

LETTER • **OPEN ACCESS**

Behavioral responses to spring snow conditions contribute to long-term shift in migration phenology in American robins

To cite this article: Ruth Y Oliver *et al* 2020 *Environ. Res. Lett.* **15** 045003

View the [article online](#) for updates and enhancements.

Environmental Research Letters



LETTER

OPEN ACCESS

RECEIVED
14 October 2019

REVISED
28 January 2020

ACCEPTED FOR PUBLICATION
30 January 2020

PUBLISHED
2 April 2020

Original content from this work may be used under the terms of the [Creative Commons Attribution 4.0 licence](#).

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.



Behavioral responses to spring snow conditions contribute to long-term shift in migration phenology in American robins

Ruth Y Oliver^{1,2,3,4,11} , Peter J Mahoney⁵, Eliezer Gurarie^{6,9}, Nicole Krikun⁷, Brian C Weeks⁸, Mark Hebblewhite⁹ , Glen Liston¹⁰ and Natalie Boelman²

¹ Department of Earth and Environmental Sciences, Columbia University, New York, NY, United States of America

² Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY, United States of America

³ Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, United States of America

⁴ Center for Biodiversity and Global Change, Yale University, New Haven, CT, United States of America

⁵ School of Environmental and Forest Sciences, University of Washington, Seattle, WA, United States of America

⁶ Department of Biology, University of Maryland, College Park, MD, United States of America

⁷ Lesser Slave Lake Bird Observatory, Slave Lake, AB, CA, United States of America

⁸ Museum of Zoology and Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, United States of America

⁹ Wildlife Biology Program, W. A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, United States of America

¹⁰ Cooperative Institute for Research in the Atmosphere, Colorado State University, Fort Collins, CO, United States of America

¹¹ Author to whom any correspondence should be addressed.

E-mail: ruth.oliver@yale.edu

Keywords: *Turdus migratorius*, migration, climate change, Arctic-boreal

Supplementary material for this article is available [online](#)

Abstract

Migratory birds have the capacity to shift their migration phenology in response to climatic change. Yet the mechanistic underpinning of changes in migratory timing remain poorly understood. We employed newly developed global positioning system (GPS) tracking devices and long-term dataset of migration passage timing to investigate how behavioral responses to environmental conditions relate to phenological shifts in American robins (*Turdus migratorius*) during spring migration to Arctic-boreal breeding grounds. We found that over the past quarter-century (1994–2018), robins have migrated ca. 5 d/decade earlier. Based on GPS data collected for 55 robins over three springs (2016–2018), we found the arrival timing and likelihood of stopovers, and timing of arrival to breeding grounds, were strongly influenced by dynamics in snow conditions along migratory paths. These findings suggest plasticity in migratory behavior may be an important mechanism for how long-distance migrants adjust their breeding phenology to keep pace with advancement of spring on breeding grounds.

One of the most pronounced and well-documented effects of global climate change has been the advancement of spring at high northern latitudes (Gray 2007), where temperatures are rising nearly two to three times faster than the global average (Gray 2007, Stocker *et al* 2013). This has caused alarm because of the important links between seasonal environmental dynamics and the phenology, reproductive success, and overall population health of many species (Moller *et al* 2008, Meller *et al* 2018). With some exceptions (e.g. Post and Forchhammer 2008, Clausen and Clausen 2013, Gauthier *et al* 2013), phenological

responses are proving especially strong in Arctic and boreal ecosystems. Plant growing seasons have advanced by nearly two days per decade at the pan-Arctic scale (Park *et al* 2019), and some animal species have shifted their migratory (e.g. Le Corre *et al* 2016) or reproductive phenologies (e.g. Réale *et al* 2003, Høye *et al* 2007) to keep pace.

There is widespread evidence that many migratory bird species are shifting the timing of their arrival to breeding grounds to match changes in local climate and phenology (Cotton 2003, Marra *et al* 2005, Rubolini *et al* 2007, Barrett 2011). These shifts are

likely driven by intense selection for philopatry (Winger *et al* 2019) coupled with the benefit of increased reproductive success associated with early arrival to the breeding grounds (Norris *et al* 2004). However, for many long-distance migratory passerines, overall shifts in migratory phenology are complicated by the uncoupling between rapidly changing conditions in their Arctic and boreal breeding grounds and the relative stability of photoperiod and environmental cues that trigger migration in their temperate and tropical wintering grounds (Farner and Follett 1966, Dawson *et al* 2001, Ramenofsky and Wingfield 2007). In addition, the high energetic costs of migration, pressure to breed, and subsequent consequences for reproductive success (Paxton and Moore 2015) force migrants to make numerous movement decisions as they travel to their breeding grounds (Alerstam 2011).

Behavioral responses to environmental conditions along migratory routes could contribute to observed phenological shifts on breeding grounds by constraining the overall window in which subsequent breeding activities may occur. Yet, we lack critical understanding of how these decisions relate to environmental conditions along migratory routes, limiting our ability to predict potential constraints on birds' ability to shift arrival timing to breeding grounds in response to ongoing and future change (Chmura *et al* 2019). This is particularly true for migratory songbirds because, while tremendous insight into songbird migration has been gleaned from light-level geolocators, until recently, global positioning system (GPS) tracking devices were too large to be worn by most species (Kays *et al* 2015), precluding direct study of individuals' fine-scale movements (McKinnon *et al* 2016). Recent advances in GPS tracking technology have generated units small enough to be placed on some songbird species, providing opportunities to test how individuals adjust their migration in response to environmental dynamics.

Here, we combined long-term observations (1994–2018) of the timing of spring migration and GPS tracking data of individuals ($n = 55$, 2016–2018) to understand potential mechanisms underlying phenological shifts of one of the most widespread, common, and recognizable passerine species in North America, the American robin (*Turdus migratorius*) (figures 1(a), (b), 2) as they migrated to Arctic-boreal breeding grounds. First, we tested whether the timing of spring migration of American robins through the Canadian boreal forest has significantly advanced over the past quarter-century. Second, we tested whether inter- and intra-seasonal dynamics in environmental conditions along migratory routes influence the migration behavior and phenology of individual American robins, including the passage timing of migration over our tagging site (Slave Lake, Alberta), timing and likelihood of stopovers, migration rates, and timing of arrival to breeding sites.

Methods

Study area

American robins were captured in the Lesser Slave Lake Provincial Park (7700 ha; 55°26' N, 114°49' W) near the town of Slave Lake in northern Alberta, Canada. The park is bordered by Lesser Slave Lake to the west and Marten Mountain (elevation: 1020 m) to the east. These two natural features serve as a funnel that concentrates bird populations over the park as they migrate through the area.

