RESEARCH ARTICLE

Factors influencing fall departure phenology in migratory birds that bred in northeastern North America

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ABSTRACT

The phenology of migrating birds is shifting with climate change. For instance, short-distance migrants wintering in temperate regions tend to delay their migration in fall during spells of warmer temperature. However, some species do not show strong shifts, and the factors determining which species will react to temperature changes by delaying their migration are poorly known. In addition, it is not known whether a slower migration or a postponed departure creates the observed delays in fall migration because most studies occur far south of the boreal breeding areas making it difficult to separate those 2 mechanisms. We used 22 yr of data at a northern observatory in eastern North America, at the southern edge of the boreal forest, to examine how 21 short-distance migrants responded to changing temperatures. We investigated if those species responding to temperature share life-history features (i.e. diet, size, total migration distance, breeding habitat, timing of migration). The period of migration in each species was, by far, the most important factor predicting the response of a species to temperature. Eight of the 13 species migrating in October changed their migration onset with temperature (usually by delaying migration by 1–2 days/°C), while the migration timing of none of the 8 species migrating in September was dependent on temperature. Furthermore, the absence of a greater migration delay by birds breeding farther from the study site (i.e. Arctic-breeding birds) suggests the mechanism is a postponed departure rather than a slower migration. We conclude that temperature variations in late fall influence the conditions on the breeding grounds, so that birds still present at that time benefit more from postponing their departure in warm weather.

Keywords: climate change, migration, phenology

Facteurs influençant la phénologie du départ automnal chez les oiseaux migrateurs se reproduisant dans le nord-est de l'Amérique du Nord

RÉSUMÉ

La phénologie des oiseaux migrateurs évolue avec les changements climatiques. Par exemple, les migrateurs de courte distance qui hivernent dans les régions tempérées tendent à retarder leur migration à l'automne pendant les périodes où la température est plus chaude. Toutefois, certaines espèces ne présentent pas de forts changements et les facteurs qui déterminent quelles espèces réagiront aux changements de température en retardant leur migration sont peu connus. De plus, on ne sait pas si une migration plus lente ou un départ différé est à l'origine des retards observés pendant la migration automnale car la plupart des études ont lieu loin au sud des aires de reproduction boréales, rendant difficile la séparation de ces deux mécanismes. Nous avons utilisé 22 ans de données d'un observatoire du nord-est de l'Amérique du Nord, à la limite sud de la forêt boréale, afin d'examiner la réaction de 21 migrateurs de courte distance aux changements de température. Nous avons cherché à savoir si ces espèces réagissant à la température avaient des caractéristiques biologiques en commun (i.e. régime alimentaire, taille, distance totale de migration, habitat de reproduction, moment de la migration). La période de migration de chaque espèce était de loin le facteur le plus important prédisant la réaction d'une espèce à la température. Huit des 13 espèces migrant en octobre ont changé leur début de migration en fonction de la température (habituellement en retardant la migration de 1–2 j/°C), alors que le moment de la migration d'aucune des huit espèces migrant en septembre ne dépendait de la température. De plus, l'absence d'un plus grand retard dans la migration des oiseaux se reproduisant plus loin de la zone d'étude (i.e. oiseaux nichant dans l'Arctique) suggère que le mécanisme est un départ différé plutôt qu'une migration plus lente. Nous concluons que les variations de température à la fin de l'automne influencent les conditions sur les aires de reproduction, de sorte que les oiseaux qui sont toujours présents à ce moment-là bénéficient davantage du report de leur départ par temps chaud.

Mots-clés: changements climatiques, migration, phénologie

INTRODUCTION

The phenology of migrating birds is altering in response to climate change (Gordo 2007, Thorup et al. 2007, McDermott and DeGroote 2017). Many studies have reported the advancement of bird migration timing in spring with earlier phenology (Sparks 1999, Marra et al. 2005, Tøttrup et al. 2006). While some studies have found similar patterns for departing birds in fall, the timing of fall migration remains rather overlooked compared to spring (Gallinat et al. 2015). Nevertheless, several studies have shown that a species' likelihood of responding to increasing fall temperatures by changing its migration timing will depend on how far south the species will migrate (Sokolov et al. 1999, Jenni and Kéry 2003, Thorup et al. 2007). While obligate, long-distance migrants (migrating over 2,000 km) may be constrained in their timing of migration by endogenous mechanisms, short-distance migrants may be more flexible in their timing and often delay their fall migration during warmer years (Gwinner 1996, Gordo 2007, Newton 2007). Two mechanisms have been suggested to cause delays in short-distance migrants with warmer temperature: a postponed departure or a slower migration (Therrien et al. 2017, Haest et al. 2019). The nature of these mechanisms, and how they act on every species, might also explain why some short-distance migrants change their migration with temperature and others do not.

The first hypothesized mechanism, a postponed departure, could occur if the conditions on the breeding grounds remain good in late autumn during years of warm weather. During warm autumns, a departure toward the wintering grounds would be less beneficial, as wintering grounds conditions usually only improve later in the season (Gordo 2007, Newton 2007). For example, late-season insects often delay their emergence in warm temperatures (Forrest 2016) such that warm autumns may create good conditions in northern locations for birds still present on the breeding grounds. Indeed, birds may wait on their breeding grounds, accumulating reserves, until the last possible date so as to improve their chances of surviving migration by having large initial reserves. Species characteristics, like diet, could therefore explain why some short-distance migrants adjust their migration timing with warmer weather and others do not, depending on how their food availability is affected by temperature (Therrien et al. 2017). For example, carnivorous raptors feeding on homeotherms might be less sensitive to temperature than passerines feeding on insects.

The second hypothesized mechanism, a slower migration speed, will affect the passage date and length of passage of a species (Liechti 2006, Therrien et al. 2017). For instance, warm temperatures are often associated with southerly headwinds, which could in turn slow down the migration of certain species and delay the date at which they will be observed at a given location on migration (Liechti 2006, Ferrarese et al. 2008). Slower migration caused by unfavorable winds is likewise expected to affect certain species more than others (Hedenström et al. 2002, Haest et al. 2019) and, again, might explain why some short-distance migrants shift their migration more strongly than others with warm temperature.

