TRACKING CHANGES IN MIGRATION FOR VAUX'S SWIFTS AND CHIMNEY SWIFTS USING COMMUNITY SCIENCE

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ABSTRACT

Climate change has resulted in changes to weather patterns with earlier springs in temperate zones, warmer winters, and more frequent droughts and high-intensity storms. These changes present challenges to migrating bird species if they are unable adjust to the changing environment. In Chapter 2, using an extensive database of observations from citizen scientists, I asked if Vaux's Swifts (*Chaetura vauxi*) altered their first arrival dates (date the first swift arrived) and peak roost occupancy dates (date the maximum number of swifts were observed at a roost) over a ten year period. I also asked if they altered migration timing in response to weather conditions experienced at migratory roosts during both spring and fall. The migration data analyzed was provided by the community science organization, Vaux's Happening over a 10-year period from 2008-2017. In spring, first arrival and peak roost occupancy advanced over time, and first arrival advanced with an increase in local wind gust speeds. During fall migration, timing did not change over time, but higher temperatures were associated with later first arrival and peak roost occupancy. Also, higher local wind speeds were associated with earlier peak roost occupancy dates. These findings may indicate that Vaux's Swifts are tracking earlier onset of spring conditions, as well as altering migration timing in response to weather conditions experienced during migration, especially during fall. In Chapter 3, I asked if Vaux's Swifts and Chimney Swifts (*Chaetura pelagica*) changed their breeding distribution, migration routes, timing of migration, or speed of migration over time. The migration data analyzed was provided by eBird and covered the years 2009-2018. My results indicate a south-east shift in the breeding centroid for Vaux's Swifts and a western shift in the breeding centroid for Chimney Swifts, as well as an eastern shift in the migration route for Vaux's Swifts, almost equal in magnitude to its eastern breeding range shift. I also found an advance in the start of spring migration for Vaux's Swifts and a delay in the start of fall migration for Chimney Swifts. Similar to my findings in Ch. 2, these results, using a much larger community-science dataset, may similarly indicate a response to earlier onset of spring conditions, and a possible delay in the onset of fall conditions. Surprisingly, my results also indicate a shift in breeding range to a more central location in North America (i.e., east for Vaux’s Swifts, west for Chimney Swifts) for both species, possibly as a result of anthropogenic changes to the environment. Results from both chapters indicate that the species show some behavioural plasticity in response to changing weather conditions and, likely, changes in the environment. What remains unclear is whether these species will be able to keep up with more extreme changes in weather and climate predicted with climate change.

Keywords: Climate change, Vaux’s Swifts, Chimney Swifts, migration, migration timing, migration route, breeding grounds

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Chapter 1: Introduction

Migratory birds travel annually from wintering grounds to breeding grounds in the spring and vice versa in the fall, typically to move from areas of low or decreasing food resources, to areas of high or increasing food resources (Dingle, 1996) and to improve survival and reproduction (Alerstam and Lindstrom 1990). In spring, individual migrants attempt to arrive at their breeding grounds first to establish the best territories and acquire high-quality mates (Cristol 1995). In temperate regions, they migrate back to their wintering grounds in the fall to avoid the harsh weather and lack of resources on breeding grounds (Jenni and Kery 2003). The high energetic cost of migration is thought to be offset by the benefits of an increase in food for young, as well as increased nest site availability (Alerstam 2011). Despite the benefits, migration remains energetically costly and exposes migrants to extreme weather conditions and increased predation risk. Timing of migration is believed to be influenced by internal endogenous cues, such as photoperiodic cues, and external environmental cues, such as temperature increases associated with the onset of spring (Akesson and Helm 2020). Timing and survival during migration can be affected by the abundance of resources, weather conditions encountered, availability of stopover sites, and anthropogenic factors (e.g., cities, agricultural lands, power lines, and wind farms).

Migratory timing has co-evolved tightly with plant and insect phenology; however, a problem arises as climate change is altering conditions experienced by birds differently throughout each phase of their annual cycle. With climate change we can expect an advance in the onset of spring conditions, warming winters, and more extreme weather conditions experienced during migration (Schwartz et al., 2006). Changes to ecosystems both in terms of available habitat as well as the timing of peak resource availability at stopover sites and breeding grounds may result in species shifting the latitude of their breeding grounds, and possibly of their wintering grounds. If these environmental changes occur at a rate at which birds cannot adequately adapt and respond to, we may see population declines due to direct mortality or phenological mismatches throughout the phases of the annual cycle (Gienapp and Bregnballe, 2012).

Mortality may result from extreme weather conditions during migration (Reid et al., 2018), a mismatch between arrival timing and peaks in food availability (Gienapp and Bregnballe, 2012), or a shift in habitat suitability and resource abundance (Parmesan, 2007; Kelly et al., 2016). Species may need to migrate to their breeding grounds earlier to arrive in time to take advantage of peaks in resource availability for themselves and their chicks, which is occurring earlier over time (Rubolini et al. 2004). However, arriving too early to the breeding grounds can result in increased mortality because of extreme weather conditions (e.g., late-season snow) or a lack of food resources (Newton, 2007). In spring, migrants are likely to be less responsive to weather conditions experienced during migration, while in fall birds should be more responsive to weather conditions experienced en route as they are not in a rush to establish territories and breed (Prytula et al., 2021).

A species' ecology and life history also influence migratory strategies and timing; for example, aerial insectivores are dependent on spring green up for primary food production (Mayor et al., 2017), as it is directly correlated with insect emergence (van Asch and Visser, 2006). Migration distance may also play a role; short distance migrants, i.e., those which migrate within North America (Bull, 2003), are potentially better able to adjust migration timing in response to climatic changes. Long distance migrants, i.e. those that migrate south of North America, may have difficulty adjusting their migration timing, as they may be more regulated by endogenous rhythms instead of environmental cues (Fraser et al., 2013; Usui et al., 2017; Lehikoinen et al., 2019). They also have farther to migrate and may be more restricted in terms of energy expenditure. Finally, they are less able to detect changes to the onset of spring conditions on the breeding grounds from their more distant wintering grounds (Visser et al. 2009).

Conditions on wintering grounds can also play a role in survival and reproduction, such as low food availability, extreme weather conditions (such as droughts), and anthropogenic effects such as agriculture and pesticide use. But this data is more difficult to obtain for long distance migrants, as the data south of North America becomes limited due to the scarcity of studies of overwintering migratory birds. Even for community science datasets like eBird, data south of the United States is sparse due to fewer users uploading data to eBird.

A difficulty that arises in the study of bird migration is determining whether the changes to their migration are a result of evolutionary adaptation or plasticity. Evolutionary adaptation refers to genetic adaptation to climate change (Charmantier and Gienapp, 2014; Merila and Hendry, 2014), whereas plasticity refers to individuals with a given genotype, or across genotypes, altering their phenotype or behaviour to their given environment (West-Eberhard 2003). Testing for evolutionary adaptation has three steps: first, there would have to be genetic change; second, the genetic change would have to be in response to climate change; and third, the change would have to result in differential survival and reproduction (Charmantier and Gienapp, 2014; Merila and Hendry, 2014). Because I was unable to test for plasticity or evolutionary changes due to the nature of the study, throughout this thesis I simply state that changes appear to be responses to changes in environmental conditions, without implying a mechanism.

Focal species

Vaux's Swifts (*Chaetura vauxi*) and Chimney Swifts (*Chaetura pelagica*) are long distance migrants and aerial insectivores that have declining populations in North America (Spiller and Dettmers, 2019; Schwitters et al. 2020; Steeves et al., 2020). Both species migrate in large species-specific flocks and roost in abandoned chimneys and hollowed out old growth trees. Both species construct nests out of stick and saliva, also nesting in chimneys and old-growth trees, during their breeding season. Vaux's Swifts overwinter in Central America, migrate across the west coast of America, and breed from California to the southern Yukon (Schwitters et al. 2020). Chimney Swifts overwinter in South America, migrate through eastern Central America, and breed along the east coast of North America from Texas to south-eastern Canada (Steeves et al., 2020). As aerial insectivores, these species may already be suffering from reduced insect abundance (Wagner, 2020) and quality (Nocera et al., 2012; Pomfret et al., 2014). However, there are a number of other potential factors responsible for the population declines for both Vaux's and Chimney swifts (Spiller and Dettmers, 2019). As long distance migrants, Vaux's swifts and Chimney swifts may also have difficulty changing their migration timing. This could leave them susceptible to a mismatch in timing between spring arrival and spring green up (Gienapp and Bregnballe, 2012; Mayor et al., 2017), resulting in missed peak insect emergence (van Asch and Visser, 2006). This mismatch could result in migrants not meeting their energetic requirements for both breeding and migration. Finally, with loss of hollowed out old-growth trees and old chimneys being capped, Vaux's swifts roost availability during migration may be a limiting factor (Bull, 2003). However, roost availability does not currently appear to be a limiting factor for Chimney swifts' (Fitzgerald et al. 2014). The two species were chosen because they are similar species with similar life history traits, with a difference in west coast versus east coast migration and breeding grounds.

Community science data

The use of community science data is becoming more popular over time as it allows for the study of species over large spatial and temporal scales. For my thesis I used two different community science data sets: Vaux's Happening was used to acquire data on Vaux's Swifts for chapter 2, and eBird was utilized to acquire data on Vaux's and Chimney Swifts for chapter 3. Vaux's Happening was utilized to test for changes in migration timing. In this program, volunteers went to known roost locations for multiple nights every year during spring and fall migration to count swifts roosting in decommissioned chimneys and one old growth tree. From these counts, I generated data on first arrival and peak roost occupancy of between the years 2008-2017. eBird was utilized to test for changes to the distributions and migration timing/routes for Vaux's Swifts and Chimney Swifts. From these data, I analyzed changes in breeding ground centroids, as well as changes in spring and fall migration route, timing, and speed between the years 2009-2018.

The purpose of my thesis is to utilize community science data to measure the ability of Vaux's swifts and Chimney swifts to alter spring and fall migration routes, speeds and timing and to shift their breeding range in response to short-term changes in weather and more persistent changes in climate-related weather patterns and over time. The goal of this thesis is to determine if Vaux's and Chimney Swifts are restricted in their migratory timing based on endogenous rhythms or are able to respond to changing weather and climate conditions and alter their migratory routes and timing.

Structure of thesis

This thesis is organized into 4 chapters: the general introduction; chapters 2 and 3 utilizing research data; and a conclusion chapter. In chapter 2, I utilize a community science data set, Vaux's Happening, coupled with local and regional weather data to determine whether Vaux's Swifts' have changed their migratory timing over time and whether these changes are driven by weather conditions. This chapter was published in the Canadian Journal of Zoology (Prytula et al. 2021). In chapter 3, I utilize eBird data to determine if Vaux's Swifts and Chimney Swifts have altered their breeding distributions, migration timing, speed, or migratory routes over time. Chapter 4 concludes my thesis, where I address potential directions for future studies, and discuss the implications my research has for conservation, and the effect of alterations to migration in an ever-changing climate.

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Chapter 2: Rapid advancement of spring migration and en route adjustment of migration timing in response to weather during fall migration in Vaux’s Swifts (*Chaetura vauxi*)

Abstract

In temperate regions of the world, climate change has generated earlier springs, later falls, and different weather patterns. These changes may prove challenging to migratory species if they are unable to adjust their migratory timing. We analyzed changes in migratory timing of Vaux’s Swifts (*Chaetura vauxi* (J.K. Townsend, 1839)) by examining first arrivals (date the first swift arrived) and peak roost occupancy (date the maximum number of swifts were observed) at migratory roosts in both spring and fall from the citizen science organization Vaux’s Happening. First arrivals and peak occupancy date in Vaux’s Swifts advanced over time from 2008 to 2017, and the timing of first arrivals advance correlated with an increase in local wind gust speeds. In contrast, fall migration timing did not change over time from 2008 to 2016, but higher temperatures were associated with later fall migration (both first arrival and peak roost occupancy) and higher local wind speeds were associated with earlier fall migration (peak roost occupancy only). Like many other migratory birds, Vaux’s Swifts may be tracking earlier spring phenology, and may also be altering their migratory timing in response to local weather conditions, especially during fall migration. Our results indicate that swifts may be able to adjust their migration to a changing climate, at least in the short term.

Key words: Vaux’s Swift, *Chaetura vauxi*, citizen science, roost, migration, climate change, weather.