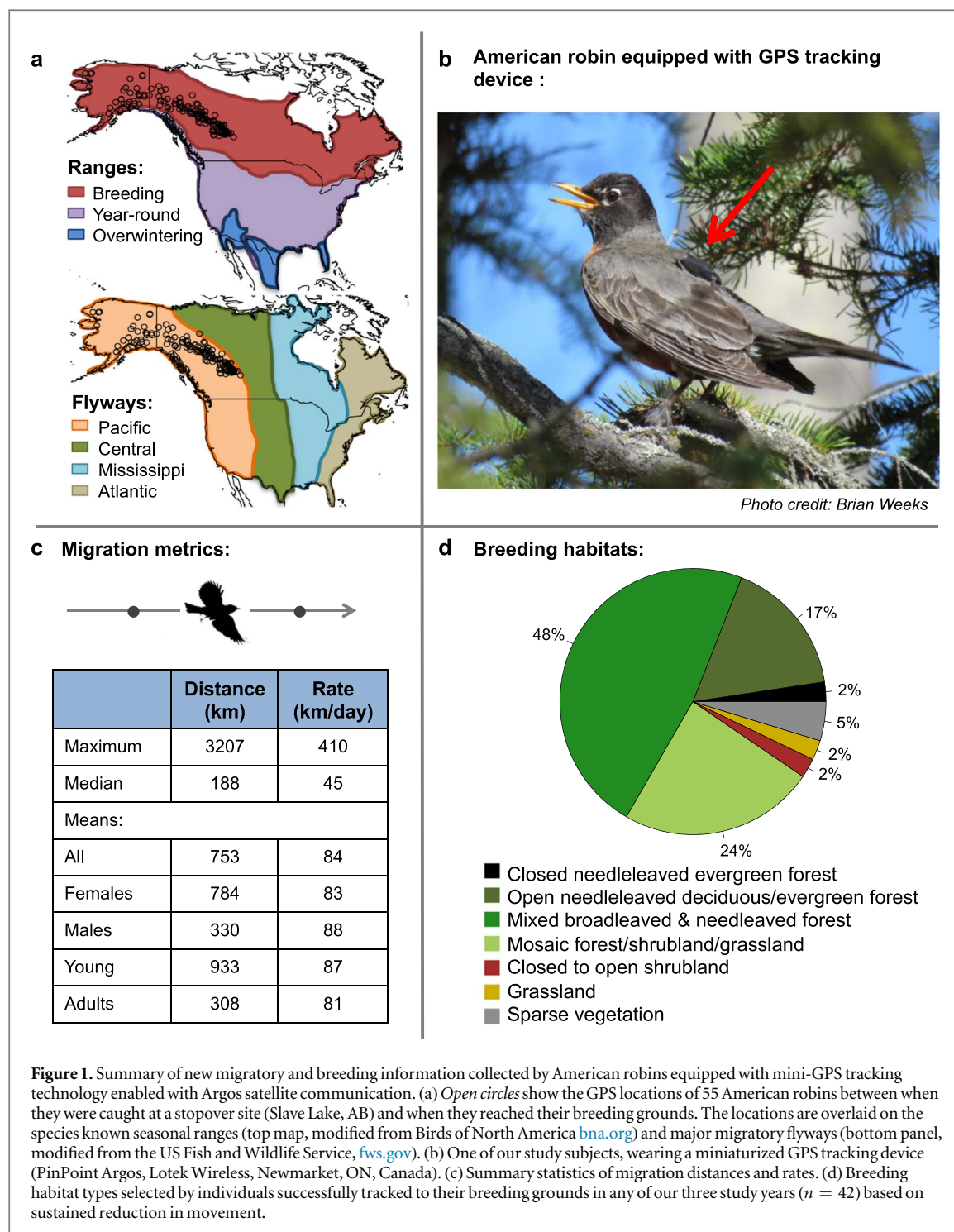
Study species

American robins are the most abundant and broadly distributed thrush species in North America. Robin breeding ranges extend from northern Alaska, Yukon, Northwest Territories, Manitoba, and Quebec to southern California, west-central Texas, the panhandle of Florida and even into Mexico along interior slopes from western Sonora and eastern Chihuahua to eastern Oaxaca (Armstrong 2016). Robins overwinter in much of North America, but are seen only rarely north of the Canada-United States border and southeastern Alaska during winter months (Armstrong 2016). Large robin migrations are witnessed over much of North America, with flock sizes ranging from a dozen to several hundred individuals. Observations at the Lesser Slave Lake Bird Observatory (LSLBO) show that robins typically arrive in the region in late April.

Field methods and robin location data

Daily estimates of individuals from the LSLBO were based on daily constant effort mist netting, visual migration counts, census for each day during spring migration over the past 25 years (1994–2018). Daily constant effort mist netting was based on twelve 30 mm mesh panel mist nets (12 m × 2.6 m) which have been established in the same location over the entire study period. Nets were deployed daily 30 min prior to sunrise and checked every 30 min. Visual migration counts were based on hourly 5 min visual overhead migration count conducted by an LSLBO staff member through binoculars from the same location daily starting 30 min prior to sunrise and ending 7 h later for a total of 8 counts per day. Census counts are based on an established 600 m census route which has remained in the same location over the entire study period. During the first three hours after sunrise, an LSLBO staff member walked the route south for 30 min, recording all birds seen or heard. Daily estimates of the total number of robins migrating through Slave Lake was estimated as the sum of estimated individuals from the three protocols.

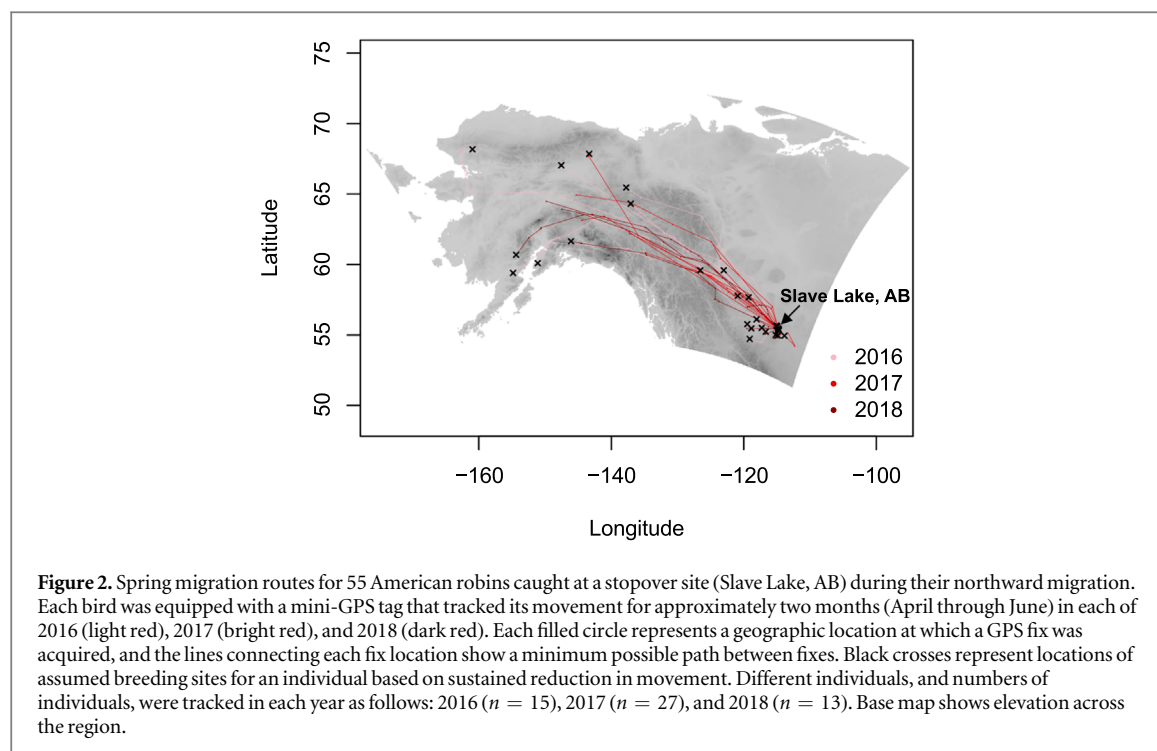
American robins were captured in mist nets from 2016 to 2018 at the LSLBO and Boreal Centre for Bird Conservation (BCBC). Mist netting occurred between April 15 and May 8 each year. The LSLBO is a part of



