Spatiotemporal dynamics of songbird breeding in arctic-boreal North America

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ABSTRACT

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The high northern latitudes of North America are undergoing rapid climatic change with acute impacts to the ecosystems in which millions of songbirds breed each year. The goal of this dissertation is to improve understanding of how concurrent and interacting changes in environmental and land surface conditions influence annual movements and habitat selections of long distance migratory birds who must navigate the mosaic of changing North American ecosystems.

Chapter 1 presents novel automated bioacoustic methods for estimating arrival dates of the songbird community to their arctic breeding grounds. Automated acoustic networks could vastly expand the spatiotemporal coverage of wildlife observations. However, the enormous datasets that autonomous recorders typically generate demand automated analyses that remain largely undeveloped. Chapter 1 demonstrates novel machine learning and signal processing techniques for estimating songbird community arrival dates near Toolik Field Station which agreed well with traditional survey estimates and were strongly related to the landscape’s snow free dates. Daily variations in vocal activity were more strongly influenced by environmental conditions prior to egg-laying dates. The success of the approaches presented in Chapter 1 indicate that variation in songbird migratory arrival can be detected autonomously. Widespread deployment of this advance could provide avian monitoring on a scale large enough to enable global-scale understanding of how climate change influences migratory timing of avian species.
Chapter 2 examines potential future changes in habitat suitability for two songbirds breeding throughout North America’s high northern latitudes – a tundra-nesting species (Lapland Longspurs (*Calcarius lapponicus*)) and a shrub-nesting species (White-crowned Sparrows (*Zonotrichia leucophyrs*)). By the late 21st century, models based on both climate and vegetation projected habitat suitability for Lapland Longspurs decreased across nearly all of the study domain (54-96%), while that for White-crowned Sparrows decreased in 69% of North America’s high northern latitudes. For both species, currently unsuitable habitats in northern Canada and Alaska are projected to provide suitable breeding habitat in the future. In contrast, models based solely on climate showed more drastic declines in habitat suitability for both species (Lapland Longspur, ~100% and White-crowned Sparrow ~80%). This discrepancy between model projections demonstrates that the future availability of suitable songbird breeding habitat for both species will be strongly dependent on how both the vegetation and climate– as opposed to climate alone - of northern ecosystems respond to ongoing climate change.

Chapter 3 investigates the environmental and ecological drivers of migratory movements of songbirds breeding at high northern latitudes. For North America alone, there is overwhelming evidence of major shifts in seasonality of meteorological conditions, snow cover, and vegetation phenology. Few studies have focused on how this suite of changes impacts long distance migratory species that annually navigate throughout the spatially and temporally dynamic mosaic of ecosystems because of technological constraints in animal tracking. However, recent advances in GPS technology have generated units small enough to be placed on songbird species. In 2016-2018 a total of 55 American robins (*Turdus migratorius*) were tracked during their spring migration through the Canadian boreal forest en route to their breeding grounds. We found a significant trend towards earlier arrival of robins to the Canadian boreal
forest over the past quarter-century, consistent with advances in spring environmental conditions. Robin stopover timing at our tagging site was delayed in response to later seasonal snowmelt, but triggered by adverse environmental conditions. Individuals breeding in regions with shorter snow-free seasons moved faster than individuals breeding in areas with longer snow-free seasons and selected locations with less favorable environmental conditions. Overall, arrival timing to breeding grounds was negatively related to snow depth and positively related to snowmelt timing. Migratory movements and timing of American robins are highly tied to seasonal environmental dynamics en route to their breeding grounds. Our findings present a unique, mechanistic understanding of how migratory birds navigate highly dynamic ecosystems.

In light of rapid global change, the use of multi-disciplinary, spatially explicit approaches similar to the ones used in this dissertation will be critical for understanding how avian taxa breeding at high northern latitudes may respond to ongoing and future change. This is important for investigating both regional and global impacts because species breeding in arctic-boreal zones perform key ecosystem services around the globe.
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INTRODUCTION

Over the past fifty years, high northern latitudes (> 45°N) have warmed twice as much as the increase in global average temperatures (Trenberth et al. 2007, Stocker et al. 2014). Warming on this scale has implications for many environmental and ecological processes. Most notably, the extent and duration of sea-ice and terrestrial snow cover are declining (Serreze et al. 2000, Comiso et al. 2008, Callaghan et al. 2011, Simmonds 2015,) and permafrost is thawing (Anisimov et al. 2007). These temperature-induced changes are altering the surface energy balance of arctic-boreal ecosystems and having cascading effects for flora and fauna in the region.

Biotic responses to global climate change are being observed throughout arctic and boreal ecosystems (Post et al. 2009). Among these are changes in vegetation phenology and community composition. There is evidence that over the past three decades the onset of the growing season in high northern latitudes at the circumpolar scale is advancing by nearly two days per decade (Park et al., 2016). However, this trend is spatially heterogeneous both in magnitude and direction, with spring arriving later in some regions (Zeng et al. 2011, Park et al., 2016). In the arctic tundra, deciduous shrubs are increasingly encroaching on non-shrub tundra, typically dominated by evergreen, graminoids, and cryptograms (Sturm et al. 2001, Hinzman et al. 2005, Tape et al. 2006). While many arctic ecosystems have increased in productivity in response to recent climate warming (Jia et al. 2003, Jia et al. 2009, Forbes et al. 2010), several boreal ecosystems appear to be declining in productivity (Goetz et al. 2005, Lloyd & Bunn 2007). This is in part due to increasingly frequent and severe drought, wildfire, and insect outbreaks (Barber et al. 2000, Kasischke & Turetsky 2006, Werner et al. 2006, Soja et al. 2007). Observed increases in frequency and extent of disturbances are likely to shift the community composition
of boreal forests towards early successional deciduous species (Rupp et al. 2000). Taken together, these changes in primary productivity and abiotic conditions may have significant, yet largely unquantified, impacts on the animals that depend on arctic-boreal ecosystems (Post et al. 2009).

Millions of songbirds migrate from every continent to breed in arctic-boreal North America (Pielou 1994, Cornelissen et al. 2001). These birds, representing over a hundred species worldwide, undertake impressive migrations seeking the short, but significant, pulse in food resources as well as lower predatory and parasitic pressures available at high latitudes compared to more temperate ecosystems (Piersma 1997, McKinnon et al. 2010). Songbirds’ reproductive success, and overall population numbers, are influenced by access to preferred breeding habitat, interactions with other species, and reproductive timing to ensure their young arrive in time to take full advantage of the peak in arthropod biomass, all of which may be altered or disrupted by global climate change (Perez et al. 2016). Songbirds are an important prey for predators in the region and perform ecosystem services, such as insect control and seed dispersal, not only on their arctic-boreal breeding grounds but also in the habitats in which they overwinter and migrate through (Sekercioglu 2006, Boelman et al. 2015). So, changes in arctic-boreal habitats have the potential to reverberate in ecosystems globally.