Studying the mechanisms of delayed fall migration is essential to understand why the migration phenology of some species changes with temperature and that of other species does not. Understanding the features that temperature-influenced species have in common might reveal which of the hypothesized mechanisms acts the strongest, as the species predicted to respond to temperature are different in the postponed departure hypothesis and the slower migration hypothesis. Some species groups, like passerines and raptors, might react differently to temperature changes due to their distinct life history (e.g., diet, size, flight mode) and characteristics such as breeding/wintering habitat might also be determinant factors. Although some studies have examined the traits that temperature-influenced migrants share in common, few factors have been identified (e.g., Ellwood et al. 2015, Therrien et al. 2017, Usui et al. 2017). While the total migration distance of a species is a good predictor of its phenological adjustment with temperature, many inter-species differences still remain unexplained (Usui et al. 2017). In addition, most studies to date have focused on converging migrating corridors, sampling different populations that might have been exposed to different weather conditions while migrating (e.g., Bennett 1952, Mueller and Berger 1961, Kim et al. 2015, Sullivan et al. 2016). For example, the North American Great Lakes migration corridor is used by both west and east coast populations (Dunn et al. 2006). While converging migration corridors are ideal to assess migration patterns over larger scales, they do not capture the particularities of the different migration cohorts passing through. Rather, bird observatories sampling a limited breeding population are better suited to identify the factors influencing migration phenology.

The Observatoire d'oiseaux de Tadoussac (hereafter "the observatory") is located along the St. Lawrence River corridor in Québec, Canada. Unlike the Great Lakes corridor, the St. Lawrence route is almost exclusively used by eastern breeding birds (Hobson et al. 2010, Hobson et al. 2015, Miller et al. 2017). In fall, boreal or Arctic breeders from northeastern Canada, both passerines and raptors, head south to reach their wintering grounds, typically southeastern Canada for northern wintering migrants (e.g., Laing and Bird 2005, Hobson et al. 2010, Miller et al. 2017; Figure 1, Appendix Figure 5). The Gulf of the St. Lawrence creates a geographical barrier for those migrating birds, which then follow its shoreline in a southwestern direction, and eventually pass the observatory (Ibarzabal 1999, Hobson et al. 2015). These Arctic and boreal breeders also migrate through the same weather system for most of their
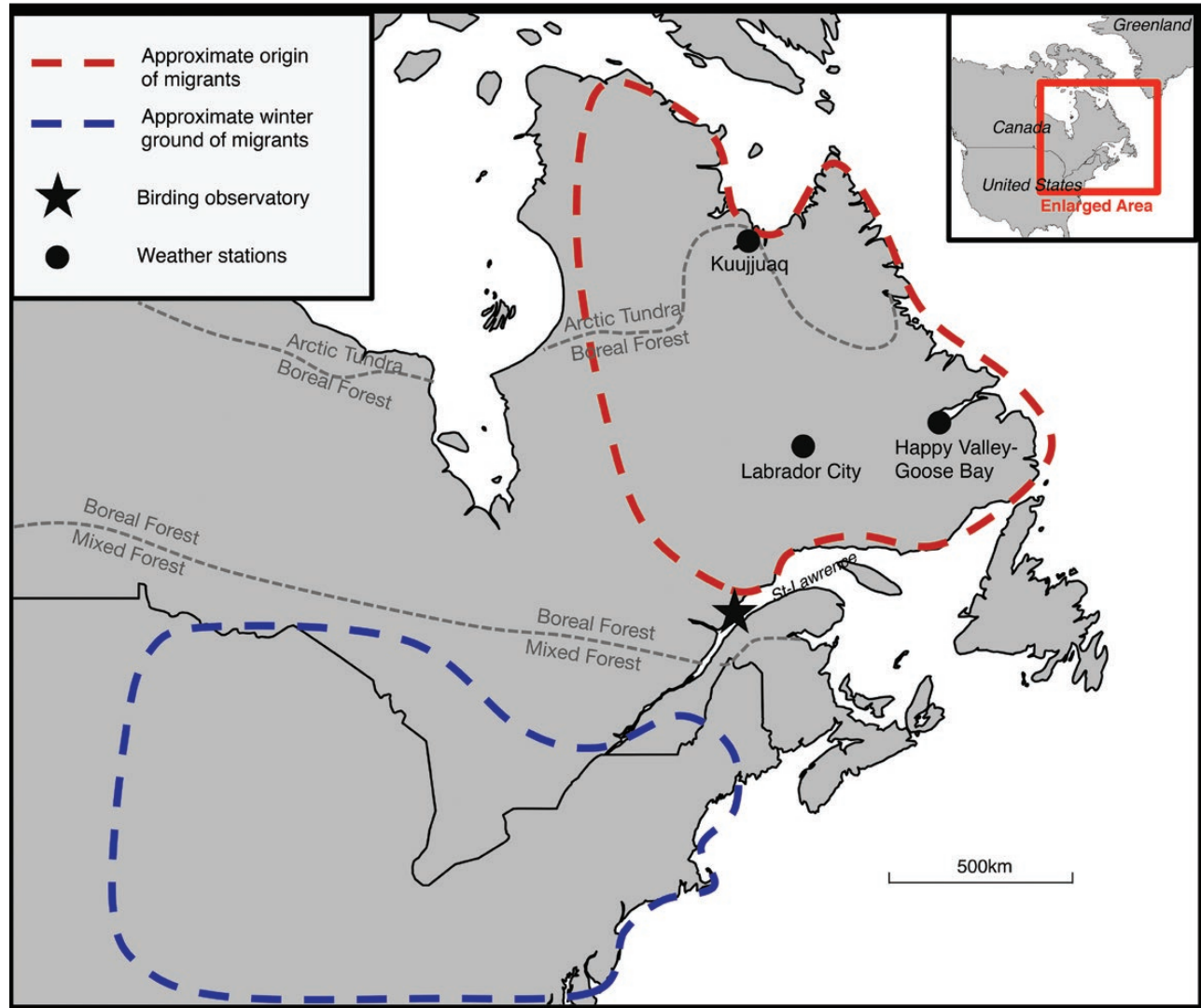
FIGURE 1. Location of the study site. Arctic and boreal breeders migrate through the same weather system for most of their movement prior to their arrival at the observatory with daily mean fall temperatures positively correlated across the breeding region: Labrador City ($\rho = 0.92$), Happy Valley-Goose Bay ($\rho = 0.96$), and Kuujjuaq ($\rho = 0.80$). The origin of migrants and winter ground was derived from eBird data (eBird 2018) to include most of the 21 species' breeding locations north of the observatory and the wintering grounds south of the observatory (see Appendix Figure 5 for more information on the exact summer and winter grounds for each species).

movement prior to their arrival at the observatory, as dramatic temperature changes co-occur throughout the years across the whole region (Jones and Kelly 1983; Figure 1).

