

Research Article

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Associations between sex, age and species-specific climate sensitivity in migration

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Abstract: Weather often plays a key role in migration timing, and temporal shifts over the past century have been heavily researched and linked to climate change. Much research is however limited by the use of arbitrary time periods during which weather is thought to most influence migration. Here, we compare the classic fixed window method to a novel sliding window approach created to determine periods of temperature sensitivity among organisms, in this case on the migration phenology of nineteen passerine species banded at the McGill Bird Observatory in Montréal, Québec, from 2005 to 2015. We found overall shorter temperature sensitivity windows in the spring than the fall migration and deemed the non-arbitrarily chosen periods of temperature sensitivity to be more useful than the classic fixed window method when used with caution. We also found significant variation in migration timing of 11 species, as well as more cases of male birds arriving in spring prior to females than the reverse. More males departed in fall before females as well. Similarly, on average, older birds arrived in spring ahead of younger individuals and departed prior to younger in the fall.

Keywords: climate sensitivity window, temperature, temporal shift, phenology, passerine, migration

1 Introduction

Animal movements, such as bird migrations, are often linked to seasonal patterns whereby individuals travel between wintering and breeding grounds to take advantage of seasonal resources, and to avoid predators

and cold weather [1-3]. Harsh winters promote long distance migrations as previously abundant food and habitat become inaccessible [2]. Because the abundance and accessibility of many food resources critically depend on temperature, changes in weather may drive changes in migration timing [4]. Examples of the influence of climate on migration include associations between the timing of emergent insects and migration of insectivorous birds [5-7], and the link between plants leafing and migratory bird arrival [8, 9]. Migrating species may also be influenced during migration by extreme weather conditions (high winds, heavy precipitation), and cold weather can delay birds at stop overs [10, 11]. As such, bird migration may be influenced by both global climate and local weather conditions, driven by altered resource availability or inclement weather inhibiting migration flights [12-14].

Evidence for changes in bird migration mediated by climate is known for both spring and fall migration periods. As spring temperatures increase, insects and plants advance their phenology, driving bird species to do the same or risk asynchrony with their food sources [15, 16]. Concurrently, as fall temperatures increase, insects and plants may be available as food for longer, delaying fall departure as individuals improve their condition to increase survival during migration. For certain species and regions, shifts in plant and insect phenology have already exceeded those of birds' migration [9], as is the case of the pied flycatcher *Ficedula hypoleuca* [17] and the great tit *Parus major* [18]. In Delta Marsh, Manitoba, Canada, shifts to earlier spring arrival dates of 43 species were significantly related to increasing temperatures between 1939 and 2001 [19]. Similarly, between 1975 and 2000, over a dozen species (two significantly) showed an overall trend for earlier spring arrival in southern Ontario, Canada [20]. While data on shifts in migration phenology are generally less available for the fall migration [21], research from southern Ontario, Canada, demonstrated that six species have significantly moved their migration to later in the fall over the same 25-year period [20]. Migratory shifts in fall may also be more variable than those of spring, as two other species in the same study showed evidence of significantly earlier

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fall migrations over the same time period [20]. Similar patterns in altered migration have been recorded around the world [22]. Some temporal patterns appear to be linked with the distance traveled by species; early fall departure has mostly been observed in long-distance migrants, while larger numbers of short-distance migrants tend to show delayed departure in fall [21, 23, 24]. Further variation can be found even within single species, as age and sex groups may migrate discretely [20].

Variation in climate-induced migratory patterns may be associated with intrinsic factors, such as sex and age. Sex is well documented in its influence on migration phenology [25, 26]. Protandry is a common phenomenon wherein male birds commonly arrive at, and depart, breeding grounds prior to female birds [27-29]. The opposite effect, protogyny, has also been documented, usually in species where the female defends the territory instead of the male [30-32]. Sex-differentiated migration is therefore likely linked to territorial control, as in most species males need to migrate earlier to secure good territories [30].

A similar differentiation in migration occurs with an individual's age. In many species, older birds complete their migration before younger ones, likely due to the latter's inexperience [33-35]. For example, juvenile savannah sparrows (*Passerculus sandwichensis princeps*) take longer migratory routes than adults [36]. In many species, younger birds also tend to remain longer on their winter territory than older birds [29, 37]. This may be a consequence of younger birds occupying low quality habitats on wintering grounds, and thus needing more time to accumulate fat storage prior to migration, or an intended delay by individuals in lower condition to avoid harsh early spring weather [38-40]. Given migration differentiation due to both sex and age, older males should be the earliest migrants [29, 33, 37, 41], leading to uneven distribution of both age and sex classes within migration. Evaluating temporal changes within a population's or species' migration thus requires the consideration of multiple influential factors.

Several methods have been used to evaluate temporal variation in migration. One common parameter used is the first arrival date (FAD) in spring and last departure date (LDD) in fall, where the first and last sighting of a bird is compared throughout the years of interest [14, 19, 20, 42]. Yet FADs and LDDs represent only a portion of migrating species' populations, especially given that males and females—and old and young birds—tend to migrate separately [20, 33, 43]. Thus, without differentiation of the age and sex of migrating individuals, biases are inherent in the data. It is also more difficult to determine the fall LDD of a species than

the spring FAD when using observation data sets, as observers better recall their first spring sighting of a bird than their last fall sighting, though both may be heavily influenced by observer effort [20, 44]. To provide a more comprehensive examination, migration can additionally be separated into multiple periods, to help determine when migration is most responsive to a particular variable of interest [20, 45]. For instance, the earliest birds in spring, and latest birds in fall, are likely to be most responsive to weather patterns because they are more likely to encounter extreme conditions [39, 46, 47].

