Canadian Journal of Zoology

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*)

Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID	cjz-2021-0089.R2
Manuscript Type:	Article
Date Submitted by the Author:	13-Sep-2021
Complete List of Authors:	Prytula, Erik; Thompson Rivers University, Department of Biological Sciences McKellar, Ann; Environment and Climate Change Canada, Canadian Wildlife Service Schwitters, Larry; Vaux's Happening Reudink, Matthew; Thompson Rivers University, Department of Biological Sciences
Is your manuscript invited for consideration in a Special Issue?:	Not applicable (regular submission)
Keyword:	Vaux's swift, citizen science, ROOST < Habitat, MIGRATION < Discipline, climate change, weather

SCHOLARONE™
Manuscripts

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. Prytula¹, A.E. McKellar², L. Schwitters³, and M.W. Reudink^{1*}

1. Department of Biological Sciences, Thompson Rivers University, Kamloops, British Columbia, Canada.
2. Environment and Climate Change Canada, 115 Perimeter Road, Saskatoon, Saskatchewan, Canada.
3. Vaux's Happening, Issaquah, WA, USA.

* Corresponding author: mreudink@tru.ca

Draft

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* 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 2008-2017, 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 2008-2016, 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.

Keywords: 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/territory (Cristol 1995) and avoiding

harsh environmental conditions during migration and at the breeding grounds (Brown and Brown 1998; Moller 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 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 & 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 2020). 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 petechial* Linnaeus 1766, Drake et al. 2014), strong westerly winds appear to slow migration and result in a later clutch initiation date, while in the Yellow-Breasted Chat (*Icteria virens auricollis* Linnaeus 1758, 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 multi-year 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 which 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* 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 to as far north as southern Yukon (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. 2012; Nocera et al. 2012; Pomfret et al. 2014). 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 species' declining population (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.

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 average flock entry typically began 2 minutes after sunset. Monitors were instructed to arrive 30 minutes before sunset and to stay at the roost for 30 minutes 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 ten swifts per second entering the roost. This rate was calculated from two live camera streams at the Monroe Wagner, WA 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 eight (as above, slow-motion video was used to estimate an exit rate of eight birds/second). 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 2008-2017 and fall migration data from 2008-2016. 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 (see Fig. S2 for example of data distribution), 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 three 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 while others, such as Chapman Elementary in Portland, OR 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 5 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 an average of 467 counts per year, with a minimum

of 224 and maximum of 702 counts. During fall migration, monitors performed an average of 367 counts per year with a minimum of 178 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 gust speed (m/s) were calculated for the three weeks prior to the average peak roost occupancy date at each roost. Weather data were retrieved from Weather Underground (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 hour intervals which varies depending on each weather station. We did not include historical weather data from airports that were greater than 100km away from the roost as it may not have been an accurate representation of the weather experienced at the roost. Unfortunately, wind direction was not available from each airport, and 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 (V-) and westerly (U-) 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 degree latitude by longitude cells across North America, with a temporal resolution of 6 hours. We chose to use a 3-week window to reflect average 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 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 three weeks preceding arrival to the roost may affect insect abundance and availability—factors which 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 degrees of latitude and 10 degrees of longitude south of each roost (Fig. S1). To capture wind conditions experienced en route during fall migration, NCEP wind data were averaged over an area of 10 degrees of latitude and 10 degrees of longitude north of each roost (Fig. S2). For spring migration, 15 degrees of latitude ensured we did not collect wind data from the wintering grounds. For fall migration, 10 degrees of latitude ensured we did not exceed the northern bound of the breeding range. Thus, weather data included the following variables: local wind, wind gust, precipitation, and temperature, and regional southerly (V-) and westerly (U-) wind.

Statistical analysis

To examine potential changes over time and associations between weather and the timing of first arrival and peak roost occupancy, we constructed a series of linear mixed models (LMMs). Models were constructed so 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 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 (CI) for models within 4 delta AICc of the top model (Burnham and Anderson 2002). The statistical software R (v. 4.0.2, R Core Team 2020) was used to analyze the data, including the packages AICcmodavg (Mazerolle 2014), 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 1). Other models within delta 4 AICc 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% confidence intervals 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 degree increase in latitude.