Using 22 yr of data from the observatory, we test for the existence of a relationship between temperature and the timing of migration (mean date and length of passage) of 21 species of short-distance migrants wintering in southern Canada or the northern United States. We then investigate if the species that do change their timing of migration in response to temperature share features in their life history (raptor or passerine), size, breeding habitat (tundra or boreal forest), wintering habitat, migration distance, or average period of passage. Finally, based on the characteristics shared by the responsive species, we infer which mechanism (change in migration speed

or departure date) determines how migration changes with temperature. If slower migration is the main mechanism, then we predict that species breeding farther from the observatory (i.e. tundra breeders) will have a greater apparent delay with warmer weather than boreal forest breeders, as differences in migration speed have more time to create a cumulative effect before the individuals are observed. Under the slow migration hypothesis, we also predict that the passage of a species will be more spread out in warm years, starting earlier and finishing later, as the whole cohort will take more time to pass through the observatory. Furthermore, if the slower migration speed is caused by the presence of unfavorable winds associated with warm weather, then we predict that species with larger body sizes and species with a more wind-assisted flight (i.e.

raptors) will have a more pronounced migration delay with temperature, as southerly winds associated with warm temperature will slow down their migration (Hedenström 1993). Under the postponed departure hypothesis, we predict that birds feeding on ectothermic organisms (e.g., passerines feeding on insects) will have a delayed migration timing with warmer weather, as their food is more dependent on warm temperature than are raptors, which forage predominantly on homeotherms (Williams 1961, Evans et al. 2006). We also predict that species migrating later in fall would be more prone to adjust their departure with temperature, because productivity of arthropods and prey habitat (e.g., leaf cover) are more dependent on temperature in late fall than in early fall, with a few degree differences being crucial to phenological processes such as leaf senescence (Fracheboud et al. 2009, Ellwood et al. 2015). Therefore, bird species still present during late fall might be more prone to adjust their departure date with temperature. Finally, we predict that birds migrating the shortest distances, and wintering in the northernmost habitats, will be more likely to delay migration with warm temperature, as differences in conditions between the breeding and wintering grounds would be more easily predicted by the birds when these 2 locations are close to each other.

METHODS

All data was collected between 1996 and 2017 at the Observatoire d'oiseaux de Tadoussac (48.15°N, 69.66°W),

Québec, Canada. The main observation point is situated 55 m above sea level, on sand dunes surrounded by boreal forest and adjacent to the estuary of the St. Lawrence River. Due to the microhabitat of the dunes being unfavorable for breeding birds, the area is visited mostly by migrating birds passing through. The funnel effect created by the estuary, where birds migrating south follow the shoreline, creates a high density of migrants passing through the region (Ibarzabal 1999). The open habitat of the dunes, cleared of vegetation every year, facilitates detection for observers. Stationary observations were carried out daily by at least one experienced birdwatcher from August 24 to November 25 in each year. The observations started ~1 hr after sunrise and lasted 5 hr or more depending on the migration flow. Only heavy rain or snow prematurely ended the observations (Berthiaume et al. 2009, Savard et al. 2011).

Twenty-one species were used for analysis. These species were chosen for being short-distance diurnal migrants (<2,000 km migration), nesting in northeastern Canada (habitats ranging from boreal forest to Arctic tundra), and wintering in southern Canada or the northern United States. Only the most common species (>15 individuals seen every year on average) were retained to ensure that phenological estimates were accurate (Table 1 provides a list of all species and characteristics).

For each species and for each year, we calculated the Mean Passage Date (MPD), defined as the mean of the passage dates of all the individuals of a given species.

TABLE 1. Study species characteristics.

Species	Scientific name	Figure abbreviations	Species type	Body size (cm)	Northernmost breeding habitat	Northernmost wintering habitat	Migration distance	Across-year Mean Passage Date
American Crow	*Corvus brachyrhynchos*	AMCR	Passerine	48.0	Boreal forest	Boreal forest	Very short	289
American Kestrel	*Falco sparverius*	AMKE	Raptor	27.0	Boreal forest	Mixed forest	Very short	258
American Pipit	*Anthus rubescens*	AMPI	Passerine	16.5	Tundra	Mixed forest	Medium	266
American Robin	*Turdus migratorius*	AMRO	Passerine	25.5	Tundra	Boreal forest	Short	294
Bald Eagle	*Haliaeetus leucocephalus*	BAEA	Raptor	85.0	Boreal forest	Boreal forest	Short	290
Cedar Waxwing	*Bombycilla cedrorum*	CEWA	Passerine	18.5	Boreal forest	Boreal forest	Very short	256
Common Grackle	*Quiscalus quiscula*	COGR	Passerine	31.0	Boreal forest	Boreal forest	Short	281
Common Raven	*Corvus corax*	CORA	Passerine	61.5	Tundra	Boreal forest	Medium	288
Dark-eyed Junco	*Junco hyemalis*	DEJU	Passerine	16.0	Tundra	Boreal forest	Medium	280
Golden Eagle	*Aquila chrysaetos*	GOEA	Raptor	90.0	Tundra	Mixed forest	Medium	296
Horned Lark	*Eremophila alpestris*	HOLA	Passerine	18.5	Tundra	Mixed forest	Medium	270
Merlin	*Falco columbarius*	MERL	Raptor	29.0	Boreal forest	Mixed forest	Short	262
Northern Goshawk	*Accipiter gentilis*	NOGO	Raptor	58.5	Boreal forest	Boreal forest	Very short	281
Northern Harrier	*Circus hudsonius*	NOHA	Raptor	53.0	Boreal forest	Mixed forest	Short	258
Peregrine Falcon	*Falco peregrinus*	PEFA	Raptor	46.0	Tundra	Mixed forest	Medium	271
Red-tailed Hawk	*Buteo jamaicensis*	RLHA	Raptor	54.5	Boreal forest	Mixed forest	Short	281
Rough-legged Hawk	*Buteo lagopus*	RTHA	Raptor	54.5	Tundra	Mixed forest	Medium	293
Rusty Blackbird	*Euphagus carolinus*	RUBL	Passerine	23.5	Boreal forest	Mixed forest	Short	269
Sharp-shinned Hawk	*Accipiter striatus*	SSHA	Raptor	30.5	Boreal forest	Mixed forest	Very short	262
Snow Bunting	*Plectrophenax nivalis*	SNBU	Passerine	17.0	Tundra	Boreal forest	Medium	307
Yellow-rumped Warbler	*Setophaga coronata*	YRWA	Passerine	14.0	Boreal forest	Mixed forest	Short	265