Changes in phenology, the timing of life history events, is among one of the most widely documented biotic responses to global climate change (Parmesan). At high northern latitudes, phenology is controlled by climatic conditions. Vegetation and lower trophic levels are influenced by weather conditions, with snow melt ultimately driving the emergence of invertebrates in the spring (Tulp & Schekkerman 2008). Invertebrates are a critical food resource for migratory songbirds, and as such their reproductive success depends on timing egg-laying so
that young can take capitalize on the peak in invertebrate abundance (Perez et al. 2016). As such, songbirds establish territories and initiate clutches as soon as conditions become suitable because of the compressed breeding season at high northern latitudes (about 4-5 weeks). Prolonged delays can be detrimental because passerines must ensure that young have sufficient time to develop and adults to molt before migrating south in the fall (Martin 1987, Verhulst and Nilsson 2008).

As spring environmental conditions continue to change at high northern latitudes (Park et al. 2016), songbirds’ reproductive success will depend in part on their ability to adjust their breeding phenology to keep in step with changes on their breeding grounds. Across the globe, migratory birds show strong phenological responses to climate change (Root et al. 2003, Thorup et al. 2007), with many populations arriving to their breeding grounds earlier, consistent with increasing spring temperatures (e.g. Mills et al. 2005, Rubolini et al. 2007, Travers et al. 2015). The onset of spring migration in is cued by photoperiod, thus departure dates from wintering grounds are largely constrained (Both & Visser 2001). However, timing of arrival to breeding grounds is influenced by food quality and environmental conditions on wintering grounds (Marra 2005), along the migratory route (Tottrup et al. 2012), and on breeding grounds (Wingfield et al. 2004). Many studies suggest that passerines breeding in the arctic adjust their breeding phenology in response to spring conditions (Custer & Pitelka 1977, Fox et al. 1987, Norment 1992, Liebezeit et al. 2014, Boelman et al. 2017). While these studies are critical in documenting local or population specific biotic responses to climate change, we are still limited in our ability to predict the phenological responses avian communities will have to future changes in climate (Turner 2014). This will require understanding the relative importance of meteorological conditions, extreme events, and modes of climate variability in determining avian arrival timing,
and this understanding is currently limited by the temporal and spatial scale that studies are typically conducted (Gordo 2007, Morisette et al. 2009).

However, the viability of future songbird populations breeding in arctic-boreal North America depends not only on their ability to cope with changes in seasonality, but also on concurrent changes in habitat quality, location, and extent (Ims & Henden 2012, Sokolov et al. 2012, Bolduc et al. 2013, Boelman et al. 2015, van Wilgenburg et al. 2018). Changes in abiotic conditions and landscape characteristics are likely to impact habitat suitability because climate and vegetation are widely known to control avian abundance and distribution at large geographic scales (Root et al. 1988, Cumming et al. 2014). For example, Brommer et al. (2012) found poleward shifts in the breeding ranges of arctic and boreal birds, consistent with warming trends. However, changes in vegetation community and structure are likely to play a key role in determining future breeding habitat. Boelman et al. (2015) predicted that breeding habitat extent would expand for a shrub-nesting species and contract for a tundra-nesting species by 2050 as deciduous shrubs continue to expand in arctic Alaska. Stralberg et al. (2015) found that lags in forest growth and succession may dramatically reduce the future extent of suitable breeding habitats of songbirds breeding in boreal ecosystems. Predicting future availability of breeding habitats will require considering not only future climate information, but also understanding how vegetation communities will respond to climate change.

In addition to changes in breeding habitat, temporal and spatial characteristics are changing in overwintering and stopover habitats, often in different ways and to different degrees (Coppack & Both 2002, Newton 2004, Norris et al. 2004, Holmes 2007). For North America alone, there is overwhelming evidence of major shifts in seasonality of meteorological conditions, snow cover, and vegetation phenology, as well increases in the frequency and
intensity of natural disturbances (i.e. wildfire) and extreme environmental conditions (i.e. drought) (Karl et al. 1993, Foley et al. 2005, Cook et al. 2007, Marlon et al. 2009). Few studies have focused on how this suite of changes impacts long distance migratory species that annually navigate throughout the spatially and temporally dynamic mosaic of ecosystems. This is because technological constraints in animal tracking have resulted in migratory routes for most species being only crudely defined, and while the breeding or overwintering grounds of a given population are known, both are seldom identified (Wikelski et al. 2007). For the same reason, animal movements and habitat selection are rarely examined in response to dynamic environmental and land surface conditions.

There is but a handful of annual, long-term bird monitoring programs spread throughout North America, and these efforts are seldom able to demystify the migratory pathways and pan-seasonal habitat selections of any given bird population. This is because traditional census surveys represent a single snapshot in time and space, making it difficult to piece together highly seasonal patterns in a population’s migration movement and habitat selections, or to determine animal behavioral responses to spatially and temporally unpredictable disturbance events (e.g. wildfire) or extreme environmental conditions (e.g. drought) (Semeniuk et al. 2012). Recent and emerging advances in space-based animal tracking technologies allow the direct measurement of animal movements across vast, remote regions through seasons and years with minimal labor (Wikelski et al. 2007). These regional-scale and near-continuous descriptions of animal locations can be linked to satellite observations of environmental and land surface conditions (Semeniuk et al. 2012, Bohrer et al. 2012, Dodge et al. 2013). The rapid pace of change in abiotic conditions in arctic-boreal ecosystems demands research over large spatial and temporal scales to understand and predict future ecological responses (Post et al. 2009, Guathier et al. 2013). In light of these
needs, this dissertation presents contributions to our understanding of the spatio-temporal dynamics of songbird breeding in arctic-boreal North America.

Chapter 1 presents novel machine learning and signal processing techniques for estimating songbird community arrival dates to their breeding grounds on the North Slope of Alaska. Acoustically derived measures of songbird arrival agreed well with traditional survey estimates of arrival. Widespread deployment of this advance could provide avian monitoring on spatiotemporal scales large enough to enable global-scale understanding of how climate change influences migratory timing of avian species.