Introduction

The timing of bird migration evolved as a trade-off between maximizing reproductive output on the breeding grounds and minimizing mortality throughout each phase of the annual cycle (Nathan et al. 2008; Alerstam 2011). Arrival timing on the breeding grounds is a balance between arriving early enough to acquire a suitable mate or territory (Cristol 1995) and avoiding harsh environmental conditions during migration and at the breeding grounds (Brown and Brown 1998; Møller et al. 2008; Hurlbert and Liang 2012). Similarly, the timing of fall migration must balance conditions on the breeding grounds following the breeding season and future conditions that will be experienced on the winter grounds and en route throughout migration (Jenni and Kery 2003). With the rapid onset of global climate change (Cook et al. 2013), a major unknown is which species or populations will be able to migrate earlier and time their arrival to take advantage of the increased food availability with the advancement of spring conditions on the breeding grounds, or adjust their migration timing in response to changes in weather and resources experienced en route.

Climate change may affect migratory timing by altering weather patterns, advancing spring phenology, and (or) changing fall phenology in temperate North America (Schwartz et al. 2006). Changes to weather patterns are predicted to alter plant and insect phenology both during migration and on the breeding grounds, which in turn may alter the optimal timing of avian migration and breeding (Kelly et al. 2016). Events in spring have been rapidly advancing, with earlier plant leaf-out and flowering, and the emergence of insects occurring 2.8 days per decade earlier in the northern hemisphere (Parmesan 2007). In response, some migratory birds have been advancing their spring migration (Rubolini et al. 2004). Species across a broad range of avian taxa, such as the Broad-tailed Hummingbird (*Selasphorus platycercus*) (McKinney et al. 2012), White Stork (*Ciconia ciconia*) (Gordo and Sanz 2006), Eurasian Blackcap (*Sylvia atricapilla*) (Bearhop et al. 2005), and European Pied Flycatcher (*Ficedula hypoleuca*) (Coppack and Both 2002; Both et al. 2005), have significantly advanced their spring migration. Changes to fall migratory timing generally appear to be weaker and more variable across species, with short-distance migrants departing breeding grounds later and long-distance migrants either departing earlier or not changing departure time at all (Jenni and Kery 2003; Brisson-Curadeau et al. 2019). In a study across Northern Europe, 80% of the variability in fall migration timing was accounted for by weather on the breeding grounds and at stopover sites versus the julian date (Haest et al. 2019).

Vegetation conditions experienced en route can influence migration timing in both spring and fall (La Sorte and Graham 2021). For example, the migratory pathways used by Painted Buntings (*Passerina ciris*) are directly associated with primary productivity during fall migration (Bridge et al. 2015). Similarly, individual Barnacle Geese (*Branta leucopsis*) time their spring migration to a "green wave" of primary productivity and arrive at stopover sites when food resources peak (Si et al. 2015). Direct effects of weather conditions experienced en route, such as temperature and wind, can also alter migratory timing (Bozó et al. 2018). Studies have documented changes in the timing of both spring and fall migration in response to weather conditions, but the responses vary between species and even populations in terms of which weather variables are associated with migration and to what extent. For example, warmer temperatures are associated with earlier arrival on the breeding grounds in Ruby-throated Hummingbirds (*Archilochus colubris* (Linnaeus, 1758)) (Courter et al. 2013). In Yellow Warblers (*Setophaga petechia* (Linnaeus, 1766)) (Drake et al. 2014), strong westerly winds appear to slow migration and result in a later clutch initiation date, whereas in the Yellow-breasted Chat (*Icteria virens auricollis* (Deppe, 1830)) (Huang et al. 2017), westerly winds are linked to a decline in survival during migration and a later arrival date at the breeding grounds.

The challenge in studying large-scale changes in migratory timing lies in the accessibility of multiyear datasets that encompass broad geographic regions. Citizen science can collect data on a much greater spatial and temporal scale than can be obtained by individual scientists, and in some cases, may provide access to private lands that may otherwise be inaccessible (Dickinson et al. 2010). Well-known citizen science programs such as eBird have proven invaluable in examining relationships between weather and bird migration for many species over large spatial scales (Hurlbert and Liang 2012; Arab et al. 2016; Newson et al. 2016). For small migratory species that are challenging to track over large spatial areas, such as the Vaux's Swift (*Chaetura vauxi* (J.K. Townsend, 1839)), citizen-science-based approaches may be the most effective approach for examining patterns of migration.

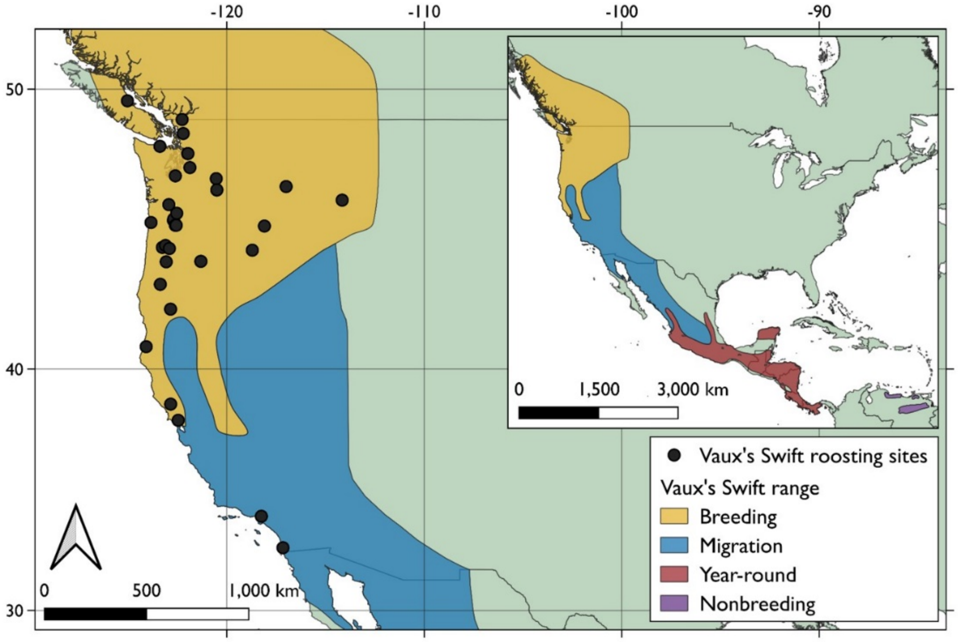
The Vaux's Swift is a long-distance aerial insectivorous bird with a declining population (Bull 2003). These birds' winter in Mexico and Central America, migrate up the west coast, flying during the day and roosting at night in chimneys or old-growth trees, and breed along the west coast from California (USA) to as far north as southern Yukon (Canada) (Figure 2.1) (Schwitters et al. 2020). During the breeding season, the swifts construct nests individually in semi-circles composed of twigs and saliva located in hollow trees or chimneys. Because these birds are aerial insectivores, changes to flying insect populations may be an important factor affecting their declines (Nebel et al. 2010; Nocera et al. 2012; Pomfret et al. 2012). In addition, changes to insect emergence timing or availability during spring and fall may influence their migration phenology. Vaux's Swifts roost with hundreds to thousands of other conspecifics in the cavities of hollowed-out old-growth trees and masonry chimneys during migration (Shuford and Gardali 2008; Schwitters et al. 2020), and the loss of old-growth trees may be another contributing factor to the declining population of the species (Bull 2003). Given Vaux's Swifts reliance on roosts, a species-specific survey that targets roosts may generate more comprehensive data than community-wide bird surveys, such as the Breeding Bird Survey, for monitoring Vaux's Swifts during migration. Vaux's Happening (https://www.vauxhappening.org/) has been in operation since 2008 and involves volunteer monitors counting Vaux's Swifts at known roosts (typically decommissioned chimneys) during spring and fall migration.

In this study, we made use for the first time of a citizen science project specific to the Vaux's Swift, Vaux's Happening, to examine trends in migration over time and the relationship between migratory timing and weather in this species. We predicted that we would detect an advance in spring migratory timing, likely due to the earlier onset of spring events in the northern hemisphere (Parmesan 2007). However, due to the pressure to migrate quickly and arrive early to the breeding grounds (Alerstam 2011; Karlsson et al. 2012; Nilsson et al. 2013), we predicted that Vaux's Swifts would be relatively unresponsive to weather conditions experienced en route to the breeding grounds. In contrast to spring migration, we predicted weaker, if any, changes in fall migratory timing across the study period (Brisson-Curadeau et al. 2019), as they were not trying to be the first on the wintering grounds to establish the best nest. However, we predicted that weather conditions experienced en route would be more strongly correlated with fall migratory timing due to comparatively reduced pressure to arrive early to the wintering grounds, which would result in birds adjusting their migratory timing based on local weather conditions.

Materials and methods

Migration data

Roost counts of Vaux's Swifts during spring and fall migration were collected by the citizen science organization Vaux's Happening, a coordinated effort involving 350 citizen scientists (https://www.vauxhappening.org/). Volunteer monitors visited sites in which Vaux's Swifts have historically roosted (Figure 2.1) and recorded the number of swifts roosting each day during northward and southward migration, with counts ranging from a few swifts to tens of thousands. To ensure that first arrival dates were recorded, monitors began visiting roosts several days before birds were predicted/expected to arrive at the site. Whenever possible, eBird was used by Vaux's Happening to track where swifts had already been sighted and project when they would arrive at a given roost. Once the first swifts were sighted, monitors began nightly roost checks (when possible). In good weather, the mean flock entry typically began 2 min after sunset. Monitors were instructed to arrive 30 min before sunset and to stay at the roost for 30 min after sunset if no swifts arrived. Experienced observers were paired with new observers for their first-time monitoring roosts. Only swifts entering roosts were counted. When large numbers of swifts were observed, monitors either counted by tens using a clicker or counts were estimated at a rate of 10 swifts/s entering the roost. This rate was calculated from two live camera streams at the Monroe Wagner, Washington, USA, roost. At this site, counts from the camera were also used during poor weather and low visibility, by estimating the number of swifts exiting the roost. In this case, the count of swifts exiting the roost was estimated by multiplying the length of video time (in seconds) during which swifts were exiting by 8 (as above, slow- motion video was used to estimate an exit rate of 8 birds/s). When camera counts and counts by monitors on site were compared, the results were similar. At the end of the season, data were submitted to the Vaux's Happening database.



Vaux's Swift range data: BirdLife International and Handbook of the Birds of the World (2019) Bird species distribution maps of the world. Version 2019.1. Available at http://datazone.birdlife.org/species/requestdis.

Figure 2.1. Distribution of Vaux's Swifts (*Chaetura vauxi*) roosts used in an analysis of spring and fall migration timing from the Citizen Science project "Vaux's Happening in North America", as well as breeding, migration, year-round, and nonbreeding ranges. WGS 84 and EPSG 3857 were used in creating the map. Range data from BirdLife International and Handbook of Birds of the World (2019). Colour version online.

Data cleaning and segmentation

We analyzed spring migration data ranging from 2008 to 2017 and fall migration data from 2008 to 2016. From these data, we extracted information on first arrival date (the date on which the first swift arrived at the roost) and peak roost occupancy (the date on which the maximum number of swifts were observed at that roost during the season). First arrival dates may represent an individual's response to environmental conditions and not the population as a whole, and the reliability of the data is sensitive to population size and observer effort (Miller-Rushing et al. 2008); therefore, we also included peak roost occupancy as an indication of a population-wide respond to environmental conditions. Spring and fall seasons were delineated each year based on known species life history (Schwitters et al. 2020) and through examining the distribution of count data at northern roosts, which indicated a strong bimodal distribution with a gap occurring in mid-July (for example of data distribution see Appendix Figure 1),1 although exact dates for spring and fall migration varied from year to year. Furthermore, the start of fall migration was confirmed each year by examining camera footage from the Monroe Wagner roost.

We restricted our analysis to roosts that had at least five observations during a season in at least 3 years, which resulted in 155 first arrival and peak roost occupancy observations in the spring, at 26 different roosts, and 148 first arrival and peak roost occupancy observations in the fall, at 28 different roosts. Because data collection was variable across sites (e.g., some sites are remote and difficult to access, whereas others, such as Chapman Elementary in Portland, Oregon, USA, attract dozens of spectators nightly during migration), we decided on an approach that would allow us to look at change over time (at least 3 years of observations) and assess peak roost occupancy (at least five observations within a season), while capturing a broad array of roosts with varying numbers of swifts rather than limit our data to only accessible sites with large numbers of swifts. Though this approach may add a degree of uncertainty to our analysis, it is unlikely to introduce systematic bias (i.e., systematically recording earlier or later arrival dates). Overall, during spring migration, monitors performed, on average, 467 counts per year, with a minimum of 224 counts and a maximum of 702 counts. During fall migration, monitors performed, on average, 367 counts per year, with a minimum of 178 counts and a maximum of 506 counts.