This phenology metric was chosen because it is robust to outliers and remains accurate even with imperfect detectability (Moussus et al. 2010). Similarly, we calculated the passage length, defined as the number of days between the date when 5% of the individuals of a species had passed and the date when 95% of the individuals had passed (Kim et al. 2015). This method ensures that uneven sample sizes among years for a species do not affect passage length calculation. In addition, the Pearson correlation between sample size and passage length averages –0.19 across all species, implying that a larger sample size does lead to an artificially large estimate of passage length.

We compiled a set of life history variables for each species. Migration distance was estimated using the citizen science website eBird (eBird 2018). We used the distance between the northernmost sighting east of the Great Lakes during summer (June–August) and the northernmost sighting east of the Great Lakes during winter (January–February). Only sightings during the study period (1996–2017) were considered. To exclude outliers and exceptional sightings, we did not consider regions (50-km quadrats) where a species was reported in less than 3 different years during the given period. Because this method is more useful to provide a species ranking of migration distance than a quantitative migration distance estimate, we transformed the migration distance into categorical variables with 3 levels for the model input: very short migration (<800 km), short migration (800–1,500 km) and medium-distance migration (>1,500 km). Breeding habitat (Arctic tundra vs. boreal forest) and wintering habitat (boreal forest vs. mixed forest) were also determined using eBird. Again, we excluded outliers of very small breeding populations or abnormal wintering locations by excluding the quadrats with fewer than 3 yr of sightings. If a species was present in more than one habitat, we retained the northernmost habitat for the analysis. The last species-specific variable, species size, was determined using the halfway point of the body size range reported in Paquin and Caron (1998).

The temperature and wind were recorded at 1000 hours every day by the observers at the site. Temperature at the observatory is highly correlated with the temperature across northeastern Québec, where the birds we studied are thought to breed and migrate (Jones and Kelly 1983). Similar assumptions are widely used in phenology studies (e.g., Barrett 2002, Askeyev et al. 2007, Kolářová and Adamík 2015, Xu et al. 2017). However, the exact temperature window that a given species responds to is crucial to migration timing at a study site, and depends on the species, yet is difficult to determinate empirically (Jarjour et al. 2017). For this reason, we opted for a sliding window approach (van de Pol and Cockburn 2011, Jarjour et al. 2017, McDermott and DeGroote 2017). We slid a 15-day window between the across-year average MPD of a species (hereafter "across-year-MPD") and 1 mo before the across-year-MPD. We then calculated the correlation between the mean temperature during each window period and the MPD. The window with the highest correlation was retained for analysis (see Appendix Table 3 for the periods retained for each species). The length of the window was set at 15 days because preliminary analysis showed that the correlations started to decline after this window length. Finally, to assess whether warmer temperatures were associated with particular winds, we compared the dominant wind direction during cold fronts (i.e. days when the maximum temperature was more than 5°C colder than the maximum of the previous day) with those of warm fronts (i.e. days when the maximum temperature was more than 5°C warmer than the maximum of the previous day).

Statistical Analysis

Generalized linear models were constructed with temperature as the explanatory variable and MPD or passage length as the response variable. To test trends unrelated to temperature, additional models were also built with year as an additional explanatory variable. Models containing both year and temperature effects were considered, as the Pearson correlation coefficient of those 2 variables was very low ($\rho = 0.09$). Interactions between species and the slope of the explanatory variable were systematically included in all models to account for variability across species. A null model, consisting of randomly generated data with the same mean and standard deviation as the actual data, was used as a reference to statistically test for the influence of the explanatory variables on each species. We allowed the variance structure of the model to vary according to the species. AIC_c was used to rank the models (Burnham et al. 2011). The residuals and variance inflation factors of the best model according to the AIC_c rank were inspected for model validation.

A second series of models was used to assess which species-specific factors were most important in determining the strength of relationships in the previous models. Species size (continuous), across-year-MPD (continuous), breeding habitat (Arctic vs. boreal forest, binary), wintering habitat (boreal forest vs. mixed forest, binary), species type (passerine or raptor, binary), and estimated migration distance (categorical) were used as explanatory variables. Statistical significance of previous models (yes/no binary variable) was used as response variable. Species type and size were never used in the same model due to correlations between the 2 variables. A logistic model was used, with the same residual inspections as described previously. AIC_c were used to rank the models. Furthermore, McFadden's pseudo R^2 (McFadden 1973) and Hosmer-Lemeshow test (Hosmer et al. 2013) were used to assess the fit of the models.

All analyses were conducted in R. We used package *nlme* (Pinheiro et al. 2016) to build linear models, *MuMIn*

(Bartoń 2017) to calculate AIC_c, *pscl* (Jackman 2017) to calculate McFadden's pseudo R^2, and *MKmisc* (Kohl 2018) to calculate Hosmer-Lemeshow H and C statistics. For all models, we first assured that the residuals were homoscedastic and not autocorrelated.

RESULTS

The number of individuals observed and MPD for each species varied greatly. The rarest species was Golden Eagle (average of 18 individuals per year) and the most abundant was American Crow (average of 4,686 individuals per year; see Appendix Figure 6 for the sample size of all species). Furthermore, we observed strong variation across years in the number of individuals observed for some species, usually passerines. The MPD varied from mid-September for earlier species to late October and early November for late species (Figure 2A), while the mean passage length of a species varied from 20 to 80 days (Figure 2B).