the Canadian Migration Monitoring Network and deploys twelve mist nets ($12\text{ m} \times 3\text{ m}$) which are opened daily for 7 h beginning 30 min before sunrise. In order to increase opportunities for capturing robins, we deployed on average six additional mist nets which were also opened daily beginning 30 min before sunrise. Weight, wing length, age, and sex of captured individuals were determined following relevant guidelines by Pyle (1997). Weight of captured individuals was determined to the nearest hundredth of a gram by placing individuals in a tared weighing tube on a digital scale. Wing chord length was measured using a flat rule

with a perpendicular stop at zero. The stop was placed against the carpal joint of the wing and the length was read at the natural tip of the wing extending down the length of the rule with no downward pressure applied to feathers. Second year birds were determined by the presence of a moult limit within the greater coverts where inner replaced formative feathers contrast with the outer retained juvenile feathers. After second year birds were determined by a lack of said moult limit. Sex was determined after age by plumage.

Individuals were then banded and outfitted with a Lotek ARGOS PinPoint GPS (Lotek Wireless, Ontario,



Canada) unit via a nylon harness. GPS units weighing either 3.5 or 4 g were fitted on individuals weighing greater than 70 or 80 g, respectively, representing less than 5% of the bird's mass. The mean body mass of individuals outfitted with 4 g tags was 84.1 g, with a mean percentage of body mass of 4.7% ($n = 8$). The mean body mass of individuals outfitted with 3.5 g tags was 79.8 g, with a mean percentage of body mass of 4.3% ($n = 47$) (figure S1 is available online at stacks.iop.org/ERL/15/045003/mmedia).

GPS units were scheduled to acquire and store their location every 48 h beginning the day after deployment and continuing for a total of 30 fixes (approximately late April to early July) and eventually upload location data via the Argos satellite system. Each unit is limited to a maximum of 30 fixes with a battery lifetime of approximately 3 months. Therefore, no individuals were tracked for more than a single spring migration.

Environmental data

We used the environmental-data automated track annotation (*Env-DATA*) system (Dodge *et al* 2013) to access environmental datasets for our analysis of robin migratory movements and habitat selection. *Env-DATA* is housed within Movebank (www.movebank.org), an open-access, online system for the management and analysis of animal movement data (Kranstauber *et al* 2011, Dodge *et al* 2013). Daily surface wind velocity data are provided by the European Centre for Medium-Range Weather Forecasts global reanalysis dataset. Daily total accumulated precipitation at the surface data are provided by the NOAA National Centers for Environmental Protection (NCEP) through the North American Regional

Reanalysis (NARR) dataset. We characterized habitat used by robins based on the GlobCover Land Cover dataset, provided by the European Space Agency.

MicroMet (Liston and Elder 2006a) and SnowModel (Liston and Elder 2006b) were used to simulate daily air temperature and snow depth distributions on a 5 km grid, over the robin migration routes, for the period 1 September 1980 through 30 June 2018. The simulated daily snow-depth distributions were processed to extract the annual snow-free date following (Liston and Hiemstra 2011). The model simulations required 3 hourly inputs of air temperature, relative humidity, wind speed and direction at 10 m above the ground, and precipitation. These were provided by NASA's Modern Era Retrospective-Analysis for Research and Applications (MERRA-2 Gelaro *et al* 2017) atmospheric reanalysis datasets. In addition, SnowModel requires spatially distributed topography and land-cover data. These were provided by the United States Geological Survey Global Digital Elevation Model (GTOPO30; 30 arc seconds, or ~1 km) dataset, and the GlobCover Land Cover (v2.2; 10 arc seconds, or ~300 m) dataset, and re-gridded to the 5 km simulation grid.

Monthly values of the strength of the Pacific decadal oscillation (PDO) were obtained from the National Oceanic and Atmospheric Administration.

Robin migration passage timing over Slave Lake, Alberta (1994–2018)

We tested for the presence of trends and the influence of environmental conditions on robin migration timing to Slave Lake, Alberta using long-term dataset collected by the LSLBO (1994–2018). Timing of migration was described using three migration phases

(date of first 5%, 50%, and 95% of total spring observations). We tested for the presence of trends in passage timing using a generalized least squares approach taking into account first order temporal autocorrelation, by incorporating first order autoregressive correlation structure. To test for the influence of environmental variables on passage timing, we performed model selection of linear models based on all possible combinations of environmental variables (monthly mean air temperature, snow depth, and precipitation for March and April, annual snow-free date, and mean strength of the PDO for the 12 months preceding arrival) and year. We restricted the inclusion of environmental variables which were highly correlated (Pearson's $|R| > 0.7$). As a result, snow-free date was excluded from being included with March and April snow-depth and March air temperature, as well as March snow depth with March air temperature and April snow depth. We ranked candidate models based on Akaike's information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002). We considered models with $\Delta AIC_c < 2$ to have strong support for associations between variables of interest.

Stopover and breeding grounds arrival timing

We modeled robin stopover timing at our tagging site in Slave Lake, Alberta and their breeding grounds, and investigated factors influencing timing using the Anderson–Gill extension to the Cox proportional hazards (Cox PH) regression modeling (Therneau and Grambsch 2013). We tested the proportional hazards assumption of Cox PH using the formula test recommended by Therneau and Grambsch (2013) and only included predictor variables which did not have significant violations of the proportionality ($P > 0.05$). We used a 365 d, recurrent, time scale to model the baseline hazard standardized to a year beginning on 1 January (Fieberg and DelGiudice 2009). In this context, 'hazard' does not represent the standard hazard of mortality, but rather the 'hazard' of arriving to a given location.

