence Berkeley National Laboratory data release. https://doi.org/10.5066/F7TX3DN0

Holmes, R. T., & Sherry, T. W. (2001). Thirty-year bird population trends in an unfragmented temperate deciduous forest: Importance of habitat change. *Auk*, *118*(3), 589–609. https://doi.org/10.2307/4089923

Horn, J. W., & Kunz, T. H. (2008). Analyzing NEXRAD Doppler radar images to assess nightly dispersal patterns and population trends in Brazilian free-tailed bats (Tadarida brasiliensis). *Integrative and Comparative Biology*, *48*(1), 24–39. https://doi.org/10.1093/icb/icn051

Horton, K. G., Gregory Shriver, W., & Buler, J. J. (2015). An assessment of spatio-temporal relationships between nocturnal bird migration traffic rates and diurnal bird stopover density. *Movement Ecology*, *4*(1), 1–10. https://doi.org/10.1186/s40462-015-0066-1

Horton, K. G., la Sorte, F. A., Sheldon, D., Lin, T. Y., Winner, K., Bernstein, G., Maji, S., Hochachka, W. M., & Farnsworth, A. (2020). Phenology of nocturnal avian migration has

shifted at the continental scale. *Nature Climate Change*, *10*(1), 63–68. https://doi.org/10.1038/s41558-019-0648-9

Horton, K. G., Nilsson, C., Van Doren, B. M., la Sorte, F. A., Dokter, A. M., & Farnsworth, A. (2019). Bright lights in the big cities: Migratory birds' exposure to artificial light. *Frontiers in Ecology and the Environment*, *17*(4), 209–214. https://doi.org/10.1002/fee.2029

Horton, K. G., Van Doren, B. M., la Sorte, F. A., Cohen, E. B., Clipp, H. L., Buler, J. J., Fink, D., Kelly, J. F., & Farnsworth, A. (2019). Holding steady: Little change in intensity or timing of bird migration over the Gulf of Mexico. *Global Change Biology*, *25*(3), 1106–1118. https://doi.org/10.1111/gcb.14540

Imlay, T. L., Mills Flemming, J., Saldanha, S., Wheelwright, N. T., & Leonard, M. L. (2018). Breeding phenology and performance for four swallows over 57 years: Relationships with temperature and precipitation. *Ecosphere*, *9*(4), e02166. https://doi.org/10.1002/ecs2.2166

Imlay, T. L., & Taylor, P. D. (2020). Diurnal and crepuscular activity during fall migration for four species of aerial foragers. *Wilson Journal of Ornithology*, *132*(1), 159–164. https://doi.org/10.1676/1559-4491-132.1.159

Inouye, D. W. (2022). Climate change and phenology. *Wiley Interdisciplinary Reviews: Climate Change*, e764. https://doi.org/10.1002/wcc.764

Kelly, J. F., & Pletschet, S. M. (2018). Accuracy of swallow roost locations assigned using weather surveillance radar. *Remote Sensing in Ecology and Conservation*, *4*(2), 166–172. https://doi.org/10.1002/rse2.66

Kelly, J. F., Ryan Shipley, J., Chilson, P. B., Howard, K. W., Frick, W. F., Kunz, T. H., Shipley, J. R., Chilson, P. B., Howard, K. W., Frick, W. F., & Kunz, T. H. (2012). Quantifying

animal phenology in the aerosphere at a continental scale using NEXRAD weather radars. *Ecosphere*, *3*(2), 1–9. https://doi.org/10.1890/ES11-00257.1

Kerby, J., & Post, E. (2013). Reproductive phenology of large mammals. *Phenology: An Integrative Environmental Science* (pp. 467–479). Springer, Dordrecht. https://doi.org/10.1007/978-94-007-6925-0_25

Kirby, R. E. (1978). Roosting of passerines over open water at night. *North American Bird Bander, 3*(3).

La Sorte, F. A., Hochachka, W. M., Farnsworth, A., Sheldon, D., Fink, D., Geevarghese, J., Winner, K., Van Doren, B. M., & Kelling, S. (2015). Migration timing and its determinants for nocturnal migratory birds during autumn migration. *Journal of Animal Ecology*, *84*(5), 1202–1212. https://doi.org/10.1111/1365-2656.12376

Lafleur, J. M., Buler, J. J., & Moore, F. R. (2016). Geographic position and landscape composition explain regional patterns of migrating landbird distributions during spring stopover along the northern coast of the Gulf of Mexico. *Landscape Ecology*, *31*(8), 1697–1709. https://doi.org/10.1007/s10980-016-0354-1

Laughlin, A. J., Sheldon, D. R., Winkler, D. W., & Taylor, C. M. (2014). Behavioral drivers of communal roosting in a songbird: A combined theoretical and empirical approach. *Behavioral Ecology*, *25*(4), 734–743. https://doi.org/10.1093/beheco/aru044

Laughlin, A. J., Sheldon, D. R., Winkler, D. W., & Taylor, C. M. (2016). Quantifying non-breeding season occupancy patterns and the timing and drivers of autumn migration for a migratory songbird using Doppler radar. *Ecography*, *39*(10), 1017–1024. https://doi.org/10.1111/ecog.01988

Laughlin, A. J., Taylor, C. M., Bradley, D. W., LeClair, D., Clark, R. G., Dawson, R. D., Dunn, P. O., Horn, A., Leonard, M., Sheldon, D. R., Shutler, D., Whittingham, L. A., Winkler, D. W., & Norris, D. R. (2013). Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. *Auk*, *130*(2), 230–239. https://doi.org/10.1525/auk.2013.12229

McLaren, J. D., Buler, J. J., Schreckengost, T., Smolinsky, J. A., Boone, M., Emiel van Loon, E., Dawson, D. K., & Walters, E. L. (2018). Artificial light at night confounds broad-scale habitat use by migrating birds. *Ecology Letters*, *21*(3), 356–364. https://doi.org/10.1111/ele.12902

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aaasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., … Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, *12*(10), 1969-1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W., & Post, E. (2010). The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3177–3186. https://doi.org/10.1098/rstb.2010.0148

Moussus, J.-P., Julliard, R., & Jiguet, F. (2010). Featuring 10 phenological estimators using simulated data. *Methods in Ecology and Evolution*, *1*(2), 140–150. https://doi.org/10.1111/J.2041-210X.2010.00020.X

Nebuloni, R., Capsoni, C., & Vigorita, V. (2008). Quantifying bird migration by a high-resolution weather radar. *IEEE Transactions on Geoscience and Remote Sensing*, *46*(6), 1867–1875. https://doi.org/10.1109/TGRS.2008.916467

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

Nilsson, C., Dokter, A. M., Verlinden, L., Shamoun-Baranes, J., Schmid, B., Desmet, P., Bauer, S., Chapman, J., Alves, J. A., Stepanian, P. M., Sapir, N., Wainwright, C., Boos, M., Górska, A., Menz, M. H. M., Rodrigues, P., Leijnse, H., Zehtindjiev, P., Brabant, R., … Liechti, F. (2019). Revealing patterns of nocturnal migration using the European weather radar network. *Ecography*, *42*(5), 876–886. https://doi.org/10.1111/ecog.04003

Panchen, Z. A., Primack, R. B., Gallinat, A. S., Nordt, B., Stevens, A. D., Du, Y., & Fahey, R. (2015). Substantial variation in leaf senescence times among 1360 temperate woody plant species: Implications for phenology and ecosystem processes. *Annals of Botany*, *116*(6), 865–873. https://doi.org/10.1093/aob/mcv015

Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., Blondel, M., Prettenhofer, P., Weiss, R., Dubourg, V., Vanderplas, J., Passos, A., Cournapeau, D., Brucher, M., Perrot, M., & Duchesnay, E. (2011). Scikit-learn: Machine Learning in Python. *Journal of Machine Learning Research*, 12, 2825–2830.

Post, E., & Forchhammer, M. C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1501), 2367–2373. https://doi.org/10.1098/rstb.2007.2207

Ren, S., He, K., Girshick, R., & Sun, J. (2017). Faster R-CNN: Towards Real-Time Object Detection with Region Proposal Networks. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, *39*(6), 1137–1149. https://doi.org/10.1109/TPAMI.2016.2577031

Rioux Paquette, S., Pelletier, F., Garant, D., & Bélisle, M. (2014). Severe recent decrease of adult body mass in a declining insectivorous bird population. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1786), 20140649. https://doi.org/10.1098/rspb.2014.0649

Rosenberg, K. v., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J. C., Panjabi, A., Helft, L., Parr, M., & Marra, P. P. (2019). Decline of the North American avifauna. *Science*, *366*(6461), 120–124. https://doi.org/10.1126/science.aaw1313

Russakovsky, O., Deng, J., Su, H., Krause, J., Satheesh, S., Ma, S., Huang, Z., Karpathy, A., Khosla, A., Bernstein, M., Berg, A. C., & Fei-Fei, L. (2015). ImageNet large scale visual recognition challenge. *International Journal of Computer Vision*, *115*(3), 211–252. https://doi.org/10.1007/s11263-015-0816-y

Russell, K. R., & Gauthreaux, S. A. (1998). Use of weather radar to characterize movements of roosting Purple Martins. *Wildlife Society Bulletin*, *26*(1), 5–16. https://about.jstor.org/terms

Russell, K. R., & Gauthreaux, S. A. (1999). Spatial and temporal dynamics of a Purple Martin pre-migratory roost. *The Wilson Bulletin*, *111*(3), 354–362. https://about.jstor.org/terms

Saldanha, S., Taylor, P. D., Imlay, T. L., & Leonard, M. L. (2019). Biological and environmental factors related to communal roosting behavior of breeding bank swallow (Riparia riparia). *Avian Conservation and Ecology*, *14*(2), 21. https://doi.org/10.5751/ACE-01490-140221

Schwartz, M. D. (2013). *Phenology: an integrative environmental science.* Dordrecht: Kluwer Academic Publishers.

Shave, A., Garroway, C. J., Siegrist, J., & Fraser, K. C. (2019). Timing to temperature: Egg-laying dates respond to temperature and are under stronger selection at northern latitudes. *Ecosphere*, *10*(12), e02974. https://doi.org/10.1002/ecs2.2974

Shutler, D., Hussell, D. J. T., Norris, D. R., Winkler, D. W., Robertson, R. J., Bonier, F., Rendell, W. B., Bélisle, M., Clark, R. G., Dawson, R. D., Wheelwright, N. T., Lombardo, M. P., Thorpe, P. A., Truan, M. A., Walsh, R., Leonard, M. L., Horn, A. G., Vleck, C. M., Vleck, D., … Stanback, M. T. (2012). Spatiotemporal patterns in nest box occupancy by tree swallows across North America. *Avian Conservation and Ecology*, *7*(1), 3-3. https://doi.org/10.5751/ace-00517-070103

Spiller, K. J., & Dettmers, R. (2019). Evidence for multiple drivers of aerial insectivore declines in North America. *Condor*, *121*(2), duz010. https://doi.org/10.1093/condor/duz010

Stepanian, P. M., Entrekin, S. A., Wainwright, C. E., Mirkovic, D., Tank, J. L., Kelly, J. F., & Schindler, D. W. (2020). Declines in an abundant aquatic insect, the burrowing mayfly, across major North American waterways. *Proceedings of the National Academy of Sciences*, *117*(6), 2987–2992. https://doi.org/10.1073/pnas.1913598117/-/DCSupplemental.y

Stepanian, P. M., Horton, K. G., Melnikov, V. M., Zrnić, D. S., & Gauthreaux, S. A. (2016). Dual-polarization radar products for biological applications. *Ecosphere*, *7*(11), e01539. https://doi.org/10.1002/ecs2.1539

Stepanian, P. M., & Wainwright, C. E. (2018). Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. *Global Change Biology*, *24*(7), 3266–3275. https://doi.org/10.1111/gcb.14051

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., MacKay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M.,

… Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, *535*(7611), 241–245. https://doi.org/10.1038/NATURE18608

Torres, S. M. (2007). Initial implementation of super-resolution data on the NEXRAD network. American Meteorological Society Annual Meeting, San Antonio, Texas. https://ams.confex.com/ams/87ANNUAL/techprogram/paper_116240.htm

Tøttrup, A. P., Thorup, K., & Rahbek, C. (2006). Changes in timing of autumn migration in North European songbird populations. *Ardea*, *94*(3), 527.

Tryjanowski, P., Kuzniak, S., & Sparks, T. (2002). Earlier arrival of some farmland migrants in western Poland. *Ibis*, *144*(1), 62–68. https://doi.org/10.1046/j.0019-1019.2001.00022.x

Twining, C. W., Shipley, J. R., & Matthews, B. (2022). Climate change creates nutritional phenological mismatches. *Trends in Ecology & Evolution*, *37*(9), 736–739. https://doi.org/10.1016/J.TREE.2022.06.009

Twining, C. W., Shipley, J. R., & Winkler, D. W. (2018). Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. *Ecology Letters*, *21*(12), 1812–1820. https://doi.org/10.1111/ELE.13156

Van Doren, B. M., Horton, K. G., Dokter, A. M., Klinck, H., Elbin, S. B., & Farnsworth, A. (2017). High-intensity urban light installation dramatically alters nocturnal bird migration. *Proceedings of the National Academy of Sciences*, *114*(42), 11175–11180. https://doi.org/10.1073/pnas.1708574114

Van Doren, B. M., Willard, D. E., Hennen, M., Horton, K. G., Stuber, E. F., Sheldon, D., Sivakumar, A. H., Wang, J., Farnsworth, A., & Winger, B. M. (2021). Drivers of fatal bird collisions in an urban center. *Proceedings of the National Academy of Sciences*, *118*(24), e2101666118. https://doi.org/10.1073/pnas.2101666118/-/DCSupplemental.y

Winkler, D. W., Dunn, P. O., & McCulloch, C. E. (2002). Predicting the effects of climate change on avian life-history traits. *Proceedings of the National Academy of Sciences*, *99*(21), 13595–13599. https://doi.org/10.1073/pnas.212251999

Wood, S., & Wood, M. S. (2015). Package 'mgcv'. R package version, 1(29), 729.

Xu, F., & Si, Y. (2019). The frost wave hypothesis: How the environment drives autumn departure of migratory waterfowl. *Ecological Indicators*, *101*, 1018–1025. https://doi.org/10.1016/j.ecolind.2019.02.024

Youngflesh, C., Socolar, J., Amaral, B. R., Arab, A., Guralnick, R. P., Hurlbert, A. H., LaFrance, R., Mayor, S. J., Miller, D. A. W., & Tingley, M. W. (2021). Migratory strategy drives species-level variation in bird sensitivity to vegetation green-up. *Nature Ecology & Evolution*, *5*(7), 987–994. https://doi.org/10.1038/s41559-021-01442-y

CHAPTER TWO

CONTINENTAL CONNECTIONS: CHANGING TEMPERATURE, WIND, AND PRECIPITATION ADVANCE THE POST-BREEDING ROOSTING PHENOLOGY OF AVIAN AERIAL INSECTIVORES

Summary

Migratory birds are under threat by climate change. Successfully conserving them requires knowing which climatic factors drive changes in their migratory behavior. Assessing the influence of weather on migratory birds is challenging, however, due to the temporal and spatial uncertainties in breeding, roosting, and wintering grounds. Weather may affect these temporally disjointed life stages separately and through carry-over effects, but they are not often studied together. Coupling migratory bird movements estimated using weather radar (NEXRAD) with long-term and large-scale environmental data allows us to overcome these spatiotemporal uncertainties. Here, I assess environmental drivers of the phenology of post-breeding roosting of aerial insectivores in the Great Lakes region (USA) by evaluating predictors during the months leading up to roosting across species' ranges. I conducted a spatially explicit time-window analysis to examine the effects of 17 gridded weather and vegetation variables on swallow peak roosting phenology in the Great Lakes, which has advanced by 4.5 days over the past two decades. Our analysis spans a 21-year (2000-2020) time series and covers areas across Canada and the northern United States. I found that peak roosting timing is paced by both local condition (headwind at 850 hPa) at the Great Lakes and distant conditions (minimum temperature, precipitation rate, and specific humidity) at the likely breeding and stopover sites, with warmer temperature advancing, headwind delaying, and high precipitation advancing the phenophases.

Time windows selected for the possible breeding and stopover sites are mostly before or around the time of roosting, with one exception during wintertime. Our results fill in some of the remaining knowledge gaps in swallows' migration ecology and, more generally, in migratory birds' responses to ongoing climate change.

Introduction

The direct and indirect impacts of climate and other anthropogenic changes are causing wildlife across the globe to face ever-increasing threats in terms of individual health, altered behavior, phenology, distribution, and population dynamics (Acevedo-Whitehouse & Duffus, 2009; Peñuelas et al., 2013; Razgour et al., 2018). Migratory birds navigate hemisphere-scale journeys and live at the forefront of climate change and must adapt through either phenotypic plasticity or microevolution (Moiron et al., 2024). Climate change is increasingly influencing migratory birds' phenology, leading many species to alter their timing of arrival or departure from breeding grounds (Jenni & Kéry, 2003; Pearce-Higgins & Green, 2012). These shifts, while evident, raise concerns about whether they are sufficient to align with shifting resource availability – a mismatch that could have severe consequences for migratory bird populations (Bairlein, 2016; Visser & Both, 2005). Therefore, determining which environmental signals are perceived by wildlife, during which period in their life cycle, and at what locations, are essential steps toward unraveling the complexities of climate-induced phenological changes (van de Pol et al., 2016). This understanding is pivotal for understanding how broader ecological processes are being reshaped by climate change (Haest et al., 2018a, 2019, 2021).

Climate-induced phenological changes are particularly complex in long-distance migrants (Miles et al., 2017), due to the diversity of environmental conditions that they experience along the journey. Therefore, it is crucial to adopt approaches that encompass multi-locality analyses,

capturing the complexities of migration patterns across diverse regions (Haest et al., 2018a, 2019, 2021). Despite this complexity, most studies on the influence of weather on migration phenology use weather variables from migration arrival areas (Gordo, 2007). Doing so inherently assumes that migration timing is primarily driven by local conditions rather than by distant conditions at the locations where migration commenced or locations where migrants navigated through. However, both local and distant conditions likely play a role in shaping migration phenology (Cotton, 2003). For instance, local temperature conditions at migration stopover sites affect arrival timing for some passerine species migrating between Africa and Europe, particularly those breeding at higher latitudes, who showed flexibility in response to local conditions en route (Aharon-Rotman et al., 2022). In contrast, distant conditions at the site where migration commenced can serve as cues for migration initiation, indirectly affecting arrival timing at later stages of migration (Gunnarsson et al., 2006; Shamoun-Baranes et al., 2006). The relative influence of local versus distant conditions can also depend on the scale of movement. For short-distance migration movements, immediate factors like wind conditions or local food availability may have a stronger influence on fine-scale migration timing (Bridge et al., 2010; Eisaguirre et al., 2018). For long-distance movements, distant environmental factors, such as temperature anomalies or precipitation patterns in breeding or non-breeding grounds, can act as drivers of migration initiation, with effects that propagate over thousands of kilometers (Both & Visser, 2001; Studds & Marra, 2007). These distinctions highlight the importance of considering the spatial and temporal scale of environmental influences when studying migration phenology.

Large spatial scale climatic variables, such as teleconnections and climate dipoles, have been shown to affect migration patterns (Strong et al., 2015; Zuckerberg et al., 2020). Notably, phenomena like El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO)

have been studied for their impact on local ecological changes, including bird spring migration timing and breeding biology (Cotton, 2003; Haest et al., 2018a; Huang et al., 2017; Hüppop & Hüppop, 2003; Laczi et al., 2019). However, teleconnection patterns, which influence temperature, precipitation, wind, extreme weather, and ocean currents, summarized into single-value indices, making it difficult to attribute these effects to specific source locations (Gordo, 2007). This complicates understanding the mechanisms by which climate change-driven shifts in environmental conditions affect different stages of the migration journey. Additionally, timing assumptions are often made when examining the relationship between weather and migration phenology (van de Pol et al., 2016). For instance, predictors are sometimes averaged over extended periods or matched directly with the phenological event. While these approaches have provided valuable insights, they may not always align with the specific biological mechanisms driving phenological events. Advances in tools like sliding window analyses now allow for a more nuanced exploration of these relationships (van de Pol et al., 2016).

More recent work on understanding climate-ecology relationships has moved away from these spatial and temporal assumptions, and instead, steps have been taken to conduct spatially and temporally explicit analysis of several climate conditions (Haest et al., 2018b, 2019, 2020, 2021). Such an exploratory approach allows for the identification of the most likely locations and times of influence and the formulation of data-driven hypotheses on these influences that can then be verified through explicit testing when future data become available. Explicit testing could involve comparing the predicted timing of phenological events based on our identified climatic influences with field observations or tracking data to further verify the spatial and temporal relationships between climate and phenology.

Several commonly studied weather variables have been examined in previous research to influence migration phenology by either delaying or advancing its timing. Temperature is among the most studied predictors of changes in phenological events, both across regions and taxa (Gordo, 2007; Root et al., 2003). It is a common environmental cue for many organisms to begin their life history events (Schwartz, 2013), be it directly (Klinner & Schmaljohann, 2020) or indirectly by changing the timing of food resource availability (Both et al., 2004). Warmer surface air temperatures are predicted to advance phenology by increasing insect activity and abundance, providing more favorable foraging conditions earlier in the season (Forrest, 2016; Scranton & Amarasekare, 2017). Precipitation, in contrast, is hypothesized to have both delaying and advancing effects depending on timing and context. High precipitation can delay phenology by creating poor flight conditions that hinder migration or roosting (Haest et al., 2020), as well as reducing flying insect activity and potentially causing short-term food shortages for aerial insectivores (Cox et al., 2019). However, in arid regions, rainfall can advance phenology by promoting vegetation growth and supporting insect populations, especially when lag effects from soil moisture prolong these favorable conditions (Gordo, 2007). Precipitation and relative humidity often reflect the availability of water sources, which in turn impacts insect abundance and distribution. That ultimately shapes foraging opportunities for obligate insectivores such as swallows and martins (Brown et al., 2002).

Other environmental variables can also serve as drivers of phenological changes in birds. Vegetation phenology, which can be measured by enhanced vegetation index (EVI), can also affect a migratory bird's spring and fall phenology (C. A. Adams et al., 2024; Robertson et al., 2024; Youngflesh et al., 2021) as some birds will 'surf' the green wave moving across latitudes. Greener vegetation is hypothesized to cue earlier phenology by providing suitable habitat and

food resources (La Sorte & Graham, 2021). Wind conditions (speed and direction) are hypothesized to delay or advance phenology depending on their alignment with migratory paths. Favorable tailwinds are expected to advance phenology by facilitating faster migration and reducing energetic costs, whereas headwinds or adverse crosswinds may delay arrival by requiring additional energy or causing stopovers (Gauthreaux et al., 2006; Haest et al., 2020; Horton et al., 2018; Liechti, 2006). Finally, surface water temperature is predicted to advance phenology by regulating the emergence of aquatic insects, a key food resource for aerial insectivores. Warmer water temperatures earlier in the season can trigger earlier aquatic insect emergence, thereby supporting earlier roosting or migratory events (Hixson et al., 2015; Twining et al., 2018).

Phenological events, such as shifts in migration timing, influenced by environmental variables that operate across varying spatial and temporal scales, sometimes require large-scale monitoring systems to effectively quantify and understand these patterns. Weather surveillance radar offers a powerful tool for this purpose, enabling the study of phenology across tens of thousands of individuals over extensive spatial areas, sometimes with insights into taxonomic group identities (Deng et al., 2023; Horton et al., 2020; Stepanian & Wainwright, 2018). During the post-breeding and pre-migratory season (Figure 2.1), some species of swallows aggregate in large numbers at their nocturnal roosting site and then disperse synchronously before dawn for foraging, leaving a unique donut-shaped signature on radar (Belotti et al., 2023; Laughlin et al., 2013). This offers a unique opportunity to investigate an understudied aspect of swallows' life history, as the daily number of swallows aloft can be estimated directly from raw radar data (Chilson et al., 2012). From this, phenological metrics describing roosting timing are derived, representing the day of the year when half (or 10%, 25%, 75%, 90%) of the cumulative number

of swallows aggregate and emerge at post-breeding roosting sites (Deng et al., 2023). In the Great Lakes region, post-breeding roosts of aerial insectivores are largely composed of Purple Martins (*Progne subis*) and Tree Swallows (*Tachycineta bicolor*), but other swallow species (e.g., Barn Swallow, Bank Swallow, and Cliff Swallow) could also mix in (Bridge et al., 2016; Kelly & Pletschet, 2018b). In the Great Lakes, roosting swallows probably include a combination of local breeders and post-breeding migrants (Fink, Auer, Johnston, Strimas-Mackey, et al., 2020). Therefore, I am expecting far-away teleconnections and short-distance conditions that could both influence the roosting phenology in this region.

With this unique 21-year (2000-2020) weather surveillance radar dataset on swallow roosting timing (Deng et al., 2023), I examine the drivers of interannual variation and long-term trends in post-breeding phenology at a large spatial scale. Specifically, I take a spatially explicit time-window analysis approach, free of preconceived assumptions about which location(s) or time window(s) influence migration timing. I seek to answer the following questions: Where, when, and to what extent are swallows responding to environmental conditions that drive the observed shift toward earlier roosting phenology in the Great Lakes, and what specific factors are influencing this change? Our findings contribute to a broader understanding of the ecological impacts of climate change on migratory species and provide valuable insights for predicting the effects of future environmental changes.

Methods

Swallow roosting phenology throughout the Great Lakes

Weather surveillance radar can detect and quantify a large number of swallows as they enter the airspace synchronously around dawn during post-breeding season, with high temporal and spatial resolution. Deng et al. (2023) provided valuable insights into phenological shifts of

the roosting swallows in the Great Lakes (defined as longitude -92° to -75° and latitude 41° to 47°) over 21 consecutive years (2000 - 2021) using 12 radar stations. The resulting dataset generated from radar was used to calculate the peak roosting date (i.e., the 50th percentile date of cumulative passage) of these aerial insectivores in the Great Lakes, which is the biological response used in this study.