We found that temperature was related to MPD but not to passage length. The MPD model with the lowest AIC_c contained temperature as the unique explanatory variable ($\Delta AIC_c = -70.9$ with second-best model; see Appendix Table 4). The variance inflation factor of this model was low (0.87). Eight out of the 22 species changed their MPD significantly with temperature, usually by 1–2 days/°C (Figure 3A). Six species showed a statistically significant positive relationship (Northern Goshawk, Snow Bunting, Dark-eyed Junco, Red-tailed Hawk, Common Raven, and Rough-legged Hawk), whereas only 2 species showed a statistically significant negative relationship (Bald Eagle and American Robin). On average, birds delayed their migration by 0.3 days/°C. The passage length model with the lowest AIC contained, again, temperature as the unique explanatory variable ($\Delta AIC_c = -25.9$ with second-best model; see Appendix Table 5). This model was a poor fit, however, with no species having a significant relationship with temperature (Figure 3B). The variance inflation factor of the model was low (0.83). Warm fronts ($n = 105$) were associated with south-southwest winds, while cold fronts ($n = 138$) were associated with west-northwest winds (Appendix Figure 7).

Most species-specific factors were not strongly associated with the strength of the relationships between temperature and MPD (Table 2). The logistic model with the lowest AIC_c contained only across-year-MPD to explain the different response to temperature among the species ($\Delta AIC_c = -2.5$ with second-best model). Species that migrated later were more likely to display a significant relationship between MPD and temperature (Figure 4). This model presented a good fit, with a McFadden's pseudo R^2 of 0.41 and a nonsignificant Hosmer-Lemeshow H and C statistic (H: $\chi^2_8 = 3.18$, $P = 0.92$; C: $\chi^2_8 = 8.68$, $P = 0.37$). Warm fronts ($n = 105$) were associated with south-southwest
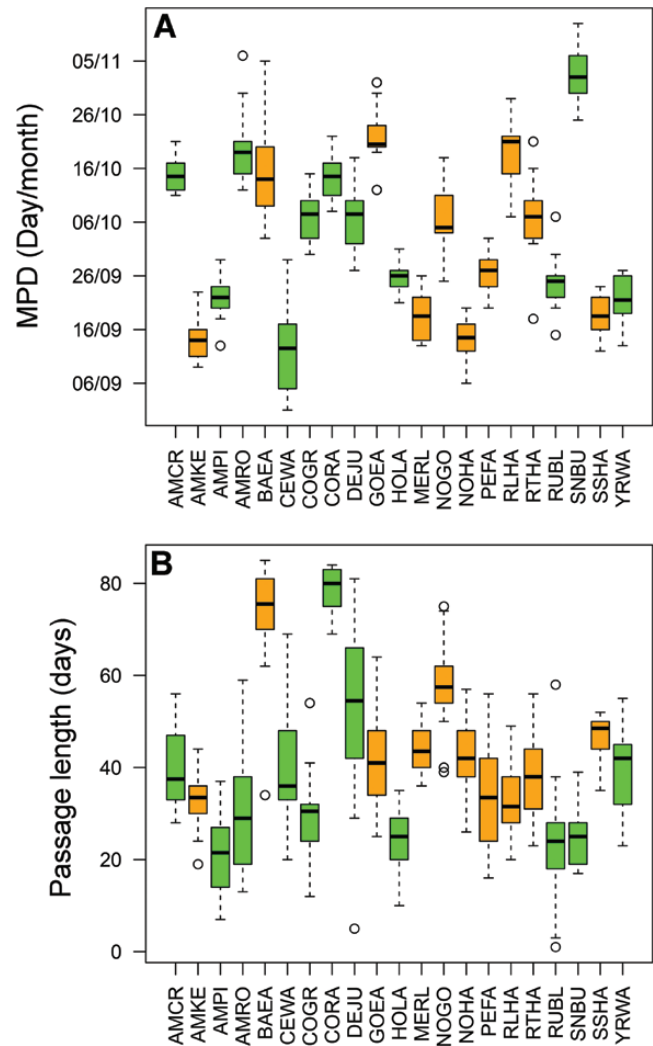

FIGURE 2. (**A**) Mean passage date (MPD) and (**B**) passage length for each species throughout the 22 yr of data collection (see Table 1 for species abbreviations). Passerine species are displayed in green and raptor species in orange.

winds, while cold fronts ($n = 138$) were associated with west-northwest winds.

DISCUSSION

Eight species out of 21 changed their fall migration phenology with temperature. All 8 species were late migrants having migration peaks in October, and most (6/8) delayed their migration in warmer weather, usually by 1–2 days/°C. The change in phenology with warmer weather for some short-distance migrants (but not all) has been known in Europe (e.g., Sokolov et al. 1999, Jenni and Kéry 2003, Jaffré et al. 2013) and North America (e.g., Frank and Conover 2017, Jarjour et al. 2017, Therrien et al. 2017, Zaifman et al. 2017). Contrary to previous studies conducted in North America, individuals from the same species observed in
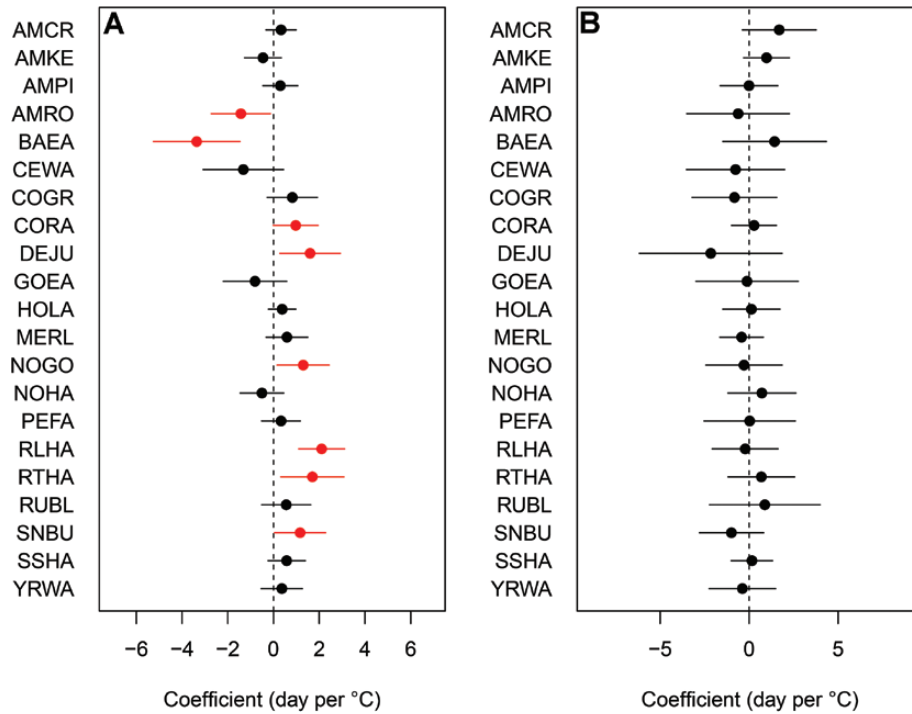
FIGURE 3. Output from (**A**) the model predicting mean passage date (MPD) and (**B**) passage length using the temperature during a species-specific 15-day window preceding migration. The coefficients are reported in days of changes in the MPD/passage length per degree Celsius. Significant coefficients ($P < 0.05$) are reported in red.