To understand factors influencing robin stopover arrival timing, we used the date on which we captured individuals at Slave Lake as a stopover event because all individuals were captured while foraging. We consider this to be stopover event as all individuals were captured while refueling, as opposed to migrating which is consistent with known flexibility in stopover behavior in passerines, as compared to other groups (Catry *et al* 2004). We generated daily records of environmental conditions for each individual starting on 1 January of the year they were observed and ending when they were captured at Slave Lake. We included sex (referenced to female), mass, wing length, and a binary age classification (second year or after second year, referenced to second year) as predictor variables, as well as snow-free date and daily mean precipitation, snow depth, and air temperature at Slave Lake were averaged

at four spatial scales (5-, 25-, 105-, and 255-km grid cells centered around Slave Lake). Snow depth and air temperature at Slave Lake averaged within a 5 km grid cell were highly correlated with the same variables averaged across larger spatial scales (25, 105, and 255-km grid cell; $R^2 > 0.95$), indicating local conditions at Slave Lake are representative of regional conditions. All further analyses were based on environmental conditions averaged across the smallest spatial resolution. To test whether arrival timing differed between years we tested for an effect of categorical year (2016–2018). We considered years to be significantly different if the 95% confidence intervals of odds ratios (exponentiated β coefficients) of included year variables did not overlap.

To test for the influence of environmental, demographic, and morphological variables on stopover arrival timing based on capture data, we performed model selection of Cox proportional hazards models of all individuals captured as part of our tagging effort ($n = 77$). We generated candidate models based on all possible combinations of variables. However, we restricted the inclusion of snow depth and air temperature as predictor variables in the same model based on a high correlation (Pearson's $|R| > 0.7$). We additionally restricted models to contain seven or fewer covariates based on the overall sample size ($n = 77$). We ranked candidate models based on Akaike's information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002), where the number of individuals observed at Slave Lake was considered the sample size. We considered models with $\Delta AIC_c < 2$ to have strong empirical support. We assessed significance of variables with robust z tests and 95% confidence intervals for odd ratios (Therneau and Grambsch 2013). We considered predictor variables significant if odds ratio confidence intervals did not overlap one. In this case, for categorical variables the odds ratio corresponds to the instantaneous odds of arrival at the location in question relative to the reference group. For continuous variables, the odds ratios correspond to a proportional change in the odds of arrival per unit change in the covariate. In all models, we estimated robust standard errors for parameter estimates based on data clustered by year. For variables that were retained in multiple top models, responses were similar across models, so we report results from the model with the lowest AIC_c value.

We modeled robin arrival to breeding grounds based on GPS locations collected over our three study years (2016–2018). Each GPS location was considered a record. We identified general breeding locations for individuals based on a sustained reduction in movement during known breeding months (June and July) (Young 1955). GPS fixes were identified as being in the general location an individual's breeding grounds based on the proximity to the final GPS location ($> 80\%$ of total distance traveled) and consistently low movement rates ($< 10 \text{ km d}^{-1}$). Arrival to breeding

grounds was designated by the first breeding ground location. In some cases, robins were not tracked completely to their breeding grounds due to GPS failure. We again considered demographic and morphological variables (sex, mass, wing length, and a binary age classification) as well as daily snow depth and air temperature in a 5 km grid cell around each GPS location. To account for the fact that individuals traveled to breeding grounds of variable distances from our tagging site, we included distance traveled from our tagging site to breeding grounds as a predictor variable. We also included an interaction term between snow-free date and distance traveled from tagging site because snow is likely to melt out later at higher latitudes. We used the same procedure for testing differences between years as we did for stopover timing to Slave Lake. To test for the influence of environmental, demographic, and morphological variables on arrival to breeding grounds, we performed the same model selection procedure as above. We tested for correlation among all environmental covariates to exclude any combinations of variables that were highly correlated (Pearson's $|R| > 0.7$). However, no covariates were found to be highly correlated. We additionally restricted all models to containing five or fewer covariates based on the sample size ($n = 55$). The overall number of individuals included in the model was 55, 42 of which had sufficient GPS data to suggest that the individual was tracked to the general breeding area, based on a sustained dramatic decrease in movement.

Migration movement rate

We investigated environmental, demographic, and morphological variables influencing movement rates during migration. We identified locations of each individual as occurring during migration, as opposed to on breeding grounds, based on the proximity to the final GPS location ($<80\%$ of total distance traveled) and the movement rate ($>10 \text{ km d}^{-1}$). To standardize our analysis we sub-sampled to only include sequential locations, hereafter referred to as steps, that were acquired 48 h apart. This resulted in 101 unique migratory steps from 17 individuals. Preliminary analysis revealed that movement rates were highly related to distance from Slave Lake and that individuals selected breeding areas throughout northwestern Canada and Alaska. The northern Rocky Mountains represent a significant geographic feature of the landscape, which several individuals traversed in the course of their migration. To test potential differences as individuals crossed the Rocky Mountains, we tested differences in migration movement rates for individuals that crossed 130°W longitude in the regions east and west of the barrier using two sample t-tests. We also tested differences in mean environmental conditions, such as snow depth, number of days before/after the snow free date, proportion of locations with snow present, and wind speeds,

experienced at the locations selected by these two regions using two sample t-tests.

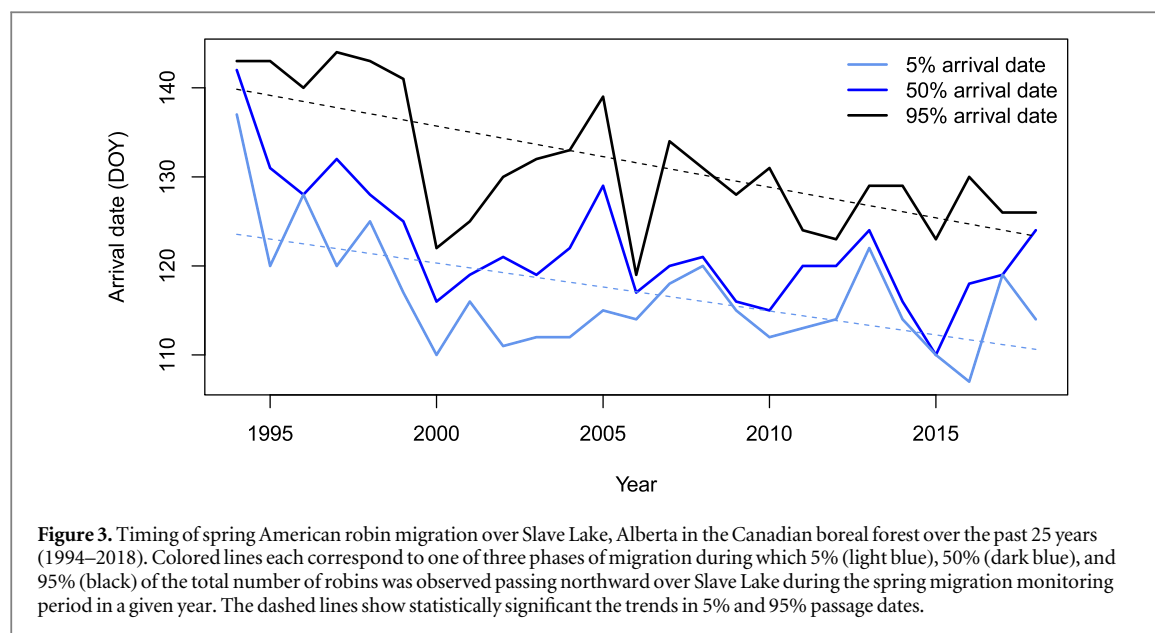
We investigated the influence of environmental conditions on migration movement rates for all individuals and the subset of individuals that crossed 130°W longitude over the entire study domain and in the regions east and west of the barrier using linear regression. We summarized environmental conditions along each step by averaging conditions at each start and end location using the following variables: snow depth, air temperature, precipitation, and zonal and meridional wind speeds and the interaction between air temperature and snow depth. We also included distance from Slave Lake in our model of migration movement rates over the entire study domain.