Environmental data

To determine the mechanisms driving phenological change, I acquired data (Figure 2.2, Supplementary Table 1) from the NCEP Reanalysis I database using the RNCEP R package (Kemp, Emiel van Loon, et al., 2012). These included mean, minimum, and maximum daily air temperature, and specific humidity at 2 m above ground, and surface convective precipitation rate, surface precipitation rate, u-wind (east/west) and v-wind (north/south) components during daytime at the 1000, 925, and 850 hPa atmospheric pressure levels. These pressure levels correspond to approximately 100, 750, and 1450 m above sea level (a.s.l.), respectively. I selected the three lowest pressure levels available from the NCEP dataset to represent environmental influences across different altitudes, focusing on those most aligned with the typical flight heights of the swallow species studied. Research on swallows and martins indicates that they rarely reach altitudes as high as 2 km during migration, with the majority of their activity occurring at much lower levels (Dreelin et al., 2018; Mateos-Rodríguez & Liechti, 2012). Aerial insectivore swallows are known to forage and migrate mainly during the day (Imlay & Taylor, 2020). I thus only analyzed daytime wind conditions. From the u- and v-wind components, I derived both wind direction and wind assistance (using the *M.Groundspeed* equation in RNCEP) at all three atmospheric pressure levels. Wind direction includes the number of days when wind comes from the reference location (headwind) and wind goes to the reference

location (tailwind), both determined by the wind direction relative to the -45º to +45º angle ranges of the grid cell to reference location direction. I used the KAPX radar station as the reference location, which is centrally located in our study area (44.9072º W, -84.7197º N). Wind assistance assumes the animal will adjust its heading and airspeed to achieve different groundspeeds in different flow conditions to achieve complete compensation (Kemp, Shamoun-Baranes, et al., 2012). Here, I defined the preferred ground speed of swallows as 4.97 m/s, which is estimated by the Purple Martins' average migration speed over land presented in a previous GPS tracking study (Lavallée et al., 2021). The preferred direction of movement was defined by pointing from the analyzed grid cell to the reference location.

I also acquired Enhanced Vegetation Index (Huete et al., 1994) (EVI) data from MODIS/Terra Vegetation Indices 16-Day L3 Global 1km SIN Grid V061 (MOD13A2.v061) from 2000 to 2021 and water surface temperature data from MODIS/Aqua Land Surface Temperature/Emissivity 8-Day L3 Global 1 km SIN Grid (MYD11A2.v061) from 2003 to 2021 (limited due to data inavailability). Nine tiles (H09V04, H10V03, H10V04, H11V03, H11V04, H12V03, H12V04, H13V03, H13V04) were downloaded to cover an area similar to the extent of NCEP data. I clipped the Aqua Land Surface Temperature data to the Great Lakes.

To prepare the MODIS data for time-window analysis, I temporally interpolated it to 1-day resolution and filled in the missing data points in the time series with a generalized additive model (GAM) using the *mgcv* R package (Wood, 2001). Due to the high spatial resolution of the original data and computation limitations, I first spatially downscaled the data by a factor of 4 using a mean function. I then modeled the value in each grid cell with ordinal date as the response variable and a tensor product interaction between the year and the day of the year as the explanatory variable with a Gaussian distribution. Smooth terms were applied to each variable:

cubic regression spline for the day of the year and p-splines for the year. The number of knots (k) was set to the minimum number of days available in each year. I then further downscaled the interpolated data by a factor of 4 for EVI and 2 for aquatic data using mean functions to ensure the analyses remained computationally efficient. This resulted in a 64 km x 64 km resolution final raster product for EVI and 16 km x 16 km for aquatic surface temperature over the Great Lakes. All datasets were standardized to the same projection (WGS84) to maintain spatial consistency.

Finding the influential "environment variable – location – time window" combinations

I conducted per-grid cell time-window analyses to quantify what, when, and where environmental conditions influenced swallow pre-migratory roosting timing in the Great Lakes. The extent of the study area includes latitudes from the southern border of the Great Lakes region to the northern breeding boundary of these roosting swallow species, covering key locations relevant to swallow breeding and post-breeding migration. I followed the methods used in previous literature (Haest et al., 2018b, 2019, 2020, 2021). Broadly, this method works by systematically testing different combinations of environmental variables and locations within their best time windows to quantify their influence on the timing of biological events. In total, I examined 33369 spatiotemporal environmental variable combinations, encompassing all pixels for all variables across the study area. Ocean masks (not including the Great Lakes) were applied to all the environmental layers to restrict our inference to terrestrial habitats. Given the large number of combinations tested, some spurious relationships are expected; therefore, I applied further steps to refine and identify the most meaningful relationships, as described in the following section.

First, I determined a linear baseline trend model for the roosting phenology by selecting the trend model (among intercept only, linear, quadratic, or cubic models) with the lowest second order Akaike Information Criterion (AICc) value (Anderson & Burnham, 2002). By incorporating a linear temporal trend (i.e., year as the independent variable) in the analysis of environmental variables, I mitigate the risk of identifying spurious climate-phenology relationships that could arise from shared year-to-year trends in both phenology and climate (Iler et al., 2016). To ensure the trend model was effective, I verified that the time series was stationary and that the residuals from the detrended data showed no autocorrelation (Haest et al., 2018a). I then performed a time window analysis independently for each of the environmental variables using the *climwin* R package (Bailey & Van De Pol, 2016) on the value of each pixel and using five randomizations to avoid false positives resulting from chance alone. With these five randomizations, I calculated the alternative probability statistics (P_c) to estimate the reliability of the results (van de Pol et al., 2016). I used a P_c cut-off limit of 0.3 to achieve the probability of false negatives less than 0.1 for data with high R^2 (0.40) and less than 0.01 for data with very high R^2 (0.80), as well as false positives less than 0.2 (Bailey & Van De Pol, 2016; van de Pol et al., 2016). The best time window for each grid cell and variable was determined using ΔAICc, i.e., the AICc difference between the testing model and the baseline model. Maps of ΔAICc, R^2, slope, and visual outputs from the *plotall* function in climwin were then generated for all pixels with a P_c<0.3.

I used September 15 as the reference day for the time window analysis, as by this time, more than 90% of the roosting birds had departed for more southern latitudes (Y. Deng et al., 2023). The minimum time window length was set to 14 days to reduce the likelihood of overfitting, as very short time windows may capture noise rather than meaningful environmental

signals (van de Pol et al., 2016). For wind, the maximum time window length was limited to 107 days (back to June) to align with the start of the breeding season and post-breeding migration, as wind is a short-term effect and unlikely to persist consistently over extended periods. In contrast, the maximum time window for temperature, precipitation, and other variables was set to 258 days (back to January) because these variables tend to have cumulative and longer-term influences on overall environmental conditions, such as habitat suitability or resource availability. I took an absolute time window approach, as opposed to the relative time window, because I focused on analyzing the environmental influence on the roosting swallow population and had the same window for all individuals. For the wind analyses, I set our target location to the reference location. To aggregate statistics within the time window ("CW_stat"), I employed the slope and mean function for EVI, calculated the number of days going to or coming from the reference location for wind, and calculated the mean for wind assistance and temperature and the sum for precipitation. This process resulted in a single aggregated value for each variable-location-time window-year combination, which was then compared to a single phenology value per year.

Using the output of the per-pixel time-window analyses (i.e., per-weather variable ΔAICc maps of the best time windows), I first, for each of the environmental variables, selected the pixels with the lowest regional ΔAICc using a 9x9 pixel window. Of these, I removed the pixels that had a P_c probability less than 0.3 but were isolated, i.e., without any adjacent pixels with a P_c probability of less than 0.3. For further analysis, I no longer included the temporal trend variables in the model since the potential spurious climate-phenology relationships have been accounted for in the earlier steps. From the remaining "candidate variables", I first removed those for which the model with the environmental variable only, i.e., without the temporal trend

included, was not better (i.e. less than two units of ΔAICc lower) than the intercept-only model. Next, I removed those that had a collinearity of higher than 0.7 with another variable from the remaining "candidates" (Dormann et al., 2013) and a lower ΔAICc value, i.e., difference with the base model, than the variable they were highly collinear with. Next, I reduced the number of variables to the top 14 performing variables with the R package *Boruta* (Kursa & Rudnicki, 2010), which identifies significantly better predictors by comparing their importance scores (calculated with Random Forest algorithm) to randomly shuffled shadow variables. In the final step, I performed a variable importance analysis based on three different methods: (1) cumulative AICc weights to identify more important variables by summing multiple models with up to four independent variables (Guthery et al., 2003) using the *MuMIn* R package[47] (2) the Boruta method (Kursa & Rudnicki, 2010); and (3) the LMG (Lindeman, Merenda, and Gold) metric (Grömping, 2015), which distributes the variance contribution among the predictor variables in linear models and is based on game theory's Shapley value. The final ranking of the variable importance was decided by the mean rank calculated using all three variable importance methods. In cases of disagreements among the three methods, I reran 100 randomizations for the top fourteen "environment variable – location – time window" combinations to generate a new ΔAICc value to make sure the result was not due to chance.

For the final assessment of the amount of variance in roosting phenology that was explained by the identified final climate/vegetation variable-location-time combinations, I first repeated the time window analysis for these variables with a 21-fold cross-validation to decrease the potential of overfitting and the resulting inflated R^2. For each of these folds, one year was left out of the model fitting process, for which a time window was then determined. The k-fold cross-validation was provided by the *slidingwin* function in the *climwin* package. I chose the

maximum number of folds (≤ 21 data points) because the estimation of R^2 improves as the number of folds increases (Bailey & Van De Pol, 2016). The final time window-location combinations were still determined through the original analysis without k-fold cross-validation since it will increase the false positive rates (Bailey & Van De Pol, 2016). The coefficient of partial determination (partial R^2) for the multivariate linear model was calculated for each final signal using the rsq R package (Zhang, 2022).

Trends in roosting phenology explained by environmental variables

To examine if environmental variables that drive interannual variations in roosting phenology are also driving overall trends, I calculated the "overall contributions" made by all the important environmental variable-location-time combinations that have a trend themselves, following the equation (Haest et al., 2019, 2020; McLean et al., 2018):

$$Environment\ variables'\ contributions\ to\ trend\ in\ roosting\ phenology = \sum_{i=1}^{n}\left(\frac{\delta Phenology}{\delta Env_i} * \frac{\delta Env_i}{\delta Year}\right)$$

, where n is the total number of the remaining environmental signals left after the variable selection process; $\frac{\delta Phenology}{\delta Env_i}$ the linear regression coefficients; and $\frac{\delta Env_i}{\delta Year}$ the trend of the selected environmental variable. The multiplicative propagation of standard errors in trend contribution can be calculated using the chain rule (Taylor, 1997):

$$SE_c = Coef_c * \sqrt{\left(\frac{SE_a}{Ceof_a}\right)^2 + \left(\frac{SE_b}{Ceof_b}\right)^2}$$

Comparison to conventional approaches investigating weather signals

To determine the effectiveness of our spatiotemporally explicit per-grid-cell time-window analysis, I compared the adjusted R^2 of our final candidates' models with two other approaches that are commonly used to investigate climate-phenology relationships. Both of these approaches use *a priori* assumptions. The most common "local, static-time" approach assumes

that the climatic impacts on the mean weighted roosting phenology occur at the location and time of observation. For this scenario, I averaged the Great Lake Region local variables from July 1 to September 31 and across space, covering the roosting period at the Great Lakes. The second "local, dynamic-time" approach assumes climatic impacts occurring at the location of observation but at a flexible time window, so I used the Great Lake Region local variables and dynamic time windows with *climwin* package. I examined all final climate variables except for wind conditions as local wind extraction at the Great Lakes region resulted in no directionality.

Within the local Great Lakes area, I extracted 20 pixels (resolution 1.9047º x 1.875º) for each of the final climatic variables (minimum temperature, specific humidity, and precipitation rate), because the spatial layers of these variables overlapped with the Great Lakes region for these 20 pixels. This resulted in 60 climate-location combinations for the "local, dynamic-time" approach.

Results

Influential location-time-variable combinations on roosting phenology

I found that five final environmental, location, and time window combinations explained 89.8% (adjusted R^2) of the interannual variation in swallows' pre-migratory roosting phenology at the Great Lakes. These were composed of a mixture of temperature, wind conditions, and precipitation at likely breeding grounds and post-breeding stopover sites (Figure 2.3). Among the top five influences, minimum temperatures and headwind at 850 hPa explained the highest proportion of variance (Table 1).

Minimum temperature ("tmin.2m") in Alberta, Canada between mid-July to mid-August alone explained around 82% of the variance. Higher minimum temperatures at this location advanced the peak roosting timing (slope = -2.79, SE = 0.30, $p < 0.0001$). Minimum temperature

at coastal New Hampshire and Massachusetts from early May to June also explained 58.8% of variance and were also negatively correlated with the peak roosting timing (slope = -2.11, SE = 0.39, $p < 0.0001$). Wind conditions ("WindCF850") between June to July had a contrasting effect, with headwind from the northeast Great Lakes at the 850 hPa pressure level (1450 m above sea level) resulting in later roosting (slope = 0.71, SE = 0.12, $p < 0.0001$, adjusted R^2 = 0.614). I observed earlier peak roosting timing (slope = -71.068, SE = 16.223, $p < 0.001$, adjusted R^2 = 0.476) as specific humidity at 2 m above ground ("shum.2m") in northern North Dakota from the end of April to June increased. Conversely, I observed later roosting timing as surface precipitation rate (prate.sfc) from the Great Salt Lake area from January to February increased (slope = 0.141, SE = 0.030, $p < 0.001$, adjusted R^2 = 0.506). Accounting for the other variables, the partial R^2 indicated that minimum temperature in Alberta, headwind, minimum temperature in coastal New Hampshire and Massachusetts, precipitation rate, and specific humidity explained 63.4%, 45.1%, 26.5%, 16.3%, and 0.05% of the additional variance, respectively (Table 1).

Contributions to the trend in roosting phenology

Over the 2000-2020 study period, only three out of the five final variables showed a temporal trend: minimum temperature at Alberta and coastal New Hampshire/Massachusetts, and wind conditions at the northeast of the Great Lakes (Figure 2.4, Table 2.2). I only report trend contributions for these three variables.

Increases in minimum temperature at Alberta advanced roosting phenology at the Great Lakes with 2.52 days, and minimum temperature in coastal New Hampshire/Massachusetts resulted in an advance of 0.84 days over 21 years. A decrease in the headwinds from the roosting

location to the northeast Great Lakes may also have contributed 1.47 days of advance in the roosting phenology.

Comparison to conventional approaches of investigating environmental drivers on phenology

None of the examined signals from the "local, static-time" approach showed a significant ($p < 0.05$) relationship with the peak roosting timing. Minimum temperature at the Great Lakes from July to September explained 9.2% of the variances ($p = 0.58$, slope = -0.94, SE = 1.69). Averaged across the same space and time period, specific humidity explained 10.9% ($p = 0.61$, slope = -1290, SE = 2483), and precipitation rate explained 9.0% ($p = 0.42$, slope = -2.31, SE = 2.83) of the variances. The "local, dynamic-time" approach had a normal distribution (Shapiro-Wilk test p-value = 0.6344) for the adjusted R^2 ranging from 0.25 to 0.67 (n = 60, median = 0.44, SD = 0.094). Only 11.7% of the examined combinations for the dynamic time-window approach had P_c value lower than 0.3, which indicated only a very small number of results being reliable.

Discussion

Data integration from weather surveillance radar and satellite-based remote sensing platforms provided a unique opportunity to examine environmental effects on biological events at large spatial and temporal scales. Specifically, I used an intensive per-grid-cell time-window analysis approach to address the current lack of knowledge on the exact location and time of influence on swallows' roosting phenology at the Great Lakes. I found that a mixture of temperature, wind condition, and humidity/precipitation at potential breeding and passage areas during pre-roosting or roosting periods were drivers of migratory phenology, either directly or indirectly — with this approach I was able to explain the vast majority of variance in migration timing.

From these environmental variables I examined, minimum temperature between mid-July to mid-August at Alberta, Canada was the most important influence on roosting timing at the Great Lakes (Figure 2.3, Table 1). This region overlapped both Tree Swallow and Purple Martin breeding locations as highlighted in eBird Status and Trend maps (Figure 2.3; Fink, Auer, Johnston, Strimas-Mackey, et al., 2020). During the specific time window of temperature influence, 75% of the swallows have emerged from roost locations at the Great Lakes (Deng et al., 2023). This suggests that the minimum temperature in Alberta likely triggers the rapid migration of swallows to the Great Lakes roosting sites, with minimal time lag during this period. Increases in minimum temperatures directly impact the intensifying heat accumulation of the summer and desiccation of the environment, creating unfavorable conditions. Additionally, increased temperatures can advance insect emergence (McMaster & Wilhelm, 1997), which could influence breeding timing and success rate and subsequently better prepare swallows for an earlier migration at the end of the breeding season. I identified a much weaker influence of minimum temperature in the northeast US (New Hampshire and Massachusetts coastal region) between mid-May to early-June (Figure 2.3, Table 2.1). This location is much closer to our focal roosting region and at a lower latitude, and swallows may time their roosting events based on the minimum temperature at their breeding ground. In our analyses, I also considered daily mean and maximum temperatures. Although they were not identified as the final influences, their effect was merely excluded because it was highly collinear (Pearson correlation coefficients > 0.7) with minimum temperature and precipitation. This means that I couldn't statistically separate their effects and hence cannot make a strong conclusion on whether it is indeed minimum, mean, or maximum temperature at the breeding grounds that affects post-breeding roosting phenology.

Wind conditions, specifically the frequency of days with headwinds at the 850 hPa pressure level (1450 m a.s.l.) during the migration season in the northeast of the Great Lakes, had a strong impact on roosting phenology at the Great Lakes. The time window for wind conditions ranged from June to July, i.e., the period right before the start of the roosting activities in the Great Lakes. As one would expect from a direct wind effect, more days with headwinds during daytime at 850 hPa at the northeastern Great Lakes led to later peak roosting times. Headwind conditions usually require higher energy expenditure from migratory birds, thus delaying swallows' readiness to take off (Liechti, 2006). Swallows are very adaptive in terms of migration strategies and sensitive to consistent wind conditions: Tree Swallows have a cross-Gulf autumn migration aided by favorable tailwinds and a circum-Gulf overland migration in the spring without strong wind assistance, following a looped trans-Gulf migration pattern (Bradley et al., 2014). Similarly, Purple Martins adjust their spring departure timing from the Yucatán Peninsula across the Gulf of Mexico based on wind speed and direction (Abdulle & Fraser, 2018). The Great Lakes themselves serve as a non-trivial ecological barrier and possibly drive swallow populations breeding in the northeast to migrate through land corridors, which are the space between (1) Lake Erie/Lake Ontario and Lake Huron, and (2) Lake Erie and Lake Ontario. The headwind variable is positioned along these migration corridors, aligning with the swallows' likely flight paths.

Wind at different altitudes also plays a critical part in shaping migration strategies. In this study, headwind influence was detected at the 850 hPa pressure level (1,450 m a.s.l.), rather than at lower altitudes (925 and 1,000 hPa), suggesting that the swallows migrating from the northeast are predominantly Purple Martins. Flight behavior data from altitudinal data loggers recorded maximum altitudes of 1,945 m for Purple Martins, 661 m for Tree Swallows, and 273 m for Barn

Swallows, further supporting this idea (Dreelin et al., 2018). Additionally, the aerial insects consumed by Purple Martins have been recorded at higher altitudes, reaching up to 922 m above ground (Helms et al., 2016). The result suggests that swallows and martins migrating through the Great Lakes utilized higher-altitude airspace during the day, likely influenced by a combination of atmospheric conditions over the lakes, prey availability, and energy trade-offs (Senner et al., 2018; Williamson & Witt, 2021).

Following these major influences, specific humidity at the potential breeding grounds and stopover sites of several roosting swallow species (May to June) also had a moderate influence on roosting phenology at the Great Lakes. The region where specific humidity influenced migration phenology extended from Alberta and southern Saskatchewan down to South Dakota (Figure 2.3, Map 2.S1). The range overlapped with migration routes of many swallow species, Tree Swallows in particular (Imlay, 2018; Imlay et al., 2020; Imlay & Taylor, 2020). Specific humidity likely influences a bird's breeding phenology and success through its effects on environmental conditions that impact key reproductive stages, such as nest building, egg laying, incubation, hatching, and provisioning (Deeming, 2011; Namasivayam-MacDonald et al., 2018). Higher specific humidity can enhance the availability of food resources for insectivorous birds by promoting plant productivity for herbivorous insects (Studds & Marra, 2007). For species like Tree Swallows, earlier egg-laying during the breeding season has been linked to greater food abundance (Nooker et al., 2005). Evidently, the timing of the breeding season was found to have carryover effect on the departure timing of the autumn migration in barn swallows (Imlay et al., 2021). This earlier initiation of reproductive activities could cascade into earlier post-breeding migration. Thus, the influence of specific humidity on the timing and success of breeding likely contributes to shifts in the timing of subsequent phenological events.

Precipitation rate at surface (prate.sfc) at the Salt Lake during winter (the month of January) surprisingly showed up in the final candidates as well. There are confirmed distributions of several roosting swallow species in the Salt Lake region, where Purple Martins have a small, isolated breeding and post-breeding range (Fink, Auer, Johnston, Ruiz-Gutierrez, et al., 2020). This result suggests that there may be a migration connection between the population passing the Salt Lake in Utah and the population roosting at the Great Lakes. Here, a drier winter corresponded to earlier roosting in the summer. This effect was evident in a 57-year study on four swallow species' breeding phenology in Canada: Barn and Tree Swallows experienced time advancements in breeding during warmer winters with reduced snow (i.e., precipitation) due to climate change (Imlay et al., 2018).

Using more localized or time-specific approaches ('local, static-time' and 'local, dynamic-time' frameworks), I was unable to explain much of the observed variance in roosting phenology. These approaches may not always capture the potential lag effects or indirect pathways through which environmental variables can influence phenological events (van de Pol et al., 2016). Migratory species engage in frequent movements, potentially traversing extensive spatial regions throughout their migration season (Berthold, 2001). While some studies in migration phenology do account for such complexities, our findings suggest that these dynamics might require further exploration in the context of post-breeding roosting phenology. Much of the current knowledge on environmental drivers of migration phenology stems from observational data, instead of experiments, meaning *a priori* assumptions have often been propagated over studies. Patterns may seem to be driven by local measures, but there is a probability of obtaining these 'significant' correlations due to spatiotemporally correlated phenomenon (Haest et al., 2018a). Based on our contrasting findings between the *a priori* approaches and our holistic analysis, I

argue that much of the research on the drivers of animal phenology would benefit from a careful examination of assumptions on time, space, and types of influences using an exploratory approach (van de Pol et al., 2016).

While our results explained much of the variance in swallows' post-breeding roosting phenology in the Great Lakes, it is important to acknowledge certain caveats that could affect the interpretation of the results. Many of the environmental variables measured, such as temperature, wind, and precipitation, are often correlated both in time and space (Li et al., 2003). For example, wind speed, which is a critical driver of migratory behavior (Liechti, 2006; Nussbaumer et al., 2022), could be indirectly correlated with other variables like temperature and precipitation, leading to potential confounding effects. While our approach allows for some degree of isolation of independent climate and weather effects on phenology, there remains the possibility that some of the relationships I observed could be spurious or influenced by unmeasured covariates. Additionally, our approach of identifying influential pixels does not imply that only these specific locations drive phenology; rather, these pixels represent a broader surrounding area of influence (Figure 2.3). Future studies incorporating finer-scale biological data and explicitly testing for interactions among predictors could help strengthen confidence in these findings and address remaining uncertainties.

Climate change is a complex and multifaceted phenomenon, operating on a global scale and occurring over extended periods, spanning decades or centuries. While change in migration systems is often gradual in response to climate change, biological responses at times are dramatic. Even within 21 years of our study period, I observed an advance in the peak roosting activity of the swallows at the Great Lakes by 4.75 days (Deng et al., 2023) due to increasing minimum temperature at potential breeding grounds and less frequent unfavorable wind

conditions (Figure 2.4). Over the next three decades, this region is projected to experience a 2.4–2.8°C temperature increase compared to historical data (1911–2005), based on the CMIP5 (ENSMN) RCP8 model (https://www.esrl.noaa.gov/psd/ipcc/cmip5/), along with weaker prevailing westerly winds during autumn migration (La Sorte et al., 2019). This suggests that favorable wind conditions for northeastern breeding populations, combined with rising temperatures in northern latitudes where these swallows breed and migrate, could further advance roosting phenology at the Great Lakes. It is also important for future studies to understand whether they are reaching their thermal limits or altering their migration behavior due to extreme heat or the increasing frequency of heat waves. Overall, trends in the examined influential environmental drivers are projected to result in advances in roosting season at the Great Lakes in the near future, with possible consequences of trophic mismatch, population changes, as well as changing ecosystem functions that aerial insectivores are playing.

Studies aiming to investigate climate change's impact on biodiversity, wildlife population, and ecosystem functioning are urgently needed in this ever-changing era. As this study shows, if we are going to understand the impacts of climate change holistically, we need to use a broader lens — both in space and time. This knowledge will be essential for developing robust and adaptive climate change strategies that can help protect vulnerable ecosystems and enhance resilience in the face of ongoing climate changes.

Figures and Tables

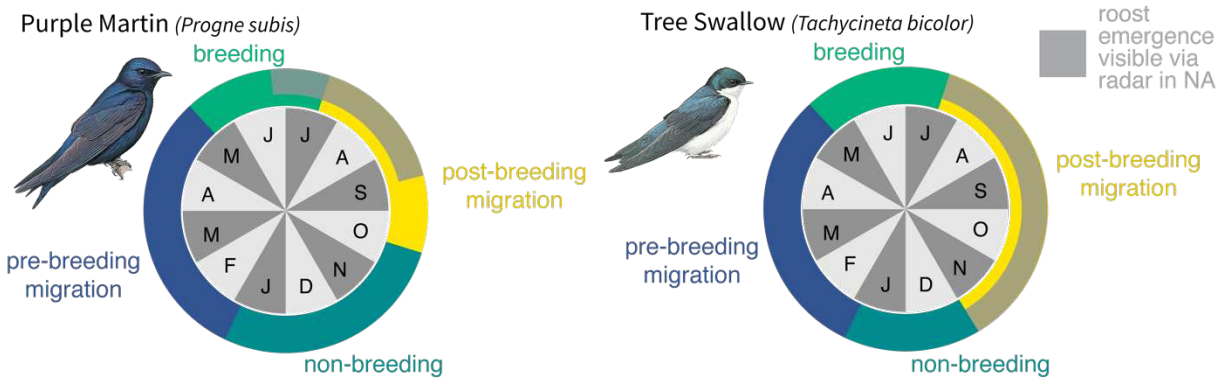

Figure 2.1. Annual cycles of Purple Martin (*Progne subis*) and Tree Swallow (*Tachycineta bicolor*), noting important life history events, including non-breeding, spring migration, breeding, and fall migration phases. Transparent grey wheel shows the period in their life history when they form large roosts in North America and can be detected on weather surveillance radar. Months are abbreviated by their first letters on the time wheel.