TABLE 2. Models linking species life history characteristics with sensitivity to temperature, ranked by AIC_c. Categorical variables are breeding habitat (Arctic or boreal forest), wintering habitat (boreal forest or mixed forest), species type (passerine or raptor) and estimated migration distance (very short, short, and medium). Variables in each model are indicated with an X.

Across-year Mean Passage Date	Size	Breeding habitat	Wintering habitat	Species type	Migration distance	AIC_c	ΔAIC_c	w_i	Cumulative w_i	LogLik
x						21.2	0	0.46	0.46	−8.3
x	x					23.6	2.5	0.13	0.59	−8.1
x				x		23.7	2.5	0.13	0.72	−8.1
				x		23.8	2.7	0.12	0.84	−8.2
	x					23.9	2.7	0.12	0.96	−8.2
x					x	26.7	5.6	0.03	0.99	−8.1
					x	29.3	8.1	0.01	1	−12.3
		x				30.5	9.4	0	1	−12.9
x		x				31	9.9	0	1	−13.2
		x		x		32.5	11.4	0	1	−13.9
x			x			32.9	11.8	0	1	−12.8
			x			34.3	13.2	0	1	−13.5

migration at Tadoussac will likely have nested in the same region (the Labrador Peninsula) and will have migrated through similar weather systems. While our estimates of the magnitude of phenological changes cannot be systematically extrapolated continent-wide, they are nonetheless likely to be representative of northeastern migration routes. Body size, species type, and breeding and wintering habitat did not predict which species changed their migration with temperature. Furthermore, passage length did not vary significantly with temperature. Thus, presumably

a postponed departure rather than a slower migration explained the observed pattern.

Migration Speed

Therrien et al. (2017) suggested the possibility of a slower migration during warm autumns. Southerly winds associated with warm temperatures at Tadoussac can slow down southward fall migration by either reducing flight speed or forcing birds to stop along the way and wait for favorable winds (Zehnder et al. 2001, Hedenström et al. 2002).
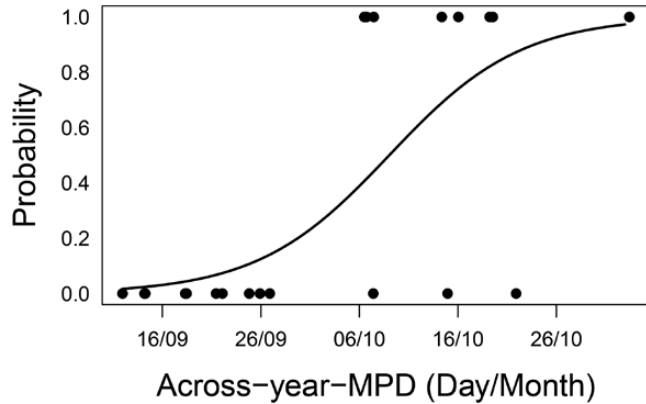
FIGURE 4. Logistic regression of the probability that a species changes its mean passage date (MPD) significantly with temperature according to its across-year-MPD. Each point represents a species tested in the model of panel **A** of Figure 3.

Subsequently, one would expect the observed migration delay to be greater in species that rely more on wind dynamics for long flights (e.g., raptors). Similarly, the size of a bird, varying greatly in our dataset, is a determinant factor in flight speed and cost (Hedenström et al. 2002). However, neither size nor species type were good predictors of the phenological responses of a species to temperature. In addition, we would expect passage length to vary with changes in migration speed, as bird cohorts would require more time to pass through the observatory during slower migration, therefore affecting passage length just as much as MPD. This was not the case, as no species changed their passage length with temperature, even when MPD was changing. These results suggest that slower migration might not be the mechanism acting on the observed phenological changes. Yet, conclusions are tentative; it is possible that southerly winds affect all birds equally, so that slower migration cannot be completely ruled out, or even that other factors than wind influence migration speed. Similarly, other mechanisms than migration speed can influence passage length, like the synchrony of departure among individuals of a species. These other factors might also be interacting with temperature and cancel the effect of migration speed on passage length. Nonetheless, whether body size, species type, or passage length can be used to detect changes in migration speed or not, a more apparent delay should realistically be observed during years of slower migration for the species breeding the farthest from the observatory. Again, this was not the case, leaving very little evidence that slower migration explains the observed phenological delays with warmer temperature.

Postponed Departure

An alternative hypothesis would be that short-distance migrants could postpone their departure from breeding grounds during warmer weather (Sparks et al. 2007,

Gallinat et al. 2015). Conditions on the breeding grounds often remain better than those on the wintering grounds during warm years, so that migrants should remain there to benefit from superior resources (Gordo 2007, Newton 2007). Species migrating mostly in October are more likely to change migration phenology with temperature than species migrating mostly in September (Figure 4). As average temperature drops quickly in late fall at our study site (Appendix Figures 8 and 9), a difference of a couple of degrees might become crucial for multiple aspects of the energetics of birds. Metabolic costs and activity of prey (for both insectivorous and carnivorous species), as well as seed production by plants (for seed-eaters), is affected most strongly after a given temperature threshold (Mellanby 1939, King and Farner 1961, Vickery and Bider 1981, Rawson et al. 1984), so that warmer temperature in the otherwise cold climate of October could be an important decision factor for postponement of departure for species still present at that time.