Chapter 2 examines potential future changes in habitat suitability for two songbirds breeding throughout North America’s high northern latitudes – a tundra-nesting species (Lapland Longspurs (Calcarius lapponicus)) and a shrub-nesting species (White-crowned Sparrows (Zonotrichia leucophyrs)). By the late 21st century, suitable breeding habitat is projected to decline for both species. However, the inclusion of future vegetation distributions moderate these declines demonstrating that the future availability of suitable songbird breeding habitat for both species will be strongly dependent on how both the vegetation and climate of northern ecosystems respond to ongoing climate change.

Chapter 3 investigates the environmental and ecological drivers of spring migratory movements of American robins (Turdus migratorius) breeding at high northern latitudes. Consistent with the well-documented advance in spring environmental conditions at high northern latitudes, robin migration to Slave Lake, Alberta has advanced over the past quarter-century. Multiple metrics of robin migratory phenology were negatively influenced by unfavorable spring environmental conditions. Our findings present improved understanding of the links between songbird migration timing and environmental conditions.
CHAPTER 1:

Eavesdropping on the Arctic: Automated bioacoustics reveal dynamics in songbird breeding phenology

Abstract

Bioacoustic networks could vastly expand the coverage of wildlife monitoring to complement satellite observations of climate and vegetation. This would enable global-scale understanding of how climate change influences phenomena like migratory timing of avian species. The enormous datasets that autonomous recorders typically generate demand automated analyses that remain largely undeveloped. We devised automated signal processing and machine learning approaches to estimate dates on which songbird communities arrived to arctic breeding grounds. Acoustically-estimated dates agreed well with those determined via traditional surveys and were strongly related to the landscape’s snow-free dates (RMSE = 1.88-3.02 days). We found that daily variation in songbird vocal activity was heavily influenced by environmental conditions, especially prior to egg laying (R² = 0.62 (before) vs. 0.21 (after)). Our novel approaches demonstrate that variation in avian migratory arrival can be detected autonomously. Large-scale deployment of this innovation in wildlife monitoring would enable the coverage necessary to assess and forecast changes in bird migration in the face of climate change.

A modified version of this chapter has been published as:

1.1 Introduction

Shifts in phenology across floral and faunal taxa are among the mostly widely documented biotic responses to global climate change (Parmesan 2006). Migratory birds show strong phenological responses to changing climate (Root et al. 2003), with many populations arriving to their breeding grounds earlier in association with rising spring temperatures (Rubolini et al. 2007). Such shifts can influence their reproductive success (Both et al. 2006), and may lead to adaptations to climate change (Charmantier & Gienapp 2014). These population-specific and often local responses, though important for monitoring biotic climate change impacts, are limited in their ability to provide global-scale assessments of phenological responses of avian communities to climate change. Large-scale spatial and temporal heterogeneity in climate change and taxonomic variability among avian species requires a global approach (Gordo 2007). The absence of such long-term, global-scale information hampers understanding of the relative influences of meteorological conditions, extreme events, and modes of climate variability (e.g. El Niño Southern Oscillation) which is necessary to identify avian species, populations, communities, and ecosystems most vulnerable to projected shifts in climate (Morisette et al. 2009, Turner 2014).

To date, wildlife responses to climate change have been measured using in situ censuses and global positioning system (GPS) tracking, both of which function poorly in monitoring whole avian communities. In situ censuses provide only point-based information, are conducted at infrequent snapshots in time and space, primarily due to their labor-intensive nature, and are subject to large sampling bias because of limited access to remote areas and observer differences (Shonfield & Bayne 2017). Although GPS tracking provides dynamic data, tagging remains costly and current tracking units are too large to place on most avian species (Kays et al. 2015).
Automated bioacoustic recorders offer a more cost-effective alternative to sample at larger spatial, temporal, and taxonomic scales (Shonfield & Bayne), but have yet to be widely deployed because bioacoustic data is complex and, despite significant advances in automated analytical methods, comprehensive toolsets remain largely undeveloped. Single recorders provide highly localized information, but recording arrays are being deployed across landscapes, recording sounds at the landscape level, or recording what constitutes a soundscape (Krause 2008).

Soundscapes are rich in information relating to wildlife abundance, community assemblage, behavior, and communication (e.g. Poole et al. 2005, Farina et al. 2011, Frommolt & Tauchert 2014, Stoeger & Zepplezauer 2014). As such, the use of bioacoustics to answer ecological questions has been increasing steadily (Shonfield & Bayne 2017). Many methodological papers have focused on comparing tallies of species presence/absence determined by experts listening to acoustic recordings versus traditional field surveys (e.g. Vold & Handel 2017). Other studies use acoustic data to test ecological hypotheses, relying on listener input from trained experts to identify species from recordings (e.g. Hart et al. 2015). Although listening to recorded data has proven a valuable technique (Shonfield & Bayne 2017), recorders typically generate enormous datasets too large to listen to. Considerable effort has gone into automating the extraction of bioacoustic information from large volumes of recorded data for use in ecological studies. For example, automated signal processing and machine learning techniques have been developed to identify species-specific vocalizations with great success in the study of marine mammals (e.g. Stafford et al. 1998), elephants (e.g. Zepplezauer et al. 2015), and nocturnal avian migration (e.g. Salamon et al. 2016). Although valuable, these techniques are fine-tuned to individual species of interest (Salamon et al. 2016), which narrows their broad application. Further, these approaches often rely on recordings with limited background noise – a
condition atypical of soundscape-level recordings (Salamon et al. 2016, Bardeli et al. 2010). Other studies sidestep the direct identification of vocalizations, and examine community-level dynamics through various ‘acoustic indices’ (e.g. Boelman et al. 2007, Sueur et al. 2008, Pieretti et al. 2011, Gage & Axel 2011). This approach has proven powerful because acoustic indices are relatively straightforward to calculate and rapidly synthesize complex soundscapes.

We took a novel approach to analyzing bioacoustic data by leveraging signal processing and machine learning techniques – borrowed from human speech recognition applications – to develop automated monitoring of migratory songbird communities breeding in arctic Alaska. Specifically, we quantified spatiotemporal dynamics in vocal activity and estimated the date on which songbird communities arrived to their breeding grounds in each of five consecutive springs.

1.2 Materials and Methods

1.2.1 Study design

This study was focused on four research sites in the foothills of the Brooks Range, Alaska (68°38’ N, 149°34’ W, elevation 760 m) in a 35 km radius of Toolik Field Station (Supplemental Fig. A.1). Data was collected over a five-year period (2010-2014) at Roche Mountonee Creek (ROMO), Imnaviat Creek (IMVT), Toolik Field Station (TLFS), and Sagavanirtok Department of Transportation (SDOT). For a full description of sites see (Boelman et al. 2015).