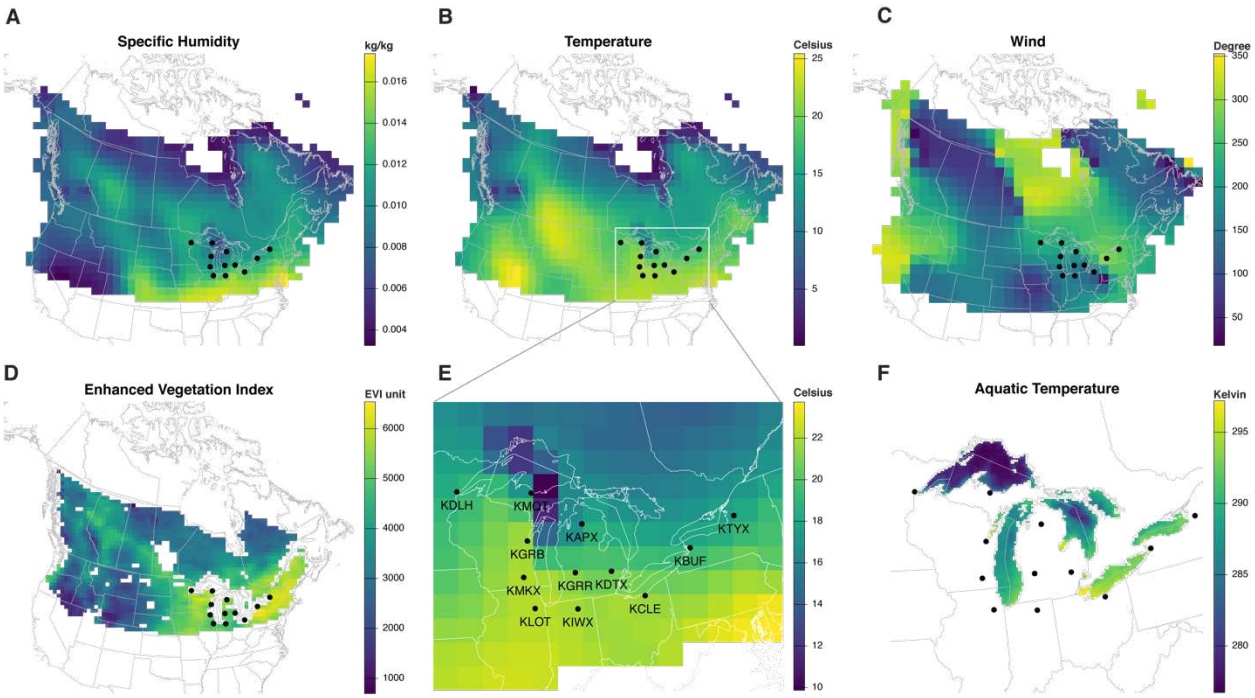

Figure 2.2. Example environmental data input from July 1st, 2003, showing the resolution and extent of the variables. Dots represent the location of radar stations included in this analysis. (A) Specific humidity at 2 meters above ground (kg/kg). (B) Mean air temperature at 2 meters above ground (degree celsius). (C) Wind direction (degree) calculated from uwind (m/s) and vwind (m/s). (D) Enhanced Vegetation Index. (E) Zoomed in location of 12 radar stations across the Great Lakes. (F) Water surface temperature (degree K), zoomed in to the Great Lakes region.

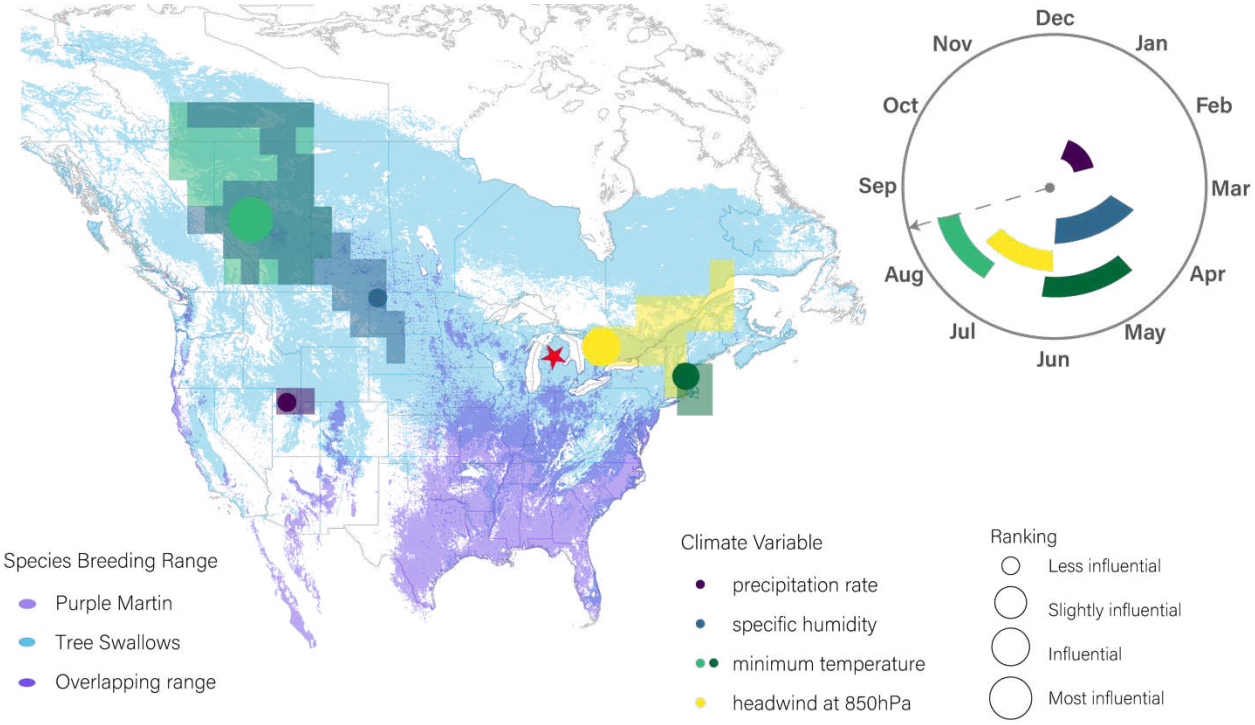

Figure 2.3. Map and time windows of the most important environmental variables identified to influence the peak post-breeding roosting timing of the aerial insectivores at the Great Lakes. The star marks the center of the roosting phenomenon detected on radars. Sizes of the marked locations correspond to the final ranking given by the variable importance analysis. The actual influential areas are larger than the representative location I show, represented by the colored transparent area (based on per-weather variable ΔAICc maps of the best time windows, Supplementary Map 1). The time window wheel represents the period of the single best time window for each environmental variable (corresponding colors). The dotted line with arrow points shows the peak roosting timing (August 16th) at the Great Lakes. Breeding abundance maps of Purple Martins (*Progne subis*) and Tree Swallows (*Tachycineta bicolor*) are overlaid, provided by eBird Status and Trends.

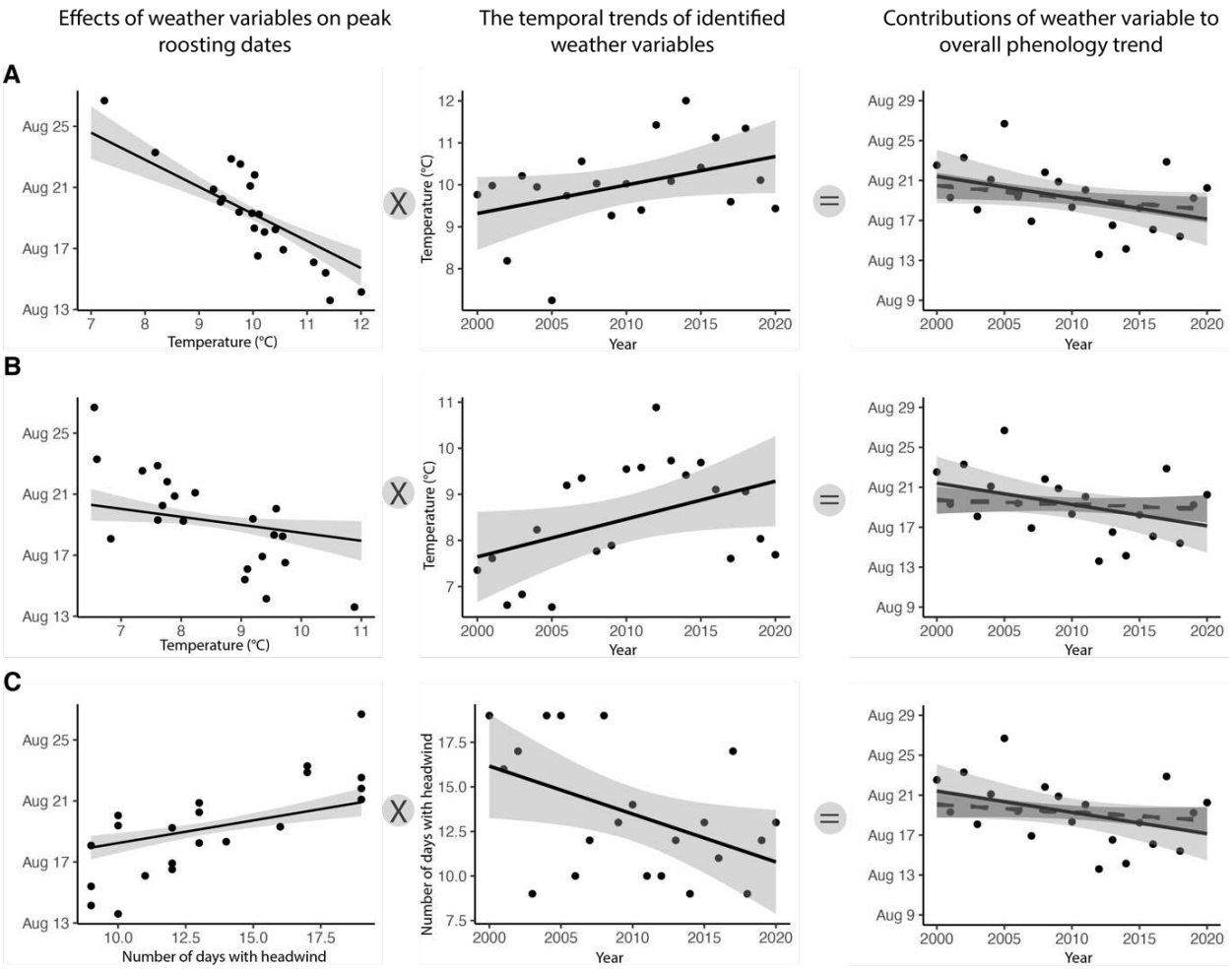

Figure 2.4. Overview of the correlations between the identified environmental signals and peak roosting timing (the first column); the temporal trends of these signals (the second column); and the resulting contribution to the overall trend of the roosting phenology using the chain rule (the third column). The solid lines on the third column plots represent the trend of roosting phenology over 21 years, and the dotted line shows the calculated contributions to the temporal trend by each signal. Ribbons around each line represent the 95% CI. Three examined signals are (A) Minimum temperature - ID 200 - Alberta, Canada. (B) Minimum temperature - ID 518 - Coastal New Hampshire and Massachusetts. (C) Wind coming from Great Lakes at 850 hPa - ID 294 - Northeast Great Lakes.

Table 2.1. Identified most influential environmental variables that are likely to influence the peak swallow roosting phenology dates at the Great Lakes, including the identified variable, location, time window (with associated uncertainty), importance ranking, and R^2. Window uncertainty means that this percent of the top models falls within the 95% confidence set.

Climate Variable	Operation	Pixel Number	Location	Interpretation	Window Open	Window Close	Window Length	Window Uncertainty	Longitude	Latitude	Mean Rank	Adjusted R^2	Partial R^2	K-fold cross-validation R^2
Minimum temperature	mean	200	Alberta, Canada	Likely breeding ground and stopover area	67	29	38	3%	-116.25	54.28	5	0.815	0.634	0.665
Precipitation rate	sum	233	Great Salt Lake area	Likely breeding ground	258	230	28	63%	-112.5	40.95	2	0.506	0.163	0.549
Minimum temperature	mean	518	Coastal New Hampshire and Massachusetts	Likely breeding ground	129	102	27	61%	-71.25	42.85	2.3	0.588	0.265	0.254
Specific humidity	sum	294	Northern North Dakota	Likely passage and stopover area	145	108	37	49%	-103.12	48.57	2	0.476	0.005	0.337
Wind coming from Great Lakes	number of days	294	Northeast Great Lakes	Likely breeding ground	103	79	24	45%	-80	45	3.7	0.614	0.451	0.244

Table 2.2. Trend contributions of three environmental variables to the roosting phenology were calculated based on the chain rule.

Climate Variable	Location	dPheno/dClimate		dClimate/dTime		dPheno/dTime	
		Coef.	SE	Coef.	SE	Coef.	SE
Minimum temperature	Alberta, Canada	-1.7735	0.2636	0.0679	0.0356	-0.1204	-0.0656
Minimum temperature	Coastal New Hampshire and Massachusetts	-0.5229	0.2301	0.0821	0.0400	-0.0429	-0.0281
Wind coming from Great Lakes	Northeast Great Lakes	0.2969	0.0702	-0.269	0.1191	-0.0798	-0.0401

REFERENCES

Abdulle, S. A., & Fraser, K. C. (2018). Does wind speed and direction influence timing and route of a trans-hemispheric migratory songbird (purple martin) at a migration barrier? *Animal Migration*, *5*(1). https://doi.org/10.1515/ami-2018-0005

Acevedo-Whitehouse, K., & Duffus, A. L. J. (2009). Effects of environmental change on wildlife health. In *Philosophical Transactions of the Royal Society B: Biological Sciences* (Vol. 364, Issue 1534). https://doi.org/10.1098/rstb.2009.0128

Adams, C. A., Tomaszewska, M. A., Henebry, G. M., & Horton, K. G. (2024). Chasing and surfing seasonal waves: Avian migration through the US tracks land surface phenology in fall, but not spring. *Journal of Animal Ecology*, *93*(7), 836–848. https://doi.org/10.1111/1365-2656.14088

Aharon-Rotman, Y., McEvoy, J. F., Kiat, Y., Raz, T., & Perlman, G. Y. (2022). Time to Move On: The Role of Greenness in Africa and Temperatures at a Mediterranean Stopover Site in Migration Decision of Long-Distance Migratory Passerines. *Frontiers in Ecology and Evolution*, *10*. https://doi.org/10.3389/fevo.2022.834074

Anderson, D. R., & Burnham, K. P. (2002). Avoiding Pitfalls When Using Information-Theoretic Methods. *The Journal of Wildlife Management*, *66*(3). https://doi.org/10.2307/3803155

Bailey, L. D., & Van De Pol, M. (2016). climwin: An R Toolbox for Climate Window Analysis. *PLOS ONE*, *11*(12), e0167980. https://doi.org/10.1371/JOURNAL.PONE.0167980

Bairlein, F. (2016). Migratory birds under threat. In *Science* (Vol. 354, Issue 6312). https://doi.org/10.1126/science.aah6647

Belotti, M. C. T. D., Deng, Y., Zhao, W., Simons, V. F., Cheng, Z., Perez, G., Tielens, E., Maji, S., Sheldon, D., Kelly, J. F., & Horton, K. G. (2023). Long-term analysis of persistence and size of swallow and martin roosts in the US Great Lakes. *Remote Sensing in Ecology and Conservation*. https://doi.org/10.1002/rse2.323

Berthold, P. (2001). *Bird migration: a general survey*. Oxford University Press.

Both, C., Artemyev, A. V, Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V, Jä rvinen, A., Metcalfe, N. B., Erik Nyholm, N. I., Potti, J., Ravussin, P.-A., Jose Sanz, J., Silverin, B., Slater, F. M., Sokolov, L. V, nos Tö rö, J., … Visser, M. E. (2004). Large–scale geographical variation confirms that climate change causes birds to lay earlier. *Royalsocietypublishing.Org*, *271*(1549), 1657–1662. https://doi.org/10.1098/rspb.2004.2770

Both, C., & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, *411*(6835). https://doi.org/10.1038/35077063

Bradley, D. W., Clark, R. G., Dunn, P. O., Laughlin, A. J., Taylor, C. M., Vleck, C., Whittingham, L. A., Winkler, D. W., & Norris, R. (2014). Trans-Gulf of Mexico loop migration of tree swallows revealed by solar geolocation. In *Current Zoology* (Vol. 60, Issue 5). https://academic.oup.com/cz/article/60/5/653/1786995

Bridge, E. S., Kelly, J. F., Bjornen, P. E., Curry, C. M., Crawford, P. H. C., & Paritte, J. M. (2010). Effects of nutritional condition on spring migration: Do migrants use resource availability to keep pace with a changing world? *Journal of Experimental Biology*, *213*(14). https://doi.org/10.1242/jeb.041277

Bridge, E. S., Pletschet, S. M., Fagin, T., Chilson, P. B., Horton, K. G., Broadfoot, K. R., & Kelly, J. F. (2016). Persistence and habitat associations of Purple Martin roosts quantified

via weather surveillance radar. *Landscape Ecology*, *31*(1), 43–53. https://doi.org/10.1007/s10980-015-0279-0

Brown, C. R., Sas, C. M., & Brown, M. B. (2002). Colony choice in Cliff Swallows: Effects of heterogeneity in foraging habitat. *Auk*, *119*(2). https://doi.org/10.2307/4089891

Chilson, P. B., Frick, W. F., Stepanian, P. M., Shipley, J. R., Kunz, T. H., & Kelly, J. F. (2012). Estimating animal densities in the aerosphere using weather radar: To Z or not to Z? *Ecosphere*, *3*(8), 1–19. https://doi.org/10.1890/es12-00027.1

Cotton, P. A. (2003). Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(21). https://doi.org/10.1073/pnas.1930548100

Cox, A. R., Robertson, R. J., Lendvai, A. Z., Everitt, K., & Bonier, F. (2019). Rainy springs linked to poor nestling growth in a declining avian aerial insectivore (Tachycineta bicolor). *Proceedings of the Royal Society B: Biological Sciences*, *286*(1898). https://doi.org/10.1098/rspb.2019.0018

Deeming, D. C. (2011). Importance of nest type on the regulation of humidity in bird nests. *Avian Biology Research*, *4*(1). https://doi.org/10.3184/175815511X13013963263739

Deng, Y., Belotti, M. C. T. D., Zhao, W., Cheng, Z., Perez, G., Tielens, E., Simons, V. F., Sheldon, D. R., Maji, S., Kelly, J. F., & Horton, K. G. (2023). Quantifying long-term phenological patterns of aerial insectivores roosting in the Great Lakes region using weather surveillance radar. *Global Change Biology*, *29*(5). https://doi.org/10.1111/gcb.16509

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., Mcclean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013).

Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dreelin, R. A., Shipley, J. R., & Winkler, D. W. (2018). Flight behavior of individual aerial insectivores revealed by novel altitudinal dataloggers. *Frontiers in Ecology and Evolution*, *6*(NOV). https://doi.org/10.3389/fevo.2018.00182

Eisaguirre, J. M., Booms, T. L., Barger, C. P., McIntyre, C. L., Lewis, S. B., & Breed, G. A. (2018). Local meteorological conditions reroute a migration. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1890). https://doi.org/10.1098/rspb.2018.1779

Fink, D., Auer, T., Johnston, A., Ruiz-Gutierrez, V., Hochachka, W. M., & Kelling, S. (2020). Modeling avian full annual cycle distribution and population trends with citizen science data. *Ecological Applications*, *30*(3). https://doi.org/10.1002/eap.2056

Fink, D., Auer, T., Johnston, A., Strimas-Mackey, M., Robinson, O., Ligocki, S., Hochachka, W., Wood, C., Davies, I., & Iliff, M. (2020). eBird status and trends. *Data Version*.

Forrest, J. R. (2016). Complex responses of insect phenology to climate change. In *Current Opinion in Insect Science* (Vol. 17). https://doi.org/10.1016/j.cois.2016.07.002

Gauthreaux, S. A., Belser, C. G., & Welch, C. M. (2006). Atmospheric trajectories and spring bird migration across the Gulf of Mexico. *Journal of Ornithology*, *147*(2). https://doi.org/10.1007/s10336-006-0063-7

Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, *35*(1–2), 37–58. https://doi.org/10.3354/cr00713

Grömping, U. (2015). Variable importance in regression models. In *Wiley Interdisciplinary Reviews: Computational Statistics* (Vol. 7, Issue 2). https://doi.org/10.1002/wics.1346

Gunnarsson, T. G., Gill, J. A., Atkinson, P. W., Gélinaud, G., Potts, P. M., Croger, R. E., Gudmundsson, G. A., Appleton, G. F., & Sutherland, W. J. (2006). Population-scale drivers of individual arrival times in migratory birds. *Journal of Animal Ecology*, *75*(5). https://doi.org/10.1111/j.1365-2656.2006.01131.x

Guthery, F. S., Burnham, K. P., & Anderson, D. R. (2003). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. *The Journal of Wildlife Management*, *67*(3). https://doi.org/10.2307/3802723

Haest, B., Hüppop, O., & Bairlein, F. (2018a). Challenging a 15-year-old claim: The North Atlantic Oscillation index as a predictor of spring migration phenology of birds. *Global Change Biology*, *24*(4). https://doi.org/10.1111/gcb.14023

Haest, B., Hüppop, O., & Bairlein, F. (2018b). The influence of weather on avian spring migration phenology: What, where and when? *Global Change Biology*, *24*(12). https://doi.org/10.1111/gcb.14450

Haest, B., Hüppop, O., & Bairlein, F. (2020). Weather at the winter and stopover areas determines spring migration onset, progress, and advancements in Afro-Palearctic migrant birds. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(29), 17056–17062. https://doi.org/10.1073/pnas.1920448117

Haest, B., Hüppop, O., van de Pol, M., & Bairlein, F. (2019). Autumn bird migration phenology: A potpourri of wind, precipitation and temperature effects. *Global Change Biology*, *25*(12), 4064–4080. https://doi.org/10.1111/gcb.14746

Haest, B., Stepanian, P. M., Wainwright, C. E., Liechti, F., & Bauer, S. (2021). Climatic drivers of (changes in) bat migration phenology at Bracken Cave (USA). *Global Change Biology*, *27*(4), 768–780. https://doi.org/10.1111/gcb.15433

Helms, J. A., Godfrey, A. P., Ames, T., & Bridge, E. S. (2016). Predator foraging altitudes reveal the structure of aerial insect communities. *Scientific Reports*, *6*(1), 1–10. https://doi.org/10.1038/srep28670

Hixson, S. M., Sharma, B., Kainz, M. J., Wacker, A., & Arts, M. T. (2015). Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: A fundamental dichotomy between freshwater and terrestrial ecosystems. *Environmental Reviews*, *23*(4), 414–424. https://doi.org/10.1139/ER-2015-0029

Horton, K. G., La Sorte, F. A., Sheldon, D., Lin, T. Y., Winner, K., Bernstein, G., Maji, S., Hochachka, W. M., & Farnsworth, A. (2020). Phenology of nocturnal avian migration has shifted at the continental scale. *Nature Climate Change*, *10*(1), 63–68. https://doi.org/10.1038/s41558-019-0648-9

Horton, K. G., Van Doren, B. M., La Sorte, F. A., Fink, D., Sheldon, D., Farnsworth, A., & Kelly, J. F. (2018). Navigating north: how body mass and winds shape avian flight behaviours across a North American migratory flyway. *Ecology Letters*, *21*(7), 1055–1064. https://doi.org/10.1111/ele.12971

Huang, A. C., Bishop, C. A., McKibbin, R., Drake, A., & Green, D. J. (2017). Wind conditions on migration influence the annual survival of a neotropical migrant, the western yellow-breasted chat (Icteria virens auricollis). *BMC Ecology*, *17*(1). https://doi.org/10.1186/s12898-017-0139-7

Huete, A., Justice, C., & Liu, H. (1994). Development of vegetation and soil indices for MODIS-EOS. *Remote Sensing of Environment*, *49*(3). https://doi.org/10.1016/0034-4257(94)90018-3

Hüppop, O., & Hüppop, K. (2003). North Atlantic Oscillation and timing of spring migration in birds. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1512). https://doi.org/10.1098/rspb.2002.2236

Iler, A. M., Inouye, D. W., Schmidt, N. M., & Høye, T. T. (2016). *Detrending phenological time series improves climate-phenology analyses and reveals evidence of plasticity*. http://data.g-e-m.dk/

Imlay, T. L., Mann, H. A. R., & Taylor, P. D. (2021). Autumn migratory timing and pace are driven by breeding season carryover effects. *Animal Behaviour*, *177*. https://doi.org/10.1016/j.anbehav.2021.05.003

Imlay, T. L. (2018). *Understanding the Drivers of Population Declines for Swallows (Family: Hirundinidae) Throughout the Annual Cycle*. Dalhousie University.