The potentially better conditions caused by warmer temperatures likely influence the species differently depending on their diet. Our sample size of 21 species only permitted us to test for differences between 2 diet types (raptor vs. non-raptor). There was no difference in the phenological response to temperature between these 2 groups. Ideally, future studies with greater species sample sizes should test for a more diversified and precise classification of diet (e.g., seeds, homeotherms, fish, fruit, insects). Nonetheless, it is noteworthy that the 2 species that advanced significantly their departure in warmer years, the American Robin and the Bald Eagle, have a unique diet compared with the other species within our dataset. The onset of migration in the Bald Eagle, the only fish-eater of our study, depends highly on prey availability (Fitzner and Hanson 1979; Elliott et al. 2011; Mandernack et al. 2012), and eagles may depart early in warm years to take advantage of fish congregations elsewhere. However, Golden Eagles, which are not piscivores, also showed a negative (albeit nonsignificant) relationship between phenology and temperature. Similarly, the American Robin depends more on fruit trees during migration than any other species within our study (Thompson and Willson 1979). The only other fruit-eating bird we examined was the Cedar Waxwing, which was one of the rare birds to also present a negative (albeit nonsignificant) relationship between phenology and temperature. Fruit production is often advanced with warmer temperature (Menzel et al. 2006), so fruit eaters might not benefit from a prolonged stay on the breeding site in warmer years.

Among the short-distance migrants selected for our study, we did not detect differences between those migrating shorter distances or wintering and breeding in different habitats. However, in other studies comparing short-distance migrants with long-distance migrants, or

species wintering in temperate regions with those wintering in tropical regions, short-distance north-wintering migrants tend more to delay their migration with warmer temperatures (Jenni and Kéry 2003, Lehikoinen et al. 2004, Gordo 2007, Therrien et al. 2017). This fits with the postponed departure hypothesis, as it would be reasonable to think that short-distance north-wintering migrants take few risks to voluntarily prolong their stay on the breeding grounds to benefit from the warmer conditions. Indeed, the wintering grounds of most species considered in this study are often located only a few hundred kilometers southward, and the individuals typically migrate through the same weather systems. Migration costs are therefore quite low and predictable, so that staying on the breeding grounds can be done without fear of later paying the costs of a postponed migration. Long-distance migrants, on the other hand, must traverse many weather systems before arriving on the wintering grounds, increasing their chance of encountering unfavorable winds that can trap migrants at a stopover site and slow down their migration (Rappole and Warner 1976, Liechti 2006). For this reason, staying for too long on their breeding grounds might be too risky for long-distance migrants, even in good weather, explaining why migration timing for these migrants has evolved to be of an obligate nature, dictated by unchanging signals such as photoperiod (Gwinner 1996).

Future work could refine our results by incorporating counts during both day and night. We observed strong variation across years in the number of individuals observed for some species. This in itself is not necessarily a problem for passage length and MPD calculations, especially if the variations are caused by fluctuations in the population, as is probably the case for passerines or passerine-eating hawks like the Sharp-shinned Hawk. However, these fluctuations may be partially caused by a large migration cohort migrating at night due to particular weather conditions. This can be the case for the Rusty Blackbird, which is known to sometimes prolong its daily migration at night, therefore potentially going unnoticed if the phenomenon occurs at the level of the observatory (Wright et al. 2018). This can be problematic for MPD and passage length estimations in some years. A partial solution to this problem would be to record nocturnal migrations by calls. Although nocturnal monitoring can only take place in particular weather conditions, and is less precise than visual observations, nocturnal monitoring could give complementary information on the presence of big night passages for a species, allowing for adjustments in MPD and passage length calculations.

More studies need to be conducted on the mechanisms of phenological changes with temperature. We found that changes in departure dates explain migration timing, but other factors might also influence birds' departure decisions. While we did not find that wind had a species-specific effect on migration timing, at least when coupled with temperature, its real impact might have been underestimated. Among raptors, those larger ones that soar extensively in migration are also those that migrate later. It is possible that the 2 variables, size and across-year-MPD, were confounded for this group. An analysis with a greater sample size for raptors would permit better discrimination of the roles of those 2 variables, and might find a greater effect of wind than what we found in this study. Finally, it would be interesting to investigate if the response to temperature might be different among individuals of a species. Different sexes and age classes of certain species are in fact known to migrate at different times (Mueller et al. 2000), and this could have an effect on the interaction with temperature.

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APPENDIX FIGURE 5. The abundance map of the 21 study species during summer (June–August) and winter (January–February), as presented on eBird (eBird 2018).

APPENDIX TABLE 3. Across-year-MPD and period with maximum correlation between across-year-MPD and temperature for each species.

| Species	Across-year-MPD (day/month)	Period (day/month) with max correlation between across-year-MPD and temperature
American Crow	15/10	18/09–02/10
American Kestrel	14/09	15/08–29/08
American Pipit	22/09	24/08–07/09
American Robin	20/10	22/09–06/10
Bald Eagle	16/10	27/09–11/10
Cedar Waxwing	12/09	26/08–09/09
Common Grackle	07/10	23/09–07/10
Common Raven	14/10	29/09–13/10
Dark-eyed Junco	06/10	07/09–21/09
Golden Eagle	22/10	27/09–11/10
Horned Lark	26/09	12/09–26/09
Merlin	18/09	02/09–18/09
Northern Goshawk	07/10	18/09–02/10
Northern Harrier	14/09	16/08–30/08
Peregrine Falcon	27/09	28/08–11/09
Red-tailed Hawk	07/10	18/09–02/10
Rough-legged Hawk	19/10	19/09–03/10
Rusty Blackbird	25/09	08/09–22/09
Sharp-shinned Hawk	18/09	02/09–18/09
Snow Bunting	02/11	19/10–02/11
Yellow-rumped Warbler	21/09	22/08–05/09
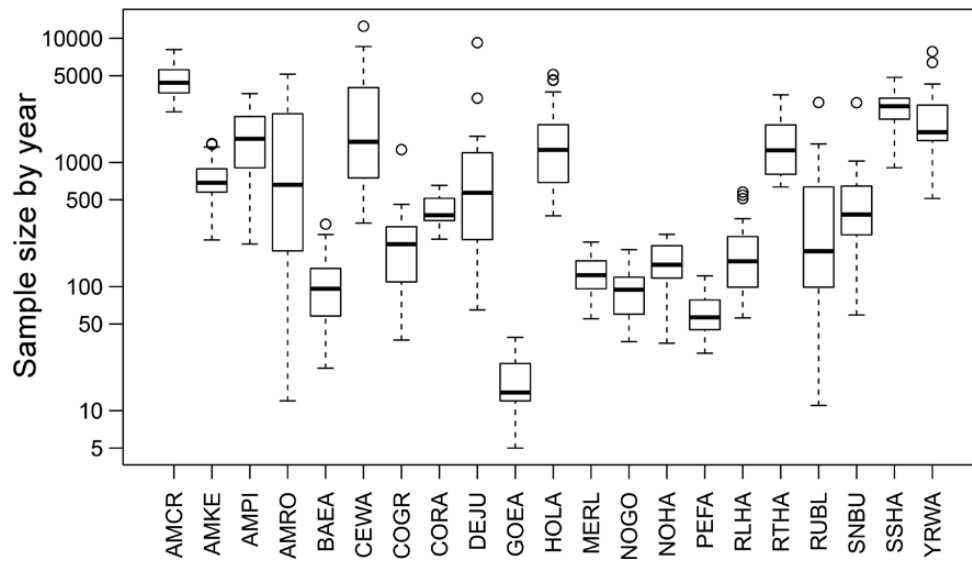
APPENDIX FIGURE 6. Sample size variation over the years for each species.