We tested for differences in movement rates and total migration rate between sexes and age classes using t-tests and tested for the influence of mass and wing lengths using linear regression. For all individuals that were tracked entirely to their breeding grounds we estimated total migration rates based on minimum distance traveled and number of days between capture at Slave Lake and arrival to breeding grounds.

Results and discussion

We found that over the previous 25 years, American robins have migrated northward over the boreal forest surrounding Slave Lake, Alberta approximately 5 days earlier per decade using a generalized least squares approach taking into account first order temporal autocorrelation (figure 3, 5% passage date: coefficient = -0.5 d yr^{-1} , $\text{se} = 0.25$, $t(23) = -2.19$, $p = 0.039$; 50% passage date: coefficient = -0.65 d yr^{-1} , $\text{se} = 0.34$, $t(23) = -1.89$, $p = 0.070$; 95% passage date: coefficient = -0.69 d yr^{-1} , $\text{se} = 0.19$, $t(23) = -3.52$, $p = 0.002$) Interestingly, our observed rate of advance in migration timing is comparable to the only other long-term study of American robin migration, that we are aware of, that found that robins advanced their arrival to a high altitude site in the Rocky Mountains by 14 d over a 19 year period (approx. 0.74 d yr^{-1}) from 1981 to 1999 (Inouye *et al* 2000). Earlier passage through Slave Lake may reflect a shift in migration timing to maintain the same arrival time to the breeding grounds as ranges expand northward (Tingley *et al* 2009), or could reflect selection to reach breeding grounds earlier as habitat and prey phenology advance both along migratory corridors and within breeding grounds (Norris *et al* 2004).

Over the same 25 year period, we found inter-annual differences in the timing of robin migration over Slave Lake, Alberta were explained by inter-annual variability not only in environmental conditions at this specific locale, but also in the strength of a continental-scale climate oscillation, the PDO (Gedalof, Mantua and Peterson 2002). Specifically, the



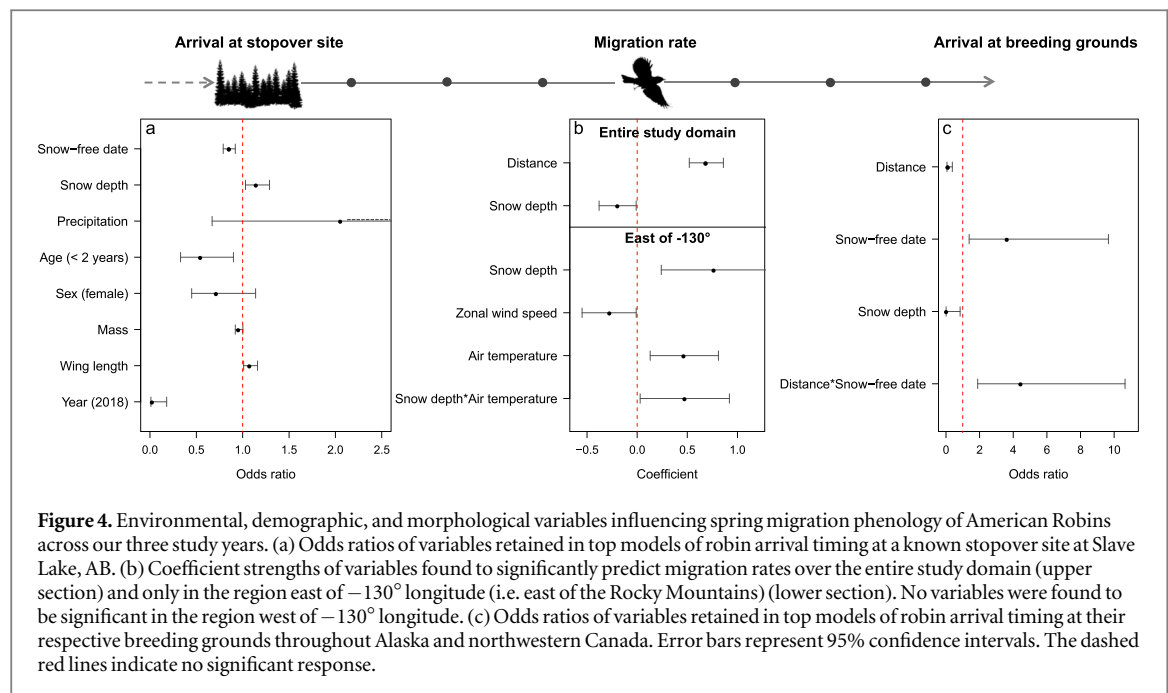
migration passage timing of robins was significantly earlier in years when the mean annual strength of the PDO was more negative (supplementary tables 1–4). Since negative phases of the PDO are associated with warm and dry winters in continental North America (Gedalof *et al* 2002), our results indicate that robins migrate earlier through the northwestern Canadian boreal forest following milder winters in the region.

Our results suggest that American robins may fine-tune their northward rates of migration based not only on local environmental conditions along the way, forging ahead when and where environmental conditions permit, but also adjust departure from overwintering grounds and migration rates according to broad-scale climatic conditions (as indexed by the PDO). Numerous previous studies have found that dynamics in migration phenology are often related in complementary ways to both local environmental conditions and large-scale climate oscillations (e.g. Marra *et al* 2005, Jonzen *et al* 2006, Macmynowski *et al* 2007). Rainio *et al* (2006) found that the majority of 75 species migrated earlier to sites in northern Europe after winters in which the North Atlantic Oscillation was higher, suggesting large-scale climate oscillations may shape inter-annual differences in seasonality along avian migratory routes more broadly than local environmental conditions (Hallett *et al* 2004). Further, several studies suggest that long-distance migrants may be able to shift arrival timing to breeding grounds by taking advantage of broad-scale climatic connections between southern overwintering areas and breeding grounds (Saino and Ambrosini 2008, Pancera *et al* 2018).

The GPS tagging data collected from individual robins migrating through Slave Lake during three consecutive springs (2016–2018) not only revealed the migratory flyway and breeding habitats used by populations which migrate through this locale (figures 1(a),

(d)), but also allowed us to relate dynamics in the migratory behavior and phenology of individual birds to environmental conditions along their migratory paths. Analysis of stopover arrival timing from the 77 robins captured in Slave Lake as part of our tagging effort, using Cox proportional hazards regression models, showed that arrival timing at this known stopover site was delayed in years with persistent local snow cover, such as occurred in 2018 (figure 4(a), supplementary tables 5–7). However, once in the general region, individuals were more likely to stopover during periods of inclement weather (i.e. deeper snow and higher precipitation) (figure 4(a), supplementary tables 5–7). By considering multiple behavioral responses (i.e. timing versus likelihood of stopovers), our results demonstrate multi-directional responses of robins to dynamics in snow conditions.