Imlay, T. L., Mills Flemming, J., Saldanha, S., Wheelwright, N. T., & Leonard, M. L. (2018). Breeding phenology and performance for four swallows over 57 years: relationships with temperature and precipitation. *Ecosphere*, *9*(4), e02166. https://doi.org/10.1002/ecs2.2166

Imlay, T. L., Saldanha, S., & Taylor, P. D. (2020). The fall migratory movements of bank swallows, riparia riparia: Fly-and-forage migration? *Avian Conservation and Ecology*, *15*(1). https://doi.org/10.5751/ACE-01463-150102

Imlay, T. L., & Taylor, P. D. (2020). Diurnal and crepuscular activity during fall migration for four species of aerial foragers. *Wilson Journal of Ornithology*, *132*(1), 159–164. https://doi.org/10.1676/1559-4491-132.1.159

Jenni, L., & Kéry, M. (2003). Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1523). https://doi.org/10.1098/rspb.2003.2394

Kelly, J. F., & Pletschet, S. M. (2018). Accuracy of swallow roost locations assigned using weather surveillance radar. *Remote Sensing in Ecology and Conservation*, *4*(2), 166–172. https://doi.org/10.1002/rse2.66

Kemp, M. U., Emiel van Loon, E., Shamoun-Baranes, J., & Bouten, W. (2012). RNCEP: Global weather and climate data at your fingertips. *Methods in Ecology and Evolution*, *3*(1), 65–70. https://doi.org/10.1111/j.2041-210X.2011.00138.x

Kemp, M. U., Shamoun-Baranes, J., van Loon, E. E., McLaren, J. D., Dokter, A. M., & Bouten, W. (2012). Quantifying flow-assistance and implications for movement research. *Journal of Theoretical Biology*, *308*, 56–67. https://doi.org/10.1016/j.jtbi.2012.05.026

Klinner, T., & Schmaljohann, H. (2020). Temperature change is an important departure cue in nocturnal migrants: Controlled experiments with wild-caught birds in a proof-of-concept study: Temperature affects departure decision. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1936). https://doi.org/10.1098/rspb.2020.1650

Kursa, M. B., & Rudnicki, W. R. (2010). Feature selection with the boruta package. *Journal of Statistical Software*, *36*(11). https://doi.org/10.18637/jss.v036.i11

La Sorte, F. A., & Graham, C. H. (2021). Phenological synchronization of seasonal bird migration with vegetation greenness across dietary guilds. *Journal of Animal Ecology*, *90*(2), 343–355. https://doi.org/10.1111/1365-2656.13345

La Sorte, F. A., Horton, K. G., Nilsson, C., & Dokter, A. M. (2019). Projected changes in wind assistance under climate change for nocturnally migrating bird populations. *Global Change Biology*, *25*(2). https://doi.org/10.1111/gcb.14531

Laczi, M., Garamszegi, L. Z., Hegyi, G., Herényi, M., Ilyés, G., Könczey, R., Nagy, G., Pongrácz, R., Rosivall, B., Szöllősi, E., Tóth, L., & Török, J. (2019). Teleconnections and

local weather orchestrate the reproduction of tit species in the Carpathian Basin. *Journal of Avian Biology*, *50*(12). https://doi.org/10.1111/jav.02179

Laughlin, A. J., Taylor, C. M., Bradley, D. W., LeClair, D., Clark, R. G., Dawson, R. D., Dunn, P. O., Horn, A., Leonard, M., Sheldon, D. R., Shutler, D., Whittingham, L. A., Winkler, D. W., & Norris, D. R. (2013). Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. *Auk*, *130*(2), 230–239. https://doi.org/10.1525/auk.2013.12229

Lavallée, C. D., Assadi, S. B., Korpach, A. M., Ray, J. D., Fischer, J. D., Siegrist, J., & Fraser, K. C. (2021). The use of nocturnal flights for barrier crossing in a diurnally migrating songbird. *Movement Ecology*, *9*(1), 1–11. https://doi.org/10.1186/S40462-021-00257-7

Li, Z., Liu, L., & Dunham, M. H. (2003). Considering correlation between variables to improve spatiotemporal forecasting. *Lecture Notes in Artificial Intelligence (Subseries of Lecture Notes in Computer Science)*, *2637*. https://doi.org/10.1007/3-540-36175-8_52

Liechti, F. (2006). Birds: Blowin' by the wind? In *Journal of Ornithology* (Vol. 147, Issue 2, pp. 202–211). https://doi.org/10.1007/s10336-006-0061-9

Mateos-Rodríguez, M., & Liechti, F. (2012). How do diurnal long-distance migrants select flight altitude in relation to wind? *Behavioral Ecology*, *23*(2). https://doi.org/10.1093/beheco/arr204

McLean, N., Van Der Jeugd, H. P., & Van De Pol, M. (2018). High intra-specific variation in avian body condition responses to climate limits generalisation across species. *PLoS ONE*, *13*(2). https://doi.org/10.1371/journal.pone.0192401

McMaster, G. S., & Wilhelm, W. W. (1997). Growing degree-days: One equation, two interpretations. *Agricultural and Forest Meteorology*, *87*(4). https://doi.org/10.1016/S0168-1923(97)00027-0

Miles, W. T. S., Bolton, M., Davis, P., Dennis, R., Broad, R., Robertson, I., Riddiford, N. J., Harvey, P. V., Riddington, R., Shaw, D. N., Parnaby, D., & Reid, J. M. (2017). Quantifying full phenological event distributions reveals simultaneous advances, temporal stability and delays in spring and autumn migration timing in long-distance migratory birds. *Global Change Biology*, *23*(4). https://doi.org/10.1111/gcb.13486

Moiron, M., Teplitsky, C., Haest, B., Charmantier, A., & Bouwhuis, S. (2024). Micro-evolutionary response of spring migration timing in a wild seabird. *Evolution Letters*, *8*(1). https://doi.org/10.1093/evlett/qrad014

Namasivayam-MacDonald, A. M., Barbon, C. E. A., & Steele, C. M. (2018). A review of swallow timing in the elderly. In *Physiology and Behavior* (Vol. 184). https://doi.org/10.1016/j.physbeh.2017.10.023

Nooker, J. K., Dunn, P. O., & Whittingham, L. A. (2005). Effects of food abundance, weather, and female condition on reproduction in Tree Swallows (Tachycineta bicolor). *Auk*, *122*(4). https://doi.org/10.1642/0004-8038(2005)122[1225:EOFAWA]2.0.CO;2

Nussbaumer, R., Schmid, B., Bauer, S., & Liechti, F. (2022). Favorable winds speed up bird migration in spring but not in autumn. *Ecology and Evolution*, *12*(8), e9146. https://doi.org/10.1002/ece3.9146

Pearce-Higgins, J. W., & Green, R. E. (2012). Birds and climate change: Impacts and conservation responses. In *Birds and Climate Change: Impacts and Conservation Responses*. https://doi.org/10.1017/CBO9781139047791

Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., Barbeta, A., Rivas-Ubach, A., Llusià, J., Garbulsky, M., Filella, I., & Jump, A. S. (2013). Evidence of current impact of climate change on life: A walk from genes to the biosphere. In *Global Change Biology* (Vol. 19, Issue 8, pp. 2303–2338). https://doi.org/10.1111/gcb.12143

Razgour, O., Taggart, J. B., Manel, S., Juste, J., Ibáñez, C., Rebelo, H., Alberdi, A., Jones, G., & Park, K. (2018). An integrated framework to identify wildlife populations under threat from climate change. In *Molecular Ecology Resources* (Vol. 18, Issue 1, pp. 18–31). Blackwell Publishing Ltd. https://doi.org/10.1111/1755-0998.12694

Robertson, E. P., La Sorte, F. A., Mays, J. D., Taillie, P. J., Robinson, O. J., Ansley, R. J., O'Connell, T. J., Davis, C. A., & Loss, S. R. (2024). Decoupling of bird migration from the changing phenology of spring green-up. *Proceedings of the National Academy of Sciences of the United States of America*, *121*(12). https://doi.org/10.1073/pnas.2308433121

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, *421*(6918). https://doi.org/10.1038/nature01333

Schwartz, M. D. (2013). Phenology: An integrative environmental science. In *Phenology: An Integrative Environmental Science*. https://doi.org/10.1007/978-94-007-6925-0

Scranton, K., & Amarasekare, P. (2017). Predicting phenological shifts in a changing climate. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(50). https://doi.org/10.1073/pnas.1711221114

Senner, N. R., Stager, M., Verhoeven, M. A., Cheviron, Z. A., Piersma, T., & Bouten, W. (2018). High-altitude shorebird migration in the absence of topographical barriers: avoiding

high air temperatures and searching for profitable winds. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1881). https://doi.org/10.1098/rspb.2018.0569

Shamoun-Baranes, J., van Loon, E., Alon, D., Alpert, P., Yom-Tov, Y., & Leshem, Y. (2006). Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? *Global Ecology and Biogeography*, *0*(0), 060822084839001-??? https://doi.org/10.1111/j.1466-822x.2006.00261.x

Stepanian, P. M., & Wainwright, C. E. (2018). Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. *Global Change Biology*, *24*(7), 3266–3275. https://doi.org/10.1111/gcb.14051

Strong, C., Zuckerberg, B., Betancourt, J. L., & Koenig, W. D. (2015). Climatic dipoles drive two principal modes of North American boreal bird irruption. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(21), E2795–E2802. https://doi.org/10.1073/pnas.1418414112

Studds, C. E., & Marra, P. P. (2007). Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, Setophaga ruticilla. *Climate Research*, *35*(1–2). https://doi.org/10.3354/cr00718

Taylor, J. R. (1997). An Introduction to Error Analysis. *Journal of the Acoustical Society of America*, *101*.

Twining, C. W., Shipley, J. R., & Winkler, D. W. (2018). Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. *Ecology Letters*, *21*(12), 1812–1820. https://doi.org/10.1111/ELE.13156

van de Pol, M., Bailey, L. D., McLean, N., Rijsdijk, L., Lawson, C. R., & Brouwer, L. (2016). Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and Evolution*, *7*(10). https://doi.org/10.1111/2041-210X.12590

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2561–2569. https://doi.org/10.1098/rspb.2005.3356

Williamson, J. L., & Witt, C. C. (2021). Elevational niche-shift migration: Why the degree of elevational change matters for the ecology, evolution, and physiology of migratory birds. In *Ornithology* (Vol. 138, Issue 2). https://doi.org/10.1093/ornithology/ukaa087

Wood, S. N. (2001). mgcv: GAMs and generalized ridge regression for R. *R News*, *1*.

Youngflesh, C., Socolar, J., Amaral, B. R., Arab, A., Guralnick, R. P., Hurlbert, A. H., LaFrance, R., Mayor, S. J., Miller, D. A. W., & Tingley, M. W. (2021). Migratory strategy drives species-level variation in bird sensitivity to vegetation green-up. *Nature Ecology & Evolution*, *5*(7), 987–994. https://doi.org/10.1038/s41559-021-01442-y

Zhang, D. (2022). Package "rsq": R-Squared and Related Measures. In *The Comprehensive R Archive Network*.

Zuckerberg, B., Strong, C., LaMontagne, J. M., St. George, S., Betancourt, J. L., & Koenig, W. D. (2020). Climate Dipoles as Continental Drivers of Plant and Animal Populations. *Trends in Ecology and Evolution*, *35*(5), 440–453. https://doi.org/10.1016/j.tree.2020.01.010

CHAPTER THREE

MEXICAN FREE-TAILED BAT (TADARIDA BRASILIENSIS) MIGRATION PHENOLOGY AND POPULATION DYNAMICS QUANTIFIED BY WEATHER RADARS IN SOUTH-CENTRAL TEXAS

Summary

Insectivorous bats play key roles in the ecosystem and agroecology by providing essential services for pest control and serving as ecotourism attractions. In Texas, this is especially true, as Mexican free-tailed bats (*Tadarida brasiliensis*) have formed the densest aggregations of mammals anywhere on the planet. However, their population status and phenology in this region are understudied, with most of the knowledge coming from just a few dense colonies. Little is known about the neighboring cave and bridge colonies throughout the south-central Texas region. Nightly, millions of bats emerge from colonies to forage around sunset – these dense aggregations in the aerial space can be captured by weather radar. I quantified the nightly number of Mexican free-tailed bats from four weather surveillances radars in Texas. Analyzing data from 53 consistent colonies over 17 years (2006-2022), I observed a region-wide decline in their abundances at an annual rate of 3.37%, with varying rates of decline across individual colonies. Pronounced decreases in overall bat activity levels were also observed annually. Phenological shifts were generally minimal except for a delay observed in the later stages of fall dispersal. This study provides the first comprehensive assessment of multi-colony abundance, population trends, and phenology shifts in Mexican free-tailed bats.

Introduction

Climate change is having profound impacts on biodiversity and ecosystems worldwide (Garcia et al., 2014). Aerial insectivores — animals that feed primarily on flying insects while on

the wing, including birds, bats, and dragonflies — are no exception, and many are declining rapidly (Ingersoll et al., 2013; Rosenberg et al., 2019). Their survival and reproduction are tightly linked to the availability of insect prey (Dunn et al., 2011; Festa et al., 2022; Twining et al., 2022), however, aerial insects are declining (Ball et al., 2021; van Klink et al., 2020; Wagner, 2020). Moreover, aerial insectivores are sensitive to shifting climate and extreme environmental conditions (Michel et al., 2021). Understanding how aerial insectivores are responding to climate change is crucial for developing conservation strategies that ensure the persistence of these ecologically important organisms.

Mexican free-tailed bats (*Tadarida brasiliensis*) are among the most numerous and densely aggregated mammals in North America (A. L. Russell et al., 2011). These migratory insectivorous species spend their non-breeding period in central and southern Mexico and migrate north to the southern United States in the spring, forming large maternity roosts that can number up to millions of individuals (Betke et al., 2008). Colonies of Mexican free-tailed bats provide important ecosystem services and economic value to humans. Roosting bats emerge on a nightly basis, they may travel upwards of 50 km away from their roosts (Williams et al., 1973), offering a pest suppression service to agricultural fields in the surrounding areas (Mainea & Boylesa, 2015). Mexican free-tailed bats consume a diverse array of insect species, including over 40 species that are harmful to agriculture (Krauel, Brown, et al., 2018). By foraging on adult insects that carry eggs, bats help to reduce pest populations over multiple generations, making a lasting impact on keeping agricultural pests below damaging thresholds across vast regions (Federico et al., 2008). Their dietary patterns are closely linked to the seasonal availability of migratory noctuid moth pests, particularly during key periods in their life cycle, such as pregnancy and pre-migration weight gain in the spring and fall, respectively (Hawkes et

al., 2023; Lee & McCracken, 2001). Ecosystem services provided by insectivorous bats significantly reduce the need for chemical pesticides, leading to substantial economic savings for the agricultural industry that amount to billions of dollars per year (Boyles et al., 2011; Kunz et al., 2011). Bats' droppings (i.e., guano) also serve as fertilizer and an alternative source of chitin and chitosan (e.g., can be used as soil conditioner) (Kaya et al., 2014). Moreover, famous maternity colonies such as Congress Bridge and Bracken Cave also have untold ecotourism values, attracting over 242,000 visitors annually to view these emergence events (Wiederholt et al., 2015).

Mexican free-tailed bat roosts may form in a variety of locations, including man-made structures (i.e., bridges, buildings, mines, tunnels, dams) and natural caves (McCracken, 2003; Wiederholt et al., 2015). Human-made structures might offer benefits such as including warmer or more stable temperatures or decreased competition with conspecifics (Horn & Kunz, 2008). However, artificial roosts tend to be more vulnerable to anthropogenic activities and may be associated with other drawbacks, such as higher parasite loads or vulnerability to extreme temperature events versus natural roosts (Crawford & O'Keefe, 2024). Thus, colonies using human-made sites may experience different costs and benefits compared to those that utilize caves.

To understand the combined effects of climate change and anthropogenic habitat change, it is important to monitor the population dynamics and phenology of Mexican free-tailed bat throughout their annual cycle. However, surveys of bats have remained challenging due to the invasive nature of in-roost surveys (Tuttle, 1979) and the resources required to count individuals as they emerge from roosts (Kunz et al., 2009). Monitoring nightly emergences may also produce underestimates due to the difficulties of counting all emerging individuals (Westcott &

McKeown, 2004) and the variable nature of bat emergences, which may change significantly in volume from night to night (Barclay et al., 2024).

NEXRAD Doppler Radar has shown great promise in monitoring daily abundance fluctuations of large aggregations of flying animals in near real-time (Belotti et al., 2023; Deng et al., 2023; Stepanian & Wainwright, 2018). With time resolutions as fine as 5-10 minutes, Doppler radar captures detailed information on their density, timing, movement speed, direction, and altitude as bats emerge from their roosts in large numbers. This has made it a popular technology for studying bat behavior and movement patterns, population trends, and phenology (Frick et al., 2012; Haest et al., 2021; Horn & Kunz, 2008; Meade et al., 2019). Radar-based counts have been shown to closely align with ground-based counts in flying foxes (Meade et al., 2019) and with thermal imaging and population censuses in Mexican free-tailed bats at Bracken Cave (Stepanian & Wainwright, 2018), the largest colony in the region. Further, NEXRAD data has been widely available since 1996, and so offers several decades of high-resolution temporal coverage of most of the entire summer range and some populations' overwintering range of Mexican free-tailed bats in the United States. However, processing and analyzing such an extensive data set present significant challenges, and most radar studies of bat emergences have been limited to the analysis of single sites or non-continuous time span (Frick et al., 2012; Horn & Kunz, 2008; Stepanian & Wainwright, 2018). Thus, population trends and responses to environmental change have not been identified at broader, policy-relevant spatial scales.

Here, I leverage advances in an AI-assisted detection and tracking system (Perez et al., 2024) in conjunction with manual screening validations to develop a data processing and analysis pipeline for monitoring free-tailed bat emergences. This approach can capture bat emergence patterns reliably even from otherwise unknown roost locations, enabling broad-scale

monitoring of Mexican free-tailed bat populations at the regional level. I applied this algorithm to process the data from four weather surveillance radars in south-central Texas spanning 2006 – 2022, encompassing approximately 260,000 square kilometers. Our analysis comprised three foci: (1) long-term phenology of different life-history phases, (2) relative abundance of each colony visible on radar, and (3) abundance trends. Our study sheds light on the plasticity of seasonal migration behavior of insectivorous bats under the impact of climate change, as well as filling in knowledge gaps in Mexican free-tailed bats' regional population status.

Methods

Data processing from weather surveillance radar

I downloaded and processed weather surveillance radar data archived on the AWS server (https://s3.amazonaws.com/noaa-nexrad-level2/index.html) for four radar stations in south-central Texas (KSJT, KDFX, KEWX, KGRK), sampling every other year from 2000 to 2022. Significant manual screening effort prevented continuous sampling of years (see next paragraph for details). Due to substantial data gaps (fewer than 40 days of data available in the NEXRAD archive) in 2000, 2002, and 2004 at some of the four radar stations, I excluded these years from our analysis. Because Mexican free-tailed bat populations use some roost sites throughout the year (i.e., overwinter in Texas), I collected data from the entire calendar year (Kasper & Yancey, 2018; Scales & Wilkins, 2007; Stepanian & Wainwright, 2018). To capture the complete nightly emergence of Mexican free-tailed bats, I downloaded radar volume scan data files from 90 minutes before to 150 minutes after local sunset for each night. The analyzed data set contains 9 years and 2893 monitoring days, which amassed to 185,776 radar scans. Each volume scan ranged from 5 to 10 minutes apart and included all elevation angles (usually starting from 0.5

degrees) below 5 km. I constrained all radar measures to a spatial range of 150 km from each radar.

For each radar scan, an AI-assisted system was used to detect and track roosts automatically (Deng et al., 2023; Perez et al., 2024), creating a bounding box that surrounds each roost detection dynamically and tracks both the spatial position and size of the roost emergence through time. Human screeners (YD, LH, EG, SS, MNM) then used the user interface accompanied by the AI system to visualize and screen the detections (Figure 3.S1) to (1) remove false positives due to precipitation, anomalous propagation, or other biological signals, (2) add roosts missed by detection algorithm (i.e., false negative), and (3) shorten the track if the bounding boxes do not adequately cover the expansion of the roost or if they include excessive background noises. Screeners were all trained using the same protocol and assessed for accuracy. The extensive screening effort totaled 188 hours, limiting our ability to screen all data from 2006 to 2022. Therefore, I restricted monitoring to even years to ensure high-quality coverage. Additionally, I eliminated volumes with reflectivity measures greater than 40dBZ to eliminate potential weather contamination. Filtering with dual-polarization radar data products wasn't feasible since the time series includes periods before dual-polarization data became available. MistNet (Lin et al., 2019), a frequently used algorithm for discriminating precipitation from biology in radar scans, regularly labeled roosts as weather, and is therefore not applicable here either.

I converted raw reflectivity factor Z_e (dBZ, Level II weather radar data product) to reflectivity η (cm^2/km^3) following the method described in Chilson et al., (2012). Radar reflectivity on the linear scale was then converted into the number of bats, using the Mexican free-tailed bat S-band radar cross-section of 4.519 cm^2 (Mirkovic et al., 2016). The methods and

equations for converting radar reflectivity to count data are detailed in Deng et al., (2023). I calculated bat counts within each detection frame across all elevation angle scans below 5 km above ground level. All radar data processing was done in Python (version 3.9.4) using *PyArt* and *pywsrlib* packages. Subsequent data analysis and visuals were conducted in R (version 4.2.2).

Range correction for roosts

As the distance from the radar increases, the curvature of the Earth and the uptilted beam angle cause the radar beam to measure airspace at a higher altitude. This results in a well-known range bias in biological data collected from radar products (e.g., reflectivity), making it appear as though fewer bats are detected at greater distances from the radar (Buler & Diehl, 2009; Kranstauber et al., 2020). Biases also exist at close ranges where the highest radar beam may undershoot the emerged bats. This bias poses challenges when comparing bat colony sizes across different locations. To address this issue, I applied a range correction method adapted from Kranstauber et al., (2020) to calculate the adjusted vertically integrated count across elevation scans. The procedure is described as follows:

(1) I first calculated the density (D) of bats within each voxel across elevation angles as

$$D = count/V_i,$$

where V_i represents the radar sampling volume for the detection bounding box within each elevation angle, calculated as:

$$V_i = \frac{0.35\sqrt{2\pi}}{2ln2}\left(\frac{\pi r_0^2 \theta_1 \phi_1 \Delta r}{4}\right)$$

where r_0 is the distance from the radar. The vertical beam width (ϕ_1) is 1°. During the super resolution upgrade in 2008, horizontal beam width (θ_1) changed from 1° to 0.5°, and radar range gate (Δr) changed from 1000 m to 250 m. Each radar station was upgraded at different dates, so I

accounted for the change of volume calculation when appropriate. Equation was adopted from Chilson et al., (2012), assuming that bats are scattered within the whole radar beam.

(2) I created an average vertical profile from the lowest altitude (that the radar can measure) to a maximum altitude of 5 km, using roost detections within a range of 10 to 60 km from the radar across all available dates. Averaged bat density was calculated within 100-meter elevation bins (50 height bins in total). I used the *beam_height* function to calculate beam height h using the R package *bioRad* (Dokter et al., 2019). For every 10-minute interval (averaged across all nights), a vertical profile was generated to account for potential changes in the bats' emergence patterns over time. From the vertical profile $d(h)$, I calculated the total vertically integrated density (VID) as:

$$VID = \int_0^{5km} d(h)dh$$

(3) Assuming the altitude distributions of Mexican free-tailed bats emergence at any location with our radar detection range (150 km) would be identical to the vertical profile created, I calculated the expected vertically integrated density ($vid_{expected}$) using the upper and lower beam heights at each radar beam angle and accounting for overlapping beams. Then, I calculated an adjustment ratio (R_{adjust}) and limited it at 10. Finally, the adjusted count was calculated using the original count and adjusting ratio.

$$vid_{expected} = \sum_{elevation\ angles} \int_{lower\ radar\ beam}^{upper\ radar\ beam} d(h)dh$$

$$count_{adjusted} = count \times R_{adjust}\text{, where } R_{adjust} = \frac{VID}{vid_{expected}}$$

Bat colony clustering and data manipulation

First radar detections of each track each night throughout all years and stations were used to group detections into high-density regions (i.e., roost locations). Specifically, I used a machine learning mean shift clustering algorithm (Python 3.9.4, scikit-learn library) to cluster the detections into groups and find the centroids of the kernel density. Bandwidth for the kernel density function strongly influenced the resulting number of clusters. I chose an optimal bandwidth of 15000 by maximizing the silhouette coefficient (0.700) and Calinski-Harabasz index (96942.876) while visually confirming the clustering results on the map. Roosts with recorded records (e.g., Bracken Cave, Congress Bridge, Devil's Hole) were given their recorded name.

I filtered out the adjusted emergence detection count higher than 6 million, since those detections were primarily the result of precipitation contamination following manual inspection and passed the 40 dBZ filter. I limited our analysis to roost clusters that persisted for at least 5 years and had at least 2 years with more than 10 days of observations. These criteria helped to ensure the accurate identification of roosts and phenology characteristics. I classified colonies as "natural" if they were known to be a cave or forest colony, and "anthropogenic" if they are found to be from bridges, highways, buildings, advertisement boards, or any other human structures. I classified the remaining clusters as "unknown" if I could not judge the colony type based on records or satellite images. Finally, I summarized the count per detection track as the 90^{th} percentile count of all the detections, ensuring a representative high count while minimizing the influence of outliers.

Examining phenology shifts

Due to significant variation in data availability among clusters, I focused on estimating region-wide phenology and phenological shifts rather than doing so on a cluster-by-cluster basis.

The daily number of emerging bats was summed across the entire south-central Texas region from all roosts that fit my criteria described above. The yearly data distribution was modeled separately in a hierarchical modeling framework using the *phenomix* R package (Wilson et al., 2023). The model structure allowed us to extract key phenological metrics from interannual distributions, propagate uncertainties, and estimate the trend of peak phenology changes. I modeled the spring and autumn portions of the bats' life history separately, as analyzing the annual phenology pattern proved challenging due to its bimodal nature.

I divided seasonal activity patterns as spring as days of year 0–200 and fall as days 201–365. In spring, I anticipated peak activity to reflect northward migration waves and the arrival of summer residents, while in fall to the emergence of pups as they take their first flights from maternity roosts. I did not attempt to extract phenology dates related to parturition (i.e., giving birth) and the end of fall dispersal (Stepanian & Wainwright, 2018). Parturition is difficult to detect through changes in abundance and may be better captured by daily emergence timing, which remains challenging to quantify by radar. Similarly, estimating the end of fall dispersal is complicated by the high variability in daily counts, likely due to multiple waves of fall migration, roost switching, and the presence of overwintering populations.

For model fitting, I calculated AIC scores for normal, Student's t, and generalized normal distributions (with symmetric and asymmetric tails) to represent the phenological processes, ultimately selecting the model with the lowest AIC (Table S1). The mean and variance controlling these distributions were estimated as random effects, allowing them to vary over time. The phenological metrics were estimated for both spring and fall and included the 25th quantile, peak, and 75th quantile dates. Weighted average percentile dates for each season-year were calculated with weights on the inverse variance. This gives higher weight to season-year

with lower variance. Trends in both the mean and variance of peak dates were estimated using weighted linear regression, which accounted for the variability in each year (i.e., the standard deviations) and were used as weights in a weighted regression.

Quantifying relative abundance and abundance trends

I fitted Bayesian hierarchical models to estimate annual trends in bat colony counts at individual roosts using the *brms* package (Bürkner, 2017). For each colony, I filtered the dataset to include only observations from that colony and modeled counts as a function of year with ordinal date as a random intercept. The response variable was treated as an integer and modeled using a negative binomial distribution to accommodate overdispersion. Each model was run using four MCMC chains, with 4,000 total iterations per chain (including a 2,000-iteration warmup).

The annual trend in regional bat abundance was estimated with all colony counts summed across the study region. Regional daily count data, calculated by summing all colony counts across the study region daily, was modeled as a function of year, with random intercepts for ordinal date. The rest of the model setup is the same as the colony-level models.