Weather data

We obtained data on weather conditions at both a local and a regional scale. For local weather, mean temperature (°C), precipitation (mm), wind speed (m/s), and wind gust speed (m/s) were calculated for the 3 weeks prior to the mean peak roost occupancy date at each roost. Weather data were retrieved from Weather Underground (https://www.wunderground.com/) and recorded from the nearest airport to the roost.

Weather Underground recorded historical weather data from local airports taken in real time at 1, 3, or 6 h intervals, which varies depending on each weather station. We did not include historical weather data from airports that were greater than 100 km away from the roost because it may not have been an accurate representation of the weather experienced at the roost. Unfortunately, wind direction was not available from each airport; therefore, we were not able to include wind direction at a local scale. However, we calculated wind at the regional scale (en route to the roost) to test the influence of southerly (Vwind) and westerly (Uwind) wind speed (m/s) from a larger area on first arrival and peak roost occupancy during spring and fall migration, following Drake et al. (2014). Using the RNCEP program (Kemp et al. 2012), regional wind data were downloaded from the National Center for Environmental Prediction (NCEP) and were averaged over 2.5° latitude by longitude cells across North America, with a temporal resolution of 6 h. We chose to use a 3-week window to reflect mean conditions experienced prior to peak roost occupancy for several reasons. For Vaux's Swifts, we do not have data on the migration speed of individuals and some individuals may spend several days or longer at individual roosts along the migratory path. In addition, our goal was to capture the conditions that the birds would experience as they migrated towards the roost, and as such, we chose to average over a longer period of time rather than obtain a simple snapshot that is subject to high variability in conditions. Finally, because Vaux's Swifts are aerial insectivores, conditions experienced in the 3 weeks preceding arrival to the roost may affect insect abundance and availability — factors that are key to fueling during migration. To capture wind conditions experienced en route during spring migration, spring NCEP wind data were averaged over an area of 15° of latitude and 10° of longitude south of each roost (Appendix Figure 2).1 To capture wind conditions experienced en route during fall migration, NCEP wind data were averaged over an area of 10° of latitude and 10° of longitude north of each roost (Appendix Figure. A2).1 For spring migration, 15° of latitude ensured that we did not collect wind data from the wintering grounds. For fall migration, 10° of latitude ensured that we did not exceed the northern bound of the breeding range. Thus, weather data included the following variables: local wind, wind gust, precipitation, temperature, and regional southerly (Vwind) and westerly (Uwind) wind.

Statistical analysis

To examine potential changes over time and associations between weather and timing of first arrival and peak roost occupancy, we constructed a series of linear mixed models (LMMs). Models were constructed so that each variable was tested on its own and with various combinations of other variables. The full model for either spring or fall included local wind (Wind; m/s), local wind gust (WindGust; m/s), local precipitation (Precip; mm), local temperature (Temp; °C), regional southerly wind (Vwind; m/s), regional westerly wind (Uwind; m/s), latitude (Lat), and year (Year). The models that we evaluated included various combinations of the above variables to evaluate all combinations. This resulted in a total of 28 models for each season, plus a null model with the intercept only. Roost was considered a random effect in each model.

All of the considered effects were additive and did not include interactive effects. We tested for multicollinearity among fixed effects, but there were no strong correlations between variables ($r < 0.56$), and variance inflation factors of fixed effects were all <2. We used Akaike's information criterion corrected for small sample size (AICc) to rank the models, and we present model-averaged 95% confidence intervals (95% CI) for models within 4 DAICc of the top model (Burnham and Anderson 2002). The statistical software R version 4.0.2 (R Core Team 2021) was used to analyze the data, including the packages AICcmodavg (Mazerolle 2020), lme4 (Bates et al. 2015), MuMIn (Barton 2009), and MASS (Venables and Ripley 2002).

Results

Spring migration

First arrival

The top model explaining variation in first arrival during spring migration included effects of year, local wind gust, and latitude (Table 2.1). Other models within 4 DAICc units included the effects of local wind, regional southerly wind, and precipitation in addition to those effects found in the top model. However, only the 95% CI for the effects of year, wind gust, and latitude did not overlap zero (Table 2.2). Swifts arrived 0.9 days earlier per year and 0.37 days earlier per unit increase (m/s) in wind gust. Swifts arrived 1.33 days later per 1° increase in latitude.

Table 2.1. Summary of top ranked models (<4 AICc from top-ranked model) using Akaike Information Criterion corrected for small sample size (AICc), explaining variation in migratory timing of Vaux's Swifts (*Chaetura vauxi*) during spring migration, 2008-2017. Roost is included in all models as a random effect. The AICc of the model, difference between the model and the top model's AICc (delta AICc), and the weight of each model (AICcWt) are shown. Vwind = regional southerly wind (m/s), Uwind = regional westerly wind (m/s), Precip = local precipitation (mm), Temp = local temperature (°C), Lat = latitude, Wind = local wind (m/s), WindGust = local wind gust (m/s).

	AICc	Delta AICc	AICcWt
First Arrival			
Year + WindGust + Lat	852.91	0	0.33
Year + Wind + WindGust + Lat	854.03	1.12	0.19
Year + Precip + WindGust + Lat	855.17	2.26	0.11
Year + Wind + WindGust + Vwind + Lat	855.84	2.93	0.08
Year + Precip + Wind + WindGust + Lat	856.32	3.41	0.06
Peak Roost Occupancy			
Year + Precip + Temp + Lat	863.06	0	0.1
Year + Precip + Lat	863.45	0.39	0.08
Year + Lat	863.45	0.4	0.08
Year + Precip + Temp + WindGust + Lat	863.61	0.56	0.08
Lat	863.79	0.74	0.07
Year + WindGust + Lat	864.03	0.98	0.06
Year + Precip + Temp + Uwind + Lat	864.06	1.01	0.06

Peak roost occupancy

The top model explaining variation in peak roost occupancy during spring migration included effects of year, precipitation, temperature, and latitude (Table 2.1). Other models within 4 DAICc units included the effects local wind and wind gust, and regional westerly and southerly wind in addition to those effects found in the top model. The 95% CI for the effects of year and latitude did not overlap zero (Table 2.2) and indicated that for their peak roost occupancy swifts arrived 0.77 days earlier per year and 1.07 days later per 1° increase in latitude.

Table 2.2. Model-averaged parameter estimates and 95% confidence intervals for variables included in the top-ranked models (<4 delta AICc units of best model) explaining variation in Vaux's Swift (*Chaetura vauxi*) first arrival and peak roost occupancy for both spring and fall migration. Bold values represent confidence intervals that do not overlap zero. Vwind = regional southerly wind (m/s), Uwind = regional westerly wind (m/s), Precip = local precipitation (mm), Temp = local temperature (°C), Lat = latitude, Wind = local wind (m/s), WindGust = local wind gust (m/s).

	Spring first arrival	Spring, peak roost occupancy	Fall, first arrival	Fall, peak roost occupancy
Year	**-0.90 (-1.58,-0.23)**	**-0.77 (-1.52, -0.01)**	-0.76 (-1.87, 0.34)	0.068 (-0.74, 0.88)
Precip	0.043 (-1.14, 1.23)	-0.85 (-2.12, 0.42)	0.62 (-1.92, 3.16)	1.5 (-0.41, 3.41)
Temp		0.61 (-0.29, 1.5)	**1.7 (0.58, 2.82)**	**0.88 (0.09, 1.67)**
Uwind		-1.85 (-4.56, 0.87)	1.02 (-1.8, 3.83)	-1.83 (-3.75, 0.086)
Vwind	-0.75 (-2.93, 1.43)	-0.36 (-2.59, 1.88)	-0.95 (-3.16, 1.26)	0.25 (-1.43, 1.93)
Wind	0.40 (-0.30, 1.10)	-0.29 (-0.98, 0.39)	**-1.33 (-2.62, -0.04)**	**-1.23 (-2.11, -0.36)**
WindGust	-0.37 (-0.64, -0.11)	-0.14 (-0.4, 0.13)	-0.085 (-0.54, 0.38)	-0.029 (-0.37, 0.31)
Lat	**1.33 (0.73, 1.94)**	**1.07 (0.45, 1.70)**	**-1.07 (-2.09, -0.05)**	-0.87 (-1.75, 0.016)

Fall migration

First arrival

The top model explaining variation in first arrival during fall migration included effects of temperature, regional southerly and westerly wind, and local wind (Table 2.3). Other models within 4 DAICc units included the effects of year, temperature, precipitation, and local wind gust in addition to those effects found in the top model. The 95% CI for the effects of temperature, local wind, and latitude did not overlap zero (Table 2.2) and indicated that swifts arrived 1.7 days later per 1° increase in temperature, 1.33 days earlier per unit increase (m/s) in local wind speed, and 1.07 days earlier per 1° increase in latitude.

Table 2.3. Summary of top ranked models using Akaike Information Criterion corrected for small sample size (AICc), explaining variation in migratory timing of Vaux's Swifts (*Chaetura vauxi*) during fall migration, 2008-2016. Roost is included in all models as a random effect.

The AICc of the model, difference between the model and the top model's AICc (delta AICc), and the weight of each model (AICcWt) are shown. Vwind = southerly wind (m/s), Uwind = Westerly wind (m/s), Precip = precipitation (mm), Temp = temperature (°C), Lat = latitude, Wind = local wind (m/s), WindGust = local wind gust (m/s).

	AICc	Delta AICc	AICcWt
First Arrival			
Temp + Uwind + Vwind + Wind	683.15	0	0.13
Year + Precip + Lat	683.75	0.6	0.1
Temp	684.09	0.94	0.08
Year + Precip + Temp + Uwind + Lat	684.47	1.32	0.07
Temp + Uwind + Vwind + Wind	685.53	2.38	0.04
Temp + Uwind + Vwind + Wind + WindGust + Lat	685.56	2.41	0.04
Precip + Temp + Uwind + Vwind + Wind	685.57	2.42	0.04
Peak Roost Occupancy			
Temp + Uwind + Vwind + Wind	626.01	0	0.2
Precip + Temp + Uwind + Vwind + Wind	626.77	0.75	0.14
Year + Precip + Temp + Wind + WindGust + Lat	628.33	2.31	0.06
Temp + Uwind + Vwind + Wind + WindGust	628.36	2.35	0.06
Year + Precip + Temp + Uwind + Vwind + Wind	629.24	3.22	0.04
Precip + Temp + Uwind + Vwind + Wind + WindGust	629.24	3.23	0.04
Precip + Temp + Uwind + Vwind + Wind + WindGust + Lat	629.56	3.54	0.03

Peak roost occupancy

The top model explaining variation in peak roost occupancy during fall migration included effects of temperature, regional westerly and southerly wind, and local wind (Table 2.3). Other models within 4 DAICc units included the effects of year, temperature, precipitation, and local wind gust in addition to those effects found in the top model. The 95% CI for the effects of temperature and local wind did not overlap zero (Table 2.2) and indicated that swifts arrived 0.88 days later per 1° increase in temperature and 1.23 days earlier per unit increase (m/s) in local wind speed. It is worth noting that although 95% CI for latitude and westerly wind did not overlap zero, they were close to doing so (<0.1 overlap of zero). Swifts tended to arrive earlier at higher latitudes and with stronger local westerly winds.

Discussion

In this study, we explored a citizen science dataset spanning 10 years to examine potential changes in migration over time and associations between weather (at both a local and a regional scale) and the timing of arrival at migratory roosts in Vaux's Swifts. We found support for our prediction that Vaux's Swift arrival date at migratory roosts advanced significantly during spring migration from 2008 to 2017, but it has not changed during fall migration (from 2008 to 2016). Though there was little association between weather conditions experienced en route and migratory timing for spring migration (only wind gust had was significant, and only for first arrivals), fall migration timing was associated with both temperature and local wind conditions experienced en route, for both first arrival and peak roost occupancy timing. Even over a relatively short (10 year) time frame, Vaux's Swifts arrived at migratory roosts earlier in spring (both first arrival and peak roost occupancy), which could be indicative of a response to the advancement of spring phenology. This rapid change is not surprising because many species across a broad range of avian taxa have exhibited significant advances in spring migratory timing, likely in response to changing spring phenology (Coppack and Both 2002; Both et al. 2005; Gordo and Sanz 2006; Mckinney et al. 2012).

Over a 10-year period, we found that Vaux's Swifts migrated earlier in spring, as evidenced by advancement in both peak roost occupancy and first arrival dates at roosts. Vaux's Swifts may have responded also to local wind gust conditions, as they showed earlier first arrivals when there were stronger wind gusts, potentially because favourable tailwinds help to accelerate migration (Haest et al. 2019). The lack of influence on timing from regional v winds that could represent tailwinds, is possibly due to the window used for regional wind data not accurately representing the migration window of Vaux's swifts. However, first arrival dates can be biased since they are influenced by individual behaviour, population size, and sampling effort, and thus may not represent population processes as a whole (Miller-Rushing et al. 2008). Furthermore, as predicted, neither local temperature nor precipitation were strong indicators of first arrival or peak roost occupancy timing during spring migration. Together, these results are consistent with findings in Chimney Swifts (*Chaetura pelagica* (Linnaeus, 1758)) and other long-distance migrants that have shown no response to weather experienced during migration, and specifically, no response to changes in temperature (Zaifman et al. 2017).

