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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*)

E.D. Prytula, A.E. McKellar, L. Schwitters, and M.W. Reudink

Abstract: 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 advanced 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.

Résumé : Les changements climatiques ont produit des printemps plus hâtifs, des automnes plus tardifs et de nouveaux régimes météorologiques. Ces changements pourraient poser des défis pour les espèces migratrices qui ne sont pas en mesure d'ajuster le moment de leurs migrations. Nous avons analysé les changements du moment des migrations de martinets de Vaux (*Chaetura vauxi* (J.K. Townsend, 1839)) en examinant leur première arrivée (date d'arrivée du premier martinet) et la pointe d'occupation d'aires de repos (date où le plus grand nombre de martinets est relevé) dans des aires de repos migratoires au printemps et à l'automne, obtenues par l'organisation de science participative « Vaux's Happening ». Les dates de première arrivée et de pointe d'occupation des martinets de Vaux sont de plus en plus hâtives au fil du temps de 2008 à 2017, et plus les vitesses des rafales locales sont grandes, plus la première arrivée est hâtive. Le moment de la migration automnale ne change toutefois pas de 2008 à 2016, mais de plus hautes températures sont associées à des migrations automnales plus tardives (en ce qui concerne tant la première arrivée que la pointe d'occupation) et de plus grandes vitesses du vent sont associées à des migrations automnales plus hâtives (seulement pour les pointes d'occupation d'aires de repos). À l'instar de nombreux autres oiseaux migrateurs, les martinets de Vaux pourraient suivre une phénologie automnale plus hâtive et pourraient aussi modifier le moment de leurs migrations en réponse aux conditions météorologiques locales, tout particulièrement durant la migration automnale. Nos résultats indiquent que les martinets pourraient être en mesure d'ajuster leurs migrations aux changements climatiques, du moins à court terme. [Traduit par la Rédaction]

Mots-clés : martinet de Vaux, *Chaetura vauxi*, science participative, aire de repos, migration, changements climatiques, météo.

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 the breeding grounds to match 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

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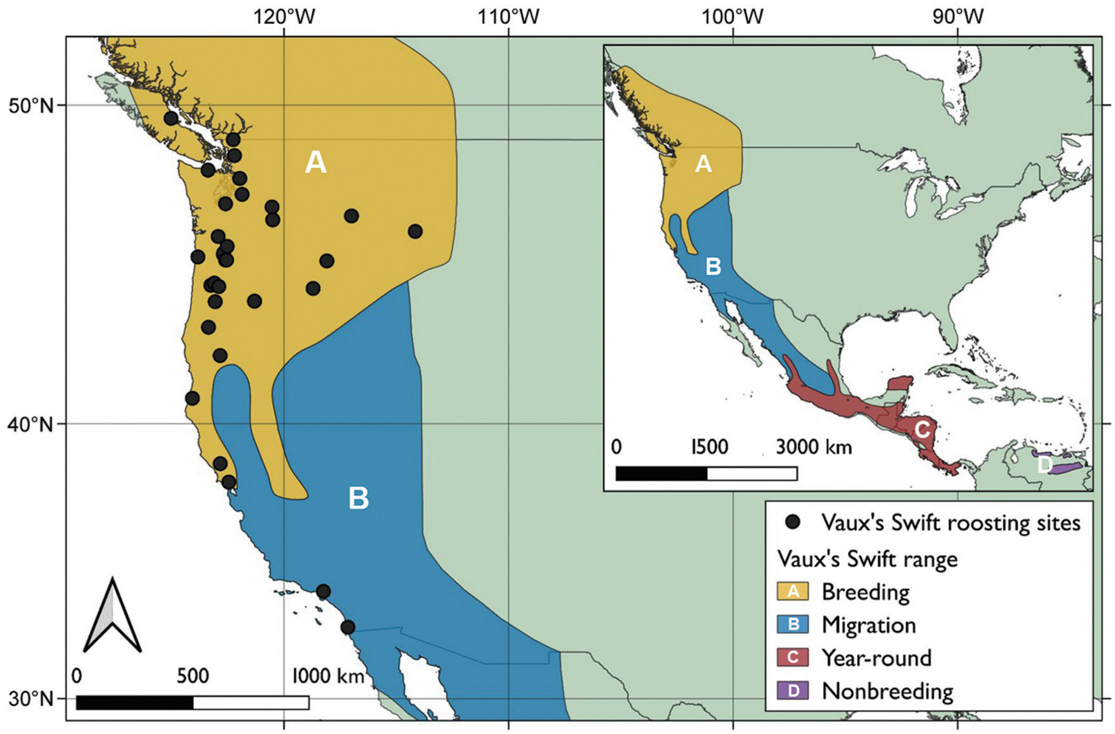
Fig. 1. Distribution of Vaux's Swifts (*Chaetura vauxi*) roosts used in an analysis of spring and fall migration timing from the Citizen Science project "Vaux's Happening in North America", as well as breeding, migration, year-round, and nonbreeding ranges. WGS 84 and EPSG 3857 were used in creating the map. Range data from BirdLife International and Handbook of Birds of the World (2019). Colour version online.