Our results indicate that predicting future migration phenology of long-distance migratory passerines to Arctic-boreal regions will require understanding of both broad-scale patterns in the advancement in spring environmental conditions, as well as the potential for increasing storm frequency and intensities (Maloney *et al* 2014). Although long-distance migrants are under pressure to reach their breeding grounds, the elevated energetic demands imposed by adverse environmental conditions (Wikelski *et al* 2003) may force them to moderate their migration behavior. For example, Briedis *et al* (2017) found that semi-collared flycatchers (*Ficedula semitorquata*) departed from their overwintering grounds in Eastern-Central Africa on approximately the same dates in two consecutive years. However, a persistent cold snap caused them to spend twice as long in the Mediterranean Basin relative to a warmer year, before continuing on to their breeding grounds. In addition, Both (2010) found that pied flycatchers (*Ficedula hypoleuca*) spring departure dates advanced, but not arrival dates



to breeding grounds due to environmental constraints along the migratory route.

Our analysis of the influence of environmental conditions along the migration paths taken by individual robins, using Cox proportional hazards regression models, revealed that the timing of arrival at their breeding grounds ($n = 42$, figure 2, see Materials and Methods for estimation of general breeding location) was significantly delayed in response to later snow-free dates, deeper snow depths, as well as the distance of a given breeding site from Slave Lake (figure 4(c), supplementary tables 8–10). Like most northern-breeding passerine populations, the robins studied herein were likely under pressure to reach their breeding grounds as their nesting season is approximately half that of populations breeding in much of the conterminous United States (James and Shugart 1974). The compressed breeding season results in a narrow window in which robins must initiate clutches to ensure sufficient time for young, including potential second broods (Young 1955), to develop, and before photorefractoriness and the onset of molt (Dawson *et al* 2001), and harsh environmental conditions cue fall migration (Verhulst and Nilsson 2008).

Our results demonstrate, that despite this pressure, persistent spring snow cover may force birds to delay movement northward, likely by limiting access to food resources *en route* and inhibiting passerine flight (Richardson 1978). Delayed arrival to breeding grounds can have a significant impact on the breeding success of passerines (Smith and Moore 2003, Newton 2004) and may constrain their ability to adjust to climatic change on their breeding grounds (Both and Visser 2001). American robins have vast differences in migration distance and timing across their range (Jahn *et al* 2019), suggesting shifts in the populations passing

through Slave Lake could play a role in long term advancement. Alternatively, advanced migration date may result from inter-generational advances, coupled with static individual migratory timing, as in Icelandic black-tailed godwits (Gill *et al* 2014), selection in response to changing environments (Charmantier and Gienapp 2014), or evolution in migratory timing programs as recently shown in pied flycatchers (Helm *et al* 2019). However, our results suggest that responses to environmental conditions *en route* may, at least in part, contribute to shifts in timing.

The responses to environmental conditions along robins' migratory route that we found are consistent with other Arctic studies that found both passerine, shorebird, and waterfowl arrival timing and breeding phenology is delayed or advanced in response to spring snow dynamics (Liebezeit *et al* 2014, Boelman *et al* 2017, Lameris *et al* 2018). In this way, our study is novel in quantitatively relating the movement of individually GPS-tagged robins to the environmental conditions along each migratory path. In lieu of this type of data, the majority of passerine migration studies have had to rely on environmental data collected at the specific locale where, and leading up to the time when, arrival data was collected (e.g. Ahola *et al* 2004, Boelman *et al* 2017). Alternatively, these studies have relied on regional-scale environmental data products that provide estimates of the conditions for large areas, and windows of time, through which birds may have migrated (e.g. Huin and Sparks 2000, Haest *et al* 2018). In contrast, the fine scales and spatiotemporally matched nature of the robin movement and environmental datasets analyzed in our study has strengthened inferences regarding factors responsible for trends and variations in the timing of when robins arrive at their breeding locations. Our results

demonstrate when, where and how dynamics in specific environmental conditions along migratory routes were related to the migration behavior and phenology of American robins, revealing that dynamics in multiple variables related to snow conditions play an overwhelmingly important role.

In addition to responding to localized and temporally transient environmental conditions, robins responded strongly to permanent features of the landscape. Impressively, while migrating between the stop-over site at Slave Lake and their respective breeding grounds, robin migration rates between consecutive GPS fixes, which are influenced by both flight speed and potential stop-overs, averaged 84 km d^{-1} and reached up to 410 km d^{-1} (figure 1(c)). Migration rates decreased with deeper snow depths (coefficient = -0.19 , $\text{se} = 0.09$, $t(90) = -2.11$, $p = 0.038$, 95% CI = $[-0.38 \text{ to } -0.01]$). Unexpectedly, we also found that migration rates increased with distance from Slave Lake (coefficient = 0.69 , $\text{se} = 0.08$, $p < 0.001$, 95% CI = $[0.52\text{--}0.86]$). Further investigation revealed that this acceleration is explained by the fact that the Alaska-breeding robins in our tracking study nearly doubled their migration rates (from 85 to 137 km d^{-1} , $t(27.5) = -1.8$, $p = 0.079$) after traversing from the east to the west side of the Rocky Mountains, potentially suggesting individuals responded to local conditions once arriving in the region (supplementary table 10). Although meridional wind speeds did not differ between locations selected by Alaska-breeding individuals, strong easterly winds prevailed west, but not east, of the Rockies (from 0.59 to -0.22 m s^{-1} , $t(25.8) = 1.72$, $p = 0.09$) (supplementary table 10). The latter could be involved in the significant acceleration of robin migration west of the Rockies. Tailwinds have been shown to increase a bird's ground speed and decrease the overall energy needed to travel the same distance, thereby conserving energy reserves (Liechti 2006). This may be especially important for spring migrants at high latitudes where food may be scarce upon arrival to breeding grounds (Richardson 1978).

Further, we found that while on the eastern side of the Rockies, the migration rates of Alaska-breeding individuals were significantly, positively related to snow depth (coefficient = 0.77 , $\text{se} = 0.26$, $p = 0.005$, 95% CI = $[0.24\text{--}1.29]$), air temperature (coefficient = 0.47 , $\text{se} = 0.17$, $p = 0.007$, 95% CI = $[0.13\text{--}0.81]$), and the interaction between snow depth and air temperature (coefficient = 0.48 , $\text{se} = 0.22$, $p = 0.036$, 95% CI = $[0.032\text{--}0.92]$), as well as negatively related to zonal wind velocity (coefficient = -0.28 , $\text{se} = 0.13$, $p = 0.043$, 95% CI = $[-0.55 \text{ to } -0.01]$) (figure 4(b)). However, we found no relation between their migration rates and environmental conditions once these same individuals had passed over to the west side of the Rockies (supplementary table 10). When we considered the migration rates of Alaska-breeding robins in combination with snow disappearance dates, we found that while on the

eastern side of the Rockies, individuals were migrating through landscapes that had been snow-free for approximately two weeks (supplementary table 10). In contrast, once these individuals had passed over to the western side, the more persistent snow cover coupled with their faster rates of migration resulted in their passage over landscapes that had become snow-free less than only two days prior (supplementary table 10). Our analysis demonstrates that as robins pass through the Rocky Mountains *en route* to Alaskan breeding grounds, they take a significant step backwards in 'seasonal time' by entering into a different climatic region where spring has only just begun, and favorable winds propel them towards their breeding grounds. Our findings suggest that together, these environmental conditions may play a large role in keeping the breeding phenology of long-distance migratory passerines well-matched to the inherently short window of suitable breeding and young rearing conditions inherent to Arctic-boreal habitats each year. In fact, as climate warming continues, fortuitous regional climatic conditions such as this may provide long-distance migrants with natural buffer zones that prove critical to overcoming both increasingly unpredictable and disjointed spatio-temporal dynamics, as well as long-term shifts, in seasonality on overwintering grounds, along migratory corridors, and on breeding grounds.