Although the acoustic analyses presented in this study do not discriminate between species, we compare the results to traditional avian surveys of the two most abundant species in our study region. Lapland Longspurs (Calcarius lapponicus) and Gambel’s White-crowned Sparrows (Zonotrichia leucophrys gambelii) are both long distance migratory passerines, which winter in
the contiguous United States (Ramenofsky, Piersma 1997) and migrate to breed in northern Alaska (Pielou 1994, Boelman 2015) where they capitalize on the brief but large pulse of food resources and relatively low predatory risk that Arctic summers offer as compared to more southern ecosystems (Pielou 1994, Piersma 1997, McKinnon et al. 2010). Typically arrival occurs in early to mid-May (27, 29). Arrival timing is of critical importance to Arctic-breeding birds who must quickly initiate clutches and complete their breeding cycles before winter’s onset (~ 90 days), and ensure that their young hatch at the peak of nutritious arthropod biomass (Rubolini et al. 2007, Pérez 2016).

1.2.2 Automated collection of landscape-level acoustic data

Acoustic recordings were taken over five breeding seasons (2010-2014), between early May and mid/late-June of each study year, thereby including the arrival, territory establishment, and clutch initiation of our two focal species (Boelman et al. 2017). Thirty-minute recordings were made four times daily (2:00, 6:00, 9:00, 21:00) to capture diurnal variation in vocal activity. Recordings were made using a digital audio recorder (722, Sound Devices, LLC, Reedsburg, Wisconsin, USA) and two microphones (MKH-30 and MKH-40, Sennheiser Electronic GmbH and Co. KG, Wedemark, Germany) at 48 kHz sample rate. The acoustic dataset contains 1200 hours of recordings capturing sounds from a range of typical local sources including rain, wind, truck traffic along the nearby Dalton Highway, mosquitoes, and a variety of bird species.

1.2.3 Traditional avian surveys

The dates of mean arrival of Lapland Longspurs and Gambel’s White-crowned Sparrows to the study region were determined by the mean date on which individuals were captured in mist nests at the four sites in 2011-2014. No Lapland Longspurs were captured in 2010, so the mean
arrival date was determined from road surveys in that year. The date of mean arrival of the songbird community to the region was determined by calculating the mean between species and sites. The mean dates of egg laying for all located nests of each species were determined based on observations of egg laying, hatching, and fledging in 2011-2014. The mean date of egg laying of the songbird community was determined by calculating the mean dates between species for each year. For full details, see (Boelman et al. 2017).

1.2.4 Environmental data collection

Air temperature, precipitation, atmospheric pressure, and wind speed data at ROMO and SDOT were collected. Environmental data for TLFS and IMVT were downloaded from the Environmental Data Center (2014) at Toolik Field Station and Imnavait Arctic Observatory Network (AON) Tussock Site, respectively. Snow cover was determined as the percentage of ground covered by snow in automated photographs. Snow cover data was only collected at two study sites (ROMO and TLFS) in 2010. For full details, see (Boelman et al. 2017).

1.2.5 Acoustic analysis overview

Our primary objectives were to: (i) estimate the arrival date of the songbird community to their arctic breeding grounds in each of our five study-years, and; (ii) determine the influence of both environmental conditions and songbird phenology on estimates of songbird vocalizations through the breeding season. We present two analytical approaches, supervised (includes listener input) and unsupervised classifications (no listener input), using a dataset collected at sub-daily intervals over five consecutive breeding seasons (Fig. 1.1). Both approaches rely on the same initial statistical characterization of the acoustic dataset to identify the presence of songbird vocalization, regardless of species.
The supervised classification approach used a linear classifier, trained on a subset of listener-determined presence/absence of songbird vocalizations, to classify every four-second segment of the dataset for the presence/absence of songbird vocalizations. The proportion of segments per day containing songbird vocalizations were then used as a relative measure of daily songbird vocal activity, referred to as the Vocal Activity Index (VAI). The performance of the classifier was assessed by the relationship between the VAI and the training dataset (Supplemental Fig. A.2). Daily time series of VAI were created for each recording site and study year (Fig. 1.2 and Supplemental Figs. A.3-A.5). To understand and interpret daily variation the VAI, we used linear models to quantify relationships between the VAI and local environmental conditions and how these relationships change based on songbird breeding phenology (Fig. 1.3 and Supplemental Fig. A.6). Finally, we used the VAI to estimate the arrival date of songbirds to their breeding grounds in each study year and compared these estimates to avian surveys conducted concurrently with acoustic recordings (Fig. 1.4).

In contrast, the unsupervised classification approach used a series of signal processing techniques and machine learning algorithms to cluster the acoustic data into potential physical sources (e.g. bird vocalizations, wind, trucks on the nearby Dalton Highway) without any training from listener input. Because the number of physical sources, and thus clusters, is not known a priori, we initially clustered the data into 100 clusters and calculated the proportion of recording segments that fell into each cluster. We then performed principal component analysis on the cluster assignment histograms to reduce the cluster assignment histograms to twenty dimensions. To identify the principal components that contained information about songbird vocalizations, we quantified the relationship between the principal components, added in succession, and the VAI (Supplemental Fig. A.2). This resulted in a time series of songbird
vocalizations, as determined by a weighted sum of the first five principal components (Fig. 1.2 and Supplemental Figs. A.3-A.5). Independent of this procedure, we used the transition in acoustic sources, as measured by the first twenty principal components, over time to estimate arrival date of songbirds to in each study year by finding the optimal boundary, and compared these estimates to avian surveys (Fig. 1.4).

1.2.6 Statistical characterization to determine presence/absence of songbird vocalizations

To identify the presence of songbird vocalizations, regardless of species, we segmented the acoustic dataset into four-second segments (the typical duration of a songbird vocalization phrase) with two seconds between consecutive clips. Each thirty-minute recording contributed 898 four-second segments, and thus a thirty-day period at a single recording site amounts to over 100,000 segments. Each four-second segment was described by a set of 54 statistical texture features known to be important for human auditory recognition: mean, variance, and sub-band entropy within auditory-scaled frequency bands (Ellis et al. 2011). The lowest five frequency bands (0-630 Hz) were excluded from analysis because songbird vocalizations are not produced at these frequencies.

1.2.7 Identifying songbird vocalizations

(1) Supervised classification.