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 delta 4 AICc 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% confidence intervals 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 degree 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 delta AICc units included the effects of year, temperature, precipitation and local wind gust in addition to those effects found in the top model. The 95% confidence intervals 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 degree increase in temperature, 1.33 days earlier per unit increase (m/s) in local wind speed, and 1.07 days earlier per 1 degree 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 delta AICc units included the effects year, temperature, precipitation, and local wind gust in addition to those effects found in the top model. The 95% confidence intervals for

the effects temperature and local wind did not overlap zero (Table 2) and indicated that swifts arrived 0.88 days later per 1 degree increase in temperature and 1.23 days earlier per unit increase (m/s) in local wind speed. It is worth noting that although confidence intervals for latitude and westerly wind did not overlap zero, they were close to doing so (<0.1 overlap of 0). Swifts tended to arrive earlier at higher latitudes and with stronger westerly winds.

DISCUSSION

In this study, we explored a citizen science dataset spanning ten years to examine potential changes in migration over time and associations between weather (at both a local and 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 2008-2017 but has not changed during fall migration (2008-2016). 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 as many species across a broad range of avian taxa have exhibited significant advances in spring migratory timing, likely in response to changing spring phenology (Both 2002; Both et al. 2005; Gordo & Sanz 2006; McKinney et al. 2012).

Over a ten-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 also responded to local wind gust conditions, as they showed earlier first arrivals when there were stronger wind gusts, potentially because favorable tailwinds help to accelerate migration (Haest et al. 2019). However, first arrival dates can be biased as 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 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 favorable 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 (Moller 2013). Vaux's Swift peak roost occupancy also tended to be earlier with increased regional westerly winds, although confidence intervals 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 to 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 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 2020). 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 which 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 Swift

populations which may be using unknown roosts along the migratory route, such as old growth trees in non-urban 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 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. 2014; Nebel et al. 2010). Finally,

Vaux's Swifts rely on old growth trees and chimneys for roosting/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 to 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 (Moller et al. 2008). The lack of relationship between migratory timing and spring weather conditions experienced en route could potentially be problematic as 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 Semi-collared Pied 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/breeding grounds, and not just what pushes/pulls them among roosts.

ACKNOWLEDGMENTS

Funding was provided by an NSERC Discovery Grant to M.W.R. and Irving K barber BC Indigenous Student Award, New Relationship Trust Scholarship, Indspire and the Ken Lepin Award for E.P. We thank E. Smith, S. Pierera, and D. Agar for their help processing data, and J. Dunne-Mucklow for GIS support and map creation. Special thanks to A. Drake for assistance with collecting and analyzing regional wind data. We also thank the many, many volunteers that assisted with data collection for Vaux's Happening over the years. Research was conducted at Thompson Rivers University and took place on the traditional lands of the Tk'emlúps te Secwépemc within Secwépemc'ulucw, the traditional and unceded territory of the Secwépemc people.

LITERATURE CITED

- Alerstam, T. 2011. Optimal bird migration revisited. *J. Ornithol.* **152**: 5-23.
- Arab, A., J.R. Courter, and Zelt J. 2016. A spatio-temporal comparison of avian migration phenology using citizen science data. *Spatial Statistics*, **18**: 234-245.
- Barton, K. 2009. Mu-MIn: Multi-model inference. R Package Version 0.12.2/r18. <http://R-Forge.R-project.org/projects/mumin/>
- Bates, D., M. Mächler, B. Bolker, and Walker, S. 2015. "Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**(1), 1–48. doi: [10.18637/jss.v067.i01](https://doi.org/10.18637/jss.v067.i01).
- Bearhop, S., W. Fiedler, R.W. Furness, S.C. Votier, S. Waldron, J. Newton, G.J. Bowen, P. Berthold, and Farnsworth, K. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* **310**: 502-504.

- 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>
- Both, C., and Visser, M.E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**: 296-298
- Both, C., R.G. Bijlsma, and Visser, M.E.. 2005. Climatic effects on spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. *J. Avian Biol.* **36**: 368-373.
- Bozó, L., T. Csörgő, and Heim, W. 2018. Weather conditions affect spring and autumn migration of Siberian leaf warblers. *Avian Res.* **9**: 33. <https://doi.org/10.1186/s40657-018-0126-5>
- Bridge, E.S., J.D. Ross, A.J. Contina, and Kelly, J.F. 2015. Do molt-migrant songbirds optimize migration routes based on primary productivity? *Behav. Ecol.* **00**: 1-9. doi:10.1093/beheco/arv199.
- Briedis, M., S. Hahn, and Adamik, P. 2017. Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird. *BMC Ecol.* **17**: 11.
- Brisson-Curadeau, É., K.H. Elliott, and Côté, P. 2019. Factors influencing fall departure phenology in migratory birds that bred in northeastern North America. *Auk*, **51**: 459.
- Brown, C.R., and Brown, M.B. 1998. Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution*, **52**: 1461–1475.
- Bull, E.L. 2003. Declines in the breeding population of Vaux's Swifts in Northeastern Oregon. *Western Birds* **34**: 230-234.