In this study, we examined how timing of migration responded to climate across an 11-year period for 19 passerine species migrating through southern Québec, Canada to determine associations of spring and fall migration with local temperature, and individual sex and age. We used the R package *Climwin* [48, 49] to determine species-specific periods of sensitivity to local temperature via a sliding window method [50-53]. Previous research used large and somewhat arbitrary time periods, usually the months during and preceding migration, therefore using a single fixed window to explain effects for many species [19, 24, 42, 44]. We also investigated whether those species with similar climatic window sizes and shifts in migratory timing share natural history characteristics, specifically, distance traveled during migration, main food resources, and breeding location (i.e., local vs. boreal breeders).

2 Methods

2.1 Data Collection

Data was collected in southern Québec, Canada, at the McGill Bird Observatory, located at McGill University's 22-hectare Stonecroft Wildlife Area, in Sainte-Anne-de-Bellevue, Québec (see Figure 1). The McGill Bird Observatory has been operating since 2004, and runs standardized spring and fall migration monitoring programs, which include daily banding, a standardized census, and incidental observations. During banding operations, birds are caught in 16 mist-nets during a five-hour period, starting 30 minutes before sunrise. The spring program runs for 45 consecutive days from mid-April to early June, and the fall program runs 90 consecutive days from early August to late October. A census observer, licensed bander, and numerous volunteers collect the data using consistent methods [57]. Data used for this study was limited to banding data.

Local mean daily temperature data was obtained from the J.S. Marshall Radar Observatory in Sainte-Anne-

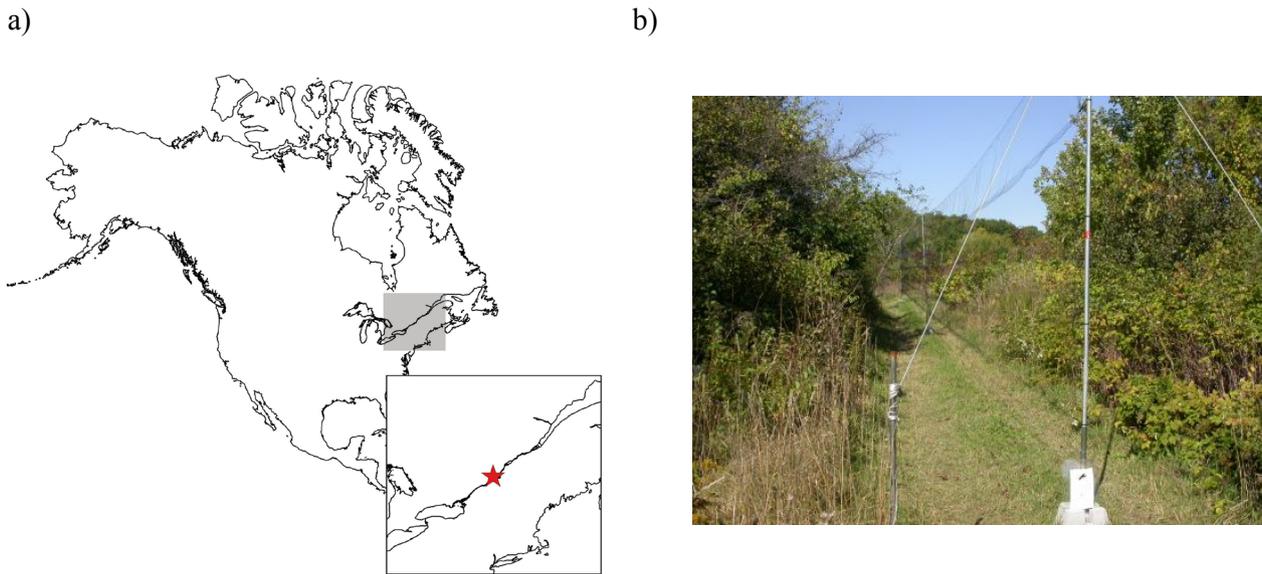


Figure 1. McGill Bird Observatory. a) Map of North America with inset showing the location of the McGill Bird Observatory (star), created with QGIS. b) An open mist net during banding operations (photo Marcel Gahbauer).

de-Bellevue. To fill data gaps that were incurred due to maintenance on the radar, we used linear relationships between the data from this station and from the Montreal/Pierre Elliott Trudeau International weather station in Dorval, 14 kilometers away, after first confirming that both datasets were correlated ($R^2_{\text{temperature}} = 0.997$). We accessed both stations' information from the Government of Canada website (http://climate.weather.gc.ca/index_e.html).

2.2 Study Species

We limited our list of study species to migrant passerines banded in every spring and fall from 2005-2015, with over 300 individual captures each, resulting in 19 species total. These were sorted into the following categories, i) local (breeding in the local area) vs. boreal breeders (at least 50% of North American population breeding further north, as described by the Boreal Songbird Initiative (<http://www.borealbirds.org>)), ii) long distance migrants (i.e., overwintering in Central or South America) vs. short distance migrants (i.e., at least part of the population winters in North America) as described by the Cornell Lab of Ornithology's Birds of North America (<https://birdsna.org/Species-Account/bna/home>) and iii) insectivorous vs. granivorous (as described by the Cornell Lab of Ornithology's Birds of North America).