Conclusions

We leveraged advanced GPS tracking technology to quantitatively link spatiotemporally-explicit environmental conditions to the migration behavior and phenology of American robins *en route* to their rapidly warming breeding grounds at high northern latitudes. Our results demonstrate that behavioral responses to environmental conditions along migratory routes may contribute to the advance in migration timing we observed through the Canadian boreal forest over the past quarter century. The improved understanding of migration behavior and phenology of passerines we have developed is critical to creating predictive models that integrate habitat preferences and movement traits into forecasts of phenological responses as the climate continues to warm.

Acknowledgments

This project was funded by NASA's Arctic-Boreal Vulnerability Experiment (NNX15AV92A to NTB, NNX15AW71A to MH, and NNX15AU20A to L Prugh (Postdoctoral advisor for PJM)) and the NSF Graduate Research Fellowship Program (DGE 16-44869 to RYO). We thank the Lesser Slave Lake Bird Observatory and Boreal Centre for Bird Conservation for providing support and logistics. We also thank Richard Krikun for his assistance and expertise.

Author contributions

NTB and RYO co-conceived this study. RYO, NTB, BCW and NK designed the field-based portion of the study. RYO executed the majority of the study, with significant guidance on analytical design and implementation from PJM, EG and MH. GL developed and provided the spatiotemporally explicit snow depth datasets required to relate robin migratory behavior to environmental dynamics. RYO and NTB co-wrote the manuscript with feedback on a previous draft from all other co-authors.

Competing interests

The authors declare no competing interests.

Data availability statement

The data that support the findings of this study are available upon request from the authors.

ORCID iDs

Ruth Y Oliver  <https://orcid.org/0000-0003-3642-3980>

Mark Hebblewhite  <https://orcid.org/0000-0001-5382-1361>

Natalie Boelman  <https://orcid.org/0000-0003-3716-2372>

References

- Ahola M, Laaksonen T, Sippola K, Eeva T, Rainio K and Lehtikoinen E 2004 Variation in climate warming along the migration route uncouples arrival and breeding dates *Glob. Change Biol.* **10** 1610–7
- Alerstam T 2011 Optimal bird migration revisited *J. Ornithol.* **152** 5–23
- Armstrong R H 2016 *Guide to the Birds of Alaska* (Portland, OR: Alaska Northwest Books)
- Barrett R T 2011 Recent response to climate change among migrant birds in northern Norway *Ringed Migration* **26** 83–93
- Boelman N T, Krause J S, Sweet S K, Chmura H E, Perez J H, Gough L and Wingfield J C 2017 Extreme spring conditions in the arctic delay spring phenology of long-distance migratory songbirds *Oecologia* **185** 69–80
- Both C 2010 Flexibility of timing of avian migration to climate change masked by environmental constraints En route *Curr. Biol.* **20** 243–8
- Both C and Visser M E 2001 Adjustment to climate change is constrained by arrival date in a long-distance migrant bird *Nature* **411** 296–8
- Briedis M, Hahn S and Adamík P 2017 Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird *BMC Ecol.* **17** 11
- Burnham K P and Anderson D R 2002 Model selection and multimodel inference: a practical information-theoretic approach *Prediction and the Power Transformation Family* ed R J Carroll and D Ruppert 1981 (New York: Springer)
- Catry P, Encarnação V, Araújo A, Fearon P, Fearon A, Armelin M and Delaloye P 2004 Are long-distance migrant passerines faithful to their stopover sites? *J. Avian Biol.* **35** 170–81
- Charmantier A and Gienapp P 2014 Climate change and timing of avian breeding and migration: evolutionary versus plastic changes *Evol. Appl.* **7** 15–28
- Chmura H E, Heather M K, Ashander J, Ehlman S M, Rivest E B and Yang L H 2019 The mechanisms of phenology: the patterns and processes of phenological shifts *Ecol. Monogr.* **89** e01337
- Clausen K and Clausen P 2013 Earlier arctic springs cause phenological mismatch in long-distance migrants *Oecologia* **173** 1101–12
- Cotton P A 2003 Avian migration phenology and global climate change *Proc. Natl Acad. Sci.* **100** 12219–22
- Dawson A, King V M, Bentley G E and Ball G F 2001 Photoperiodic control of seasonality in birds *J. Biol. Rhythms* **16** 365–80
- Dodge S, Bohrer G, Weinzierl R, Davidson S C, Kays R, Douglas D, Cruz S, Han J, Brandes D and Wikelski M 2013 The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data *Mov. Ecol.* **1** 3
- Farner D S and Follett B K 1966 Light and other environmental factors affecting avian reproduction *J. Anim. Sci.* **25** 90–115
- Fieberg J and DelGiudice G D 2009 What time is it? Choice of time origin and scale in extended proportional hazards models *Ecology* **90** 1687–97
- Gauthier G, Bety J, Cadieux M-C, Legagneux P, Doiron M, Chevallier C, Lai S, Tarroux A and Berteaux D 2013 Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the canadian arctic tundra *Phil. Trans. R. Soc. B* **368** 20120482
- Gedalof Z, Mantua N J and Peterson D L 2002 A multi-century perspective of variability in the pacific decadal oscillation: new insights from tree rings and coral: new insights from tree rings and coral *Geophys. Res. Lett.* **29** 57–1–4
- Gelaro R *et al* 2017 The modern-era retrospective analysis for research and applications, version 2 (MERRA-2) *J. Clim.* **30** 5419–54
- Gill J A, José A A, Sutherland W J, Appleton G F, Potts P M and Gunnarsson T G 2014 Why is timing of bird migration advancing when individuals are not? *Proc. R. Soc. B* **281** 20132161
- Gray V 2007 Climate change 2007: the physical science basis summary for policymakers *Energy Environ.* **18** 433–40
- Haest B, Hüppop O and Bairlein F 2018 The influence of weather on avian spring migration phenology: what, where and when? *Glob. Change Biol.* **24** 5769–88
- Hallett T B *et al* 2004 Why large-scale climate indices seem to predict ecological processes better than local weather *Nature* **430** 71–5
- Helm B, Benjamin M V D, Hoffmann D and Hoffmann U 2019 Evolutionary response to climate change in migratory pied flycatchers *Curr. Biol.* **29** 3714–3719.e4
- Huin N and Sparks T H 2000 Spring arrival patterns of the cuckoo *cuculus canorus*, nightingale *lusciniia megarhynchos* and spotted flycatcher *musciapa striata* in britain *Bird Study* **47** 22–31
- Høye T T, Post E, Møltøfte H, Schmidt N M and Forchhammer M C 2007 Rapid advancement of spring in the high arctic *Curr. Biol.* **17** R449–51
- Inouye D W, Barr B, Armitage K B and Inouye B D 2000 Climate change is affecting altitudinal migrants and hibernating species *Proc. Natl Acad. Sci.* **97** 1630–3
- Jahn A E, Susannah B L, Phillips L M, Ryder T B and Williams E J 2019 First tracking of individual American robins (*Turdus migratorius*) across seasons *Wilson J. Ornithol.* **131** 356–9
- James F C and Shugart H H 1974 The phenology of the nesting season of the American robin (*Turdus migratorius*) in the United States *Condor* **76** 159
- Jonzen N *et al* 2006 Rapid advance of spring arrival dates in long-distance migratory birds *Science* **312** 1959–61
- Kays R, Crofoot M C, Jetz W and Wikelski M 2015 Terrestrial animal tracking as an eye on life and planet *Science* **348** aaa2478