We found stronger associations between migratory timing and fall weather conditions experienced en route, which could suggest that Vaux's Swifts are altering migratory timing and time spent at migratory roosts to optimize survival during southward migration (Jenni and Kery 2003). Unlike spring arrival, associations between weather and migratory timing were observed in both first arrivals and peak roost occupancy, suggesting that they may have been collective individual level responses. Earlier fall migration dates were associated with lower temperatures, potentially due to cold snaps resulting in reduced insect availability (Jenni and Kery 2003). Higher local wind speeds measured at the closest weather stations to roosts were also associated with earlier arrivals at migratory roosts. As above, local wind could affect migratory timing through favourable tailwinds (Haest et al. 2019), although we were unable to measure the direction of local winds. In addition, wind speed could affect stopover by decreasing flying insect availability or capture efficiency (Møller 2013). Vaux's Swift peak roost occupancy also tended to be earlier with increased regional westerly winds, although the 95% CI for this effect overlapped zero and so any presumed effect is likely weak. Local wind seemed to have a stronger association with migration timing than regional wind patterns, which could be due to the large-scale effects being less representative of what individual birds experience during migration compared with local weather. However, Drake et al. (2014) found that high regional westerly winds at stopover sites were associated with lower survival and later arrival to the breeding grounds in Yellow Warblers, potentially due to an association between westerly winds and extreme weather events in Western Canada. Thus, the effects of weather events on migratory timing may be species- and season-specific and may be influenced by the migration ecology of the species (e.g., Vaux's Swifts propensity to use migratory roosts may help buffer against the effects of extreme weather events).

Many studies of migratory timing in response to climate and weather have focused on spring migration, while fewer have focused on fall migration, likely because the complexity of drivers of fall migration and the prolonged nature of fall migration make it challenging to study (Gallinat et al. 2015). Yet, understanding responses to climate change will require consideration of avian phenology across the full annual cycle. Citizen science programs such as eBird have become increasingly popular for studying avian migration and the effects of climate change, as they allow for the examination of migration timing over broad geographic regions and long time periods (Arab et al. 2016; La Sorte and Graham 2021). Programs such as Vaux's Happening that use a targeted approach in terms of counting a specific species at designated locations annually likely allow for a greater and more consistent detection of individuals and population-level patterns for species such as Vaux's Swifts that migrate to specific known locations at high concentrations. However, since this program focuses on known historical roosts, most of which are artificial (i.e., decommissioned chimneys), our results may not extend to other Vaux's Swift populations that may be using unknown roosts along the migratory route, such as old-growth trees in nonurban areas. Furthermore, shifts in use between known and unknown roosts could result in perceived changes in migration phenology when the population as a whole may not be changing. Future studies may benefit from combining Vaux's Happening and eBird data to overcome some of these issues.

We did not examine associations between weather conditions experienced during the breeding or wintering period and migration timing, due to uncertainty in terms of where individual swifts had bred or wintered. Migratory connectivity and the exact wintering locations of Vaux's Swifts remain poorly studied (Reudink et al. 2015; Schwitters et al. 2020) and would benefit from additional research using individual tracking techniques such as light-level geolocators, banding, or stable isotope analysis. Individual tracking would have had additional benefits in our study: specifically, without being able to identify individual swifts, it is possible that some degree of temporal and spatial autocorrelation may have occurred which we were not able to control for if the same swifts were using multiple roosts across the broad spatial scales of our study area. Follow-up studies should also examine the role of carry-over effects from wintering or breeding ground conditions on migratory timing.

Many long-distance migrants initiate spring migration primarily based on endogenous rhythms rather than response to environmental conditions (Both and Visser 2001), a characteristic that may make them especially vulnerable to climate change and shifting spring phenology. Our results suggest that Vaux's Swifts may be adjusting aspects of their migration based on external factors in the fall, which may allow them to better adjust to rapidly changing spring phenology. In addition, as aerial insectivores, swifts are vulnerable to changes in insect populations and human use of pesticides (Nocera et al. 2012; Pomfret et al. 2012; Nebel et al. 2010). Finally, Vaux's Swifts rely on old-growth trees and chimneys for roosting or nesting, both of which are declining due to continued deforestation and changing construction techniques as well as the decommissioning of old chimneys (Bull 2003).

In conclusion, we documented a rapid advance in Vaux's Swifts spring migration timing and stronger associations between migratory timing and weather experienced en route during fall migration compared with spring migration. Questions remain as to the causal factors resulting in advanced spring migration, and whether the changes are a result of behavioural plasticity, or if they are a long-term adaptation that will be able to keep up with the changing climate and prevent further population decline (Møller et al. 2008). The lack of relationship between migratory timing and spring weather conditions experienced en route could potentially be problematic since climate change could result in more extreme weather conditions. An inability to adjust phenology to extreme weather events could result in a delay in spring arrival and survivorship during migration, much like the cold spell that resulted in low rates of return to the breeding grounds in the long-distance migrant Semicollared Flycatchers (*Ficedula semitorquata* (Homeyer, 1885) (Briedis et al. 2017). In contrast, we found strong relationships between migratory timing and weather conditions experienced en route during fall migration, which could allow Vaux's Swifts to track future changes in local weather patterns. With inclusion of the effect of weather variables on wintering and breeding grounds, we may learn more about what causes swifts to leave these wintering or breeding grounds, and not just what pushes or pulls them among roosts.

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Chapter 3: eBird data reveal shifts in breeding distribution, migration timing, and migration routes of two North American swift species

Abstract

Climate change has resulted in changes in ecosystems and weather patterns due to earlier onset of spring weather, later onset of fall weather and more extreme weather patterns. With the changing environment migratory birds may experience challenges adjusting to the new conditions. We asked if Vaux's Swifts (*Chaetura vauxi*) and Chimney Swifts (*Chaetura pelagica*) were able to change their breeding range over time. Also, we test changes to migration routes, timing of migration, or speed of spring and fall migration over time. We utilized community science data from eBird that spanned from 2009-2018 to test changes in migration. Our results show that Vaux's Swifts shifted their breeding centroid south-east and Chimney Swifts shifted their breeding centroid west. There was also a shift in Vaux's Swifts migration route to the east, almost proportionate in magnitude to its eastern shift in breeding range. Vaux's Swifts displayed an advance in their start of spring migration, and Chimney Swifts exhibited a delay in the start of fall migration. These responses may be due to earlier onset of spring and a possible delay of colder temperatures associated with the onset of fall conditions. My results indicated that both species are breeding further away from the coastline and more towards central North America, potentially due to increased human population densities along the coast. These results indicate that the Vaux's and Chimney Swifts display some behavioural plasticity in response to the changing environmental, and weather patterns. What remains unclear is if this behavioural plasticity will be enough to prevent further population loss in the two species of swift, in the face of climate change.

Introduction

For migratory birds, migration timing and routes have evolved through a series of trade-offs, balancing a suite of selective pressures that favour early arrival to the breeding grounds to maximize reproductive success (Cristol 1995), while synchronizing food availability to peak nestling resource demands (Häfker et al., 2017), avoiding predation during migration (Häfker r et al., 2017), and avoiding severe weather conditions during migration and on the breeding grounds (Reid et al., 2018). Arriving too early on the breeding grounds can result in encountering inhospitable conditions that may lower survival rates (Newton, 2007), and arriving too late can result in a poorer territory, missed peak resource abundance as well as time constraints on rearing young (Gienapp and Bregnballe, 2012). The timing of migration is dictated by both internal endogenous cues (Berthold, 1996; Conklin et. Al 2010: Akesson and Helm 2020), and external environmental cues (Akesson and Helm 2020; Both 2010). What remains unclear, however, is how migratory birds will respond to a rapidly changing climate. The earth has already warmed by 1.0 °C from the preindustrial era to 2020, with a projected total increase of 1.5 °C estimated to occur between the years of 2030-2052 (Fawzy et al. 2020). Changes in global temperatures will increase the frequency and severity of droughts, floods, and sea level rise (Malhi et al. 2020), and will alter plant and insect phenology (Ahmed 2020). With a change in temperature, we can expect a change in weather patterns, advancement of spring phenology, and changes to fall phenology (Schwartz et al., 2006). As a result, the timing of resource availability during each phase of the annual cycle may be altered (Parmesan, 2007; Kelly et al., 2016), as will the weather conditions experienced by birds during migration. The rapid change to the tightly co-evolved relationship between migration timing and resource availability during migration may result in temporal mismatches, resulting in reduced survival and reproduction.

Different species of birds will respond to environmental cues with different changes to migratory routes, timing, and speed (Knudsen et al., 2011) based on their different life history traits. Some species of birds appear to be altering the timing of migration in response to changes in both temperature (Hurlbert and Liang, 2012; Bozó et al., 2018; Prytula et al., 2021), wind (Bozó et al., 2018; Prytula et al., 2021), and precipitation (Studds and Mara 2011). In response to differences in environmental cues as well as fueling requirements, birds may change migratory routes (Supp et al. 2015), the speed in which they migrate, daily flight duration, and the amount of time spent at stopover sites (Nilsson et al. 2013). Climate change may also result in changes to breeding distributions, as northern latitudes and higher elevations could become more favourable for breeding (Hitch and Leberg 2007; Campos-Cerqueira et al. 2017). Due to endogenous rhythms constraining changes in migration timing, some species may respond to environmental cues by choosing different migratory routes but maintaining migratory timing (Alerstam, Hake and Kjellen, 2006; Vardanis et al., 2011). La Sorte et al. (2013) found migrants in the western flyway of North America chose migratory routes with higher primary production and greener conditions in the spring and less productive and potentially more direct routes in the fall, while migrants in the eastern flyway of North America chose areas with maximum greenness for both spring and fall.

Changes in migratory timing are not consistent across different species of migratory birds. For example, while the Black-throated Blue Warbler (*Setophaga caerulescens*) has been migrating 1.1 days earlier per decade over the past 50 years (Covino et al. 2020), other species are not changing migration timing in response to environmental cues, possibly due to a lack of behavioural plasticity (Both et al., 2006). The ability to modify migratory timing can have important consequences, as Møller et al. (2008) showed that European bird species that did not advance their migration timing were more likely to be in decline (Møller, Rubolini and Lehikoinen, 2008). Some studies have found that long-distance migrants may have greater difficulty in adjusting their migration timing compared to short-distance migrants, which could potentially leave them vulnerable to climate change (Knudsen et al., 2011; Calvert et al., 2012; Fraser et al., 2013; Usui et al., 2017; Lehikoinen et al., 2019). However, results are inconsistent as some long-distance migrants have advanced their spring arrival more than short distance migrants (Both et al., 2005; Jonzén et al., 2006; Knudsen et al., 2011). One reason long-distance migrants may have difficulty altering their migratory timing in response to climate change may be because they are less able to detect changes in the earlier onset of spring from their wintering grounds (Visser et al. 2009), and instead rely on endogenous rhythms to time migration (Both and Visser, 2001). Long-distance migrants may also be constrained in their ability to change their speed of migration and/or departure date from the wintering grounds, resulting in a mismatch between arrival on the breeding grounds and optimal breeding conditions (Fraser et al., 2013). Finally, seasonality is likely to play a role in migratory birds' responses to climate change. Birds are generally under greater time constraints to arrive early in spring to establish high quality territories and find the best mates (Cristol, 1995), and thus may be more likely to advance their spring migration than fall migration (Prytula et al. 2021). During fall migration, they may be more responsive to weather variables experienced en route to the wintering grounds (La Sorte et al., 2013; Prytula et al. 2021).

In the past, studies of migratory timing and migration routes often utilized bird banding, but data was dependent on recaptures, resulting in limited sample sizes and biases due to variation in recovery effort across the range (Thorup and Conn 2009). More recently, tracking devices such as satellite trackers, GPS loggers, and light-level geolocators have been used to track individual birds, but such studies can be limited by cost, sample size, weight of devices, and coverage of different populations (Bridge et al. 2011; Stanley et al. 2012). However, large-scale community science databases provide an unparalleled resource for detecting changes in migration and distribution over broad spatial and temporal scales (Heim et al. 2020). These databases allow for the study of species across their entire range over multiple years, sometimes decades, and in locations not always accessible to scientists (Dickinson et al., 2010). Community science takes many different forms and may vary from database to database on whether or not they have structured objectives, planned data analysis, and rigorous protocols (Callaghan et al. 2019b; Kelling et al. 2019). In this study, we make use of eBird, which is considered a semi-structured database (Kelling et al. 2019), to analyze changes to the migration and distribution of two long-distance migratory swift species in North America, the Vaux's Swift (*Chaetura vauxi*) and the Chimney Swift (*Chaetura pelagica*).