2.3 Pre-analysis Data Treatment

We used data from the years 2005 to 2015 inclusively. Banding occurred each year from April 16th to June 4th (spring) and August 1st to October 31st (fall). For the sliding window method portion of our analyses, we used presence data from April 15th to June 15th (spring) and July 15th to November 15th (fall), to fully encompass the dates when banding occurred. When analyzing a species' presence for this approach, we used the binomial method and assigned a value of 1 to each day that an individual of the species was banded and 0 to a day that none were banded (including those outside of the banding period). Similarly, when performing sliding window analyses with age and sex, dates were assigned a 1 on days when the studied sex (male or female) or age (old or young) was banded. During the spring migration, we considered a second-year individual a young bird, and an after-second year an old bird [58]. In the fall, a young bird was a hatch-year, while an after-hatch year bird was an older individual [58]. We separated the species' migration distributions into periods by calculating the 10th, 50th and 90th percentile passage dates (hereafter, timing measures) for both seasons. The FADs for spring and the LDDs for fall were noted, and we calculated an average median capture date across the study period for each species in both seasons.

2.4 Statistical Analysis

2.4.1 Climate sensitivity window

We performed all statistical analyses with R version 3.2.4 [59]. Average values are reported with \pm SD. Climwin [48, 49] is an R package created to determine a climate sensitivity window, or time period where climate most affects a biological response of interest. Climwin uses a sliding window approach, that is, the program varies the start and end dates of an interval of days to examine every possible window of climate. The program then allows users to determine which of these climate windows best explains the occurrence of a response of interest, by ranking the windows via model goodness-of-fit (AICc weights) [48, 49]. In our research, the climate data was the mean daily temperature, and the response of interest was the passage of a species at the bird observatory in southern Québec. In other words, this program can tell us over which days (hereafter, window) local temperature most affected when a species would be present at the observatory. We set the program to create and compare windows starting as far as 150 days before the bird's presence to 30 days after in both spring and fall migrations. The analysis outputs the open and close dates of the best-fit climate windows and the effect size, which in our case is how many days earlier or later a species' arrival at the observatory varies per degree of temperature change (unit: days/°C).

We examined the association of local temperature with the migration phenology over the 11-year period for each species (including all age and sex classes), as well as for sex and age classes separately. We compared both sexes' species-specific sensitivity windows' sizes and shifts in migration timing (days/°C) using Student's t-test for normally distributed data (R library stats, function `t.test`, R Development Core Team 2016) and Mann-Whitney-Wilcoxon test for non-normally distributed (R library stats, function `wilcox.test`, R Development Core Team 2016). The same was done to compare both ages' window sizes and shifts in migration timing. We used generalized linear models (R library stats, function `glm`, R Development Core Team 2016) to examine how diet, migration strategy and breeding status (both separately and together as predictor variables) affect the size of species-specific sensitivity windows, as well as how they have affected any shifts in migration.

Finally, the main purpose of the sliding window method in our research is to find windows of time when local daily temperature most influence presence at the banding site. These species-specific sensitivity windows are meant to replace the larger, months-long fixed periods

typically used in past literature to examine weather's effect on migration: spring months preceding and during migration (01 March to 31 May) [19, 42, 44] and fall months during migration (01 August to 31 October) [10, 24]. To compare the sliding window method to the fixed windows, we performed two sets of regression analyses: i) median arrival date of a species vs average temperature during the species-specific sensitivity window for 2005-2015, and ii) median arrival date vs the average temperature of the fixed window for 2005-2015. Using a paired t-test (R library stats, function `t.test`, R Development Core Team 2016), we compared the means of the resulting trendline slopes and R^2 values from both these sets of graphs to determine how strongly the sliding and fixed windows differ. We also compared each species' sensitivity window and timing shift to its average migration length.

2.4.2 Timing of migration

We evaluated multicollinearity using the Pearson product-moment correlation coefficient among the representative timing measures (FAD, 10th, 50th, 90th spring and fall quantiles and LDD) (R library stats, functions `pairs` and `cor.test`, R Development Core Team 2016). The correlation matrix revealed that none of the important timing measures were consistently correlated with each other across all species, as such all were included in subsequent analyses. We used a Pearson's correlation test (R library stats, function `cor`, R Development Core Team 2016) between year and each of the representative timing measures to determine whether any species had arrived earlier, later or remained unchanged over the years. We performed Fisher's exact tests (R library stats, function `fisher.test`, R Development Core Team 2016) to determine whether diet, migration distance, or breeding location were significantly associated with variation in migratory phenology.

To compare males and females, we included only the nine species where more than 67% of individuals captured were identified to sex level. We used generalized linear models (binomial link) to examine the effect of sex and year on the migration phenology (described as presence or absence) (R library stats, function `glm`, R Development Core Team 2016). Similarly, we compared older birds and younger ones for the 19 species, all of which had more than 67% of captures identified to age level. We used generalized linear models (binomial link) to examine the effect of age and year on the migration phenology (R library stats, function `glm`, R Development Core Team 2016). We also used general linear models to check for

interactions between sex and age affecting the timing of spring arrival or fall departure for these nine species.

We predicted that spring arrival dates will be negatively correlated with temperature, while fall departure dates will be positively correlated [20]. For species with sex and age data available, we also predicted that males and older birds migrate before females and younger birds [30, 33]. We predicted that the climate window would be narrower in spring than fall, for adults than juveniles, and for males than females, given that birds in the former groupings face the strongest pressures for migration. We also predicted that short-distance migrants, local breeders and granivores would have longer climate windows than long-distance migrants, boreal breeders and insectivores, because the latter groups must move faster to reach their more distant breeding grounds or follow their emerging food source. Given that significant warming can be seen at the global scale through the latter half of the 20th century [54, 55], and temperatures have continued to increase [56], understanding how climate influences bird migration could allow us to predict how future fluctuations may alter these movements.