We employed linear discriminant analysis to develop a linear classifier to determine the presence/absence of songbird vocalizations in each segment, based on their associated texture features. The linear classifier was trained using a random subset of recording segments manually scored for the presence/absence of songbird vocalizations based on listener input. The training dataset consisted of 6000 example segments (< 1% of the total dataset).
A hyper-plane was fit to the training dataset to separate the two classes (presence/absence of songbird vocalizations) based on their texture features. A receiver operating characteristic curve (ROC) was used to investigate the performance of the classifier as the decision threshold was varied and find the area under the curve (AUC), a measure of the classifier’s performance above random classification. The classifier’s decision threshold was adjusted to the equal area rate, where the true positive rate and true negative rate are equal. The resulting classifier was used to classify the entire acoustic dataset for the presence/absence of songbird vocalizations. Calculating the proportion of four-second segments per day containing songbird vocalizations gave a score of relative vocal activity, the VAI. The VAI ranges from 0 to 1, where 0 represents no songbird vocalizations in any segments recorded in a day, and 1 means all segments contained vocalizations.

The performance of the classifier was assessed by comparing the proportion of segments containing songbird vocalizations in a thirty-minute recording as determined by the classifier and by listening. The closeness of fit to a linear relationship was quantified with a linear regression. The difference between the values from the classification output and the manual listening was measured as the root-mean-square error. Although each four-second segment was scored for the presence/absence of songbird vocalization, for the remaining analysis we reduced the temporal resolution to a daily VAI.

(2) Unsupervised classification.

To identify four-second segments with similar acoustic characteristics without listener input, we employed vector quantization to cluster segments based on their associated texture features for each thirty-day recording period independently. Vector quantization reduces multidimensional data by grouping neighboring vectors, in this case texture features, to a
predefined number of prototype vector codewords, or clusters (Gray 1984, Rabiner & Juang 1993). A codebook of 100 characteristic vectors was trained using 10,000 randomly selected texture feature vectors from each thirty-day period recording period. The training vectors were grouped using the K-means clustering algorithm, which iteratively updates the location of the codeword vectors until the average Euclidean distance to the associated training vectors falls below a predetermined threshold (Rabiner & Juang 1993). The entire thirty-day recording period was then quantized into the 100 codewords by minimizing the Euclidean distance of each four-second segment’s texture feature vector to the codewords. This associated each four-second segment with a codeword. The codeword assignments of the entire dataset were summarized by histograms of codeword assignments over 100 four-second segments (approximately ten minutes).

The codeword histograms were reduced through principal component analysis via singular value decomposition, which lowers the dimensionality of a dataset by finding the optimal subspace, based on minimizing the sum of the square perpendicular distances of the given set of points to the subspace (Krzanowski 1998). Principal component analysis was performed for each thirty-day recording period independently. On average, the first twenty principal components explained 72% of the variability in the codeword datasets, we thus restricted each thirty-day period to the first twenty principal components.

To investigate the relationship of the resulting principal components to the presence of songbird vocalizations, we compared their scores to the VAI. To match the temporal resolution of the VAI, principal component scores were averaged to give mean daily scores. A series of linear models were used to quantify the relationship between the VAI and the principal components added in succession for each thirty-day recording period independently. For
example, the VAI of each thirty-day recording period as predicted by linear models based on the following: (1) the first principal component’s scores; (2) the first two principal components’ scores, etc. The mean and standard error of $R^2$ values was found for model input configuration replicates across study years and sites. The appropriate number of principal components to use in a time series of songbird vocalizations was considered the first combination that on average explained 70% of the variance in the VAI. The fitted values from the multivariable models were used to generate a time-series of the weighted sum of the selected principal components. The ability of the weighted sum of principal components to replicate the VAI was measured by the root-mean-square-error.

1.2.8 Arrival date estimation

(1) Supervised classification.

Arrival date of the bulk of the songbird community breeding in the vicinity of our four recording sites was calculated as the first recording date on which a given site’s VAI exceeded 50% of its maximum value for that year. The sensitivity of arrival date estimates to thresholds ranging from 30-70% was investigated.

(2) Unsupervised classification.

The songbird community arrival date was estimated by analyzing scores of the first twenty principal components over time and finding the optimal segmentation boundary at each site for each year. We constrained our analysis to the time period prior to May 25th because songbirds are known to arrive to our study site in this time window (Wingfield et al. 2004, Boelman et al. 2017). Despite identifying the principal components that were strongly related to the VAI, and thus songbird vocalization, we included the first twenty principal components in this portion of the analysis in order to develop an arrival date estimation procedure that is
independent of any listener input.

The optimal segmentation boundary in the principal component scores was found using a Bayesian Information Criterion (BIC)-based algorithm, a common approach to segmenting audio information (Cettolo et al. 2005). Our BIC-segmentation tested all possible segmentation boundaries up to May 25th by fitting Gaussian mixture models on either side of the boundary. Boundary placements were scored by the sum of the negative log of the likelihoods of the associated models. We considered the optimal boundary placement to be that which minimized the score criterion. Songbird community arrival date was estimated as the date of the optimal segmentation boundary.

To validate both the supervised and unsupervised classification approaches to estimating the songbird community arrival date, we averaged arrival date estimates among recording sites for each year and compared them to avian survey estimates conducted concurrently (although at a coarser spatial resolution, see Avian surveys). The root-mean-square error was used to quantify the ability of both classification approaches to replicate survey estimates.

1.2.9 The influence of environmental conditions and songbird phenology on VAI

Relationships between the VAI and environmental conditions were investigated at each site and year (twenty replicates) with linear models. To identify which covariates were significantly predictive of the VAI we used stepwise regression with backward variable selection. Multivariable linear models were built for each thirty-day recording period independently with the following suite of environmental covariates as predictor variables: snow cover, temperature, wind speed, atmospheric pressure, and precipitation. Predictor variables were iteratively removed by the following procedure: (1) generating a linear model using all available environmental covariates; (2) performing a F-test; and (3) eliminating variables one at a time that
were not statistically significant ($p < 0.1$). This procedure was repeated until only the environmental covariates that had a statistically significant linear relationship to the VAI remained. Models for 2010 at the SDOT and IMVT sites did not include snow cover as a potential covariate because data were not available (see *Environmental data*).

Linear models were built for each of the twenty (four sites, five years) thirty-day recording periods using only the environmental covariate(s) determined to be statistically significant, hereafter referred to as significant multivariable models. Linear models were also built for each thirty-day period between VAI and each environmental covariate in isolation, hereafter referred to as single variable models.