I defined the total bat activity (i.e., a population impact metric) as the sum of daily counts across the entire season (Belotti et al., in review). This metric is important for assessing the population's ecological impact, as it likely correlates with both predation effort and the amount of aerial insect biomass consumed. It is also robust to highly variable bat activity patterns since individual bats do not forage every evening (Barclay et al., 2024). The total bat activity was estimated according to the spring and fall season models with *phenomix* package (Wilson et al., 2023). I extracted the derived totals (predicted across all days within a year) with their 95%

confidence interval separately using the spring and fall data. I examined the trends in spring and fall population impacts, estimated using weighted linear regression.

Results

In total, I detected 53 consistent Mexican free-tailed bat roosts across the sampling area of the four weather surveillance radars used in this study. Of these, I detected all previously recorded colonies of Mexican free-tailed bats in southern Texas that I were able to cross-reference (Figure 3.1), including both bridge-dwelling colonies (e.g., Congress Avenue Bridge and McNeil Bridge near downtown Austin) and cave-dwelling colonies (e.g., Bracken Cave, Davis Cave, Rucker Cave, Frio Cave, Ney Cave, Eckert James River Cave, among others). Across our study period, 45 colonies were detected by radar on more than 100 days, and 17 colonies were detected on more than 1,000 days. From 2006 to 2022, each radar station detected Mexican free-tailed bat roosts on an average of 259 days per year.

Range correction

Emergence detections most impacted by the range bias were those located at mid-to-far distances (67–150 km) and very close distances (0–7 km) from the radar, where radar beams missed (overshoot or undershoot) more than half the target volume area. Prior to range correction, distance from the radar accounted for 2.64% of the variance in emergence counts, with a slope estimate of -1.67 ± 0.02 (SE). After applying the correction, the influence of distance was significantly reduced, explaining only 0.43% of the variance, with a slope estimate of -0.81 ± 0.03 (SE).

Phenology

Between 2006 and 2022 in the South-Central Texas region, the variance weighted average 25th percentile, peak, and 75th percentile dates for spring were April 30th, May 26th, and

June 21st (ordinal days 119, 145, and 171, respectively), and for fall August 13th, September 8th, and October 3rd (ordinal days 225, 250, 275; Figure 3.2A).

All spring phenology metrics showed non-significant trends across the sampling time from 2006 to 2022. The 25th percentile date showed -0.18 days per year change ($R^2 = 0.03$, $t = -0.452$, $p = 0.665$), peak spring emergence -0.43 days per year change ($R^2 = 0.12$, $t = -0.969$, $p = 0.365$), and the 75th percentile date -0.67 days per year change ($R^2 = 0.20$, $t = -1.328$, $p = 0.226$) (Figure 3.2B). During fall, both the 25th percentile (0.13 days per year change, $R^2 = 0.01$, $t = 0.840$, $p = 0.428$) and peak emergence showed a non-significant trend (0.23 days per year change, $R^2 = 0.34$, $t = 1.890$, $p = 0.101$) (Figure 3.2B). However, the 75th percentile date was significantly delayed by 0.34 days per year ($R^2 = 0.48$, $t = 2.539$, $p = 0.039$).

Colony size and abundance trends

I identified 37 colonies that yielded at least five years of data and more than 10 nights of emergence counts per year, including Bracken cave, Frio cave, Bamberger ranch preserve, Congress bridge, McNeil bridge, Devil's Sinkhole, and Ney cave (Figure 3.3). Evidence of a declining abundance trend was found in 56.8% of these colonies (Figure 3.4), with annual trends ranging from -10.6% (Ney Cave) to -1.7% (Bracken Cave). In contrast, only 10.8% of colonies showed evidence of an increasing trend, with growth rates ranging between 1.6% (cluster 13) and 4.3% (cluster 24) per year. At the regional scale, bat abundance declined by 3.37% per year (95% CI: -4.04% to -2.68%). Significant fluctuation in daily emergence counts was also observed across colonies. The standard deviation of ordinal date (random effect in the model) represents daily variability within each colony. The mean standard deviation in emergence days across all colonies was 0.62 (SE = 0.03). However, variability differed between colonies, ranging

from as low as 0.19 to as high as 1.11. This indicates that some colonies experienced much greater fluctuations in their daily emergence counts than others.

The total bat activity (i.e., the population impact), which was defined as the sum of daily counts across the entire season, is declining at a rate of 17.41 ± 5.00 (SE) million per year ($p = 0.010$) in the spring and declining at a rate of 15.13 ± 2.90 (SE) million per year ($p = 0.001$) in the fall (Figure 3.5). Annually, with spring and fall data combined, the population impact is declining at an alarming rate of 33.01 ± 7.51 (SE) million per year ($p = 0.003$). Regression models without the year 2022 showed that annual and spring population impact does not have a significant trend ($p = 0.769$), however, fall is declining at a rate of 12.00 ± 3.92 (SE) million per year ($p = 0.020$).

Discussion

Our study provides the first comprehensive assessment of multi-colony abundance, population trends, and phenology in Mexican free-tailed bat roosts across south-central Texas. I analyzed data from 53 consistently occupied colonies from a 17-year period from 2006 to 2022. Our findings reveal a region-wide decline in bat abundance, with varying degrees of decline observed across individual colonies. Pronounced decreases in bat activity levels were also observed annually, including in both the spring and fall, with the steepest decline in 2022 driving much of the overall downward trend. Phenological shifts were generally minimal, except for a delay in the later stages of fall dispersal.

I observed a trend of the overall declining bat activity and colony abundance in the region, with many well-known colonies showing noticeable population declines (Figure 3.4-3.5). This regional decline suggests broader ecological stressors affecting the species, including potentially diminishing insect prey availability, increased extreme weather events, and habitat

degradation (Krauel, Ratcliffe, et al., 2018; Maxwell et al., 2019; Neece et al., 2018; Rodhouse et al., 2019). I observed a substantial drop in overall abundance in 2022, potentially due to the dramatic impact of the cold snap event in 2021 (Doss-Gollin et al., 2021). Bats are highly susceptible to extreme weather conditions (Adams et al., 2024), especially during critical life stages like the overwintering period (Foley et al., 2020; Schorr & Siemers, 2021). Such extreme events can have lasting effects on bat populations, with reduced survival and reproductive success carrying over into subsequent years, compounding their impact on colony size and activity (Linton & Macdonald, 2018). With climate change predicted to increase the frequency of extreme weather events, such as cold snaps, droughts, cyclones, and heatwaves, the long-term conservation of insectivorous bats will require adaptive management strategies that account for these challenges — for example, by incorporating extreme weather events into bat vulnerability assessments and adaptation plans (Maxwell et al., 2019).

Our estimates of Mexican free-tailed bat colony abundance highlight important seasonal dynamics that underscore the varying roles of different colonies throughout the year. For instance, Frio Cave supports the largest bat populations during the spring migration period (Figure 3.3), when females (mostly pregnant) arrive at maternity roosts to give birth to the only pup. Usually, some males are present as well during spring, suggesting potential mating activity (Reichard et al., 2009). In contrast, Bracken Cave emerges as a crucial summer roosting site, hosting millions of bats during the breeding season. Meanwhile, bridge colonies, like Congress and McNeil Bridges, become more important in the winter, sheltering overwintering bats when other colonies have mostly dispersed or migrated. These seasonal shifts emphasize the need for conservation assessments that address the distinct ecological role and periods of peak activity of each colony (Festa et al., 2022; Neece et al., 2018). Protecting key roosts year-round is essential,

but targeted conservation efforts—such as safeguarding maternity caves during summer and preserving bridge habitats that support overwintering populations—will help maintain the survival and reproduction of the bats.

Additionally, there were large fluctuations in daily counts within each colony, which complicated population estimates. The fission-fusion social structure of Mexican free-tailed bat, where individuals frequently move between colonies, as well as their varying site fidelity, means that population numbers at a single colony can fluctuate dramatically depending on when surveys are conducted (Kerth et al., 2011). This presents challenges for accurately estimating regional abundance, especially given the limited surveying capacity across such a vast area. Without consistent monitoring, these fluctuations may mask true population trends, making it difficult to assess the extent of population declines or recovery efforts (Barclay et al., 2024). More frequent and widespread surveying could help mitigate this issue, providing more reliable data to inform conservation strategies.

Phenological patterns observed through radar data reveal changes that correspond to fluctuations in bat colony size or activity across the annual cycle (Stepanian & Wainwright, 2018). Long-term radar datasets, therefore, provide a valuable tool for tracking phenological shifts and abundance trends over time (Stepanian et al., 2019). Our study found an advanced but not significant phenological shifts in the spring activity timings of Mexican free-tailed bats, but late fall phenological dates showed a significant delay (Figure 3.2). Previous research at Bracken Cave showed evidence of spring migration and pup flight advancement but no significant trend of fall dispersal (Stepanian & Wainwright, 2018). However, unlike this site-specific finding, our analysis encompassed a broader, regional scale, and I extracted phenological metrics differently. The delayed fall dispersal that I observed in the south-central Texas region may be related to

increased autumn precipitation in or around the region (Haest et al., 2021). Rain might increase the energy costs of flight and thus delay departures (Mcguire et al., 2012; Voigt et al., 2011). Higher precipitation is also associated with high insect abundance (Krauel, Brown, et al., 2018) and altered insect phenology (Forrest, 2016), thus potentially benefiting bats departing later. One possible explanation for the lack of significant spring phenological shifts could be that Mexican free-tailed bats are cued more strongly by environmental factors in their wintering grounds for the migration (Haest et al., 2021) rather than by local conditions in their roosting sites. As migratory species, bats may be responding more to changes in the availability of resources or conditions at wintering sites, which could buffer them from the effects of local climate variability at their roosts. However, there could be a risk of phenological mismatch if prey availability shifts due to warming temperatures (Krauel et al., 2015). This has important implications for understanding how Mexican free-tailed bats may be affected by climate change.

Continued monitoring is crucial to mitigate potential impacts on Mexican free-tailed bat populations and to detect any emerging phenological shifts in the future. Our approach offers several advancements, namely assessing population size and trends using NEXRAD data, including creating a robust, standardized, and nearly continuous time series. The deployment of a machine-learning pipeline that dynamically tracked roosts was also crucial for improving the automation of bat counts (Perez et al., 2024). To improve the reliability and comparability of colony abundance estimates across varying distances, I developed a range correction method that will be an important step in radar data processing for aeroecology studies (Buler & Diehl, 2009; Kranstauber et al., 2020).

Expanding the use of radar technology to monitor Mexican free-tailed bats on broader spatial and temporal scales could provide the comprehensive data needed to better understand the

drivers behind their declines, potentially through increased monitoring across the full range of the species. These declines hold significant ecological and economic implications, as reductions in insectivorous bat populations may lead to an increase in crop-damaging pests, amplifying broader environmental challenges (Tuneu-Corral et al., 2023). It is critical to understand how daily environmental factors influence bat emergence behavior, as this relationship offers key insights into phenology shifts and their potential variability across regions. This approach presented in this study hopefully not only advances our understanding of Mexican free-tailed bat population but also enables more informed conservation efforts in the face of ongoing climate change.

Figures and Tables

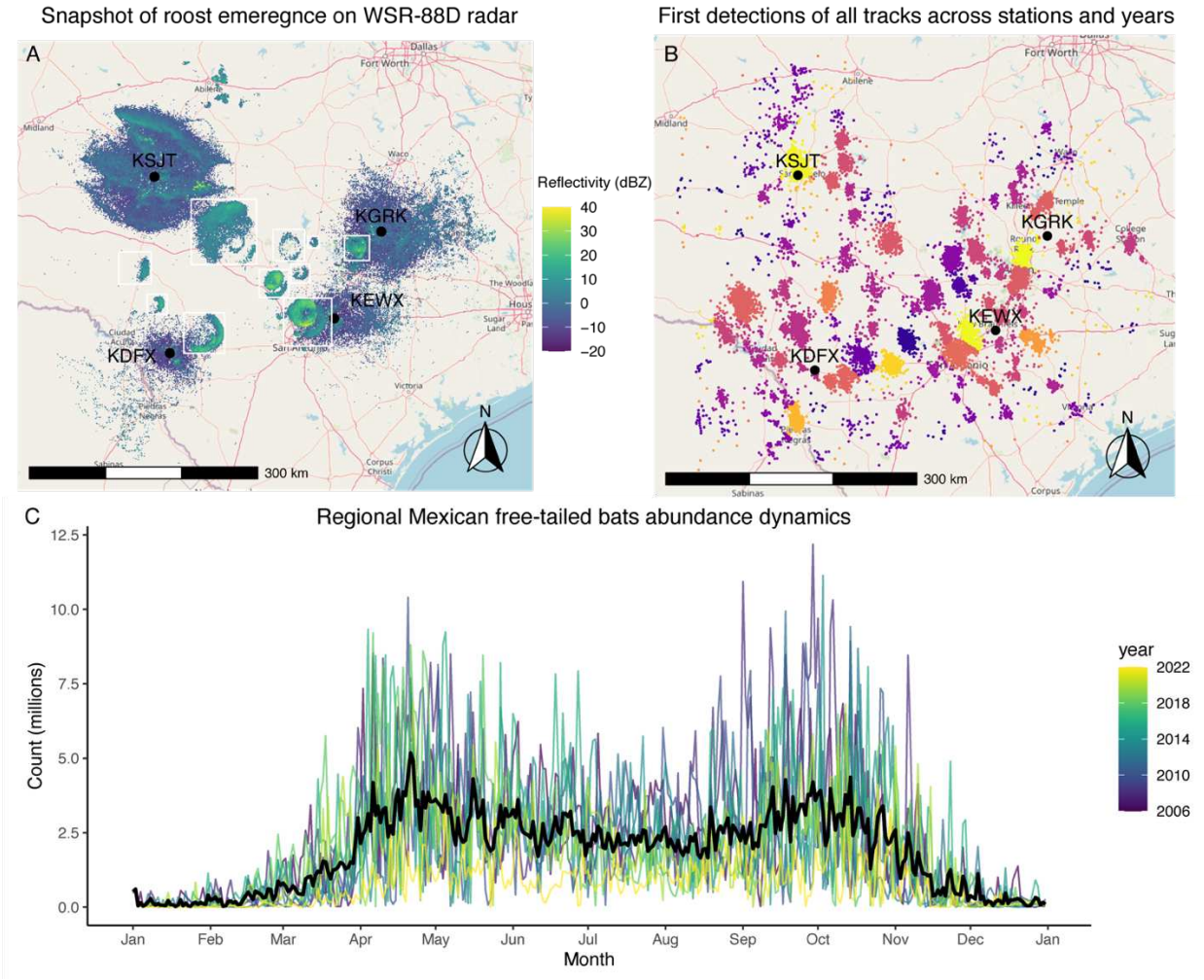

Figure 3.1. (A) Composite of 0.5° tilt radar reflectivity from four NEXRAD sites (KSJT, San Angelo; KGRK, Dallas/Fort Worth; KDFX, Austin/San Antonio; KEWX, San Antonio) on July 15th, 2023, around 01:45:00 UTC (8:45 PM CDT) with a base map from OpenStreet. Ten donut-shaped rings indicate Mexican free-tailed Bat roost emergence. (B) First detections of nightly emergence across all years (2006 – 2022). Each colony (identified by the clustering algorithm) is denoted by a different color. (C) South-central Texas regional Mexican free-tailed bats abundance dynamics. Distinct stages of spring migration, late-summer reproduction, and seasonal variations are shown in each year (colored lines). These patterns are also reflected in the regional mean abundance (black line).

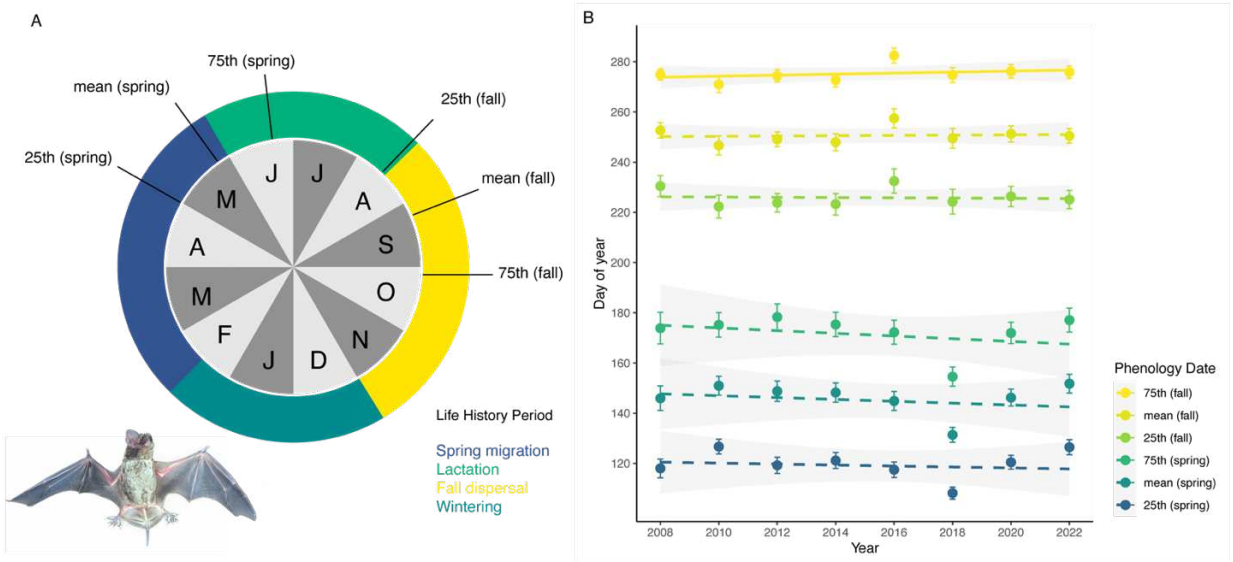

Figure 3.2. Phenology of Mexican free-tailed bat emergence in spring and fall from 2006 to 2022. (A) Life history annual cycle of Mexican free-tailed bats (color wheel). The averaged date for each phenology metric across the study period was denoted on the wheel. Photo credit: Bat Conservation International. (B) The temporal trends in spring and fall emergence dates across years for three different metrics: 25th percentile, mean (peak), and 75th percentile dates with 95% confidence intervals, with corresponding dashed lines showing non-significant ($p > 0.05$) weighted regression trend, and solid lines showing significant trend ($p < 0.05$).

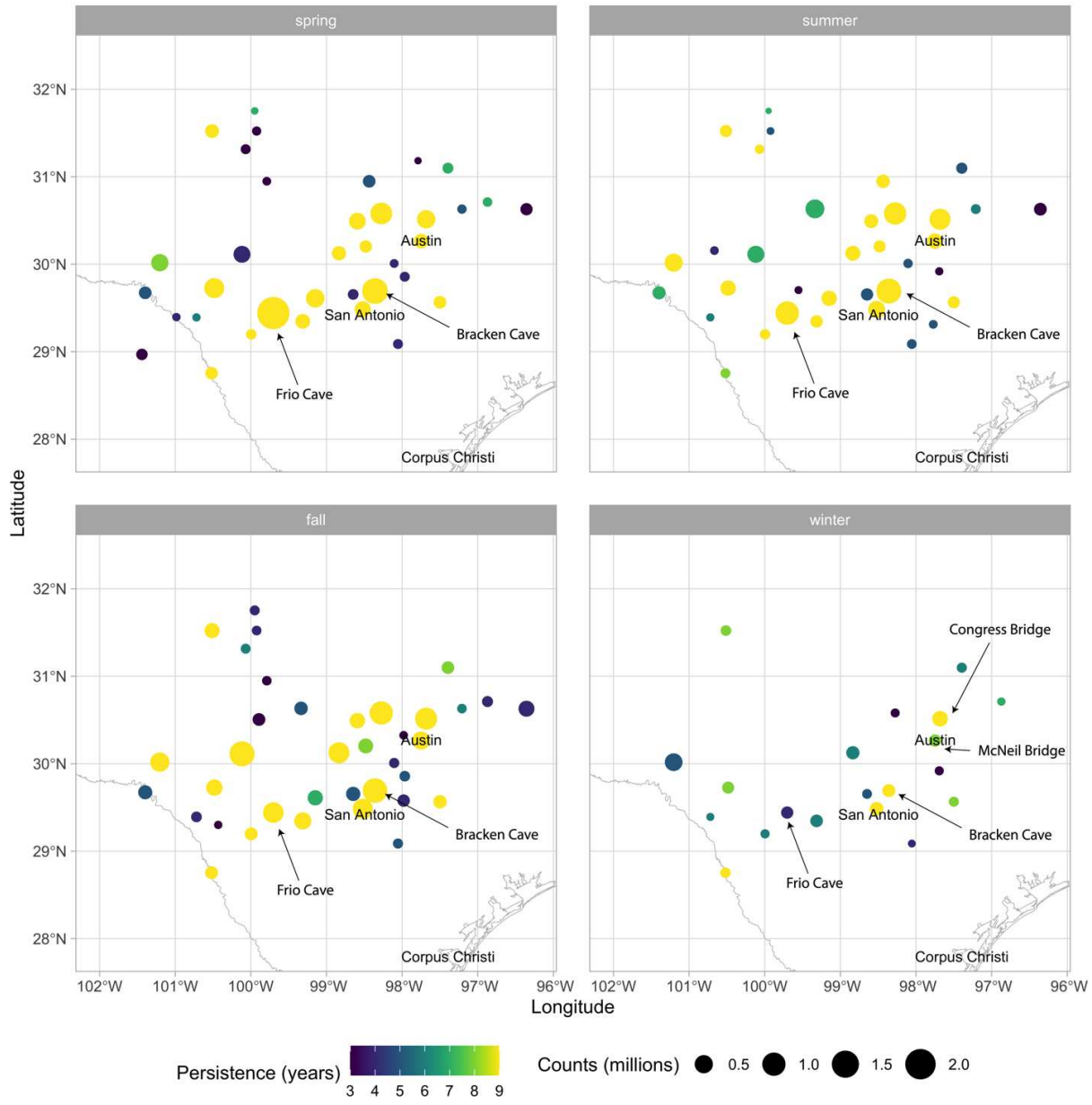

Figure 3.3. Colony abundance summarized across years for each colony, displayed by season. Only colonies with more than two years of seasonal persistence are shown. Point size indicates the 90th percentile abundance across years, while color represents the colony's persistence during the corresponding months. Seasons are defined as follows: spring (March–May), summer (June–August), fall (September–November), and winter (December–February).

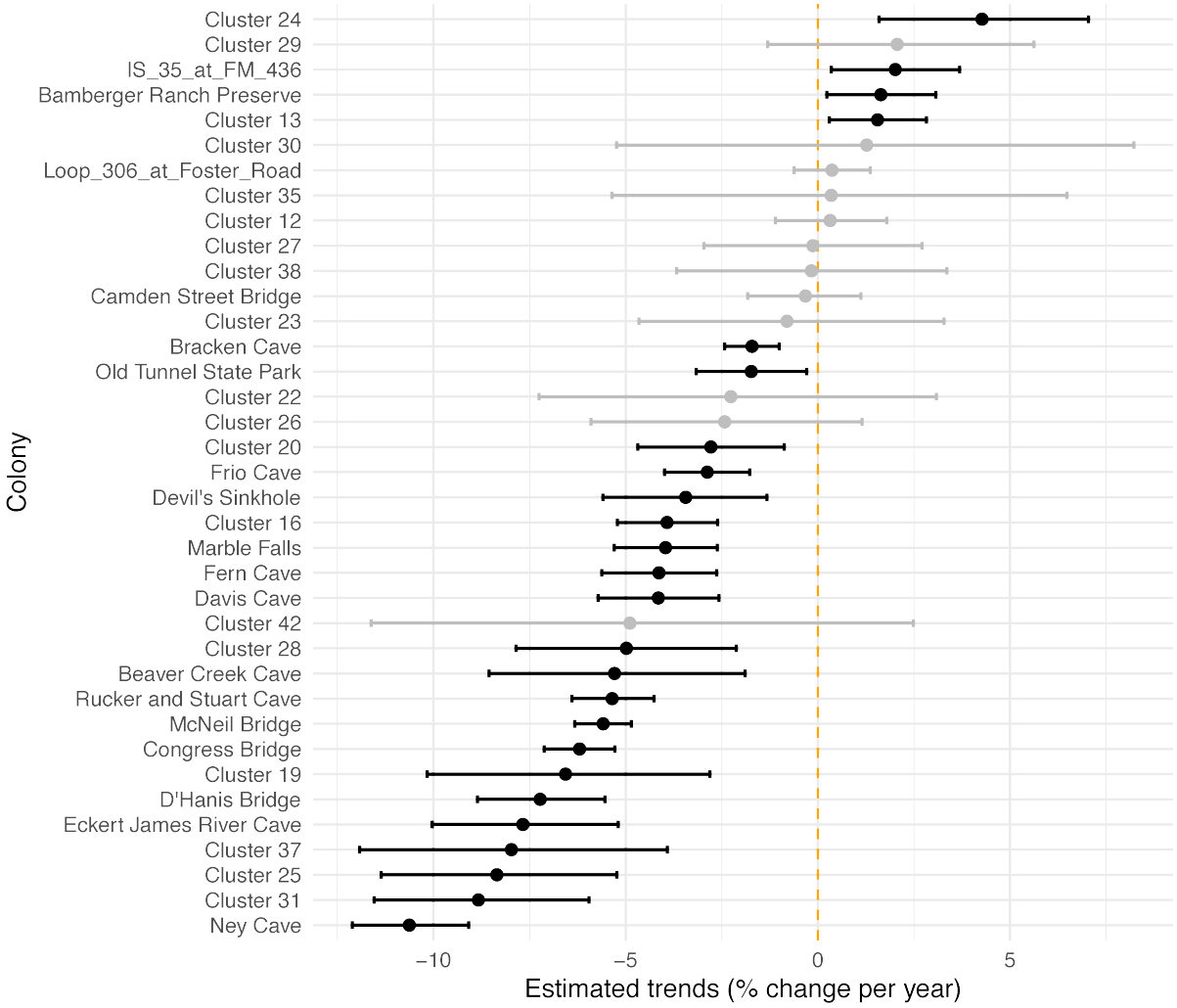

Figure 3.4. Posterior abundance trends at the colony levels, with points indicating mean estimates and error bars representing 95% credible intervals. The greyed-out estimates are overlapping aero, while the blackened points are not overlapping zero. The dashed orange line indicates no change as a reference point.