3 Results

A list of species with their total sample size, diet, breeding and migration classifications appears in Table 1 of the Supplemental Material.

3.1 Sliding Window Approach

The average temperature sensitivity window's length in spring was 38 ± 43 days and the average migration shifted earlier by 0.21 ± 0.05 days/ $^{\circ}$ C. In the fall, the sensitivity window's length averaged 105 ± 26 days and migration shifted later by 1.08 ± 0.38 days/ $^{\circ}$ C. The best climate window for each species is listed in Table 1, and the illustrations of each species-specific sensitivity window and model goodness-of-fit (AICc model weight) can be found in the Supplemental Material. The average temperature sensitivity window for each sex showed the male's spring migration was 25 ± 23 days, with migration moving earlier by 0.19 ± 0.08 days/ $^{\circ}$ C, while the female's window was 15 ± 12 days and shifted earlier by 0.12 ± 0.17 days/ $^{\circ}$ C. In the fall, the male window size was 82 ± 39 days and their migration shifted later by 1.09 ± 0.39 days/ $^{\circ}$ C, and the female was 101 ± 23 days and shifted later by 0.96 ± 0.30 days/ $^{\circ}$ C (see Figure 2).

During spring migration, blackpoll warblers (*Setophaga striata*) experienced the largest shift, migrating earlier by 0.33 days/ $^{\circ}$ C. The white-crowned sparrow (*Zonotrichia leucophrys*) experienced the smallest shift, migrating earlier by 0.12 days/ $^{\circ}$ C. During fall migration, magnolia warblers (*Setophaga magnolia*) shifted the most, migrating later by 1.64 days/ $^{\circ}$ C, and common grackles (*Quiscalus quiscula*) experienced the smallest shift, moving later at 0.29 days/ $^{\circ}$ C.

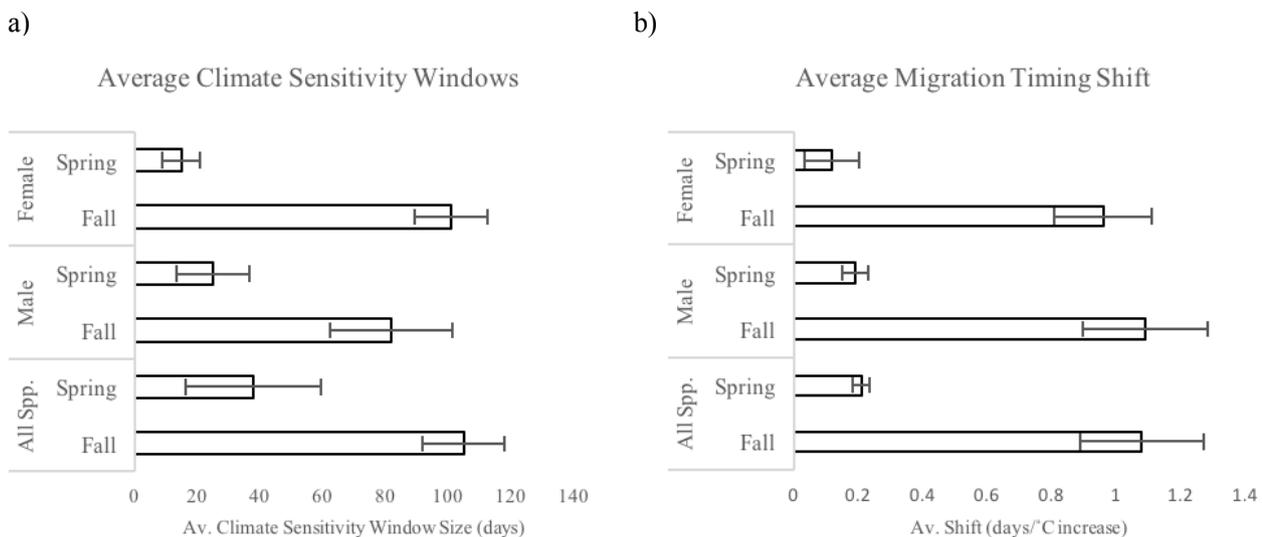


Figure 2. Sliding window analysis seasonal comparisons. Comparisons between spring and fall migration of average temperature sensitivity window length (left) and average migration timing shift (right), from sliding window method for all species ($n = 19$) and between males and females ($n = 9$). Standard deviation presented as error bars.

Table 1. Passerine species and their best climate sensitivity window model (temperature as predictor variable). The window close and open dates are the day of the examined timeframe where the period of sensitivity begins and ends, with positive values being days before the presence of a species at the observatory and negative being days after a species is present. Window size is the number of days between the open and close days, and the shift is the number of days the migration shifts for each °C increase over the 11-year period (negative value shifts earlier; positive shifts later).