Songbirds’ propensity to vocalize is known to change throughout their breeding season - with higher levels of singing when individuals are searching for mates and lower levels after clutches are initiated (Wilson & Bart 1985). We explored how relationships between the VAI and environmental conditions changed based on songbird phenology. The thirty-day recording periods were segmented based on the mean clutch initiation date for Lapland Longspurs and White-crowned Sparrows as determined by avian surveys (see *Avian surveys*). The same suite of significant multivariable and single variable linear models, described above, was constructed for the time window prior to clutch initiation (on average, 22 days) and the time window following clutch initiation (on average, 8 days). This analysis was only performed for the years 2011-2014 because clutch initiation dates were not available for 2010 (see *Avian surveys*). The proportion of variance ($R^2$) explained by the predictor variables was found for each model. The mean and standard error of $R^2$ values was found for model input configuration replicates. Two sample t-tests of mean $R^2$ values were performed to compare model input configurations.
Figure 1.1: Outline of bioacoustic methodology. We present two analytical approaches, supervised and unsupervised classifications. Both approaches rely on the same initial statistical characterization of the acoustic dataset to identify songbird vocalizations, regardless of species. The supervised approach used a linear classifier to classify every four-second segment of the dataset for the presence/absence of songbird vocalizations, trained on a subset of listener-determined scores (<1% of dataset). The proportion of segments per day containing songbird vocalizations was used as a relative score, referred to as the Vocal Activity Index (VAI). Arrival dates were estimated as the first date that exceeded 50% of the maximum value of the VAI. The unsupervised approach used a series of signal processing and machine learning techniques to cluster the acoustic data into potential physical sources (e.g. vocalizations, wind, trucks) without training from listener input. Because the number of physical sources is not known a priori, we initially clustered the data into 100 clusters. We then performed principal component analysis on the histograms of cluster assignments to reduce data to twenty dimensions. Arrival dates were estimated as the optimal segmentation boundary in principal components, as measured by the fit of Gaussian distributions on either side of the boundary.
1.3 Results and Discussion

1.3.1 Quantifying songbird community vocal activity

We explored both supervised (which includes listener input) and unsupervised (no listener input) classification approaches (Fig. 1.1) to build seasonal time series of daily avian vocal activity (Fig. 1.2). The supervised classification yielded a score of the relative proportion

![Figure 1.2: Songbird community vocal activity estimated by supervised and unsupervised approaches.](image)

(a)-(e) Songbird daily Vocal Activity Index (VAI), snow cover (blue), and air temperature (red) near Toolik Field Station (TLFS) between 2010-2014. (f)-(j) Weighted sums of the first five principal components at the same site and time. Grey boxes identify the available recording period for acoustic data. Daily VAI and weighted sums for the entire dataset at all field sites can be found in the Supplemental Materials (figs. S3 to S5).

21
of segments containing songbird vocalizations each day - the Vocal Activity Index (VAI) – which agreed well with our listener generated scores ($R^2 = 0.65$, RMSE = 0.19) (Supplemental Fig. A.2). The unsupervised classification yielded a weighted sum of principal components that were strongly related to results from the supervised approach ($R^2 = 0.7$, RMSE = 0.11) (Supplemental Fig. A.2). Time series generated by both approaches showed substantial variation in the songbird community’s vocal activity levels among days, weeks, years, and recording sites (Fig. 1.2 and Supplemental Figs. A.3-A.5).

1.3.2 Influence of environmental conditions and breeding phenology on vocal activity

![Figure 1.3. Influence of environmental conditions and breeding phenology on songbird community vocal activity. Proportion of variance in the Vocal Activity Index explained by environmental covariates as determined by linear models. To identify environmental covariates that were significantly predictive ($p < 0.1$) of the VAI, we used stepwise regression with backward variable selection based on a F-test to build linear models for each recording period independently. Single variable linear models were also built with each environmental covariate in isolation. The same suite of linear models was built for the period before and after egg laying dates for the two most abundant songbird species. Points represent mean $R^2$ (across sites and years) +/- standard error. Black points indicate linear models built with data over the entire 30-day study period. Red and blue points indicate linear models built considering the period before and after the mean egg laying dates, respectively.](image-url)
We found that daily fluctuations in snow cover, air temperature, wind speed, atmospheric pressure, and precipitation had a significant impact on the VAI and explained a large proportion of variance ($R^2 = 0.52 +/- 0.06$) (Fig. 1.3 and Supplemental Fig. A.6). Our acoustically-derived findings agree with previous in situ work showing breeding songbirds require snow-free patches of tundra to supply critical food and shelter (Wingfield et al. 2004, Grabowski et al. 2013, Boelman et al. 2017), while cold conditions exacerbate the high energetic costs associated with singing (Gaunt et al. 1996, Krause et al. 2016), suggesting songbirds are either absent or silent during unfavorable conditions.

We found the VAI was more strongly influenced by environmental conditions prior to, compared to following, egg laying dates for two of the most abundant songbird species in the region - Lapland Longspurs (*Calcarius lapponicus*) and Gambel’s White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) ($R^2 = 0.62 +/- 0.07$ vs. $0.21 +/- 0.08$, respectively, $p < 0.1$). We attribute this to the fact that vocal activity changes with male pairing status and breeding phenology, with singing decreasing drastically after egg laying (Wilson & Bart 1985). Our findings demonstrate that the correct interpretation of avian vocal activity to estimate relative songbird abundance requires pairing of acoustic data collection with meteorological data, as well as consideration of the study communities’ breeding phenology. This could be partially realized by leveraging existing environmental monitoring networks (e.g. National Science Foundation’s Arctic Observing Network (AON), National Ecological Observing Network (NEON), and Long Term Ecological Research (LTER) network), which could be expanded to include and power microphone and recording arrays.
1.3.3 Songbird community arrival dates

![Graph](image)

**Fig. 1.4. Acoustically-derived estimates of songbird arrival to breeding grounds and relationship to snow-free dates.**

(a) Songbird community mean arrival dates to their breeding grounds near Toolik Field Station, Alaska over a five-year period (2010-2014) using supervised and unsupervised bioacoustic approaches compared to traditional avian surveys. Standard error bars reflect averages across four recording sites for acoustically-derived estimates. (b) Songbird community arrival dates for each site over a five-year period (2010-2014) estimated from supervised and unsupervised bioacoustics approaches compared to the date on which the landscape surrounding the recording unit fell below 10% snow coverage.

Across our five study-years, acoustically-derived estimates of arrival dates were strongly related to those determined via traditional avian surveys of two of the most locally abundant...
species (supervised: RMSE = 3.02 days and unsupervised: RMSE = 1.88 days) (Fig. 1.4 and Supplemental Fig. A.7). This success derives from the fact that migratory songbirds vocalize intensely soon after they arrive to suitable breeding territories because of the immense pressure to initiate breeding in the Arctic (Wingfield et al. 2004). To assess the accuracy of our acoustically-derived arrival date estimates we compared them to an alternative method to estimate arrival timing based on traditional avian surveys. Differences in arrival estimates between these two methods may be due in part to the fact that acoustic sensors were able to sample more frequently than human observers. However, the inability of bioacoustic methods to distinguish absence from silence limits their accuracy. Using multiple techniques in tandem could help quantify uncertainty in available methods in the short term and inform interpretation of results. Doing so is particularly important to assess variability and trends in songbird phenology in light of global climate change.