- Charmantier, A. and Gienapp, P. 2014. Climate change and timing of avian breeding and migration: Evolutionary versus plastic changes. *Evol. App.* **7**: 15-28.
- Cook, J., D. Nuccitelli, S.A. Green, M. Richardson, B. Winkler, R. Painting, R. Way, P. Jacobs, and Skuce, A. 2013. Quantifying the consensus on anthropogenic global warming in the scientific literature. *Environ. Res. Lett.* **8**: 024024.
- Coppack, T., and Both, C. 2002. Predicting life-cycle adaption of migratory birds to global climate change. In: Both C. & T. Piersma (eds) *The avian calendar: exploring biological hurdles in the annual cycle*. Proc . 3rd Conf. European Om. Union, Groningen, August 2001. *Ardea*, **90**: 369-378.
- Covino, K.M., K.G. Horton, and Morris, S.R. 2020. Seasonally specific changes in migration phenology across 50 years in the Black-throated Blue Warbler. *Auk*, **137**: 1–11.
- Courter, J.L., R.J. Johnson, W.C. Bridges, and Hubbard, K.G. 2013. Assessing migration of Ruby-Throated Hummingbirds (*Archilochus colubris*) at broad spatial and temporal scales. *Auk*, **130**: 107-117.
- Cristol, D.A. 1995. Early arrival, initiation of nesting, and social status: An experimental study of breeding female red-winged blackbirds. *Behav. Ecol.* **6**: 87–93.
- Dickinson, J.L., B. Zuckerbeg, and Bonter, D.N. 2010. Citizen Science as an Ecological Research Tool: Challenges and Benefits. *Ann. Rev. of Ecol. Evol. and Syst.* **41**: 149–72.
- Drake, A., C.A. Rock, S.P. Quinlan, M. Martin, and Green, D.J. 2014. Wind speed during migration influences the survival, timing of breeding, and productivity of neotropical migrant, *Setophaga petechiai*. *PLoS ONE* **9**: e97152. Doi:10.1371/journal.pone.0097152.

- Gallinat, A.S., R.B. Primack, and Wagner, D.L. 2015. Autumn, the neglected season in climate change research. *Trends Ecol. Evol.* **30**: 169-176.
- Gordo, O. and Sanz, J.J. 2006. Climate change and bird phenology: a longterm study in the Iberian Peninsula. *Global Change Biol.* **12**: 1993–2004.
- Haest, B., O. Huppopp, M. Pol, and Bairlein, F. 2019. Autumn bird migration phenology: A potpourri of wind, precipitation and temperature effects. *Global Change Biol.* **25**: 4064-4080.
- Huang, A.C., C.A. Bishop, R. McKibbin, A. Drake, and Green, D.J. 2017. Wind conditions on migration influence the annual survival of a neotropical migrant, the western yellow-breasted chat (*Icteria virens auricollis*). *BMC Ecol.* **17**: 29.
- Hurlbert, A.H., and Liang, Z.A. 2012. Spatiotemporal variation in avian migration phenology: citizen science reveals effects of climate change. *PLoS One* **7**: e31662.
- Jenni, L., and Kery, M. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proc. R. Soc. Lond. B* **270**: 1467–1471
- Karlsson, H., C. Nilsson, J. Backman, and Alerstam, T. 2012. Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. *Anim. Behav.* **83**: 87–93.
- Kelly, J.F., K.G. Horton, P.M. Stepanian, K.M. de Beurs, T. Fagin, E.S. Bridge, and Chilson, P.B. 2016. Novel measures of continental-scale avian migration phenology related to proximate environmental cues. *Ecosphere* **7**:e01434

- Kemp, M.U., L.E. Emiel van, J. Shamoun-Baranes J, and W. Bouten. 2012. RNCEP: global weather and climate data at your fingertips. *Methods Ecol Evol* 3: 65–70.
(doi:10.1111/j.2041-210X.2011.00138.x)
- La Sorte, F.A., and Graham, C.H. 2020. Phenological synchronization of seasonal bird migration with vegetation greenness across dietary guilds. *J. Anim. Ecol.* **90**: 343-355.
- Mazerolle, M.J. (2020). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1, <https://cran.r-project.org/package=AICcmodavg>.
- McKinney, A.M., P.J. CaraDonna, D.W. Inouye, B. Barr, C.D. Bertelsen, and Waser, N.M. 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology*, **93**: 1987-1993.
- Miller-Rushing, A., T. Lloyd-Evans, R. Primack, and P. Satzinger. 2008. Bird migration times, climate change, and changing population sizes. *Global Change Biology*, 14(9), 1959-1972.
- Moller, A.P. 2013. Long-term trends in wind speed, insect abundance and ecology of an insectivorous bird. *Ecosphere* **4**: 1-11.
- Moller, A.P., D. Rubolini, and Lehikoinen, E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are degrading. *Proc. Nat. Sci. USA* **105**:16195-16200.
- Nathan, R., W.M. Getz, E. Revillac, M. Holyoak, R. Kadmon, D. Saltz, and Smouse, P.E. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences USA*. **105**: 19052–19059.