Species	Window Open	Window Close	Window Size	Temperature mediated shift (days)
Spring				
Red-eyed vireo	128	119	9	-0.23
Ruby-crowned kinglet	114	-25	139	-0.29
Gray catbird	125	109	16	-0.18
Northern waterthrush	129	100	29	-0.26
Tennessee warbler	127	111	16	-0.29
Nashville warbler	117	108	9	-0.15
Common yellowthroat	126	108	18	-0.18
American redstart	128	118	10	-0.23
Magnolia warbler	128	110	18	-0.22
Yellow warbler	122	104	18	-0.2
Blackpoll warbler	131	108	23	-0.33
Myrtle warbler	119	73	46	-0.18
Wilson's warbler	115	-27	142	-0.24
White-crowned sparrow	115	108	7	-0.12
White-throated sparrow	130	117	13	-0.21
Song sparrow	37	-30	67	-0.19
Swamp sparrow	18	-28	46	-0.21
Baltimore oriole	116	112	4	-0.13
Common grackle	150	63	87	-0.18
Fall				
Red-eyed vireo	117	-30	147	1.10
Ruby-crowned kinglet	124	27	97	1.55
Gray catbird	114	-27	141	0.87
Northern waterthrush	95	-21	116	1.20
Tennessee warbler	116	-26	142	1.29
Nashville warbler	98	0	98	0.95
Common yellowthroat	108	-24	132	1.41
American redstart	99	-30	129	1.49
Magnolia warbler	98	-5	103	1.64
Yellow warbler	57	-27	84	0.82
Blackpoll warbler	79	36	43	1.13
Myrtle warbler	117	22	95	1.33
Wilson's warbler	90	0	90	1.26
White-crowned sparrow	123	29	94	1.24
White-throated sparrow	110	23	87	0.76
Song sparrow	106	-1	107	0.72
Swamp sparrow	98	16	82	0.31
Baltimore oriole	75	-30	105	1.17
Common grackle	107	15	92	0.29

Five of the glm tests examining the effect of diet, breeding status and/or migration distance on the temperature sensitivity window and on the shift in migration returned significant results. Tests with single predictor variables in spring showed that temperature sensitivity window length was shorter for insectivores than granivores ($t_{18} = -2.17$, $p = 0.044$), while longer for short-distance migrants than long-distance ones ($t_{18} = 2.45$, $p = 0.025$). Insectivores also shift for later departures with higher temperatures in fall ($t_{18} = 3.78$, $p = 0.002$). An earlier median migration date in spring significantly increased temperature sensitivity window size ($t_{18} = -4.48$, $p < 0.001$), and a test combining diet, status and migration distance together as predictor variables also showed significance ($t_{18} = 2.93$, $p = 0.010$), linking insectivores to later fall departures in warmer years.

Regressions between median arrival date of each species and the average temperature during species-

specific sensitivity windows were compared via a Student's paired t-test to regressions of median arrival date and average temperature during fixed windows. Comparing their slopes and R^2 values showed non-significantly different means in both ($t_{37} = -0.65$, $p = 0.521$, $t_{37} = -0.42$, $p = 0.679$). A Pearson's correlation showed a weak positive correlation between the two groups' slopes $r_{36} = 0.49$, $p = 0.002$ (Figure 3), and an even weaker negative one between the R^2 values $r_{36} = -0.10$, $p = 0.536$. In both spring and fall, neither the sex nor age classes were significantly different one from the other in terms of the length of sensitivity window or the size of shift. The temperature sensitivity window length correlated with the average migration length (spring: $r_{17} = 0.64$, $p = 0.003$; fall: $r_{17} = 0.29$, $p = 0.236$) while timing shift also correlated with average migration length (spring: $r_{17} = 0.10$, $p = 0.687$; fall: $r_{17} = -0.36$, $p = 0.125$).