Vaux's Swifts and Chimney Swifts are both long-distance migratory aerial insectivores that migrate in flocks of hundreds to thousands, using abandoned chimneys and hollow old-growth trees as migratory roosts (Steeves et al., 2020; Schwitters et al., 2021). Chimney Swifts overwinter in South America, migrate through eastern Central America and breed from Texas to as far north as south-eastern Canada (Steeves et al., 2020). Vaux's Swifts are a slightly smaller counterpart to the Chimney Swift; they overwinter in Mexico and Central America, migrate through the west coast of North America, and breed from California to the Yukon (Schwitters et al., 2021). Both swift species have declining populations that are likely caused by multiple drivers: they are long distance migrants; have declining food abundance due to a decline in aerial insects; and have specific roosting needs that could be subject to habitat loss (Spiller and Dettmers, 2019).

In our study we made use of data from eBird to analyze trends in breeding season latitude and longitude, as well as spring and fall migration (referred to as 'migratory seasons') routes, timing, and speed over a 10-year period for Vaux's Swifts and Chimney Swifts. We predicted that both species' breeding centroids would shift northward over time, as conditions at higher latitudes are becoming more temperate in the northern hemisphere (Hitch and LeBerg, 2007). We had no *a priori* expectation of changes to migratory routes; rather, we predicted that both species would continue to utilize the same migratory routes. We predicted that both species would begin spring migration earlier over time (Prytula et al., 2021). Trends in fall migration are often inconsistent and unpredictable (Jenni and Kery, 2003; Van Buskirk et al., 2009), and it has previously been found that Vaux's swifts have not changed their fall migration timing in recent years (Prytula et al. 2021). Thus, we had no *a priori* expectation that either species would shift their fall migration timing or speed. Similarly, we had no *a priori* expectation that either species would increase their speed over time due to the already high energetic requirements of long-distance migration (Nebel et al. 2010).

Methods

All statistical analyses were performed in R (v4.0.2 R Core Team 2022). Presence data for Vaux's Swifts and Chimney Swifts from 2009-2018 was gathered from the community science database eBird (Available online www.eBird.org). The eBird database includes information on whether observations were incidental or collected while travelling or stationary. Observation effort is also recorded, including the length of observation, distance travelled while observing, and how many observers were included. Finally, if all birds observed were identified and recorded, the checklist is considered “complete”, which allows for the “zero-fill” of data for locations where species were not present. We utilized the *auk* package (v0.4.0, Strimas-Mackey et al., 2018) to filter the data to include checklists that met the eBird criteria of best practices. Specifically, we included lists that were “Travelling” or “Stationary” and excluded “Incidental” and “Historical” data. We also only included lists where observations lasted for a duration between 0-5 hours, observers travelled a distance between 0-5 kilometers, and records were considered “complete” (Strimas-Mackey et al., 2020). We subsequently added counts of 0 to the checklists that did not include Vaux’s or Chimney Swift observations to “zero-fill” the data.

Occurrence centroid- hex grids

We used the methodology developed by Supp et al. (2015) and subsequently utilized by Sonnleitner et al. (In Press), to compile presence data for Vaux’s and Chimney Swifts from 2009-2018 and generate equal-area icosahedron hex grids (23,323 km^2) based on an icosahedron map overlaying North America using the *dggridR* package (v2.0.3; Barnes, 2018). We summarized daily presence for each hex cell as the total number of binned checklists with a swift present in the hex cell divided by total number of checklists for each date (Figure 3.1). The weighted daily mean location was then calculated using the central longitude and latitude of each cell to measure spatial variation in presence data over time. To track migration on an annual basis, we used Generalized Additive Models (GAM; package *mgcv*; Wood 2011) to model these mean locations for each species and produce smoothed paths of migration (Figure 3.1). From these smooth paths we extracted population-level occurrence centroids with latitude and longitude for each species for each day of the year.

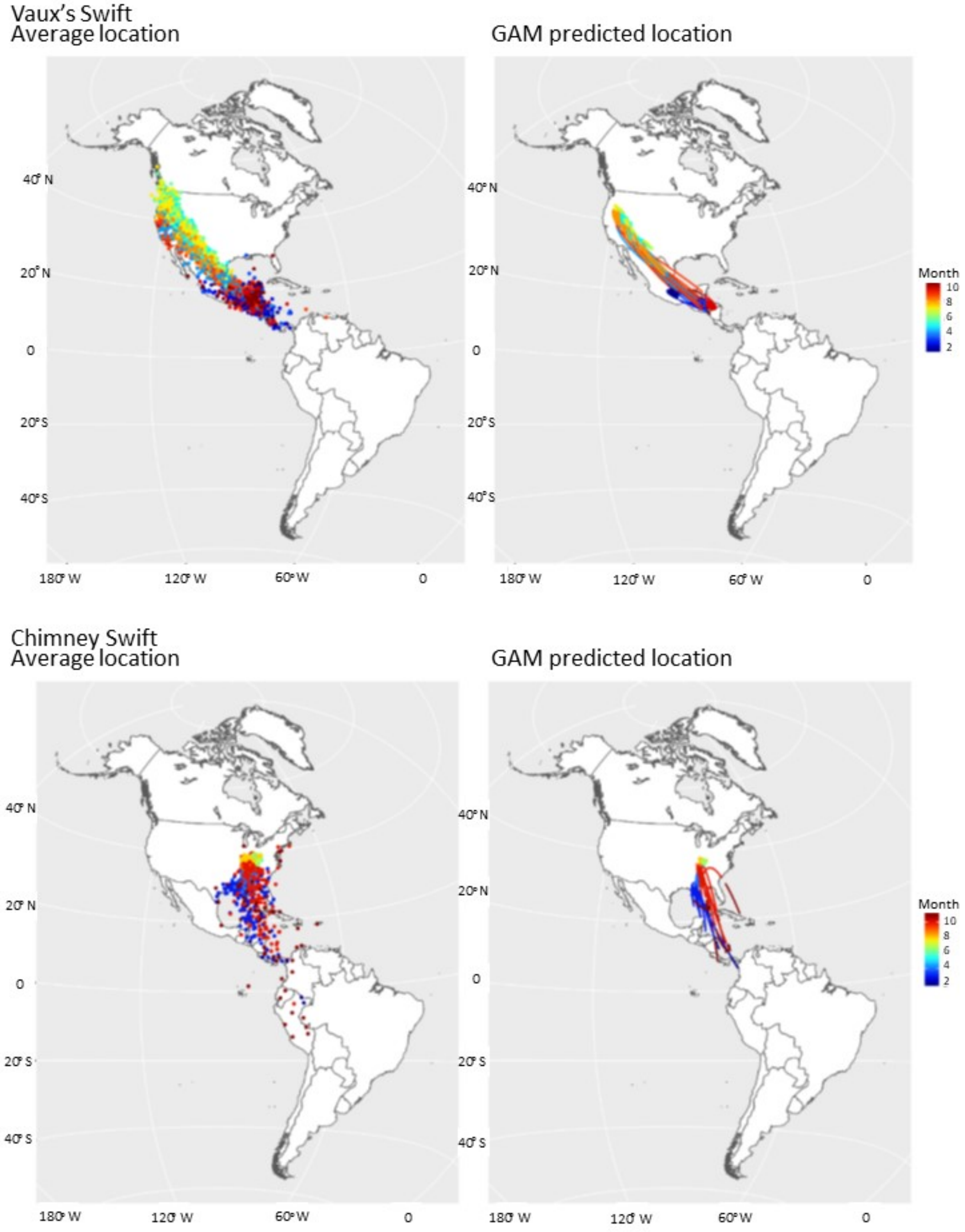

Figure 3.1. Mean location of swift populations over 10 years (2009-2018) for Vaux's Swifts and Chimney Swifts through spring and fall migration and on the breeding grounds. Left panel: points represent the daily mean weighted population centroid, coloured by month. Right panel: lines represent the migration path predicted by population centroids, coloured by month.

Breeding/migration distributions

For the breeding season, the maximum latitude and median longitude were calculated for the population centroids between June 23- August 12 (ordinal dates 175-225) for each species each year. For spring and fall migrations, the median longitude was calculated during each migratory season (between the start and end of each migration as calculated in Migration timing, below). Median longitudinal values were once again used to minimize the effects of potential outliers, or edge cases when the population was near breeding or non-breeding grounds.

Migration timing

We defined seasons of the annual cycle based upon whether the predicted population-level centroid was stable at latitude thresholds, and thus the latitude of the population centroid was no longer changing. At its minimum latitude, the species was considered to be on its wintering grounds, and at its maximum latitude, the species was considered to be on its breeding grounds. At these latitudinal thresholds migration was not occurring. We utilized the methodology of Supp et al. (2015) to generate estimates of migration timing regarding when the birds leave their wintering grounds and arrive back at their wintering grounds. We first established a latitudinal threshold by using the minimum latitude of upper limit of the 99% Confidence band of predicted daily location for: start of spring migration Jan 1- March 20 (ordinal date 1-80) and; end of fall migration Oct 11- Dec 10 (ordinal date 285-345). For migration to or from the breeding grounds we used the maximum latitude of the lower limit of the 99% confidence interval to estimate end of spring migration within the period March 20- June 23 (ordinal 80-175) and start of fall migration within the period Aug 12- Oct 11 (Ordinal 225-285).

The dates on which the population centroids crossed these thresholds gave us coarse estimates of migration start and end dates for each season, for each species per year. Following this, we used segmented regression to calculate more precise break points in latitude and ordinal dates which more accurately reflected the start and end of migration for spring and fall (*segmented* package v1.0-0, Vito and Muggeo 2008; Supp et al., 2015). Because the data for Chimney Swifts overwintering in South America was too sparse to accurately generate GAMs, we were unable to generate values for the start of spring migration and end of fall migration for this species.

Migration speed

Maximum population-level daily speed of migration was calculated as the median date of the five fastest days (km/day) of population centroid movements for each season (Supp et al., 2015). We chose the median date to minimize the effect of potential outliers. We searched for the fastest spring migration dates between January 1st-June 23rd (ordinal dates 1-175) and the fastest fall migration dates from August 12th-December 5th (ordinal dates 225-340). To ensure the speeds at the start and end of migration were not excluded, date ranges extended into breeding and overwintering seasons. Because there was little movement during the non-breeding period, we did not expect that this would alter our calculations of maximum migration speed.

Examining changes in breeding/migration distributions, migration timing, and migration speed over time

We constructed a series of linear models to examine changes over time in maximum breeding latitude and median breeding longitude, median migratory longitude for both migratory seasons, the start and end of migration for both seasons, and maximum daily migration speed for both migration seasons. In each model, we included both species and year as main effects and a species by year interaction term. If there was a significant species year interaction, we conducted a post-hoc analysis using separate linear regressions to analyze the relationship between year and the response variable for each species. If there was no significant species by year interaction, it was subsequently removed from the model. Post-hoc analyses were run using the *lsmeans* package (V2.30-0, Lenth 2018) utilizing the Tukey method to control for multiple testing. An alpha value of 0.05 was used to determine significance. The *DHARMa* package (v0.4.3; Hartig 2021) was used to assess model assumptions and fit. Results are presented as model estimates when slope interpretation was required, or as type III ANOVAs (*car* package v3.0-8; Fox and Wesiberg, 2019). All figures were created using the *ggplot2* package (v3.3.2; Wickham, 2016).

Results

Maximum breeding latitude

When examining changes to the maximum breeding latitude, we detected a significant year by species interaction ($F_{1,9}$= 72.92; p<0.0001). We then examined the relationship between maximum breeding latitude and year separately for each species (Figure 3.2). The maximum breeding latitude for Vaux's Swifts shifted 1.20 degrees south per year from 2009-2018 (r^2=0.89, p<0.0001, DF=9), while Chimney Swifts did not change their maximum breeding latitude over time (r^2=0.0005, p=0.35, DF=9) (Table 3.1).