Further, in each study year, acoustically-derived arrival dates differed among our four recording sites which were spread along a 70 km transect, with arrival occurring earliest at the southernmost site in almost all cases. Relative to other study years, in 2013 – a spring characterized by persistent snow cover and cold temperatures (Boelman et al. 2017, Krause et al. 2016) – our bioacoustic approaches identified a one to nine day delay in the arrival of songbird communities to their breeding grounds (Fig. 1.4). In addition, inter-annual and spatial differences in arrival dates were strongly related to the date on which the landscape surrounding each microphone became snow-free (i.e. snow cover < 10%) using our supervised approach ($R^2 = 0.59, p < 0.01$) (Fig. 1.4). The relationship between snow-free and arrival dates for the unsupervised approach was relatively weak ($R^2 = 0.13, p = 0.15$), suggesting that the unsupervised approach is less sensitive to small variations in snow-free dates than the supervised
approach. This is most likely due to methodological differences in estimating arrival dates between the supervised and unsupervised approaches. Arrival date estimates from the supervised approach are based solely on the Vocal Activity Index, whereas the unsupervised approach estimates arrival by incorporating information from other acoustic sources which may dampen the seasonal transition in songbird vocal activity (for more information see Materials and Methods). Our results suggest that while both bioacoustic methods successfully estimated large differences in arrival dates, the supervised approach may be superior to the unsupervised approach in estimating arrival timing in response to small spatiotemporal differences or changes in snow melt timing resulting from climate change. Again, quantifying error associated with arrival estimates by comparing alternate methods could improve our ability to assess trends related to global change.

Millions of songbirds migrate each spring to breed in the Arctic (Pielou 1994). Although the onset of spring migration is cued by photoperiod (Ramenofsky 2007), arrival and settlement are influenced by environmental conditions en route and on breeding grounds (Boelman et al. 2017, Krause et al. 2016, Tøttrup et al. 2012). Shifts in the arrival of spring due to climate change may be spatially heterogeneous along migratory routes (Buitenwerf et al. 2015). While traditional avian surveys have used timing of the onset of singing to estimate date of migratory species’ arrival to breeding grounds as far back as the nineteenth century (e.g. Gordo 2008), efforts to extract arrival timing from digital acoustic datasets have been rare (e.g. Buxton et al. 2016). We contend that arctic ecosystems in particular merit autonomous methods of data collection because they are changing rapidly and are difficult to survey because they are vast and remote (Seddon et al. 2016). Climate impacts on arrival timing, which may influence breeding
success, could reverberate globally, as Arctic-breeding songbirds perform important ecosystem services worldwide (Sekercioglu 2006).

1.4 Conclusions

The direct application of our automated analytical approaches to monitor avian phenology may be possible in other ecosystems and for the study of other vocal taxa (e.g. insect or amphibian species). Our unsupervised approach is likely to work best in ecosystems with similar high seasonality in vocal activity, such as occurs along migratory stop-overs or in other ecosystems with strong seasonality in environmental conditions. Our supervised approach can be easily calibrated for other ecosystems and species via some initial listener input and training. Automated bioacoustic networks present an advantage over traditional surveys because they can be deployed to sample more economically over longer periods and in more remote areas, and they preserve a long-term observational dataset that can be reanalyzed and thus reduce observer biases (Shonfield & Bayne). Our success demonstrates that automated bioacoustic networks are well poised to integrate with ground-based and remotely sensed observations of environmental conditions and vegetation to enhance understanding of how climate influences phenological responses of wildlife that use vocal forms of signaling and communication such as birds, amphibians, social mammals, insects, and many other species.
CHAPTER 2:

Biotic interactions moderate future decline and northward shift of songbird breeding habitat at high northern latitudes of North America

Abstract

The high northern latitudes (HNLs) of North America are undergoing rapid climatic change with acute impacts to the ecosystems in which millions of songbirds breed. Changes to songbird breeding habitat suitability are likely to result from concurrent changes in climate and vegetation in the region. The goal of this study was to make spatially explicit projections of future habitat suitability for songbirds breeding throughout North America’s HNLs – a tundra habitat specialist (Lapland Longspurs \( \text{(Calcarius lapponicus)} \)) and a habitat generalist (White-crowned Sparrows \( \text{(Zonotrichia leucophyrs)} \)). Ecological niche models were generated using species occurrence records, a suite of climate variables, and a plant functional type dataset to characterize the biotic characteristics of breeding habitats and project potential future changes. By the late 21st century (2051-2080), models based on both climate and vegetation projected decreases in habitat suitability across North America’s HNLs for Lapland Longspurs (54-96%) and White-crowned Sparrows (69%). For both species, currently unsuitable habitats in high northern Canada and Alaska are projected to become suitable breeding habitat in the future. In contrast, models based solely on climate showed more drastic declines in habitat suitability for both species (Lapland Longspur, ~100% and White-crowned Sparrow, ~80%). This discrepancy between model projections demonstrates that future suitable songbird breeding habitat for both species will strongly depend on how both the vegetation and climate— as opposed to climate alone - of northern ecosystems respond to ongoing climate change. Our results suggest that improved
forecasts of species’ responses to global change will depend on the inclusion of biotic interactions.

2.1 Introduction

In the face of global climate change, habitat changes may be especially acute at high northern latitudes (> 45°N) where temperature increases over the past fifty years have been the greatest (Trenberth et al. 2007). Warming on this scale has major environmental and ecological consequences for wildlife that depend on North America’s tundra and boreal ecosystems. Documented changes include longer growing seasons and increased vegetation productivity in many tundra ecosystems (Park et al. 2016), as well as major changes to vegetation community structure and composition, such as the expansion of shrub species (Tape et al. 2006, Walker et al. 2006). In contrast, boreal ecosystems have shown declines in productivity (Goetz et al. 2005) due to temperature-induced drought (Barber et al. 2000) and increasing frequency, intensity, and coverage of wildfire and insect outbreaks (Kasischke & Turetsky 2006, Werner et al. 2006, Soja et al. 2007). Evidence suggests that many of these trends are likely to continue in the future (Flannigan et al. 2005, Pearson et al. 2013).