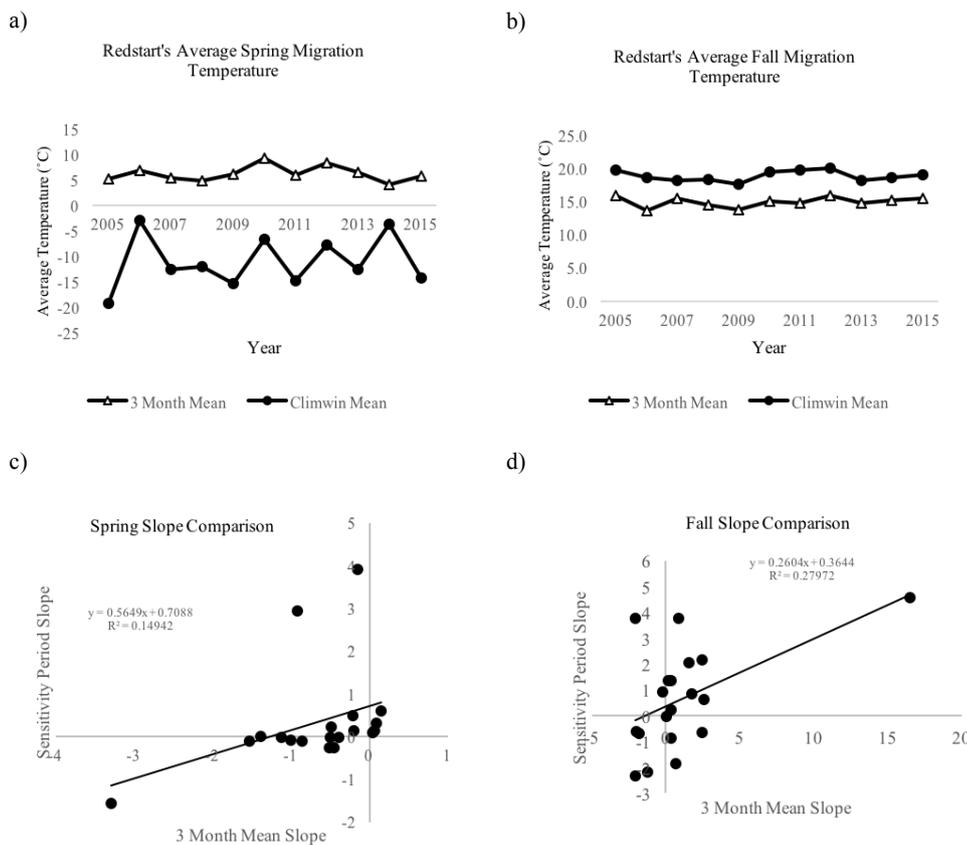


Figure 3. Sliding window approach compared to typical results. Top: The average temperature across the 3 month mean (March-May in spring, August-October in fall) typically used to determine the influence of weather on migration is compared each year against the average temperature of the American redstart's period of temperature sensitivity from the sliding window analyses during (a) spring and (b) fall migration (redstart photo Simon Duval). The period of temperature sensitivity is colder and more variable from year to year in the spring, and generally more stable and warmer in the fall. Bottom: Comparisons between two sets of regression slope values i) slopes from comparing the median arrival date to average best fitted window temperature and ii) slopes from comparing median arrival date vs the 3 month mean temperatures, for all species ($n = 19$) in (c) spring and (d) fall migration, depicting little similarity between the two methods. temperatures, for all species ($n = 19$) in (c) spring and (d) fall migration, depicting little similarity between the two methods.

3.2 Variation in Timing of Migration

A total of 11 of the 19 species demonstrated a significant change in the timing of their spring or fall migration over the 11-year period examined (Table 2), but no species had an entire season's timing measures (all of: 10th, 50th, 90th and LDD or FAD) of their migration change significantly, and none moved towards a later spring migration over time. The American redstart (*Setophaga ruticilla*) had the most variation in migration timing, arriving earlier at the FAD, 10th, and 50th spring quantiles, and the 10th and 50th fall quantiles; its LDD shifted later. The redstart was one of three species whose FAD moved earlier. There was no significant association between migration distance and breeding location and variations in migration timing.

Comparatively, there was a significant association between changes in migration timing and feeding habits, with 10 of 14 insectivores showing significant differences (Fisher's exact test, $p = 0.020$), and only one out of five granivores, the white-throated sparrow (*Zonotrichia albicollis*), showing evidence of a temporal change in migration.

3.3 Sex and Age Distributions

Males arrived significantly before females in the spring for eight of the nine species tested, the exception being the Baltimore oriole (*Icterus galbula*). In the fall, three of the nine species had males departing significantly

Table 2. Passerine species with significant changes in timing measures of their migration between 2005-2015 in southern Québec, Canada. Timing measures included: first arrival date of a species on site in spring (FAD), last departure date of a species in fall (LDD), and the 10th, 50th and 90th percentile passage dates for both spring and fall migrations, i.e. dates after which 10, 50 and 90% of the total population migrated through.

Species	Timing Measure	Pearson's r coefficient	p-value	Average change (days/year)	Direction of change
Red-eyed vireo	FAD	-0.75	0.008	0.5	earlier
Red-eyed vireo	Spring 10th	-0.75	0.008	0.5	earlier
Northern waterthrush	Spring 50th	-0.67	0.024	0.3	earlier
Tennessee warbler	Fall 10th	0.65	0.032	1	later
Nashville warbler	Spring 90th	-0.73	0.011	1.4	earlier
Common yellowthroat	Spring 50th	-0.68	0.021	0.2	earlier
Common yellowthroat	Fall 50th	-0.63	0.038	0.6	earlier
American redstart	FAD	-0.82	0.002	1	earlier
American redstart	Spring 10th	-0.68	0.021	0.2	earlier
American redstart	Spring 50th	-0.60	0.051	0.6	earlier
American redstart	Fall 10th	-0.63	0.036	0.6	earlier
American redstart	Fall 50th	-0.75	0.007	1.1	earlier
American redstart	LDD	0.77	0.005	1.4	later
Magnolia warbler	Spring 50th	-0.78	0.005	1	earlier
Magnolia warbler	Spring 90th	-0.61	0.044	0.8	earlier
Magnolia warbler	Fall 50th	0.81	0.002	1.2	later
Myrtle warbler	Spring 90th	-0.75	0.007	0.9	earlier
Myrtle warbler	Fall 90th	0.68	0.022	0.5	later
Wilson's warbler	FAD	-0.68	0.021	0.9	earlier
Wilson's warbler	Fall 10th	0.75	0.007	1.1	later
Wilson's warbler	Fall 50th	0.90	<0.001	1.4	later
White-throated sparrow	Fall 10th	0.78	0.004	0.6	later
White-throated sparrow	Fall 50th	0.93	<0.001	0.9	later
Baltimore oriole	Spring 50th	-0.67	0.025	1	earlier

before females, and two had females leaving before males (Table 3). Older birds arrived significantly earlier than young birds in the spring for 12 of the 19 species tested. In the fall, eight of the 19 had older birds departing earlier than young birds, and two had younger leave before older (Table 4). Breeding location, migration strategy and diet had no effect on the spring arrival time of either sex or

age classes, nor on their fall departure time. Only three of the nine species tested, American redstart, common yellowthroat (*Geothlypis trichas*) and Nashville warbler (*Oreothlypis ruficapilla*), showed a significant interaction between sex and age affecting capture dates, all three during the fall season ($t = -2.85$, $p = 0.004$; $t = 3.68$, $p < 0.001$; $t = -2.30$, $p = 0.022$).