- Nebel, S., A. Mills, J. D. McCracken, and P. D. Taylor. 2010. Declines of aerial insectivores in North America follow a geographic gradient. *Avian Conservation and Ecology - Écologie et conservation des oiseaux* 5(2): 1. [online] URL: <http://www.ace-eco.org/vol5/iss2/art1/>
- Newson S., Moran N.J., Musgrove, A.J., Pearce-Higgins, J.W., Gillings, S., Atkinson, P.W. et al. 2016. Long-term changes in the migration phenology of UK breeding birds detected by large-scale citizen science recording schemes. *Ibis* **158**: 481–495.
- Nilsson, C., R.H. Klaassen, and Alerstam, T. 2013. Differences in speed and duration of bird migration between spring and autumn. *Am Nat.* **181**: 837-845. doi:10.1086/670335
- Nocera, J.J., J.M. Blais, D.V. Beresford, L.K. Finity, C. Grooms, L.E. Kimpe, K. Kyser, N. Michelutti, M.W. Reudink. and J.P. Smol. 2012. Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous chimney swifts. *Proc. R. Soc. B*. 2793114–3120. <https://doi.org/10.1098/rspb.2012.0445>
- Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Chang. Biol.* **13**: 1860–72.
- Pomfret, J. K., J.J. Nocera, T.K. Kyser, and W.M. Reudink. (2000). Linking population declines with diet quality in Vaux's swifts. *Northwest Science*, 88, 305–313. <https://doi.org/10.3955/046.088.0405>
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

- Reudink, M.W., S.L. Van Wilgenburg, L.S. Steele, A.G. Pillar, P.P. Marra, and McKellar, A.E. 2015. Patterns of migratory connectivity in Vaux's Swifts at a northern migratory roost: A multi-isotope approach. *Condor: Ornith. App.* **117**: 670–682.
- Rubolini, D., Spina, F., and Saino, N. 2004. Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behav. Ecol.* **15**: 592– 601.
- Schwartz, M.D., R. Ahas, and Aasa, A. 2006. Onset of spring starting earlier across the northern hemisphere. *Global Change Biol.* **12**: 343-351.
- Schwitters, L., D. Schwitters, E.L. Bull, and Collins, C.T. 2020. Vaux's Swift (*Chaetura vauxi*), version 1.0. In *Birds of the World* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.vauswi.01>
- Si, Y., Q. Xin, W.F. de Boer, P. Gong, R.C. Ydenberg, and Prins, H.H.T. 2015. Do arctic breeding geese track or overtake a green wave during spring migration? *Sci. Rep.* **5**: 8749. DOI 10.1038/srep08749
- Shuford, W.D., and Gardali, T. 2008. California Bird Species of Special Concern: A Ranked assessment of species, subspecies, and distinct populations of birds of immediate conservation concern in California. *Studies of Western Birds*, **1**: 254-259.
- Smith, E.L., M.W. Reudink, P.P. Marra, A.E. McKellar, Van Wilgenburg, S.L. 2019. Breeding origins and migratory connectivity of a declining aerial insectivore at a northern roost site. *The Condor: Ornithol. App.* **121**: 1-12
- Venables, W.N., and Ripley, B.D. 2002. *Modern Applied Statistics with S*, Fourth edition. Springer, New York. ISBN 0-387-95457-0, <https://www.stats.ox.ac.uk/pub/MASS4/>.

Zaifman, J., Shan, D., Ay, A., and Jimenez, A.G. 2017. Shifts in Bird Migration Timing in North American Long-Distance Migrants Are Associated with Climate Change. *International Journal of Zoology*. 2017: 1-9.

Draft

Figure Legends

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.

Draft

Table 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

Table 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)

Table 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).

	<i>AICc</i>	<i>Delta AICc</i>	<i>AICcWt</i>
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

Draft

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>.

269x190mm (150 x 150 DPI)