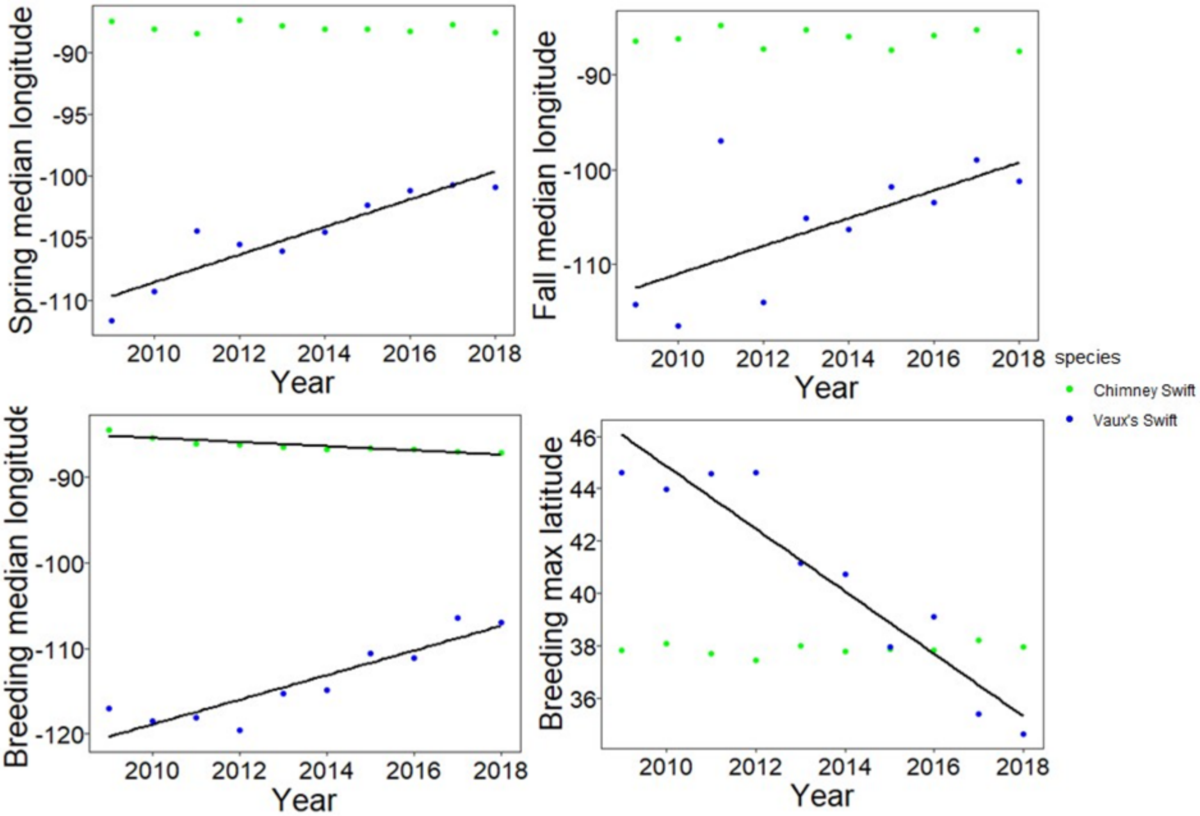

Figure 3.2. Changes in the spring and fall median longitude during migration, and the breeding median longitude and maximum latitude for Vaux's and Chimney Swifts, calculated from daily population centroid longitudes and latitudes predicted using GAMs.

Median longitude of breeding centroid

When examining changes to the median longitude of the breeding centroid (Figure 3.2), the year by species interaction was statistically significant ($F_{1,9}$= 51.92; p<0.00001). Vaux's Swifts shifted the median longitude of their breeding centroid east 1.44 degrees per year from 2009-2018 (r^2=0.81, p<0.0001, DF=9) (Table 3.1), while Chimney Swifts shifted their median longitude 0.24 degrees west per year from 2009-2018 (r^2=0.80, p<0.0001, DF=9) (Table 3.1).

Changes in migration routes (2009-2018)

Spring median longitude

When examining the median longitude of spring migration (Figure 3.2), we found a significant year by species interaction ($F_{1,9}$= 47.86; p=0.000004). Vaux's Swifts shifted their median longitude 1.12 degrees east per year from 2009-2018 (r^2= 0.84, p=0.0001, DF=9) (Table 3.1), while Chimney Swifts did not show a significant change in median longitude over time ($r^{2=}$0.015, p=0.32, DF=9).

Fall Median longitude

Similar to spring migration, there was a significant year by species interaction for the median longitude of fall migration ($F_{1,9}$= 6.16; p=0.025). Vaux's Swifts shifted their fall median longitude 1.46 degrees east per year from 2009-2018 (r^2=0.35, p=0.04, DF=9) (Table 3.1), while Chimney Swifts did not change over time (r^2=-0.087, p=0.61, DF=9; Figure 3.2).

Table 3.1. Direction and magnitude of significant changes in Vaux's Swift and Chimney Swift breeding distribution, migration timing, and migration routes over a 10-year period based on eBird data.

	Vaux Swift	Chimney Swift
Max breeding latitude	1.2° South/year (p<0.0001)	No change
Median breeding longitude	1.4° East/year (p<0.0001)	0.24° West/year (p<0.0001)
Spring median longitude	1.1° East/year (, p=0.0001)	No change

Fall median longitude	1.5° East/year (p=0.04)	No change
Start of spring migration	Advanced 1.4 days/year (p=0.0006)	NA
End of spring migration	No change	No change
Start of fall migration	No change	Delayed 4.2 days/year (p=0.035)
End of fall migration	Delayed 1.6 days/year* (p=0.06)	NA
Max speed spring	No change	No change
Max speed fall	No change	No change

* Non-significant (p = 0.06) trend

Changes to Timing of Migration (2009-2018)

Spring timing

Because Chimney Swifts did not have sufficient data from eBird to calculate the start of spring migration, we ran a linear model for only Vaux's Swifts to examine potential changes to the start of spring migration. The start of spring migration advanced 1.35 days per year from 2009-2018 for Vaux's Swifts (r^2=-0.77, p=0.0006, DF=9) (Table 3.1). Both species had sufficient data to calculate end of spring migration. We found no year by species interaction for the end of spring migration ($F_{1,9}$= 3.65; p=0.07), and subsequently removed the interaction term from the model. Following removal of the interaction term, we found no effect of either species ($F_{1,9}$=0.0007; p=0.98) or year ($F_{1,9}$=0.53; p=0.48), indicating that the end of spring migration did not change for either species over time.

Fall timing

When we examined changes to the start of fall migration, we observed a significant year by species interaction ($F_{1,9}$= 7.81; p=0.013). We then ran linear models for each species and found no change over time for the start of fall migration for Vaux's Swifts (r^2 =0.074, p=0.23, DF=9), but we found that Chimney Swifts delayed their start of fall migration 4.2

days per year from 2009-2018 (r^2=0.38, p=0.035, DF=9 (Table 3.1). Because Chimney Swifts did not have sufficient data from eBird to calculate the end of fall migration, we ran a linear model for only Vaux's Swifts to examine change over time. The resulting model indicated that the end of fall migration was delayed 1.64 days per year from 2009-2018, though this pattern was not significant (r^2=0.30, p=0.06, DF=9).

Speed of Migration (2009-2018)

Speed during spring migration

When examining changes in the speed of spring migration over time, we found no year by species interaction ($F_{1,1}$= 3.65; p=0.07), and we therefore removed it from the model. Following removal of the interaction term, we found an effect of species ($F_{1,1}$=16.48; p=0.0008), but not year ($F_{1,1}$=0.017; p=0.89), with Vaux's Swifts (mean +/- SD: 102.7 +/- 32 km/day) having a faster migration speed than Chimney Swifts (49.6 +/- 24.5 km/day).

Speed during fall migration

For speed of fall migration, the year by species interaction was not significant ($F_{1,1}$=2.92; p=0.11) and was removed from the model. Following removal of the interaction term, neither species ($F_{1,1}$=0.15; p=0.70), nor year was significant ($F_{1,1}$=0.16; p=0.70), indicating the speed of fall migration did not change over time or differ between the two species.

Discussion

In this study we used a 10-year community science dataset spanning from 2009-2018 to analyze population level changes in breeding grounds distribution, as well as migration routes, timing and speed for Vaux's Swifts and Chimney Swifts (Table 3.1). Although both species shifted their breeding centroid, they did not shift their breeding centroid in the expected northern direction; instead, Vaux's Swifts shifted their breeding centroid to the southeast and Chimney Swifts shifted their breeding centroid to the west. Although we did not predict a change in migration routes, Vaux's swifts shifted their migratory routes east in both spring and fall. In contrast, Chimney Swifts did not display a change in migratory route, which either indicates that they are either less responsive to environmental pressures, are more constrained in their ability to respond, or that they did not experience the same environmental pressures as Vaux's Swifts. We also found support for our prediction that Vaux's Swifts departed wintering grounds earlier. However, contrary to our prediction that there will be no change in fall migration timing, Chimney Swifts left their breeding grounds later over time. We found support for our prediction that there would be no change in speed of migration for both species of Swifts.

There are many documented changes in the breeding ranges of avian species in response climate change (Thomas and Lennon, 1999; Hitch and Leberg, 2007; Devictor et al., 2008; Zuckerberg et al., 2009; Potvin et al., 2016), often with a northern range expansion accompanied by a southern range contraction (Hitch and LeBerg, 2007, Rushing et al. 2020), and sometimes a southern range expansion (Rushing et al. 2020). Hovick et al. (2016) documented a southern shift in breeding range for 24% of 277 species, possibly due to uneven warming of North America, adaptation to new climates (Parmesan et al., 2006), habitat modification (Archaux, 2004), or inter species interactions (Lenoir et al., 2010). In contrast, the southern breeding centroid shift for Vaux's Swifts in our analysis is consistent with historical findings that there are aerial insectivore declines in northern North America, and increased populations in their southern range (Nebel et al. 2010). For Vaux's Swifts, the southern shift of the breeding centroid by 1.2 degrees per year could result in reduced energy expenditure due to a shorter migration distance (Coppack et al., 2008; Nebel et al., 2010). However, because distributions on the breeding grounds and wintering grounds can shift independently of one another and under different environmental conditions (Curley et al. 2020), and due to the fact that we only examined breeding centroid shifts, we cannot say whether there have been shifts to overall migration distance experienced by individuals that could influence their energy expenditure.

The breeding centroid and migration route shift to the east for Vaux's Swifts and the breeding centroid shift to the west for Chimney swifts may be a result of increased human population density along the coasts of North America (Neumann et al., 2015) resulting in a loss of potential habitat (Isaksson 2018). Recently, Sonnleitner et al. (in press) also found that the migration routes of Eastern and Western Bluebirds have been pushed away from the coastline and towards central North America, possibly as a result of human encroachment on the coast lines. A loss of old growth trees and chimney roosts could also be associated with changes to migration routes and breeding distributions for Vaux's Swifts (Bull, 2003), though this is unlikely to be the case for Chimney Swifts, as nestable chimneys do not seem to a limiting factor for Chimney Swift populations (Fitzgerald et al. 2014). However, with suitable chimneys being capped at approximately 5% per year, nest site availability may soon become an issue (Kearney-McGee 2012, COSEWIC 2018). Increases in human population density would also decrease food quality due to an increase in agriculture and therefore pesticides (Nocera et al., 2012; Pomfret et al., 2012; Møller et al., 2021), as well as decrease food abundance due to increased vehicle traffic (Martin et al., 2018). The eastern shift in the Vaux's Swift migration route appears to be correlated with an eastern shift in the breeding range for Vaux's Swifts. With climate change generating asynchronous changes in insect abundance and phenology across latitudes and longitudes (Parmesan, 2006; Aukema et al. 2008; Kozlov 2008) parts of the breeding grounds could potentially become more or less productive, resulting in changes in migration route to arrive at more productive breeding grounds. However determining this would require a further tracking study combined with productivity studies across the breeding centroid.

Vaux's Swifts left their wintering grounds earlier over time and exhibited a trend to arrive back at their wintering grounds later over time. A recent analysis of Vaux's Swift migration found that first arrivals and peak roost occupancy advanced from 2008-2017 during spring migration (Prytula et al. 2021), which aligns with our finding that Vaux's Swifts are leaving wintering grounds earlier over time. Chimney Swifts left their breeding grounds later over time, possibly as a result of environmental changes on the breeding grounds. Leaving the wintering grounds earlier may have been due to a change in environmental conditions on the wintering grounds, which has been shown to be a factor in other long distance migratory species (Haest et al., 2020; Koleček et al. 2020). Arriving at wintering grounds later could be a response to increasingly harsh environmental conditions during fall migration (Jenni and Kery, 2003; Prytula et al., 2021). For both swift species, not altering parts of their spring and fall migration timing may be indicative of endogenous rhythms overpowering any response to environmental cues, or that the environmental cues are unimportant. Vaux's swifts not changing the start of fall migration may be an indication that the shift in their breeding grounds may have adequately accounted for changes in the environment or that any environmental changes at the end of the season were not strong enough to drive changes to fall departure timing. There is also the possibility that greater variability obscured any trends.