Table 3. Passerine species with significant sex differentiation in migration timing between 2005-2015 in southern Québec, Canada. Earlier group indicates which sex arrived before the other in spring and which sex departed first in the fall.

Species	Migration	t-value	df	p-value	Earlier group
Ruby-crowned kinglet	Spring	-27.01	601	<0.001	Males
Nashville warbler	Spring	-2.44	114	0.016	Males
Common yellowthroat	Spring	-6.22	329	<0.001	Males
American redstart	Spring	-2.32	132	0.021	Males
Yellow warbler	Spring	-2.47	530	0.013	Males
Myrtle warbler	Spring	-8.02	483	<0.001	Males
Wilson's warbler	Spring	-2.75	213	0.006	Males
Common grackle	Spring	-3.01	242	0.002	Males
Ruby-crowned kinglet	Fall	11.4	3351	<0.001	Males
Nashville warbler	Fall	-1.98	724	0.047	Females
Yellow warbler	Fall	-2.00	226	0.045	Females
Myrtle warbler	Fall	9.14	5154	<0.001	Males
Wilson's warbler	Fall	4.15	333	<0.001	Males

Table 4. Passerine species with significant age differentiation in migration timing between 2005-2015 in southern Québec, Canada. Earlier group indicates which age class (younger or older) arrived before the other in spring and which departed first in the fall.

Species	Migration	t-value	df	p-value	Earlier group
Gray catbird	Spring	-4.07	176	<0.001	Older
Tennessee warbler	Spring	-4.01	578	<0.001	Older
Nashville warbler	Spring	-3.55	115	<0.001	Older
Common yellowthroat	Spring	-5.26	327	<0.001	Older
American redstart	Spring	-3.72	111	<0.001	Older
Magnolia warbler	Spring	-7.00	413	<0.001	Older
Yellow warbler	Spring	-1.55	534	<0.001	Older
Blackpoll warbler	Spring	-2.30	230	0.022	Older
Wilson's warbler	Spring	-2.98	216	0.003	Older
White-crowned sparrow	Spring	-2.45	132	0.015	Older
Swamp sparrow	Spring	-2.69	162	0.007	Older
Baltimore oriole	Spring	-7.57	206	<0.001	Older
Red-eyed vireo	Fall	-12.10	879	<0.001	Younger
Ruby-crowned kinglet	Fall	2.70	3326	0.006	Older
Tennessee warbler	Fall	-9.94	1103	<0.001	Younger
Common yellowthroat	Fall	4.12	961	<0.001	Older
American redstart	Fall	7.74	1284	<0.001	Older
Magnolia warbler	Fall	16.8	2230	<0.001	Older
Wilson's warbler	Fall	4.95	342	<0.001	Older
White-crowned sparrow	Fall	1.97	427	0.049	Older
White-throated sparrow	Fall	5.13	3686	<0.001	Older
Song sparrow	Fall	2.55	2454	0.010	Older

4 Discussion

Our study examined shifts in migration phenology of passerines species, and both the sensitivity to, and relationship with, changing climate over time. Even in the relatively short time period (11 years) we investigated, more than half of the 19 passerine species demonstrated significant changes in their migration phenology; overall spring arrival dates have moved earlier, while fall departures have varied considerably. Using a novel analytical technique, we present the time window in climate that most clearly predicted the timing of migration for migratory birds, and the relationship between migration phenology and climate. Our findings support the general trends observed of migratory phenology shifting with warmer temperatures to earlier spring migration and some delayed migration in fall [19, 20], and provides additional information on variation of climate-associated phenological changes and aspects of species' ecology. Lastly, we demonstrate additional evidence of sex and age-differentiated migration, and species-specific shifts in migration timing.

4.1 Climate sensitivity windows and changes in migration phenology over time

As predicted, we found that temperature sensitivity windows were shorter in the spring than the fall. We also found shifts for earlier migration in the spring and shifts for later migration in the fall. The effect of temperature on the change in migration phenology was nearly three times as strong in the fall than in the spring. This suggests greater plasticity in the timing of fall migration compared to the spring, likely because fall migration is generally slower (even months longer [60]), due to slower traveling speeds [61] and prolonged stays at stopover sites [62], because there are fewer constraints on the timing of fall migration than on spring's. While non-significant, the average male's sensitivity window for the effects of temperature is longer than the female's in spring, but reversed in the fall, perhaps due to the pattern of inexperienced males making their first journey back to their breeding grounds in spring, but returning to their wintering grounds more quickly as adult males to claim good territories in fall [30, 36].

We found several notable effects of diet, breeding status, and migration distance on the length of temperature sensitivity windows and shifts in migratory phenology. Short-distance migrants had significantly longer spring temperature sensitivity windows than

long-distance migrants, which may be attributed to a shorter travel distance to reach their breeding grounds; they may be less pressed and more likely to delay when faced with poor weather [21, 63]. Similarly, insectivores had significantly shorter spring temperature sensitivity windows than granivores; perhaps insectivores closely followed warming temperatures and emerging insects [64]. These insectivorous birds were also more likely to remain on their breeding grounds with warmer fall temperatures, potentially making use of extended feeding opportunities. Species with earlier median migration dates tended to have longer sensitivity windows in fall, implying that those that migrate earlier in the season can be influenced by temperature for longer periods of time. When diet, breeding status and migration distance were looked at together as predictor variables, an insectivorous diet influenced temperature-mediated migration shifts in the fall, again shifting towards later departure.