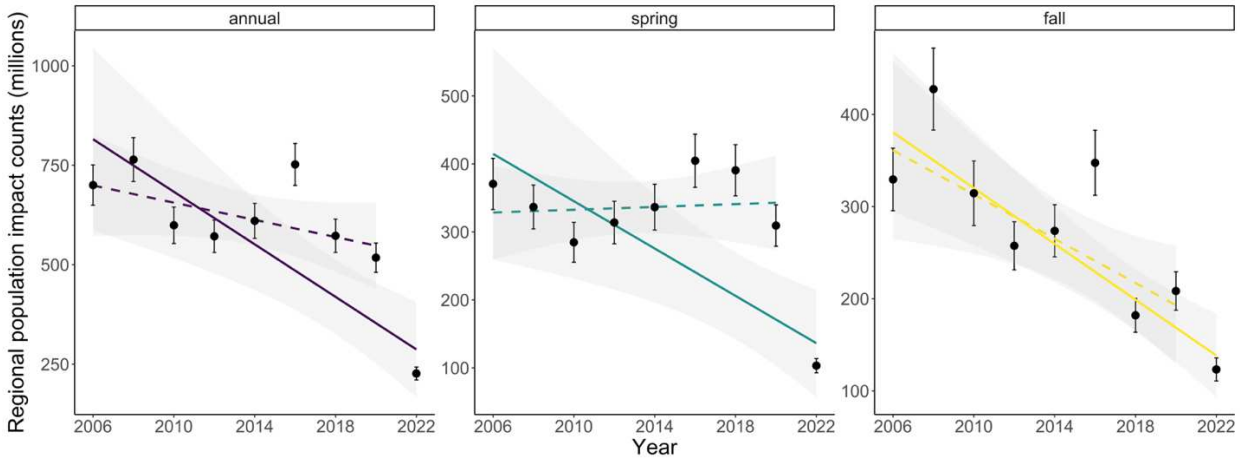

Figure 3.5. Regional population impact (daily abundance sum) annually, in spring, and in fall from 2006 to 2022. Error bars represent the standard deviations of the population impact within the season (or the whole year). The solid lines represent the weighted linear regression fit, and shaded areas indicate 95% confidence intervals from 2006 to 2022. The dashed lines represent the weighted linear regression fit from 2006 to 2020.

REFERENCES

Adams, A. M., Trujillo, L. A., Campbell, C. J., Akre, K. L., Arroyo-Cabrales, J., Burns, L., Coleman, J. T. H., Dixon, R. D., Francis, C. M., Gamba-Rios, M., Kuczynska, V., McIntire, A., Medellín, R. A., Morris, K. M., Ortega, J., Reichard, J. D., Reichert, B., Segers, J. L., Whitby, M. D., & Frick, W. F. (2024). The state of the bats in North America. *Annals of the New York Academy of Sciences*. https://doi.org/10.1111/nyas.15225

Ball, L., Still, R., Riggs, A., Skilbeck, A., Shardlow, M., Whitehouse, A., & Tinsley-Marshall, P. (2021). *The Bugs Matter Citizen Science Survey: counting insect 'splats' on vehicle number plates reveals a 58.5% reduction in the abundance of actively flying insects in the UK between 2004 and 2021.*

Barclay, R. M. R., Monteiro, T. A., Miller, E. N., & Hiles, L. E. (2024). Fluctuations in Bat-house Colony Size May Hamper Estimation of Population Changes. *Journal of North American Bat Research*, *1*(1), 1–10.

Belotti, M. C. T. D., Deng, Y., Zhao, W., Simons, V. F., Cheng, Z., Perez, G., Tielens, E., Maji, S., Sheldon, D., Kelly, J. F., & Horton, K. G. (2023). Long-term analysis of persistence and size of swallow and martin roosts in the US Great Lakes. *Remote Sensing in Ecology and Conservation*. https://doi.org/10.1002/rse2.323

Belotti, M. C. T. D., Gerber, B., Zhao, W., Deng, Y., Simons, V. F., Perez, G., Kelly, J. F., Maji, S., Sheldon, D., & Horton, K. G. (in Review). Aggregating three sources of long-term trends of swallows and martins to identify priority conservation areas in the Great Lakes region.

Betke, M., Hirsh, D. E., Makris, N. C., McCracken, G. F., Procopio, M., Hristov, N. I., Tang, S., Bagchi, A., Reichard, J. D., Horn, J. W., Crampton, S., Cleveland, C. J., & Kunz, T. H.

(2008). Thermal Imaging Reveals Significantly Smaller Brazilian Free-Tailed Bat Colonies Than Previously Estimated. *Journal of Mammalogy*, *89*(1), 18–24. https://doi.org/10.1644/07-MAMM-A-011.1

Boyles, J. G., Cryan, P. M., McCracken, G. F., & Kunz, T. H. (2011). Economic importance of bats in agriculture. In *Science* (Vol. 332, Issue 6025). https://doi.org/10.1126/science.1201366

Buler, J. J., & Diehl, R. H. (2009). Quantifying bird density during migratory stopover using weather surveillance radar. *IEEE Transactions on Geoscience and Remote Sensing*, *47*(8), 2741–2751. https://doi.org/10.1109/TGRS.2009.2014463

Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*. https://doi.org/10.18637/jss.v080.i01

Chilson, P. B., Frick, W. F., Stepanian, P. M., Shipley, J. R., Kunz, T. H., & Kelly, J. F. (2012). Estimating animal densities in the aerosphere using weather radar: To Z or not to Z? *Ecosphere*, *3*(8), 1–19. https://doi.org/10.1890/es12-00027.1

Crawford, R. D., & O'Keefe, J. M. (2024). Improving the science and practice of using artificial roosts for bats. *Conservation Biology*, *38*(1). https://doi.org/10.1111/cobi.14170

Deng, Y., Belotti, M. C. T. D., Zhao, W., Cheng, Z., Perez, G., Tielens, E., Simons, V. F., Sheldon, D. R., Maji, S., Kelly, J. F., & Horton, K. G. (2023). Quantifying long-term phenological patterns of aerial insectivores roosting in the Great Lakes region using weather surveillance radar. *Global Change Biology*, *29*(5). https://doi.org/10.1111/gcb.16509

Dokter, A. M., Desmet, P., Spaaks, J. H., van Hoey, S., Veen, L., Verlinden, L., Nilsson, C., Haase, G., Leijnse, H., Farnsworth, A., Bouten, W., & Shamoun-Baranes, J. (2019).

bioRad: biological analysis and visualization of weather radar data. *Ecography*, *42*(5), 852–860. https://doi.org/10.1111/ecog.04028

Doss-Gollin, J., Farnham, D. J., Lall, U., & Modi, V. (2021). How unprecedented was the February 2021 Texas cold snap? *Environmental Research Letters*, *16*(6). https://doi.org/10.1088/1748-9326/ac0278

Dunn, P. O., Winkler, D. W., Whittingham, L. A., Hannon, S. J., & Robertson, R. J. (2011). A test of the mismatch hypothesis: How is timing of reproduction related to food abundance in an aerial insectivore? *Ecology*, *92*(2), 450–461. https://doi.org/10.1890/10-0478.1

Federico, P., Hallam, T. G., McCracken, G. F., Purucker, S. T., Grant, W. E., Correa-Sandoval, A. N., Westbrook, J. K., Medellín, R. A., Cleveland, C. J., Sansone, C. G., López, J. D., Betke, M., Moreno-Valdez, A., & Kunz, T. H. (2008). Brazilian free-tailed bats as insect pest regulators in transgenic and conventional cotton crops. *Ecological Applications*, *18*(4). https://doi.org/10.1890/07-0556.1

Festa, F., Ancillotto, L., Santini, L., Pacifici, M., Rocha, R., Toshkova, N., Amorim, F., Benítez-López, A., Domer, A., Hamidović, D., Kramer-Schadt, S., Mathews, F., Radchuk, V., Rebelo, H., Ruczynski, I., Solem, E., Tsoar, A., Russo, D., & Razgour, O. (2022). Bat responses to climate change: a systematic review. *Biological Reviews*. https://doi.org/10.1111/brv.12893

Foley, N. M., Petit, E. J., Brazier, T., Finarelli, J. A., Hughes, G. M., Touzalin, F., Puechmaille, S. J., & Teeling, E. C. (2020). Drivers of longitudinal telomere dynamics in a long-lived bat species, Myotis myotis. *Molecular Ecology*, *29*(16). https://doi.org/10.1111/mec.15395

Forrest, J. R. (2016). Complex responses of insect phenology to climate change. In *Current Opinion in Insect Science* (Vol. 17). https://doi.org/10.1016/j.cois.2016.07.002

Frick, W. F., Stepanian, P. M., Kelly, J. F., Howard, K. W., Kuster, C. M., Kunz, T. H., & Chilson, P. B. (2012). Climate and weather impact timing of emergence of bats. *PLOS One*, *7*(8). https://doi.org/10.1371/journal.pone.0042737

Garcia, R. A., Cabeza, M., Rahbek, C., & Araújo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. In *Science* (Vol. 344, Issue 6183). American Association for the Advancement of Science. https://doi.org/10.1126/science.1247579

Haest, B., Stepanian, P. M., Wainwright, C. E., Liechti, F., & Bauer, S. (2021). Climatic drivers of (changes in) bat migration phenology at Bracken Cave (USA). *Global Change Biology*, *27*(4), 768–780. https://doi.org/10.1111/gcb.15433

Hawkes, W. L., Davies, K., Weston, S., Moyes, K., Chapman, J. W., & Wotton, K. R. (2023). Bat activity correlated with migratory insect bioflows in the Pyrenees. *Royal Society Open Science*, *10*(8). https://doi.org/10.1098/rsos.230151

Horn, J. W., & Kunz, T. H. (2008). Analyzing NEXRAD doppler radar images to assess nightly dispersal patterns and population trends in Brazilian free-tailed bats (Tadarida brasiliensis). *Integrative and Comparative Biology*, *48*(1), 24–39. https://doi.org/10.1093/icb/icn051

Ingersoll, T. E., Sewall, B. J., & Amelon, S. K. (2013). Improved Analysis of Long-Term Monitoring Data Demonstrates Marked Regional Declines of Bat Populations in the Eastern United States. *PLoS ONE*, *8*(6). https://doi.org/10.1371/journal.pone.0065907

Kasper, S., & Yancey, F. D. (2018). Year-round bridge colony of mexican free-tailed bats (tadarida brasiliensis mexicana) in trans-pecos Texas. *Texas Journal of Science*, *70*(1). https://doi.org/10.32011/txjsci_70_1_article4

Kaya, M., Seyyar, O., Baran, T., & Turkes, T. (2014). Bat guano as new and attractive chitin and chitosan source. *Frontiers in Zoology*, *11*(1). https://doi.org/10.1186/s12983-014-0059-8

Kerth, G., Perony, N., & Schweitzer, F. (2011). Bats are able to maintain long-term social relationships despite the high fission-fusion dynamics of their groups. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1719). https://doi.org/10.1098/rspb.2010.2718

Kranstauber, B., Bouten, W., Leijnse, H., Wijers, B. C., Verlinden, L., Shamoun-Baranes, J., & Dokter, A. M. (2020). High-resolution spatial distribution of bird movements estimated from aweather radar network. *Remote Sensing*, *12*(4). https://doi.org/10.3390/rs12040635

Krauel, J. J., Brown, V. A., Westbrook, J. K., & McCracken, G. F. (2018). Predator–prey interaction reveals local effects of high-altitude insect migration. *Oecologia*, *186*(1), 49–58. https://doi.org/10.1007/s00442-017-3995-0

Krauel, J. J., Ratcliffe, J. M., Westbrook, J. K., & McCracken, G. F. (2018). Brazilian free-tailed bats (Tadarida brasiliensis) adjust foraging behaviour in response to migratory moths. *Canadian Journal of Zoology*, *96*(6), 513–520. https://doi.org/10.1139/cjz-2017-0284

Krauel, J. J., Westbrook, J. K., & Mccracken, G. F. (2015). Weather-driven dynamics in a dual-migrant system: moths and bats. *The Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.12327

Kunz, T. H., Betke, M., Hristov, N. I., & Vonhof, M. J. (2009). Methods for assessing colony size, population size, and relative abundance of bats. *Ecological and Behavioral Methods for the Study of Bats*, 133–157.

Kunz, T. H., de Torrez, E. B., Bauer, D., Lobova, T., & Fleming, T. H. (2011). Ecosystem services provided by bats. In *Annals of the New York Academy of Sciences* (Vol. 1223, Issue 1). https://doi.org/10.1111/j.1749-6632.2011.06004.x

Lee, Y.-F., & McCracken, G. F. (2001). Timing and Variation in the Emergence and Return of Mexican Free-tailed Bats, Tadarida brasiliensis mexicana. *Zoological Studies*, *40*(4), 309–316. http://www.sinica.edu.tw/zool/zoolstud/40.4/309.pdf

Lin, T. Y., Winner, K., Bernstein, G., Mittal, A., Dokter, A. M., Horton, K. G., Nilsson, C., Van Doren, B. M., Farnsworth, A., La Sorte, F. A., Maji, S., & Sheldon, D. (2019). MistNet: Measuring historical bird migration in the US using archived weather radar data and convolutional neural networks. *Methods in Ecology and Evolution*, *10*(11), 1908–1922. https://doi.org/10.1111/2041-210X.13280

Linton, D. M., & Macdonald, D. W. (2018). Spring weather conditions influence breeding phenology and reproductive success in sympatric bat populations. *Journal of Animal Ecology*, *87*(4). https://doi.org/10.1111/1365-2656.12832

Mainea, J. J., & Boylesa, J. G. (2015). Bats initiate vital agroecological interactions in corn. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(40). https://doi.org/10.1073/pnas.1505413112

Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, *11*(8). https://doi.org/10.1098/rsbl.2015.0552

Maxwell, S. L., Butt, N., Maron, M., McAlpine, C. A., Chapman, S., Ullmann, A., Segan, D. B., & Watson, J. E. M. (2019). Conservation implications of ecological responses to extreme weather and climate events. In *Diversity and Distributions* (Vol. 25, Issue 4). https://doi.org/10.1111/ddi.12878

McCracken, G. F. (2003). Estimates of population sizes in summer colonies of Brazilian free-tailed bats (Tadarida brasiliensis). *Monitoring Trends in Bat Populations of the United States and Territories: Problems and Prospects*.

Mcguire, L. P., Guglielmo, C. G., Mackenzie, S. A., & Taylor, P. D. (2012). Migratory stopover in the long-distance migrant silver-haired bat, Lasionycteris noctivagans. *Journal of Animal Ecology*, *81*(2). https://doi.org/10.1111/j.1365-2656.2011.01912.x

Meade, J., van der Ree, R., Stepanian, P. M., Westcott, D. A., & Welbergen, J. A. (2019). Using weather radar to monitor the number, timing and directions of flying-foxes emerging from their roosts. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-46549-2

Michel, N. L., Hobson, K. A., Morrissey, C. A., & Clark, R. G. (2021). Climate variability has idiosyncratic impacts on North American aerial insectivorous bird population trajectories. *Biological Conservation*, *263*. https://doi.org/10.1016/j.biocon.2021.109329

Mirkovic, D., Stepanian, P. M., Kelly, J. F., & Chilson, P. B. (2016). Electromagnetic Model Reliably Predicts Radar Scattering Characteristics of Airborne Organisms. *Scientific Reports 2016 6:1*, *6*(1), 1–11. https://doi.org/10.1038/srep35637

Neece, B. D., Loeb, S. C., & Jachowski, D. S. (2018). Variation in regional and landscape effects on occupancy of temperate bats in the southeastern U.S. *PLoS ONE*, *13*(11). https://doi.org/10.1371/journal.pone.0206857

Perez, G., Zhao, W., Cheng, Z., Carolina, M., Belotti, T. D., Deng, Y., Simons, V. F., Tielens, E., Kelly, J. F., Horton, K. G., Maji, S., & Sheldon, D. (2024). Using spatiotemporal information in weather radar data to detect and track communal roosts. *Remote Sensing in Ecology and Conservation*. https://doi.org/10.1002/RSE2.388

Reichard, J. D., Gonzalez, L. E., Casey, C. M., Allen, L. C., Hristov, N. I., & Kunz, T. H. (2009). Evening emergence behavior and seasonal dynamics in large colonies of Brazilian free-tailed bats. *Journal of Mammalogy*, *90*(6). https://doi.org/10.1644/08-MAMM-A-266R1.1

Rodhouse, T. J., Rodriguez, R. M., Banner, K. M., Ormsbee, P. C., Barnett, J., & Irvine, K. M. (2019). Evidence of region-wide bat population decline from long-term monitoring and Bayesian occupancy models with empirically informed priors. *Ecology and Evolution*, *9*(19). https://doi.org/10.1002/ece3.5612

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J. C., Panjabi, A., Helft, L., Parr, M., & Marra, P. P. (2019). Decline of the North American avifauna. *Science*, *366*(6461), 120–124. https://doi.org/10.1126/science.aaw1313

Russell, A. L., Cox, M. P., Brown, V. A., & McCracken, G. F. (2011). Population growth of Mexican free-tailed bats (Tadarida brasiliensis mexicana) predates human agricultural activity. *BMC Evolutionary Biology*, *11*(1). https://doi.org/10.1186/1471-2148-11-88

Scales, J. A., & Wilkins, K. T. (2007). Seasonality and fidelity in roost use of the Mexican free-tailed bat, Tadarida brasiliensis, in an urban setting. *Western North American Naturalist*, *67*(3). https://doi.org/10.3398/1527-0904(2007)67[402:SAFIRU]2.0.CO;2

Schorr, R. A., & Siemers, J. L. (2021). Population dynamics of little brown bats (Myotis lucifugus) at summer roosts: Apparent survival, fidelity, abundance, and the influence of winter conditions. *Ecology and Evolution*, *11*(12). https://doi.org/10.1002/ece3.7573

Stepanian, P. M., & Wainwright, C. E. (2018). Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. *Global Change Biology*, *24*(7), 3266–3275. https://doi.org/10.1111/gcb.14051

Stepanian, P. M., Wainwright, C. E., Frick, W. F., & Kelly, J. F. (2019). Weather surveillance radar as an objective tool for monitoring bat phenology and biogeography. *The Journal of Engineering*, *2019*(20), 7062–7064. https://doi.org/10.1049/JOE.2019.0595

Tuneu-Corral, C., Puig-Montserrat, X., Riba-Bertolín, D., Russo, D., Rebelo, H., Cabeza, M., & López-Baucells, A. (2023). Pest suppression by bats and management strategies to favour it: a global review. *Biological Reviews*, *98*(5). https://doi.org/10.1111/brv.12967

Tuttle, M. D. (1979). Status, Causes of Decline, and Management of Endangered Gray Bats. *The Journal of Wildlife Management*, *43*(1). https://doi.org/10.2307/3800631

Twining, C. W., Shipley, J. R., & Matthews, B. (2022). Climate change creates nutritional phenological mismatches. *Trends in Ecology & Evolution*, *37*(9), 736–739. https://doi.org/10.1016/J.TREE.2022.06.009

van Klink, R., Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A., & Chase, J. M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, *368*(6489). https://doi.org/10.1126/science.aax9931

Voigt, C. C., Schneeberger, K., Voigt-Heucke, S. L., & Lewanzik, D. (2011). Rain increases the energy cost of bat flight. *Biology Letters*, *7*(5). https://doi.org/10.1098/rsbl.2011.0313

Wagner, D. L. (2020). Insect declines in the anthropocene. In *Annual Review of Entomology* (Vol. 65). https://doi.org/10.1146/annurev-ento-011019-025151

Westcott, D. A., & McKeown, A. (2004). Observer error in exit counts of flying-foxes (Pteropus spp.). *Wildlife Research*, *31*(5). https://doi.org/10.1071/WR03091

Wiederholt, R., López-Hoffman, L., Svancara, C., McCracken, G., Thogmartin, W., Diffendorfer, J. E., Mattson, B., Bagstad, K., Cryan, P., Russell, A., Semmens, D., & Medellín, R. A. (2015). Optimizing conservation strategies for Mexican free-tailed bats: a

population viability and ecosystem services approach. *Biodiversity and Conservation*, *24*(1), 63–82. https://doi.org/10.1007/S10531-014-0790-7/FIGURES/2

Williams, T. C., Ireland, L. C., & Williams, J. M. (1973). High Altitude Flights of the Free-Tailed Bat, Tadarida brasiliensis, Observed with Radar. *Journal of Mammalogy*, *54*(4), 807–821.

Wilson, S. M., Anderson, J. H., & Ward, E. J. (2023). Estimating phenology and phenological shifts with hierarchical modeling. *Ecology*, *104*(7). https://doi.org/10.1002/ecy.4061

CHAPTER FOUR

FORECASTING THE NIGHTLY EMERGENCE OF MEXICAN FREE-TAILED BATS

Summary

Understanding how environmental conditions drive flexible behaviors is key to revealing evolutionary influences and predicting species responses to climate change. This study explores the drivers of the emergence intensity of one of the largest concentrations of mammals on the planet, namely Mexican free-tailed bats (Tadarida brasiliensis) in south-central Texas. Leveraging weather surveillance radar data across 53 colonies and 9 years, I developed a predictive model with high predictive accuracy, explaining over 75% of the variance in observed emergence counts. Positive associations were found between emergence activity and air temperature, relative humidity, and southeastern winds. Natural roosts supported more bat activity than anthropogenic roosts, which make up the majority of roost sites. This characterization of nightly emergence provides a critical advance in understanding behavioral plasticity in balancing predation risk, internal and environmental conditions, and offers a tool for effective population monitoring and public outreach.

Introduction

Behavioral plasticity enables species to exploit changeable environmental and internal conditions to maximize fitness (Beever et al., 2017; Wong & Candolin, 2015). Individuals are incentivized to forage in conditions that maximize chances of prey availability and minimize the risks of predation (Rydell et al., 1996) while responding to changeable energetic demands due to reproductive status. Such behavioral adaptability not only enhances survival but also serves as a mechanism for coping with the pressures of environmental change (Festa et al., 2022). This is especially true for gregarious species, who navigate the challenges of group decision-making

under environmental variability, in ways of synchronized foraging, collective predator avoidance, and information sharing (Kerth, 2008; Patriquin & Ratcliffe, 2016). By balancing individual needs with collective benefits, gregarious species exemplify how behavioral plasticity not only sustains survival but also reinforces the resilience of social structures under environmental pressure (Akçay & van Cleve, 2012).

Mexican free-tailed bats (*Tadarida brasiliensis*) are a subtropical migratory species that roost in very large, dense aggregations. In the evening, individuals leave the roost to forage, typically emerging prior to dark as part of a rapid, swirling stream (Figure 4.1A). During this exodus, individuals are subject to high predation pressure (Duvergé et al., 2000), whereby they must balance the tradeoff of departing earlier to meet energic demands at the risk of elevated predation from diurnal predators, or delay but increase the effect of conspecific competition for nearby prey resources (Kunz, 1982). Insectivorous bats are flexible foragers and can choose to forgo foraging in suboptimal conditions (Rydell, 1989). Individuals may choose not to emerge at all at some nights, especially in conditions associated with low foraging success (e.g., precipitation) or high energetic costs (e.g., low temperatures) (Frick et al., 2012). For pregnant or lactating females, however, the decision to forage may be more constrained due to increased energetic needs. Pregnant females are also more vulnerable to predators due to increased body weight (upwards of 25%) that can reduce their flight speed and maneuverability (Kunz & Hood, 2000). Thus, the reproductive state can interact with environmental factors to influence individual decisions about when and whether to emerge, revealing how both intrinsic and extrinsic factors shape the behavioral plasticity of this species in a complex, dynamic environment.

Identifying the environmental and behavioral cues used by mass-emerging bats has remained challenging due to a paucity of broad-scale datasets, particularly those that might encompass bat activity across multiple roosts. Because their mass emergences involve the movements of sometimes millions of individuals from some sites, the accuracy of historical records of bat emergences has been called into question (Barclay et al., 2024). Technologically assisted monitoring of emergence counts, such as those using computer vision to count bats in thermal imagery, has recently improved the accuracy of such counts, but this technology remains deployed on a site-by-site basis (Betke et al., 2008; Hristov et al., 2010). The Next Generation Radar (NEXRAD) system has provided high temporal resolution data, with recordings captured every 5 to 10 minutes over several decades, resulting in a continuous and extensive dataset (Stepanian & Wainwright, 2018). South-central Texas is particularly well-covered by this network, with multiple radar stations offering comprehensive monitoring. This region also supports the densest aggregations of Mexican free-tailed bats on earth (Russell et al., 2011), whose nightly emergence events can be observed on radar (Figure 4.1B). The combination of comprehensive radar data and the unique ecological significance of these bat populations makes this region an ideal setting to examine population-level behavioral plasticity in response to various environmental conditions.

The aim of this study was to utilize the NEXRAD network in South Central Texas to predict daily patterns in the nocturnal emergence of Mexican free-tailed bats and identify key factors driving these patterns. I build on previous research linking emergence behavior to various environmental cues (Frick et al., 2012; Horn & Kunz, 2008), focusing more on how the combination of temporal, weather, and spatial variables are related to nightly emergence size differences. I aim to contribute to the understanding of how Mexican free-tailed bats adaptively

respond to dynamic environmental conditions, with implications for broader conservation efforts amid changing global climates.

Methods

Emergence count data

I obtained data on the nightly emergence counts of Mexican free-tailed bats from weather surveillance radar, following the methodology in Chapter 3. Data were collected biennially from 2006 to 2022 across four radar stations (KEWX, KDFX, KGRK, KSJT) in south-central Texas, covering a total of 9 years. I extracted data from each radar station from 90 minutes before to 150 minutes after local sunset. Mexican free-tailed bats in this region can be observed roosting year-round, with high emergence activity occurring from March through November. For analysis, I included only colonies with at least two years of data and more than 10 days of detections per year, resulting in a dataset of 35,383 emergence events from 53 colonies. Each emergence event included multiple detections with associated bat counts and time stamps (Figure 4.1B), which were used to calculate metrics such as time from sunset and time from moonrise.

Predictive variables and selection

I selected 31 predictive variables were included in the models, informed by on previous studies on the factors that could have a potential influence on the nightly emergence of bats (e.g., Haest et al., 2021; Krauel et al., 2015, 2024; Lee & McCracken, 2001; Meyer et al., 2016). I downloaded 9 environmental variables from the North American Regional Reanalysis dataset (Mesinger et al., 2006; 32-kilometer spatial resolution and 3-hour updates), including air temperature, visibility, precipitation rate, air pressure, relative humidity, total cloud cover, northward and eastward wind. Each variable was summarized as daily mean and nightly (local time 18 and 21 pm) mean. Previous night's emergence count, precipitation, and temperature

differences were also included. As a climate index, the monthly Palmer Drought Severity Index (Alley, 1984) was averaged across southern, south-central, and the Edwards Plateau regions of Texas. I also incorporated variables as proxies of predation risk, such as sunset time, moonrise time, and moon illumination. These variables estimate environmental light levels, thus influencing prey visibility and the risk of predation. To further improve the model's predictive power, I included variables such as ordinal date, latitude, longitude, and distance from the radar.