We found no changes to the maximum speed of migration (calculated as a change in the population centroid) for either species of swifts, which may be due to the energetic cost of migration already being so high for these long-distance migrants (Fraser et al., 2013; Hurlbert and Liang 2012). As the speed of migration and timing of arrival on the breeding grounds was calculated as a population centroid, we were unable to test for changes in the speed and arrival timing for individuals trying to migrate quickly and arrive first at the breeding grounds (Alerstam 2011; Karlsson et al. 2012; Prytula et al., 2021). Vaux's Swifts may not be altering speed in response to different environmental cues during migration but instead are choosing more suitable migration routes to migrate.

While there are advantages to working with population-level community science data that may not be possible based on tracking of individual birds via banding or tracking devices, such datasets present their own difficulties in terms of data reliability and generating data sets that are not spatially or temporally biased (Dickinson et al. 2010). We were limited to 10 years of data due to sparse data from years prior to 2009, and we were also unable to calculate the start of spring migration and end of fall migration for Chimney Swifts due to a lack of sufficient records from South America, where there was less use of eBird. To account for spatial bias created by frequently visited known locations, aka 'hotspots', (Prendergast et al., 1993; Callaghan et al., 2019a), areas near human settlements (Kelling et al. 2015), and easily accessible areas such as near homes (Luck et al., 2004; Dickinson et al., 2010) and roads (Kadmon, Farber, and Danin, 2004; Dickinson et al., 2010), we used equal area hexagonal grids (Strimas-Mackey et al., 2018). Temporal bias can be a problem in community science datasets due to observers being more likely to collect data on weekends (Courter et al. 2013). Weekend bias can be accounted for by using weekly/biweekly data points (Strimas-Mackey et el., 2018), but this would reduce the amount of data and likely result in less accurate start/end dates of migration. However, we do not feel that greater sampling occurrences on weekends would have biased our results. Requiring all community science databases to require data collection information (number/duration/time of visits, distance traveled) as well as structured protocols in data collection could improve the reliability and quantity of community science data that can be utilized for study (Callaghan et al. 2019b; Kelling et al. 2019).

Future studies could analyze changes in the wintering grounds of Vaux's Swifts and Chimney Swifts over time, as some species experienced a shift in wintering grounds, due to movement towards areas that were formerly too cold (Chamorro et al. 2019). As swifts are long distance migrants, they may winter closer to their breeding grounds as the climate changes, as was found for 21 of 24 species of European birds in a 73-year period (Visser et al., 2009). In addition, future studies could attempt to utilize individual tracking information such as GPS, geolocators or banding data in combination with community science to create more accurate migratory route information (Heim et al. 2020), as well as examine the concurrent influence weather patterns on migratory timing (Prytula et al., 2021). Tracking data would assist in removing spatial and temporal biases, while the addition of using weather data would enable us to examine the role of environmental conditions and environmental productivity on migration.

In conclusion, we documented a change in migratory timing, migration route, and breeding centroid for Vaux's Swifts, and a change in breeding centroid, and start of fall migration for Chimney Swifts over a ten-year period. These changes could be important as it suggests short-term behavioural plasticity in response to climate change. As our study only encapsulated a short ten-year period, our findings may demonstrate shifts resulting from short-term climatic cycles rather than broader scale climate change. To capture the effects of climate change as a whole, migration data would likely need to encapsulate a timeline long enough to capture multiple short-term cycles. It is interesting Vaux's Swifts altered their migration routes in both spring and fall but Chimney Swifts did not. This difference could be due to foraging differences between the two species, as Vaux's swifts forage mostly above forests and water (Bull 1993), while currently Chimney swifts favour industrial areas with thermal currents (Wheeler 2013) and developed landscapes (Kearney-Mcgee 2012). Another possibility is that Chimney swifts have less behavioural plasticity in migration than Vaux's swifts, which could result in population declines if they are unable to alter their migratory timing (Møller, Rubolini and Lehikoinen, 2008), speed (Hedenstrom, 2008), distance, or routes in response to climate change and are more greatly constrained by crossing the Caribbean during migration.

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Chapter 4: Conclusion

The goal of my thesis was to use community science data to test if Vaux's Swifts and Chimney Swifts have altered their spring and fall migration timing and routes over time, and whether they are responding to local and regional weather patterns during migration. With climate change altering ecosystems and changing weather patterns, mismatches between spring phenology and migration timing may lead to population declines. Both research chapters tested if swifts are changing migratory patterns over time and utilized community science data to achieve this goal. Chapter 2 utilized the community science dataset Vaux's Happening to test if Vaux's Swifts are responding to changes in local and regional weather conditions experienced during migration. Chapter 3 utilized community science data from eBird to test if Vaux's Swifts and Chimney Swifts changed their breeding grounds range, spring and fall migration routes, migration timing, and migratory speed over time. This resulted in the testing of similar patterns using two different, yet complimentary, community science datasets.

My chapter 2 results suggest Vaux's Swifts have exhibited a trend towards earlier spring migration, as I found that Swifts advanced arrival at roosts by 0.77- 0.99 days per year over a 10-year period. Wind gusts also appear to be influencing Vaux's Swifts migration; birds arrive earlier at roosts in gustier conditions; other weather conditions (e.g., temperature) did not seem to affect spring migration. This finding is consistent with studies indicating that during spring migration, some long distance migrants do not respond to changes in temperature and other weather variables (Zaifman et al., 2017). Fall migration results showed Vaux's Swifts migrated 0.88-1.7 days later per 1 degree increase in temperatures, indicating that warmer temperatures tend to delay the start of fall migration. In addition, Vaux's swifts migrated 1.23-1.33 days earlier in years with higher local wind speeds, possibly due to favourable tail winds (Haest et al., 2019), or wind speed decreasing availability of flying insects (Møller 2013), thus reducing time spent at roosts. These results suggest that Vaux's Swifts are not attempting to migrate to their wintering grounds as fast as possible and are more responsive to weather conditions encountered en route in order to optimize survival (Jenni and Kery, 2003; Prytula et al., 2021). However, the data for chapter 2 was limited to specific roosts during migration, and thus my study was unable to test for changes in breeding range, migration routes, or speed, all of which may influence swifts' arrival times to roosts. I was able to examine some of these other patterns using a larger-scale community science dataset, eBird, as well as compare and contrast these findings in a congeneric swift species.

In chapter 3, I found that both Vaux's Swifts and Chimney Swifts shifted their breeding grounds, longitude towards the center of the continent in North America, but only Vaux's Swifts changed their breeding range latitude. This longitudinal shift of the breeding ground centroids may be in response to anthropogenic factors due to increasing human population densities along the coastline (Neuman et al., 2015) and shifts in suitable habitat due to environmental changes. Vaux's Swifts also shifted their migration route eastward, matching the change in the breeding range. However, this shift in migration route was not present in Chimney Swifts, perhaps because they experienced a considerably smaller magnitude of shift in breeding grounds longitude compared to Vaux's Swifts. Vaux's Swifts advanced their start of spring migration and Chimney Swifts delayed their start of fall migration, but no other changes to timing were discovered using eBird data. Although both species were able to make changes to their migratory cycle, it is unclear whether or not the changes will be enough to prevent population declines in the face of increasing environmental changes. As Vaux's Swifts and Chimney Swifts, as well as aerial insectivores as a whole, already have seen population declines, increasing environmental changes may further exacerbate them. Vaux's Swifts' ability to change their breeding grounds, migration routes, and advance their start of spring migration suggests that the species possesses at least some behavioural plasticity in migratory timing, an attribute that may help buffer against further population declines in response to climate change. Chimney Swift's ability to change their breeding grounds and start of fall migration also suggests behavioural plasticity, but of a smaller magnitude.

Vaux's Swifts shifting their mean breeding ground centroids to a more southern location may result in a decrease in energy expenditure associated with distance migrated, at least for some individuals (Coppack et al., 2008). The shift of both Vaux's Swifts breeding grounds and their migration route eastward, away from coastal regions where human populations are more densely populated (Neuman et al., 2015), and to areas with potentially better habitat (Nebel et al., 2010), possibly indicates that Vaux's Swifts have options for roosting and nesting sites and may not be as constrained as previously thought. However, if human encroachment and environmental change further pushes populations southeast, Vaux's Swifts may reach a limit at which there is no longer suitable habitat. Loss of habitat and roosting/nesting trees could also put limits on Vaux's Swifts' ability to change migration routes or breeding areas.

The shift in migration route for Vaux's Swifts may be due to the eastern shift in breeding grounds, as the population began to start migrating from the more eastern location they may have utilized the more accessible eastern route. Or, Vaux's Swifts shifted their migration route east due to conditions experienced during migration. Those conditions could be influenced by anthropogenic effects such as increased human populations, pesticide use, agriculture, etc. (Nocera et al., 2012; Pomfret et al., 2012; Møller et al., 2021), or environmental effects, such as asymmetric changes in spring green up and insect abundance within the ecosystem (Nebel et al., 2010). The ability to shift migration routes and breeding grounds may reduce mortality during migration, as they are able to maintain timing while also responding to conditions en route (Stanley et al. 2012). The earlier spring migration of Vaux's Swifts detected with eBird data in chapter 3 is interesting as it mirrors results found in chapter 2 with Vaux's Happening data. The advancement of spring migration may be indicative of a change in spring onset at the wintering grounds. The lack of change in arrival at the breeding grounds may indicate that the advancement on the onset of spring conditions may not be experienced equally throughout migration. It is interesting to note that there was no change in arrival to or departure from the breeding grounds concurrent with the southern shift in the location of the breeding ground centroid, even though the southern shift would result in some individuals within the population potentially migrating a shorter distance to the breeding grounds, as well as experiencing different photoperiodic cues. Finally, if the onset of spring continues to advance, populations may not be able to keep up due to constraints imposed by endogenous rhythms (Both and Visser 2001).

Chimney Swifts did exhibit some capacity to make changes to their breeding grounds and migration timing, but less drastically than Vaux's Swifts. Therefore, either Chimney Swifts did not encounter similar environmental changes as Vaux's Swifts, or those changes were present, and Chimney Swifts were not able to respond to them. The postponement to the onset of fall migration in Chimney Swifts may be due to a delay in the onset of fall conditions possibly associated with warming temperatures on the breeding grounds (Prytula et al. 2021).

Strengths of the study

By using large-scale community science data, I was able to analyze changes in migration over large temporal and geographic scales. This thesis not only helps strengthen the knowledge base regarding both Vaux's and Chimney Swift migratory behaviour and breeding ranges, but utilizes methods that can be applied to other community science data sets (such as the Breeding Bird Survey, or SwiftWatch). My work has also been able to utilize data for both spring and fall, where a large portion of scientific research has neglected the study of fall migration (Gallinat et al. 2015). My work has elaborated on Nebel et al.'s (2010) results showing that Vaux's Swifts are moving their breeding grounds southward over time possibly because of changes in aerial insect populations, as well as underlying ecosystem changes. Finally, my research also showed that two separate community science datasets (Vaux's Happening and eBird) provided similar results, with both research chapters showing that Vaux's Swifts advanced their spring migration, further giving confidence in the reliability of the results for Vaux's Swifts.

Limitation of the study and future directions

Because I used community science data, my study was limited in terms of data availability. There was sufficient data for analysis for only about 10 years in each chapter (chapter 2 included data from 2008-2017; chapter 3 included data from 2009-2018). I was also limited in terms of the season of data collection, as chapter 2 could not include wintering or breeding ground data and chapter 3 did not include wintering ground data. Misidentification of swifts can be an issue with community science as well, but was not expected with Vaux's Happening due to the size and location of the flocks entering the roost, that was accounted for with eBird by utilizing the grid system in which the centroids are averages that would negate outliers. Community science can also be prone to spatial bias due to participants focusing on known hotspots, and collecting data at easy to access locations (Dickinson et al., 2010), and temporal bias due to volunteers collecting data on weekends (Courter et al. 2013), but this is becoming less of an issue as the traditional Monday to Friday work week becomes less common. Spatial bias can be accounted for by creating a grid and binning data into areas of equal size, and temporal bias can be accounted for by utilizing weekly/biweekly data points (Strimas-Mackey et al., 2018). In chapter 2 of my study there may be spatial bias as the community science program focused on known roost locations, which neglects 'cold spots' or roosts in which aren't monitored but may have Vaux's Swifts roost within them. This could be accounted for by utilizing individual tracking information to find the roosts, and a possible expansion of the organization to account for data at those locations. Chapter 2 was not likely subject to temporal bias as members of the program continually tracked Vaux's Swifts as they moved northwards and thus volunteers were alerted to visit roosts days before the arrival of Vaux's Swifts. In chapter 3, spatial bias was accounted for by utilizing equal area hexagonal grids, however I did not utilize weekly/biweekly data points as it would generate inaccurate migration timing results.