While using the sliding window method identified a specific temperature sensitivity window for each species, the analytical difference between using the specified window vs. an arbitrarily derived and fixed climate window in further migration phenology research remains unclear from our findings. Our analyses comparing the results using either the species-specific window's dates or the arbitrarily derived three-month fixed window (March-May or August-October) failed to reveal any significant differences. Similarly, only weak links were seen when looking at each species' average migration length against the size of its temperature sensitivity window or of its timing shift, suggesting that the length of the sensitivity period or the size of the shift is not simply dictated by the length of a species' migration period. The spring sensitivity window was the only one significantly positively correlated to migration length, such that a longer migration period is related to longer periods of temperature sensitivity in this season. We must also note that we are limited by locality, as the local weather in southern Québec cannot realistically be expected to accurately depict conditions where long distant migrants begin their migration; some species' periods of climate sensitivity begin while the individuals are too far to be influenced by local weather. The method is necessarily correlative (we did not experimentally manipulate climate) and it is possible that timing of migration at our study site is largely the consequence of decisions made based on climate at distant wintering sites. Yet, our findings clearly show that there are windows in time that far better predict the associations seen between shift in migration phenology and climate, and we suggest that

future research could be improved making use of these species-specific climate sensitivity windows.

4.2 Sex- and age-differentiated migration

In agreement with the well-described phenomenon of protandry evident in several studies [29, 32], we found that males arrived significantly before females during spring migration in almost all of our studied passerine species with available data. Since males almost exclusively defend a territory among these species, these findings concur with research that links protandry to territorial control [30-32]. The only species where no significant difference was found between the sexes is the Baltimore oriole. The males of this species differ from the others in that they defend much smaller breeding territories, and will share foraging territories [65, 66].

Similar to the findings during the spring migratory period, the departure dates of the nine species in the fall showed three with a significant trend for males departing prior to females, and two with females departing before males. This is a higher proportion of sex-differentiated species than has previously been seen in fall [28, 67]. The fall migration is generally slower than the spring's because of reduced traveling speeds and long stopovers, as previously discussed [60-62]. The spring migration is generally more sex-differentiated than the fall [21, 28], which is known for some cases of protogyny (females departing first) [31, 32], consistent with our results.

We found that older birds arrived significantly before younger ones in 12 of 19 species (spring), and departed before younger in 8 of 19 (fall) during our study period. Younger birds departed before older in only two species in fall. No life history trait was strongly linked to a species having older birds arrive earlier. Our results support previous evidence that age-differentiated migration is more prevalent in the spring than the fall [33], possibly because of common errors in correctly aging young individuals [68], but likely due to the migration to the wintering ground being less rushed than the arrival on the breeding territories [61, 62]. In addition, young hatch year birds in fall usually wait longer than older birds before beginning their first migration, because of their slower fat accumulation [69].

Studying the interaction between sex and age for each species revealed that older male American redstarts or Nashville warblers are likely to migrate early in the fall, while older male common yellowthroats tend to migrate later. This latter species does not usually show differential age migration timing in fall [70].

4.3 Cases of species-specific variation in migration timing

One particularly interesting case was the locally breeding, long-distance traveling American redstart. The American redstart demonstrated the greatest changes for both spring and fall migrations of any species. In spring, three of the redstart's four timing measures moved significantly earlier; only its 90th quantile remained relatively constant. The earlier redstart migration may be linked directly to food availability, as this species is known to take advantage of emerging aquatic insects, an important early food source [40]. For the fall, the redstart has moved its LDD significantly later, as expected for a species that may wish to take advantage of extended warmth and insects [20, 24]. Interestingly, redstarts are not considered multi-brooded, a characteristic often associated with later fall departures [20, 23]. This discrepancy could partially explain why the redstart's 10th and 50th fall quantiles moved significantly earlier, while their LDD has moved later; the birds have been arriving and breeding earlier since 2005, but since they only raise a single brood, the adults finish their reproductive cycle quickly and depart early [37]. Many hatch year birds with little experience are left behind and prolong their time on the breeding grounds while the extended warmth keeps the area accessible [20, 24, 71], which may explain this species' later LDD and significantly age-differentiated migration.

Another species of note is the white-throated sparrow, the only granivorous bird of five in this study to have significantly altered its migration temporally. Its 10th and 50th fall quantiles moved later, suggesting that more individuals are delaying their flight to the wintering grounds. Some research shows that this species switches to a more insect-based diet in the fall before migrating to wintering grounds [72]. We hypothesize that perhaps the species is extending its time on the breeding grounds during the increasingly warmer fall months to take advantage of the mix of available food resources, thus delaying its migration southwards.

While bird migration is an extensively studied phenomenon, newly emerging technologies, analytical methods, and growing long-term datasets will undoubtedly revolutionize our understanding in the future. Our study demonstrates the use of a new statistical tool to determine species-specific periods of climate sensitivity during migration, quantify the direction and magnitude of the climate-associated shifts in migration over time, and provides information in how these climate-sensitivity windows and climate-associated migration shifts may vary with species' ecology. Our research also

demonstrates that temporal change of migration can occur over relatively short periods of time among passerine species, and adds support for well-known age and sex differentiations in migration phenology. We suggest that further research linking climate and bird migration may well make use of climate-sensitivity windows, and that more work is needed to understand both the correct spatial and temporal-scale of climate data.

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