- Kranstauber B, Cameron A, Weinzerl R, Fountain T, Tilak S, Wikelski M and Kays R 2011 The movebank data model for animal tracking *Environ. Modelling Softw.* **26** 834–5
- Lameris T K, van der Jeugd H P, Eichhorn G, Dokter A M, Bouten W, Boom M P, Litvin K E, Ens B J and Nolet B A 2018 Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch *Curr. Biol.* **28** 2467–2473.e4
- Liebezeit J R, Gurney K E B, Budde M, Zack S and Ward D 2014 Phenological advancement in arctic bird species: relative importance of snow melt and ecological factors *Pol. Biol.* **37** 1309–20
- Liechti F 2006 Birds: blowin' by the wind? *J. Ornithol.* **147** 202–11
- Liston G E and Elder K 2006a A meteorological distribution system for high-resolution terrestrial modeling (MicroMet) *J. Hydrometeorol.* **7** 217–34
- Liston G E and Elder K 2006b A distributed snow-evolution modeling system (snow model) *J. Hydrometeorol.* **7** 1259–76
- Liston G E and Hiemstra C A 2011 The changing cryosphere: pan-arctic snow trends (1979–2009) *J. Clim.* **24** 5691–712
- Le Corre M, Dussault C and Côté S D 2016 Weather conditions and variation in timing of spring and fall migrations of migratory caribou *J. Mammal.* **98** gyw177
- Macmynowski D P, Terry L R, Ballard G and Geupel G R 2007 Changes in spring arrival of nearctic-neotropical migrants attributed to multiscalar climate *Glob. Change Biol.* **13** 2239–51
- Maloney E D *et al* 2014 North American climate in CMIP5 experiments: II. Assessment of twenty-first-century projections *J. Clim.* **27** 2230–70
- Marra P P, Charles M F, Mulvihill R S and Moore F R 2005 The influence of climate on the timing and rate of spring bird migration *Oecologia* **142** 307–15
- McKinnon E A, Macdonald C M, Gilchrist H G and Love O P 2016 Spring and fall migration phenology of an arctic-breeding passerine *J. Ornithol.* **157** 681–93
- Meller K, Piha M, Vähätalo A V and Lehikoinen A 2018 A positive relationship between spring temperature and productivity in 20 songbird species in the boreal zone *Oecologia* **186** 883–93
- Moller A P, Rubolini D and Lehikoinen E 2008 Populations of migratory bird species that did not show a phenological response to climate change are declining *Proc. Natl Acad. Sci.* **105** 16195–200
- Newton I 2004 Population limitation in migrants: population limitation in migrants *Ibis* **146** 197–226
- Norris D, Ryan P P, Marra T K, Kyser T W, Sherry and Ratcliffe L M 2004 Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird *Proc. R. Soc. B* **271** 59–64
- Pancerasa M, Ambrosini R, Saino N and Casagrandi R 2018 Barn swallows long-distance migration occurs between significantly temperature-correlated areas *Sci. Rep.* **8** 1–9
- Park T *et al* 2019 Changes in timing of seasonal peak photosynthetic activity in northern ecosystems *Glob. Change Biol.* **25** gcb.14638
- Paxton K L and Moore F R 2015 Carry-over effects of winter habitat quality on En route timing and condition of a migratory passerine during spring migration *J. Avian Biol.* **46** 495–506
- Post E and Forchhammer M C 2008 Climate change reduces reproductive success of an arctic herbivore through trophic mismatch *Phil. Trans. R. Soc. B* **363** 2367–73
- Pyle P 1997 *Identification Guide to North American Birds: I.* (Bollinas, CA: Slate Creek Press)
- Rainio K, Laaksonen T, Ahola M, Vähätalo A V and Lehikoinen E 2006 Climatic responses in spring migration of boreal and arctic birds in relation to wintering area and taxonomy *J. Avian Biol.* **37** 507–15
- Ramenofsky M and Wingfield J C 2007 Regulation of migration *BioScience* **57** 135–43
- Richardson W J 1978 Timing and amount of bird migration in relation to weather: a review *Oikos* **30** 224–72
- Rubolini D, Ap Møller K, Rainio and Lehikoinen E 2007 Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among european bird species *Clim. Res.* **35** 135–46
- Réale D, Andrew G M A, Boutin S and Berteaux D 2003 Genetic and Plastic responses of a northern mammal to climate change *Proc. R. Soc. B* **270** 591–6
- Saino N and Ambrosini R 2008 Climatic connectivity between africa and europe may serve as a basis for phenotypic adjustment of migration schedules of trans-saharan migratory birds *Glob. Change Biol.* **14** 250–63
- Smith R J and Moore F R 2003 Arrival fat and reproductive performance in a long-distance passerine migrant *Oecologia* **134** 325–31
- Stocker T F *et al* 2013 *Climate Change 2013: The Physical Science Basis.* (Cambridge: Cambridge University Press)
- Therneau T M and Grambsch P M 2013 *Modeling Survival Data: Extending the Cox Model* (Berlin: Springer)
- Tingley M W, Monahan W B, Beissinger S R and Moritz C 2009 Birds track their grinnellian niche through a century of climate change *Proc. Natl Acad. Sci.* **106** 19637–43
- Verhulst S and Nilsson J-Å 2008 The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding *Phil. Trans. R. Soc. B* **363** 399–410
- Wikelski M, Elisa M T, Raim A, Diehl R H, Larkin R P and Henk Visser G 2003 Costs of migration in free-flying songbirds *Nature* **423** 704–704
- Winger B M, Giorgia G A, Pegan T M and Weeks B C 2019 A long winter for the red queen: rethinking the evolution of seasonal migration *Biol. Rev.* **94** 737–52
- Young H 1955 Breeding behavior and nesting of the eastern robin *Am. Midland Naturalist* **53** 329–52