Community science databases have different classifications in terms of their level of structure. eBird is considered a semi-structured database as it gives participants the option to report information on how they collected data, but this information is not required (Kelling et al. 2019). With the implementation of more structured protocols, for eBird as well as other datasets, community science would be able to increase the amount of useable data and therefore have more data for scientific research. This could create a trade-off, as stricter protocols may result in more analyzable data, but could also deter community scientists from the more complex database. With increased data reliability scientists would potentially be able to utilize data moving forward to capture the effects of climate change on migration more accurately. The fact that community science data is sparse below the US/Mexico border is also problematic for the study of long-distance migrants. However, individual tracking information such as with GPS and geolocation could result in complimentary data for wintering grounds data of individuals within the population (Heim et al. 2020), The use of individual tracking data could also assist with bias by identifying areas distant from recent sample, known as 'cold spots', and help track migration timing of individuals in the population (Callaghan 2019; Heim et al. 2020). This individual tracking information could also identify changes with individuals within the population, and not just populations as a whole. In chapter 2 I focused on first arrivals, and peak roost occupancy, where first arrivals does analyze changes to the individuals arriving first at roosts but including individual tracking information could help identify roosts not already known. In chapter 3 we focused on population centroids, therefore I was unable to detect if individuals within the population changed in arrival at the breeding grounds. Finally, for both chapters, I was unable to test if individuals within the population are shifting breeding grounds, migration routes or migration timing from year to year, or merely if new generations of swifts changed their migration strategies.

In chapter 2, I used local and regional weather data, but future studies could investigate additional measurements to represent climate such as the Normalized Difference Vegetation Index (NDVI) to measure primary productivity, or the North Atlantic Oscillation (NAO) and El Niño/Southern Oscillation (ENSO), as these weather patterns have been shown to affect other long distance migrants breeding in North western North America (Nott et al., 2002). In chapter 3, I was limited to tracking population centroids for migration timing, which is not the same thing as individual movements within the population. Therefore, my study was unable to account for the drivers of these changes — for example, changes to the breeding centroid could occur if all individuals moved south over time, or through a reduction in population density in the northern portion of the range, or through increased population density in the southern portion of the range.

Implications for conservation

My results highlight relationships between changes in the annual cycle of Vaux's Swifts and Chimney Swifts and changes in the environment. In addition, my work indicates that Vaux's swifts may be relatively insensitive to spring weather conditions Vaux's Swifts). There may be continued shifts of breeding ground locations and migration routes towards central North America and away from the coasts as human settlements continue to expand more rapidly in coastal areas (Seto et al. 2011, Neumann et al. 2015). If the onset of spring continues to advance, Vaux's Swifts may continue to advance their spring migration. Chimney Swifts may also further delay fall migration as fall continues to warm, potentially delaying migration further. There could also be a northward shift of the wintering grounds, and/or a further southward shift in the breeding grounds thereby reducing the distance long distance migrants would need to travel and the required energy expenditure of migration (Coppack et al., 2008). However, with more extreme changes to the weather and environment these changes may not prove to be enough to prevent further population decline. The species may reach a limit in which they can no longer keep shifting migration patterns to accommodate more extreme conditions. All told, my results suggest that both Vaux's Swifts and Chimeny Swifts may be able to buffer against the phenological changes caused by climate change through quickly modifying their migration routes and timing; however, like all migratory birds, and especially aerial insectivores, these birds face numerous threats. Future work should focus on assessing the conditions of the wintering grounds as loss of habitat, human encroachment, as well as agriculture and pesticide use, may be important factors driving population declines.

In conclusion, my study has demonstrated that two swift species in North America have adjusted different components of their annual cycles over time and in relation to environmental factors, but that there are species-specific differences in the direction and degree of response. I also show the value of different but complimentary community science datasets for detecting changes to migration patterns over time. Future work could build on these results by utilizing an approach that addresses the annual cycle, a longer-term dataset that captures responses to climate change as a whole (or at least the start of population declines for the two species), as well as analyzing changes to all aerial insectivores within North America.

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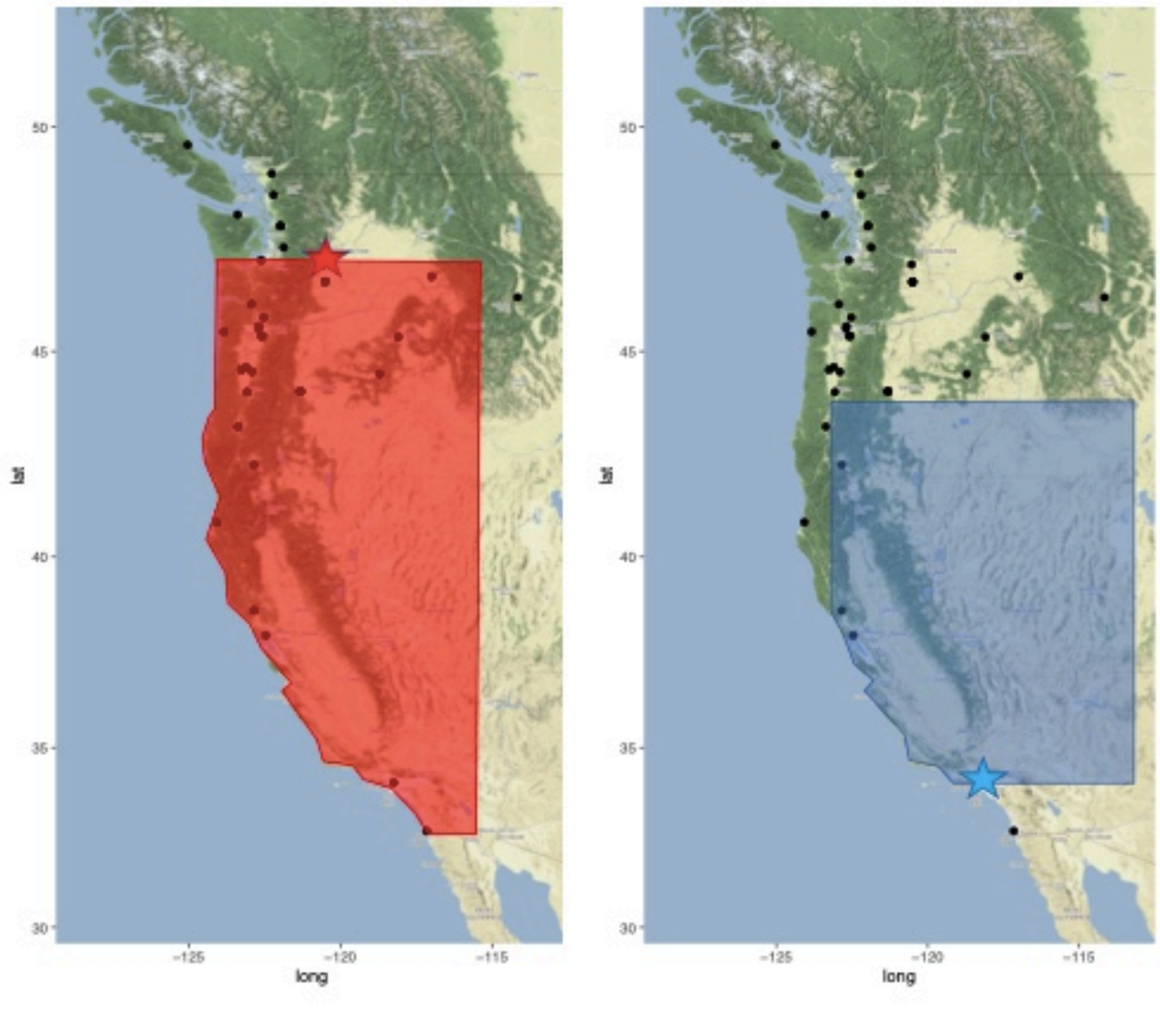
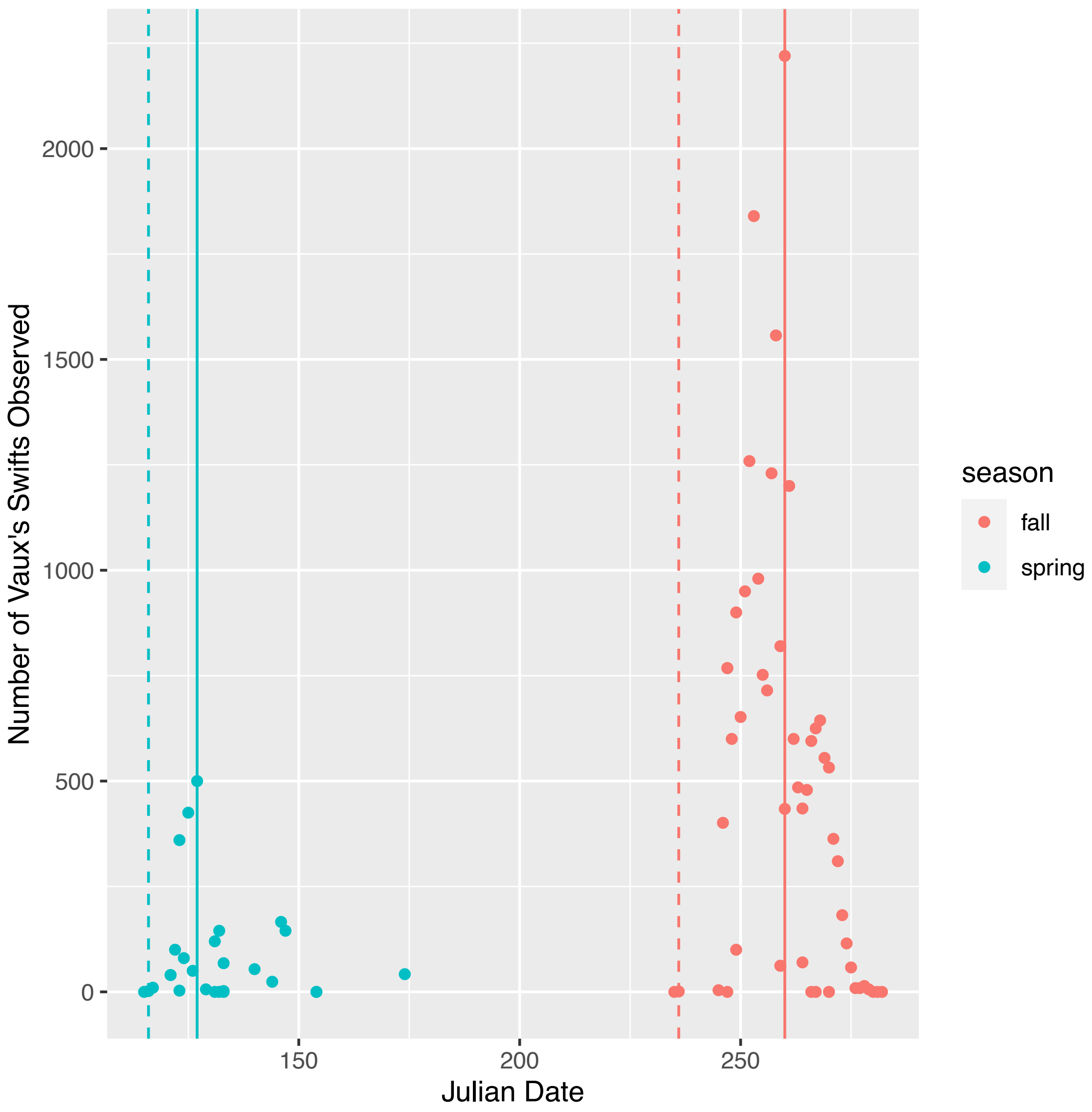
Appendix



Appendix Figure 1. Example of regional wind data collected in the three weeks prior to peak arrival at migratory roosts. Left: During spring migration we averaged wind data over a 10° latitude (5° east, 5° west) by 15° longitude area south of the roost (red star) Right: During fall migration we averaged wind data over a 10° latitude (5° east, 5° west) by 10° longitude area north of the roost (blue star).



Appendix Figure 2. Example of data used to calculate first arrival (dashed line) and peak roost occupancy (solid lines) from The Boys and Girls Club roost in Bend, OR in 2012. First arrival dates were the calculated as the first day Vaux's Swifts (*Chaetura vauxi*) were observed at the roost site; peak roost occupancy was calculated as the date of maximum occupancy at the roost site.