Modeling and validation

I used an approach combining Random Forest and Generalized Additive Models to analyze nightly bat emergence. Random forest was implemented to maximize the predictive accuracy, leveraging its ability to handle complex interactions and nonlinearities (Simon et al., 2023). However, because the random forest model does not easily provide interpretable relationships between predictors and the response variable, I also used the Generalized Additive Model to quantify and visualize how key environmental and temporal factors influence bat emergence dynamics. To address multicollinearity and select relevant features, I fitted a Regularized Random Forest (RRF) model using the training dataset (70% of total nights) with a default regularization parameter (γ=0.5, a modest amount of regulation). The RRF model penalizes correlated variables, enhancing feature selection by emphasizing predictors that contribute unique information (Deng & Runger, 2013). I visualized variable importance from the RRF to identify a subset of variables that had high importance scores over other correlated predictors. I then fitted a standard random forest model using the reduced set of uncorrelated variables to develop a predictive model for nightly bat emergence counts with *randomForest* package in R (Breiman et al., 2018). I fitted the random forest model with 500 trees, and 6 predictors were randomly selected at each split. No transformation on the response variable. The

random forest model was also trained on the same 70% of the data, and its performance was evaluated on the 30% test dataset by calculating the R-squared value (percent of the variance in the real data explained by the predictors) to assess predictive accuracy.

Using the same subset of uncorrelated variables, I then fitted Generalized Additive Models (GAM) in *mgcv* package in R (Wood, 2001). GAMs were fitted with Gaussian error distribution on log-transformed emergence count to evaluate the relationships between selected predictors and the emergence size. Log transformation was applied to the response variable to improve model fit by stabilizing variance and addressing overdispersion in count data (Siegfried & Hothorn, 2020). I assessed concurvity among covariates at each step, applying a threshold of 0.9 on the "worst-case scenario" concurvity index to identify variables with smooth terms that could be replaced by other predictors. This resulted in the stepwise removal of 4 highly redundant variables (i.e., lunar illumination, night precipitation rate, daily averaged visibility, and distance from radar) to improve interpretability and reduce model complexity. The final GAM was selected based on a combination of deviance explained and Akaike information criterion.

Results

The top random forest model for predicting nightly bat emergence counts explained 75.12% of the variance in the test data (Figure 4.2A). The random forest model with the same set of predictors, except the previous night's emergence count, explained 52.65% of the variance of the same test data. The top 5 most important variables, evaluated based on the percent of mean decrease in model accuracy, were time since sunset, previous day bat emergence count, time since moonrise, latitude, and daily eastwards wind (10 m), ranked from the most to least (Figure 2B).

The top generalized additive model included 15 environmental, temporal, and spatial variables (N = 185,776, deviance explained = 66.2%). For environmental conditions, air temperature (Figure 4.3A) and temperature differences compared to the previous day (Figure 4.3B) were positively associated with counts, with higher bat emergence observed at warmer temperatures and more positive temperature differences. Relative humidity (Figure 4.3C) displayed a non-linear but positive relationship, with a peak at 75% of humidity. Both eastward (Figure 4.3D) and northward wind speed (Figure 4.3E) influenced emergence counts, with higher activities observed at stronger eastward and southward winds. Temporal factors, including time from sunset (Figure 4.3F), significantly affected emergence, with activity peaking one to two hours after sunset. Seasonal variation was also apparent, with counts fluctuating across seasons (Figure 4.3G). The number of emerging bats peaked in the spring (around mid-April), followed by a decline and a secondary, smaller peak in late summer (around mid-July). After this, numbers gradually decreased toward the end of the year. The nightly bat emergence count is positively correlated with the previous night's emergence count (Figure 4.3H). The number of bats supported at each roost was strongly influenced by the roost type (Figure 4.3I), with natural roosts supporting higher bat emergence counts (mean = 345,807) than anthropogenic (mean = 249,672) or unknown roosts (mean = 191,050).

Discussion

In this study, I examined how environmental conditions shape emergence patterns in Mexican free-tailed bats throughout their annual cycle, during which they have varying energetic needs related to migration and reproduction. Our findings revealed a distinct seasonal pattern in emergence intensity. In spring, emergence activity peaks, coinciding with the arrival of migrants and the heightened energy requirements of reproduction (Lee & McCracken, 2001; Stepanian &

Wainwright, 2018). There was a more stable count pattern in summer and fall, likely driven by the combined demands of newly foraging pups and adults preparing for migration (Lee & McCracken, 2001; Rascón & Hernández-Velázquez, 2010).

Mexican free-tailed bats generally emerge from their roosts after sunset, though some emergence also occurs before sunset (Figure 4.3F). As the fastest flying bat species, Mexican free-tailed bats may have greater flexibility in adjusting their emergence timing, balancing predation risk and foraging opportunities, as their high flight speed may help compensate for travel time (McCracken et al., 2016). In late summer, reproductive females were observed to emerge earlier in the evening due to the high energy demands of lactation (Lee & McCracken, 2001). Emergence time is also affected by diet, with *Lepidoptera* (e.g., moths) feeders like Mexican free-tailed bats tending to emerge later until full darkness, especially on bright moonlit nights, to align with prey activity (Jones & Rydell, 1994). Aerial-hawking bats often emerge 15-30 minutes after sunset, during or after peak insect activity (Rydell et al., 1996). The average emergence time for Mexican free-tailed bats was found to be 11 minutes after sunset (Herreid & Davis, 1966). However, in our study, the radar-derived emergence start time is around 25 minutes after sunset, with peak emergence time around 100 minutes after sunset. This delay is likely due to the requirement that bats reach a certain altitude to be detected by radar, resulting in a later recorded timing relative to ground-based monitoring. Therefore, to obtain a comprehensive understanding of bat temporal activity patterns, it's important to consider detection biases, as well as ensure that monitoring spans a sufficient duration to capture both the onset and continuation of bat emergence.

Beyond light conditions, environmental conditions also play an important role in shaping emergence activity. Insectivorous bats are more active under warmer temperatures, as higher

temperatures typically enhance aerial insect abundance and lower the energy expenditure for physical regulation (Meyer et al., 2016). Additionally, temperature differences compared to the previous night as a predictor may capture unique bat foraging preferences, which may be separated from the prey availability, which is controlled by the same night air temperature. Relative humidity is another important factor, likely due to its impact on the bats' water retention. Higher relative humidity (65-95%) was found to be associated with larger bat populations in cave habitats (Herreid, 1963) and increased flight activity in some insectivorous bats (Lacki, 1984). Humid nights can generally be more favorable for bats to forage, as they help reduce the risk of dehydration. I also found a positive association between southeast winds and bat emergence. This potentially indicates that larger colonies (e.g., Bracken Cave) prefer southeast winds, which could facilitate foraging journeys toward agricultural fields located southeast of the colony roosts. Southeast winds would thus provide an optimal tailwind for bats, reducing energy expenditure on their outbound journey to abundant food resources (McCracken et al., 2016).

Our predictive model of activity predicts Mexican free-tailed bat emergence intensity with high accuracy, achieving an overall accuracy rate of 75%. This performance metric demonstrates the model’s effectiveness in capturing the nuances of bat emergence behavior across varied environmental conditions and temporal ranges. Notably, while the previous night's count was a significant predictor, our model still maintained high variance explained (53%) when this variable was omitted, indicating the robustness of our other predictors in capturing emergence behavior. This model can be useful for management and conservation of the species by enhancing the accuracy of emergence count surveys, which is a common metric for assessing bat populations and monitoring trends (Kunz et al., 2009). However, our findings also highlight

high levels of nightly variation in emergence count over the course of the season (Figure 4.2B), which may dramatically alter population estimates (Barclay et al., 2024). By guiding surveys to days associated with high emergence activity, managers could get more reliable estimates of bat colony sizes, aiding in population assessments and conservation decisions. Emergence count surveys should take place over successive days and cover days with optimal environmental conditions for bat emergence and foraging (Hoying & Kunz, 1998; Kunz & Anthony, 1996; O'Shea & Bogan, 2003). Additionally, our results provide a robust mechanism for correcting for the effect of emergence counts under sub-optimal conditions, such that a projected range of likely counts could be estimated post-hoc for recent or historical counts of Mexican free-tailed bats.

Mexican free-tailed bat activity in south-central Texas relies heavily on both natural and anthropogenic roosts (Figure 4.3I). More bat activity is sourced from natural roosts (44%) than of anthropogenic roosts (32%). However, the majority of bat colonies (66%) were anthropogenic. These findings underscore the conservation importance of preserving both roost types. Cave disturbances remain a major threat to bats globally (Furey & Racey, 2015), while the protection of anthropogenic roosts is increasingly crucial for maintaining bat populations (Voigt et al., 2015). Given recent evidence of declines in Mexican free-tailed bat populations in the region that nonetheless differ across roost type (Chapter 3), minimizing disturbance should be a key priority for managers working to protect bats already vulnerable to multiple threats (Adams et al., 2024).

The findings in this study also have implications for public outreach and engagement. Mexican free-tailed bat emergences represent a unique natural phenomenon that attracts millions of ecotourists (Boyles et al., 2011; Kunz et al., 2011), offering a prime opportunity for

community involvement and education. The model results are sufficient to inform an accurate real-time forecasting tool. Such a tool could inform visitors about the intensity and timing of a forecasted emergence, which could enhance public awareness and foster positive human-bat relationships, ultimately contributing to greater support for bat conservation efforts.

Figures and Tables

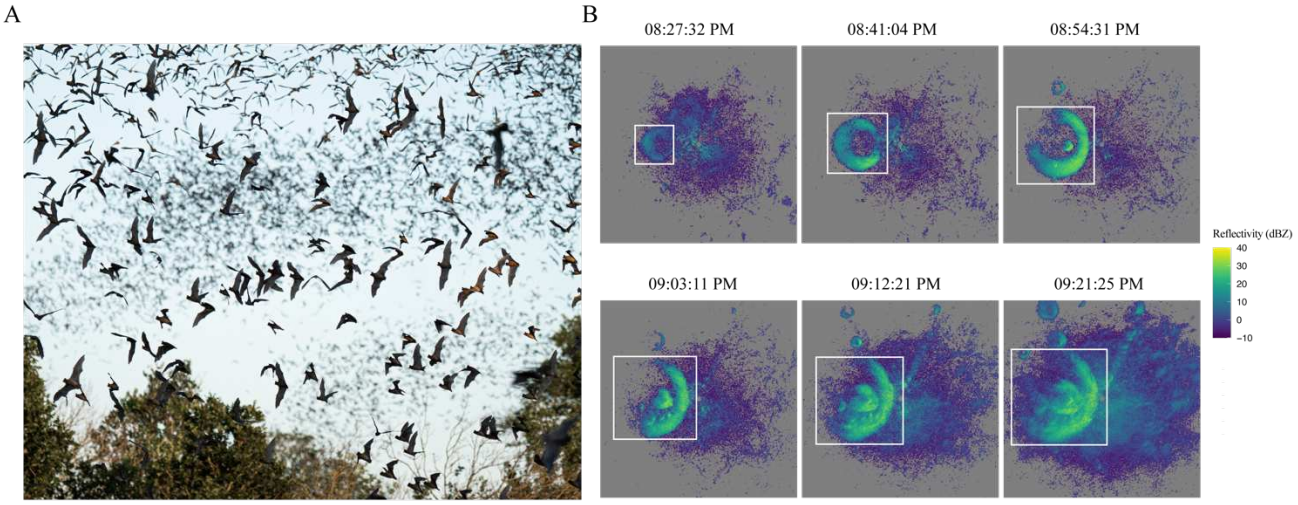

Figure 4.1. Mexican free-tailed bats night emergence event at Bracken cave on June 22nd, 2024, observed (A) on the ground and (B) on weather surveillance radar KEWX (San Antonio, TX) station at the lowest radar beam angle between 8:27 – 9:22 PM local time (every other radar scan). Box indicates the roost ring from Bracken cave emergence.

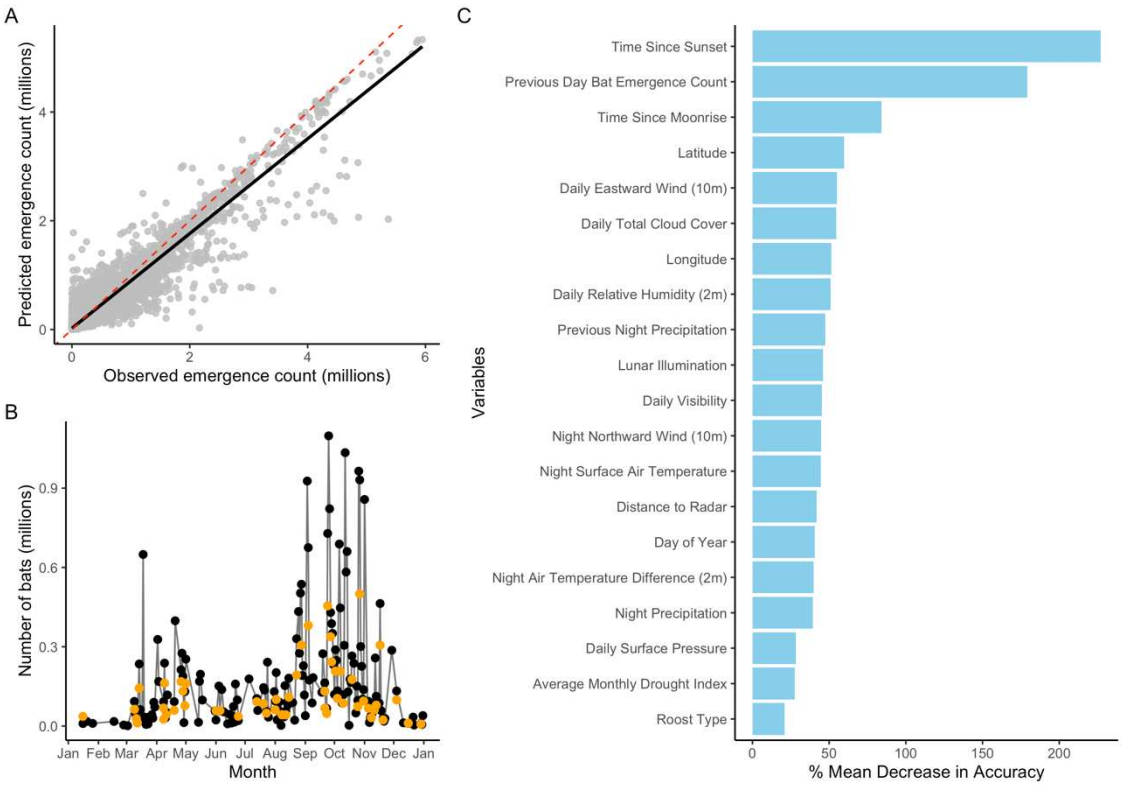

Figure 4.2. (A) Scatterplot of predicted versus observed bat emergence counts, with the black line indicating model fit (R^2 = 75.12%) and the red dashed line indicating the 1:1 line. Test data shown were not used in model training, representing 30% of the unique days of the original dataset. (B) Example of the variation in nightly 90th percentile count at Congress Bridge in 2010. Black points show the observed count. Orange points show the predicted averaged count from the random forest model on the test dataset. (C) Predictor importance based on percent of mean decrease in accuracy, ranked in descending order.

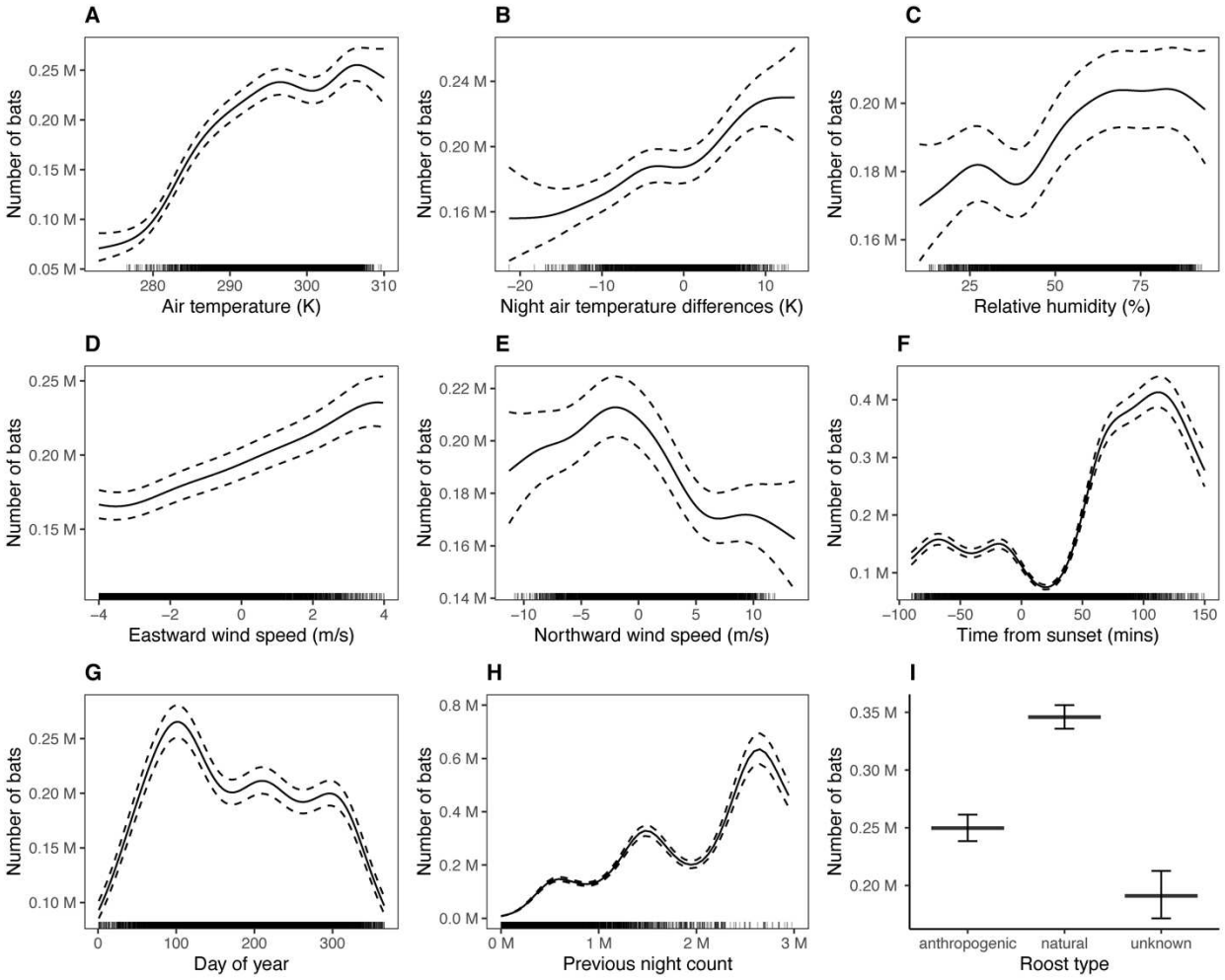

Figure 4.3. Generalized additive model (GAM) predictions showing the influence of key variables on nightly bat emergence size (n = 185,776) while holding other covariates at their mean values. Variables with high collinearity were dropped from the model. Solid lines represent the estimated effects of each variable, while dashed lines indicate the standard errors of the smooth terms. Rugs on the x-axis display the frequency distribution of each variable. Y-axis limits vary across panels to highlight subtle changes in each variable's effect. The response variable was modeled on a log scale but has been back transformed to the original scale for interpretability. Variables include: (A) daily averaged air temperature; (B) differences in night air temperature compared to the previous night; (C) relative humidity at surface level; (D) eastward wind speed; (E) northward wind speed; (F) time from sunset; (G) day of the year (ordinal date); (H) emergence count from the previous night; (I) roost types. The full model details are provided in Supplementary Figure S1.

REFERENCES

Adams, A. M., Trujillo, L. A., Campbell, C. J., Akre, K. L., Arroyo-Cabrales, J., Burns, L., Coleman, J. T. H., Dixon, R. D., Francis, C. M., Gamba-Rios, M., Kuczynska, V., McIntire, A., Medellín, R. A., Morris, K. M., Ortega, J., Reichard, J. D., Reichert, B., Segers, J. L., Whitby, M. D., & Frick, W. F. (2024). The state of the bats in North America. *Annals of the New York Academy of Sciences*. https://doi.org/10.1111/nyas.15225

Akçay, E., & van Cleve, J. (2012). Behavioral responses in structured populations pave the way to group optimality. *American Naturalist*, *179*(2). https://doi.org/10.1086/663691

Alley, W. M. (1984). The Palmer Drought Severity Index: limitations and assumptions. *Journal of Climate & Applied Meteorology*, *23*(7). https://doi.org/10.1175/1520-0450(1984)023<1100:TPDSIL>2.0.CO;2

Barclay, R. M. R., Monteiro, T. A., Miller, E. N., & Hiles, L. E. (2024). Fluctuations in Bat-house Colony Size May Hamper Estimation of Population Changes. *Journal of North American Bat Research*, *1*(1), 1–10.

Beever, E. A., Hall, L. E., Varner, J., Loosen, A. E., Dunham, J. B., Gahl, M. K., Smith, F. A., & Lawler, J. J. (2017). Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment*, *15*(6). https://doi.org/10.1002/fee.1502

Betke, M., Hirsh, D. E., Makris, N. C., McCracken, G. F., Procopio, M., Hristov, N. I., Tang, S., Bagchi, A., Reichard, J. D., Horn, J. W., Crampton, S., Cleveland, C. J., & Kunz, T. H. (2008). Thermal Imaging Reveals Significantly Smaller Brazilian Free-Tailed Bat Colonies Than Previously Estimated. *Journal of Mammalogy*, *89*(1), 18–24. https://doi.org/10.1644/07-MAMM-A-011.1

Boyles, J. G., Cryan, P. M., McCracken, G. F., & Kunz, T. H. (2011). Economic importance of bats in agriculture. In *Science* (Vol. 332, Issue 6025). https://doi.org/10.1126/science.1201366

Breiman, L., Cutler, A., Liaw, A., & Wiener, M. (2018). Package 'randomForest' - Breiman and Cutler's Random Forests for Classification and Regression. *CRAN Repository*.

Deng, H., & Runger, G. (2013). Gene selection with guided regularized random forest. *Pattern Recognition*, *46*(12). https://doi.org/10.1016/j.patcog.2013.05.018

Duvergé, P. L., Jones, G., Rydell, J., & Ransome, R. D. (2000). Functional significance of emergence timing in bats. *Ecography*, *23*(1). https://doi.org/10.1111/j.1600-0587.2000.tb00258.x

Festa, F., Ancillotto, L., Santini, L., Pacifici, M., Rocha, R., Toshkova, N., Amorim, F., Benítez-López, A., Domer, A., Hamidović, D., Kramer-Schadt, S., Mathews, F., Radchuk, V., Rebelo, H., Ruczynski, I., Solem, E., Tsoar, A., Russo, D., & Razgour, O. (2022). Bat responses to climate change: a systematic review. *Biological Reviews*. https://doi.org/10.1111/brv.12893

Frick, W. F., Stepanian, P. M., Kelly, J. F., Howard, K. W., Kuster, C. M., Kunz, T. H., & Chilson, P. B. (2012). Climate and weather impact timing of emergence of bats. *PLOS One*, *7*(8). https://doi.org/10.1371/journal.pone.0042737

Furey, N. M., & Racey, P. A. (2015). Conservation ecology of cave bats. In *Bats in the Anthropocene: Conservation of Bats in a Changing World*. https://doi.org/10.1007/978-3-319-25220-9_15

Haest, B., Stepanian, P. M., Wainwright, C. E., Liechti, F., & Bauer, S. (2021). Climatic drivers of (changes in) bat migration phenology at Bracken Cave (USA). *Global Change Biology*, *27*(4), 768–780. https://doi.org/10.1111/gcb.15433

Herreid, C. F. (1963). Temperature Regulation of Mexican Free-Tailed Bats in Cave Habitats. *Journal of Mammalogy*, *44*(4). https://doi.org/10.2307/1377140

Herreid, C. F., & Davis, R. B. (1966). Flight Patterns of Bats. *Journal of Mammalogy*, *47*(1). https://doi.org/10.2307/1378071

Horn, J. W., & Kunz, T. H. (2008). Analyzing NEXRAD doppler radar images to assess nightly dispersal patterns and population trends in Brazilian free-tailed bats (Tadarida brasiliensis). *Integrative and Comparative Biology*, *48*(1), 24–39. https://doi.org/10.1093/icb/icn051

Hoying, K. M., & Kunz, T. H. (1998). Variation in size at birth and post-natal growth in the insectivorous bat Pipistrellus subflavus (Chiroptera: Vespertilionidae). *Journal of Zoology*, *245*(1). https://doi.org/10.1017/S0952836998005020

Hristov, N. I., Betke, M., Theriault, D. E. H., Bagchi, A., & Kunz, T. H. (2010). Seasonal variation in colony size of brazilian free-tailed bats at carlsbad cavern based on thermal imaging. *Journal of Mammalogy*, *91*(1). https://doi.org/10.1644/08-MAMM-A-391R.1

Jones, G., & Rydell, J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *346*(1318). https://doi.org/10.1098/rstb.1994.0161

Kerth, G. (2008). Causes and consequences of sociality in bats. In *BioScience* (Vol. 58, Issue 8). https://doi.org/10.1641/B580810

Krauel, J. J., Reynolds, D. R., Westbrook, J. K., & McCracken, G. F. (2024). Insect migrations and the ecology, behavior, and population dynamics of bats. In *A Natural History of Bat Foraging* (pp. 139–156). Elsevier. https://doi.org/10.1016/B978-0-323-91820-6.00005-X

Krauel, J. J., Westbrook, J. K., & Mccracken, G. F. (2015). Weather-driven dynamics in a dual-migrant system: moths and bats. *The Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.12327

Kunz, T. H. (1982). Roosting ecology of bats. *Ecology of Bats*. https://doi.org/10.1007/978-1-4613-3421-7_1

Kunz, T. H., & Anthony, E. L. P. (1996). Variation in the timing of nightly emergence behaviour in the little brown bat, Myotis lucifugus (Chiroptera: Vespertilionidae). In *Contributions in Mammalogy - A memorial volume honouring Dr J Knox Jones Jr*.