**APPENDIX TABLE 4.** Models linking mean passage date with temperature, ranked by AIC_c.

Temperature	Year effect	AIC_c	ΔAIC_c	w_i	Cumulative w_i	LogLik
x		2789.1	0	1	1	−1317.9
	x	2860	70.9	0	0	−1322.2
x	x	2869.9	80.8	0	0	−1358.4

APPENDIX TABLE 5. Models linking passage length with temperature, ranked by AIC_c.

Temperature	Year effect	AIC_c	ΔAIC_c	w_i	Cumulative w_i	LogLik
x		3369.7	0	1	1	−1608.2
	x	3395.6	25.9	0	1	−1621.2
x	x	3410.7	41	0	1	−1597.5
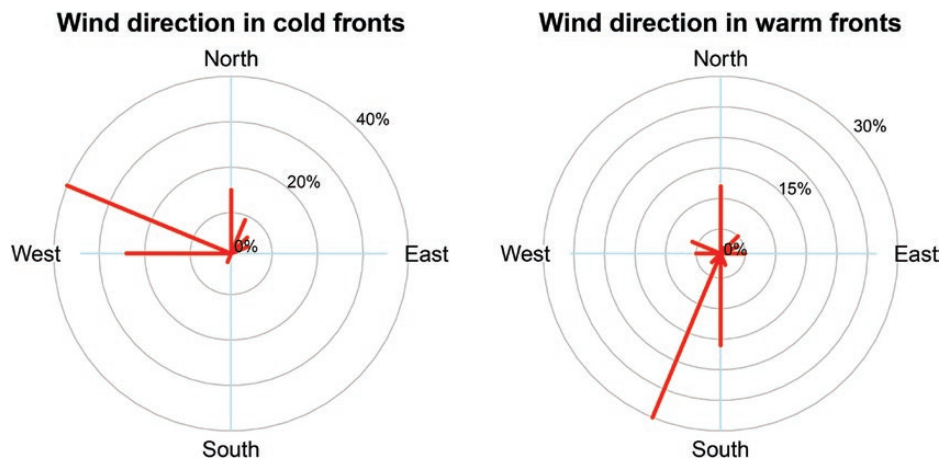
APPENDIX FIGURE 7. Relative recurrence of wind directions during cold fronts and warm fronts at the Tadoussac birding observatory.
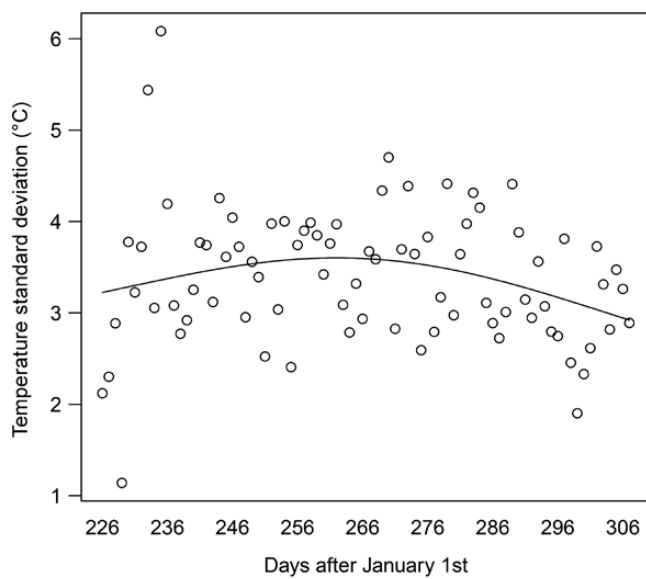
APPENDIX FIGURE 8. Across-year standard deviation of the study-site temperature in fall (1996–2017). A generalized linear model was used for the fitted line.
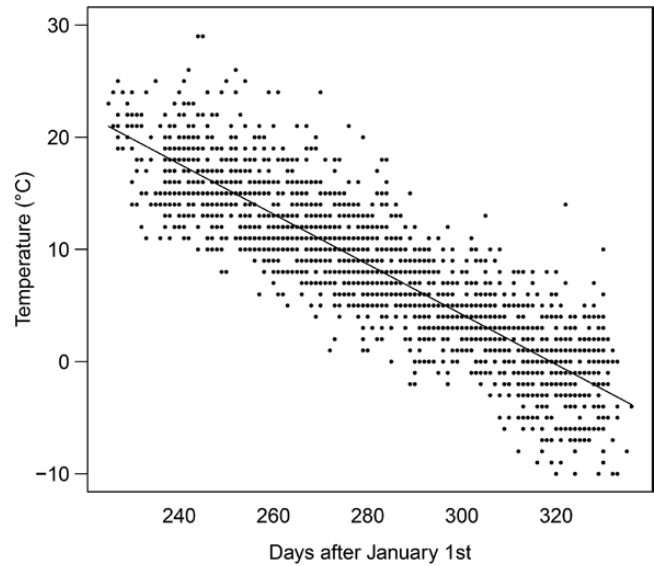
APPENDIX FIGURE 9. Temperature recorded in fall at the study site (1996–2017). A linear model was used for the fitted line.