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* (Swainson, 1827)) (McKinney et al. 2012), White Stork (*Ciconia ciconia* (Linnaeus, 1758)) (Gordo and Sanz 2006), Eurasian Blackcap (*Sylvia atricapilla* (Linnaeus, 1758)) (Bearhop et al. 2005), and European Pied Flycatcher (*Ficedula hypoleuca* (Pallas, 1764)) (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 (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* (Linnaeus, 1758)) are directly associated with primary productivity during fall migration (Bridge et al. 2015). Similarly, individual Barnacle Geese (*Branta leucopsis* (Bechstein, 1803)) 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 (auricollis) (*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. 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) (Fig. 1) (Schwitters et al. 2020). During the breeding season, the swifts construct nests 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 leading to 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 eBird, 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 advancement 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). 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 (Fig. 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 projected to arrive at the site. Whenever possible, eBird was used 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.

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 Supplementary Fig. S1),[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

[1]Supplementary figures are available with the article at https://doi.org/10.1139/cjz-2021-0089.

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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 (Supplementary Fig. S2).[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 (Supplementary Fig. S2).[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 (AIC_c) to rank the models, and we present model-averaged 95% confidence intervals (95% CI) for models within 4 ΔAIC_c 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 (Bartoń 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 1). Other models within 4 ΔAIC_c 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). 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 1. Summary of top-ranked models (<4 ΔAIC_c from top-ranked model), using Akaike's information criterion corrected for small sample size (AIC_c), that explain the variation in migratory timing of Vaux's Swifts (*Chaetura vauxi*) during spring migration, 2008–2017.

	AIC_c	ΔAIC_c	AIC_c weight
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

Note: Roost is included in all models as a random effect. The AIC_c of the model, difference between the model and the top model's AIC_c (ΔAIC_c), and the weight of each model (AIC_c weight) are shown. Vwind is regional southerly wind (m/s); Uwind is regional westerly wind (m/s); Precip is local precipitation (mm); Temp is local temperature (°C); Lat is latitude; Wind is local wind (m/s); WindGust is local wind gust (m/s).

Peak roost occupancy

The top model explaining variation in peak roost occupancy during spring migration included effects of year, precipitation, temperature, and latitude (Table 1). Other models within 4 ΔAIC_c 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) and indicated that swifts arrived 0.77 days earlier per year and 1.07 days later per 1° increase in latitude.

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 3). Other models within 4 ΔAIC_c 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) 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.

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 3). Other models within 4 ΔAIC_c 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

Table 2. Model-averaged parameter estimates and 95% confidence intervals (in parentheses) for variables included in the top-ranked models (<4 ΔAIC_c units of best model) that explain the variation in Vaux's Swift (*Chaetura vauxi*) first arrival and peak roost occupancy for both spring and fall migration.

	Spring migration		Fall migration	
	First arrival	Peak roost occupancy	First arrival	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)

Note: Values in boldface type represent confidence intervals that do not overlap zero. Vwind is regional southerly wind (m/s); Uwind is regional westerly wind (m/s); Precip is local precipitation (mm); Temp is local temperature (°C); Lat is latitude; Wind is local wind (m/s); WindGust is local wind gust (m/s).

Table 3. Summary of top-ranked models (<4 ΔAIC_c from top-ranked model), using Akaike's information criterion corrected for small sample size (AIC_c), that explain the variation in migratory timing of Vaux's Swifts (*Chaetura vauxi*) during fall migration, 2008–2016.

	AIC_c	ΔAIC_c	AIC_c weight
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

Note: Roost is included in all models as a random effect. The AIC_c of the model, difference between the model and the top model's AIC_c (ΔAIC_c), and the weight of each model (AIC_c weight) are shown. Vwind is southerly wind (m/s); Uwind is westerly wind (m/s); Precip is precipitation (mm); Temp is temperature (°C); Lat is latitude; Wind is local wind (m/s); WindGust is local wind gust (m/s).

and local wind did not overlap zero (Table 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 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 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). 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 true population-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, 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 phenotypic 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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