Kunz, T. H., Betke, M., Hristov, N. I., & Vonhof, M. J. (2009). Methods for assessing colony size, population size, and relative abundance of bats. *Ecological and Behavioral Methods for the Study of Bats*, 133–157.

Kunz, T. H., de Torrez, E. B., Bauer, D., Lobova, T., & Fleming, T. H. (2011). Ecosystem services provided by bats. In *Annals of the New York Academy of Sciences* (Vol. 1223, Issue 1). https://doi.org/10.1111/j.1749-6632.2011.06004.x

Kunz, T. H., & Hood, W. R. (2000). Parental Care and Postnatal Growth in the Chiroptera. In *Reproductive Biology of Bats*. https://doi.org/10.1016/b978-012195670-7/50011-4

Lacki, M. J. (1984). Temperature and humidity-induced shifts in the flight activity of little brown bats. *The Ohio Journal of Science*, *84*(5).

Lee, Y.-F., & McCracken, G. F. (2001). Timing and Variation in the Emergence and Return of Mexican Free-tailed Bats, Tadarida brasiliensis mexicana. *Zoological Studies*, *40*(4), 309–316. http://www.sinica.edu.tw/zool/zoolstud/40.4/309.pdf

McCracken, G. F., Safi, K., Kunz, T. H., Dechmann, D. K. N., Swartz, S. M., & Wikelski, M. (2016). Airplane tracking documents the fastest flight speeds recorded for bats. *Royal Society Open Science*, *3*(11). https://doi.org/10.1098/rsos.160398

Mesinger, F., DiMego, G., Kalnay, E., Mitchell, K., Shafran, P. C., Ebisuzaki, W., Jović, D., Woollen, J., Rogers, E., Berbery, E. H., Ek, M. B., Fan, Y., Grumbine, R., Higgins, W., Li, H., Lin, Y., Manikin, G., Parrish, D., & Shi, W. (2006). North American regional reanalysis. *Bulletin of the American Meteorological Society*, *87*(3). https://doi.org/10.1175/BAMS-87-3-343

Meyer, G. A., Senulis, J. A., & Reinartz, J. A. (2016). Effects of temperature and availability of insect prey on bat emergence from hibernation in spring. *Journal of Mammalogy*, *97*(6), 1623–1633. https://doi.org/10.1093/jmammal/gyw126

O'Shea, T., & Bogan, M. (2003). Monitoring trends in bat populations of the United States and territories: problems and prospects. *Publications of the US Geological …*.

Patriquin, K. J., & Ratcliffe, J. M. (2016). Should i stay or should i go? Fission-fusion dynamics in bats. In *Sociality in Bats*. https://doi.org/10.1007/978-3-319-38953-0_4

Rascón, J., & Hernández-Velázquez, F. D. (2010). Population structure of migratory Mexican free-tailed bats Tadarida brasiliensis mexicana (Chiroptera) in a Chihuahuan Desert roost. *Chiroptera Neotropical*, *16*(1).

Russell, A. L., Cox, M. P., Brown, V. A., & McCracken, G. F. (2011). Population growth of Mexican free-tailed bats (Tadarida brasiliensis mexicana) predates human agricultural activity. *BMC Evolutionary Biology*, *11*(1). https://doi.org/10.1186/1471-2148-11-88

Rydell, J. (1989). Feeding activity of the northern bat Eptesicus nilssoni during pregnancy and lactation. *Oecologia*, *80*(4). https://doi.org/10.1007/BF00380082

Rydell, J., Entwistle, A., & Racey, P. A. (1996). Timing of Foraging Flights of Three Species of Bats in Relation to Insect Activity and Predation Risk. *Oikos*, *76*(2). https://doi.org/10.2307/3546196

Siegfried, S., & Hothorn, T. (2020). Count transformation models. *Methods in Ecology and Evolution*, *11*(7). https://doi.org/10.1111/2041-210X.13383

Simon, S. M., Glaum, P., & Valdovinos, F. S. (2023). Interpreting random forest analysis of ecological models to move from prediction to explanation. *Scientific Reports*, *13*(1). https://doi.org/10.1038/s41598-023-30313-8

Stepanian, P. M., & Wainwright, C. E. (2018). Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. *Global Change Biology*, *24*(7), 3266–3275. https://doi.org/10.1111/gcb.14051

Voigt, C. C., Phelps, K. L., Aguirre, L. F., Corrie Schoeman, M., Vanitharani, J., & Zubaid, A. (2015). Bats and buildings: The conservation of synanthropic bats. In *Bats in the Anthropocene: Conservation of Bats in a Changing World*. https://doi.org/10.1007/978-3-319-25220-9_14

Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, *26*(3). https://doi.org/10.1093/beheco/aru183

Wood, S. N. (2001). mgcv: GAMs and generalized ridge regression for R. *R News*, *1*.

APPENDIX

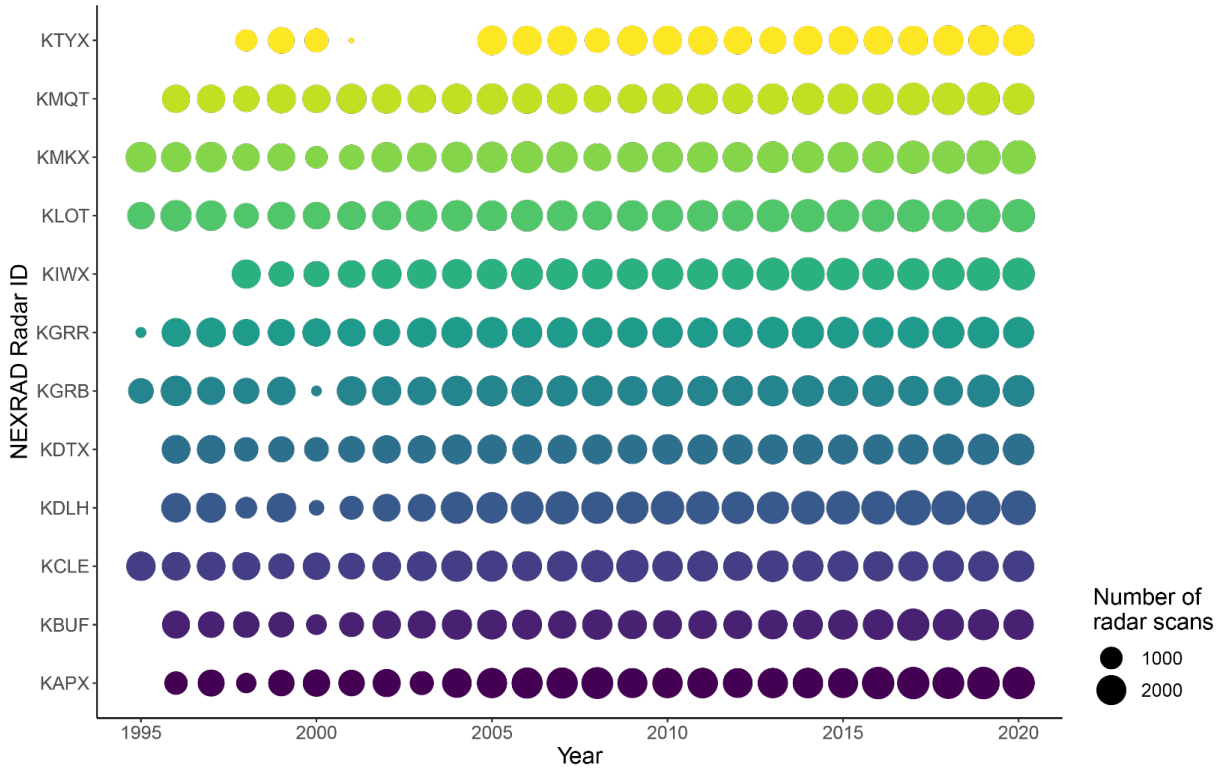

Figure 1.S1: Data density for 12 radar stations from 1995 to 2020. Data points within the plot represent the number of available annual radar scans from 30 minutes before sunrise and 90 minutes after sunrise taken from June 1st to October 31st.

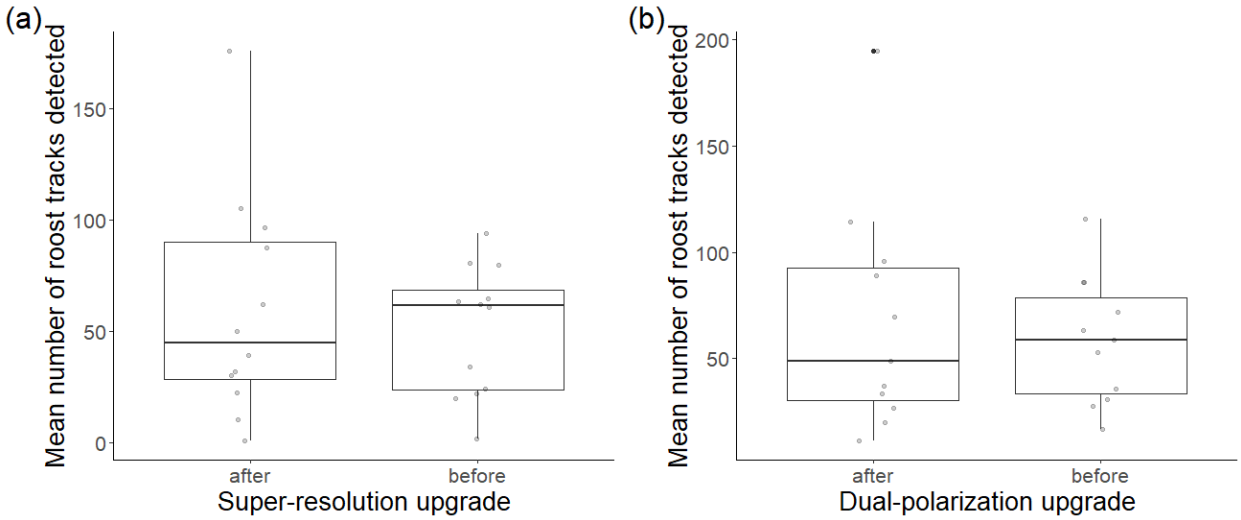

Figure 1.S2: Comparison of the mean number of roost tracks detected before and after (a) super-resolution upgrade in 2008; (b) dual-polarization upgrade in 2013. Each point represents a mean number of roost detections within a 150 km range around a radar station of all years before or after the upgrade (the year of upgrade is not included). The paired samples Wilcoxon test showed that there was no statistical significance between the two groups for the super-resolution upgrade (p-value = 0.6221) and the dual-polarization upgrade (p-value = 0.5195).

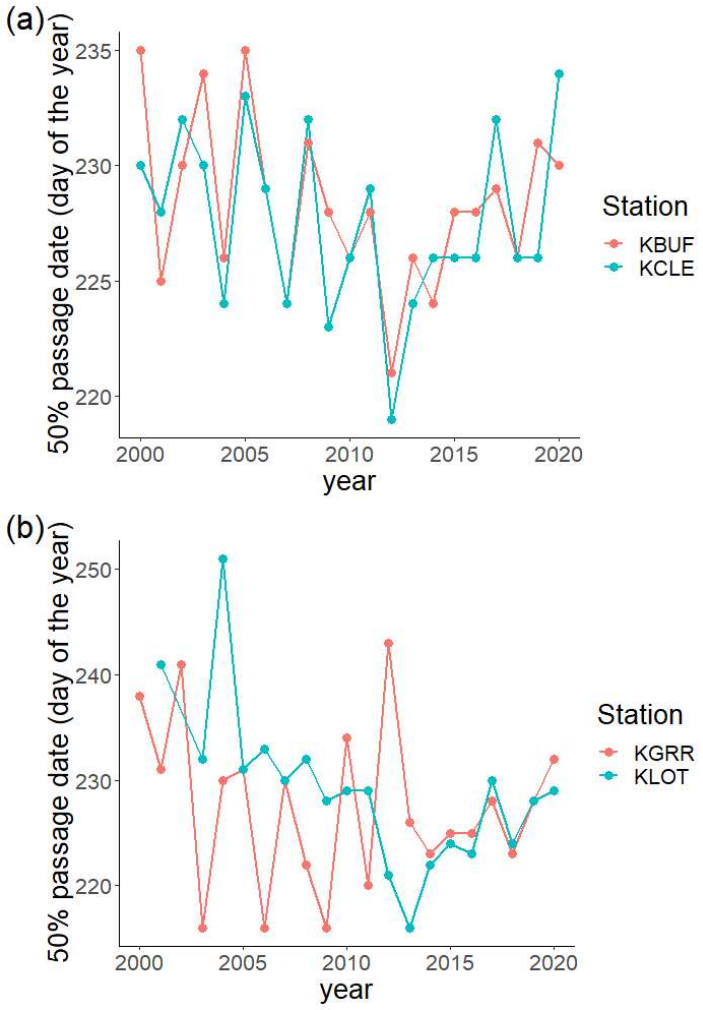

Figure 1.S3: Peak roosting activity (50% passage dates) between two pairs of stations. (a) KBUF and KCLE stations have a significant positive Pearson's correlation coefficient: 0.736. (b) KGRR and KLOT have a non-significant Pearson's correlation coefficient: 0.001.

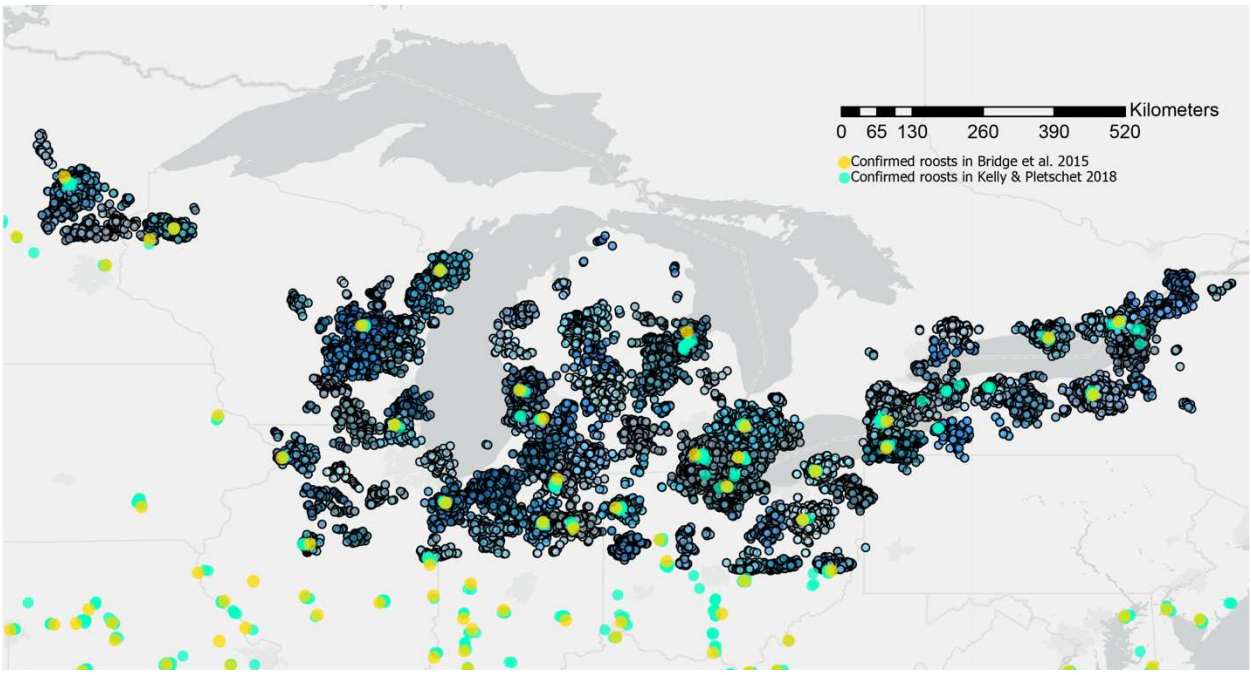

Figure 1.S4: Roost detections in this study (different shades of blue, with each unique color representing a roost cluster) as well as known swallow roosts in the Bridge et al. 2015 paper (yellow) and in Kelly & Pletschet, 2018 (cyan). Roost detection clusters from this study are plotted as smaller points, colored by different cluster ID. The map was generated in ArcGIS Pro 2.4.0. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Map 2.S1. ΔAICc maps of the identified best time windows for all variables examined, weather radar station locations at the Great Lakes, and the top 5 most influential signals. The ΔAICc values represent the difference between the AICc value of the model using the optimal time window for each pixel and the AICc value of the baseline linear trend model. ΔAICc values are displayed only for pixels with a probability P_c value < 0.3, indicating that the relationship between the identified time window and the peak roosting date is unlikely to have occurred by chance.

https://yutingdeng.shinyapps.io/Supplementary_Map_Shiny/

Table 2.S1. Properties of original and post-processing weather and vegetation variables that were acquired from the NCEP Reanalysis I database and MODIS database.

Variable type	Name	Number of variables for analysis	Spatial resolution	Analyzed grid cells	Number of rows x columns	Temporal resolution
Temperature	'air.2m', 'tmax.2m', 'tmin.2m'	3	1.9047° x 1.875°	663	13 x 51	1 day
Precipitation	'shum.2m', 'cprat.sfc', 'prate.sfc'	3	1.9047° x 1.875°	663	13 x 51	1 day
Wind	'uwnd', 'vwind' at 850, 925, 1000 hPa used to calculate 'wind direction' (from and to) and 'wind assistance"	9	2.5° x 2.5°	429	11 x 39	1 day
Enhanced vegetation index (EVI)	MOD13A2.V61	1	1km x 1km (Aggregated into 64km x 64km)	1437127 (Aggregated into 4370)	2419 x 5941 (Aggregated into 38 x 115)	1 day (interpolated from 16-day)
Water surface temperature	MYD11A2.v061	1	1km x 1km (Aggregated into 16km x 16km)	1345604 (Aggregated into 21160)	916 x 1469 (Aggregated into 115 x 184)	1 day (interpolated from 8-day resolution)

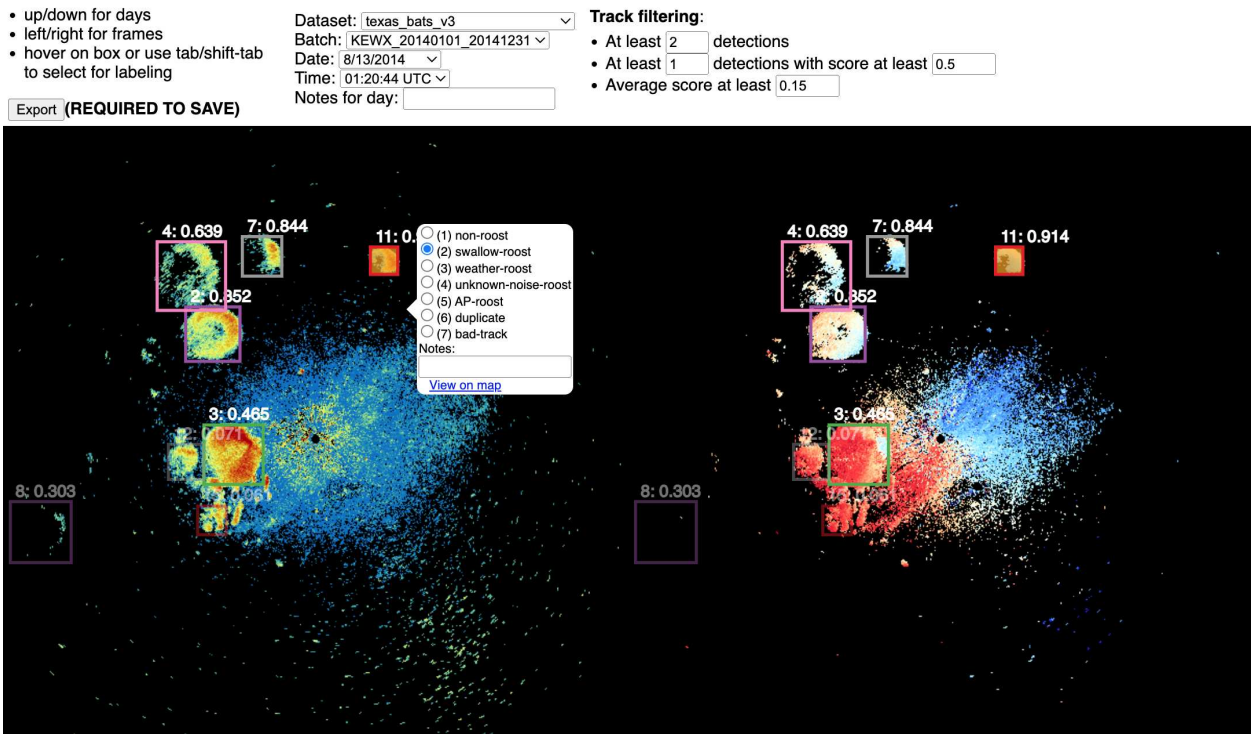

Figure 3.S1. User screening interface of the AI-assisted detection and tracking system on Mexican free-tailed bats' nightly emergence. Each bounding box shows a positive ID by the algorithm based on the current track filtering parameters. Screeners can change the label of each detection to one of the seven labels.

Table 3.S1. AIC values for models run with *phenomix* R package.

Data distribution	Model distribution	AIC	
		Spring	Fall
lognormal	Student's *t*	**4767.556**	4133.549
lognormal	Normal (Guassian)	4782.578	**4117.487**
lognormal	Generalized normal	4795.915	NA
lognormal	Double Student's *t*	NA	NA
lognormal	Double normal	NA	NA
lognormal	Double generalized normal	NA	NA

*NA indicates the model did not converge or the standard error extracted as NAs
*Bold indicates the final chosen model

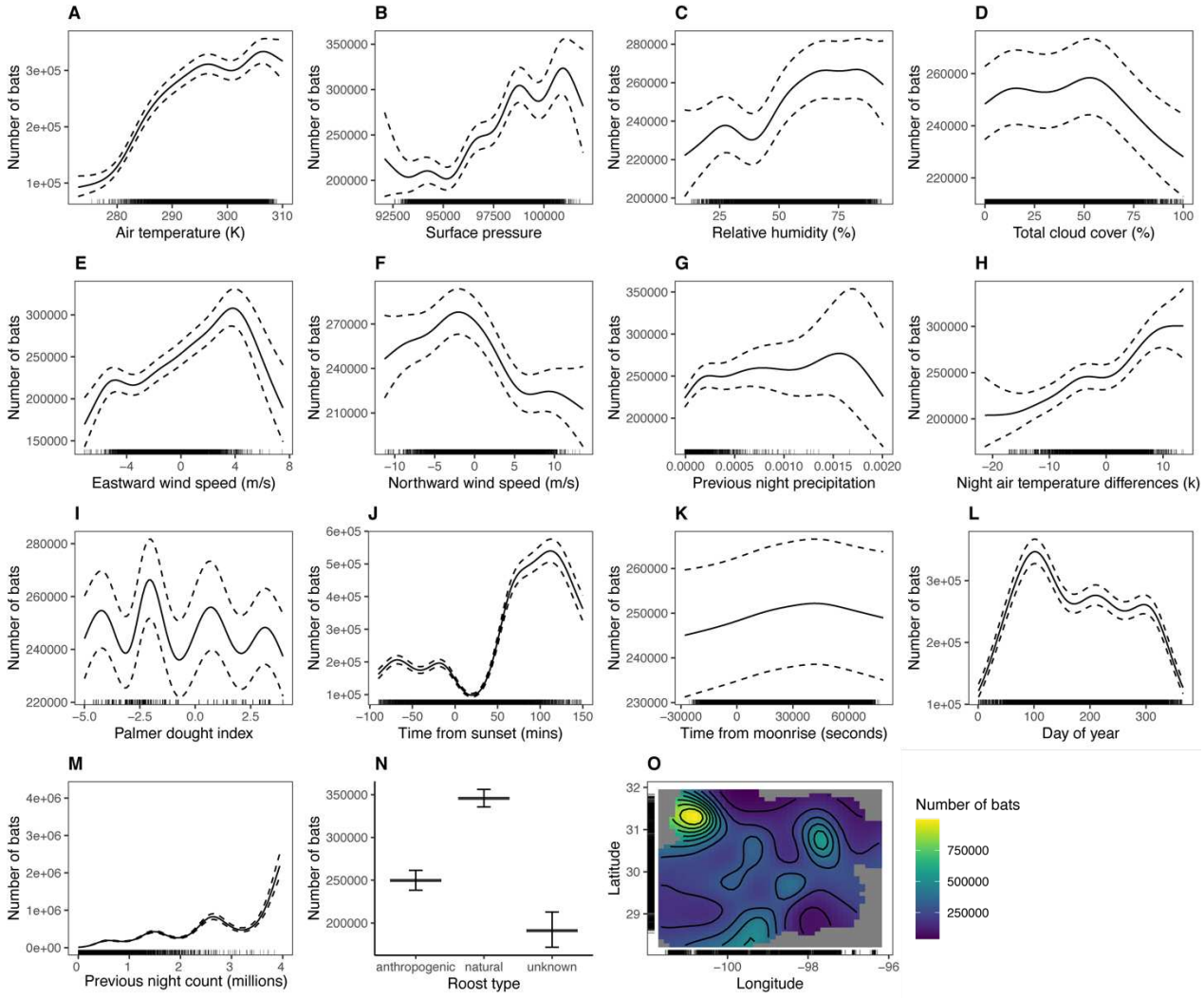

Figure 4.S1. Generalized additive model (GAM) full predictions showing the influence of key variables on nightly bat emergence size (n = 185,776). Variables with high collinearity were dropped from the model. Solid lines represent the estimated effects of each variable (holding other covariates at their mean values), while dashed lines indicate the standard errors of the smooth terms. Rugs on the x-axis display the frequency distribution of each variable. Y-axis limits vary across panels to highlight subtle changes in each variable's effect. The response variable was modeled on a log scale but has been back-transformed to the original scale for interpretability. Variables include: (A-H) weather conditions on the day of and the previous day, (I) drought index, and (J-O) other spatial, temporal, and roost types.

Table 4.S1. Variable names, data levels, and time resolutions.

	Variable	Level	Timescale
avg_drought_index	Palmer drought index		Monthly
air.sfc	Air temperature	Surface	8x Daily
air.2m	Air temperature	2m	8x Daily
vis	Visibility	Surface	8x Daily
prate	Precipitation Rate	Surface	8x Daily
pres.sfc	Pressure	Surface	8x Daily
rhum.2m	Relative Humidity	Surface	8x Daily
tcdc	Total cloud cover	Entire Atmosphere Considered as a Single Layer	8x Daily
uwind.10m	U-wind	10 m	8x Daily
vwind.10m	V-wind	10 m	8x Daily

* uwind is the wind velocity toward east and vwind is the wind velocity toward north