Every spring, millions of songbirds rely on North American high northern latitudes (HNLs) as breeding grounds (Pielou 1994, Cornelissen et al. 2001), yet how they will be affected by concurrent changes in climate and vegetation is poorly understood. It is well established that climate and vegetation strongly control avian abundance and geographical distribution at large spatial scales (Root 1988, Cumming et al. 2014), which likely reflect physiological limitations associated with energetic costs exerted on both the birds themselves and the vegetation they depend on for nutrition and shelter (Hayworth & Weathers 1984, Root 1988). Previous
observational studies that have employed data collected in the North American Breeding Bird Survey (BBS) show strongly species-specific trends in the more than 400 species annually surveyed since 1966, with consistent declines in some species and increases in others (Sauer et al. 2013). While it is generally assumed that species will track rising temperatures by shifting ranges to higher latitudes or elevations, recent studies show that responses may be more complex. Currie and Venne (2017) analyzed the geographical distributions of 21 species monitored through the BBS and found only slight evidence that they tracked temperature changes from 1979-2010. Similarly, Huang et al. (2017) found multi-directional shifts in abundance of 57 species surveyed in the BBS over the past forty years, suggesting that multi-faceted environmental changes are influencing species distributions.

Increased availability of species occurrence records and global environmental datasets has allowed large-scale studies of geographic distributions of habitat suitability through ecological niche modeling (Phillips et al. 2006). The ability of such models to accurately characterize the abiotic conditions of known avian habitats has spurred efforts to model the outcome of many species under future environmental scenarios. Many of these studies predict marked changes in North American bird habitats that are likely to impact species distributions and population trajectories (Peterson 2003, Matthews et al. 2011, Stralberg et al. 2015). For example, Stralberg et al. (2015) investigated outputs of ecological niche models for 80 boreal bird species and found that the strength of distributional responses to changing environmental conditions was much greater than statistical noise inherent in projected climate data.

Empirical evidence shows that biotic interactions influence species distributions at large geographical scales (Heikkinen et al. 2007, Kissling et al. 2012, Pérez-Rodríguez et al. 2013) and influences species responses to environmental change (Araújo & Luoto 2007, Gilman et al. 2010,
Tylianakis et al. 2008). Yet, the inclusion of biotic interactions in niche models remains uncommon (Anderson 2017). Given that vegetation properties play a major role in bird habitat preferences (MacArthur and MacArthur 1961), it follows that previous studies have demonstrated improvements to habitat models across a variety of ecosystems when they are included (Seoane et al. 2004, Cumming et al. 2014, Goetz et al. 2014). Yet few studies focused on future projections of avian habitats have included future vegetation distributions in niche modeling efforts. One exception is Matthews et al.’s (2011) study of the eastern United States that found more realistic projections of future avian distributions when future shifts in vegetation, based on regression tree models, were included. Despite this, future vegetation shifts are typically omitted, likely due to both the cost associated with creating and maintaining high-resolution vegetation maps (Lillesand et al. 1994), and the challenges in projecting future vegetation distributions (Thuiller et al. 2008).

The goal of this study is to make spatially explicit projections of future habitat suitability for two songbird species breeding throughout North America’s HNLs – Lapland Longspurs (Calcarius lapponicus), a tundra habitat specialist and White-crowned Sparrows (Zonotrichia leucophyrs), a habitat generalist (Chilton et al. 1995, Hussel et al. 2002). We employed a maximum entropy ecological niche model (Maxent) that uses statistical associations among occurrences of the focal bird species with present-day climate and plant functional types (PFTs) to define the current ecological niches of each species. We then projected future habitat suitability for each species by using two future climate projections for the late 21st century (2051-2080), as well as future predictions of PFT distributions derived from a dynamic vegetation model customized for HNLs. Due to the poleward shift in woody vegetation associated with warmer temperatures, we expected to find that the preferred breeding habitat of
tundra habitat specialists would undergo continental-scale declines, while that of habitat generalists would expand by the late 21st century. We also expected that including future shifts in vegetation cover type in future projections of breeding habitat suitability would moderate songbird responses to climate change due to a lagged response of vegetation cover to changes in climate.

2.2 Materials and Methods

2.2.1 Climate data: present-day and future

We described the “present-day” climate using climate variables from the WorldClim database, which constitutes a 30-year average from 1960-1990 (Hijmans et al. 2005). WorldClim includes a series of 19 global climate variables interpolated from weather station data (30 arc s spatial resolution) (Hijmans et al. 2005) (Table 2.1). Climate variables for 2051-2080 were drawn from daily temperature and precipitation outputs based on baseline historical observations

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<th>Climate Variable</th>
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<td>1. Annual mean temperature</td>
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<td>2. Mean diurnal range (mean of monthly(max temp-min)</td>
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<td>3. Isothermality (2/7)*100</td>
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<td>4. Temperature seasonality (standard deviation*100)</td>
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<td>5. Max temperature of warmest month</td>
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<td>6. Min temperature of coldest month</td>
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<td>7. Temperature annual range (5-6)</td>
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<td>8. Mean temperature of wettest quarter</td>
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<td>10. Mean temperature of warmest quarter</td>
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<td>11. Mean temperature of coldest quarter</td>
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<td>12. Annual precipitation</td>
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<td>13. Precipitation of wettest month</td>
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<td>14. Precipitation of driest month</td>
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<td>15. Precipitation seasonality (coefficient of variation)</td>
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(climate research unit, CRU TS 3.0 1996-2005) adjusted with monthly anomalies from the Community Climate System Model version 4 (CCSM4) Coupled Model Intercomparison Project phase 5 (CMIP5) simulations for RCP4.5 and 8.5 scenarios (Taylor et al. 2012, Harris et al. 2014) (0.5° spatial resolution, subsampled to match the resolution of the present-day climate variables). RCP8.5 represents an upper bound of the greenhouse gas emission pathways established in the IPCC’s Fifth Assessment Report, with radiative forcing reaching 8.5 Wm$^{-2}$ by 2100 (Collins et al. 2013). In contrast, RCP4.5 corresponds to an intermediate scenario, with radiative forcing stabilizing at 4.5 Wm$^{-2}$ by 2100 (van Vuuren et al. 2011). Climate layers were restricted to the domain between 45°N-72°N and 52°W-169°W.

### 2.2.2 Vegetation distribution: present-day and future

We used observations (Zhang et al. 2013) and modeled future vegetation to describe changes in vegetation distributions in our study domain with the following PFTs: boreal needleleaf evergreen and deciduous forests; shade-intolerant broadleaf deciduous forests; tall and short shrubs; temperate C$_3$ grassland; arctic tundra open-ground vegetation types (shrub; graminoid and forb; and cushion forb, lichen, and moss); wetland graminoids and mosses; and cropland. Zhang et al. (2013) describe vegetation in the study domain based on a composite map of observed pan-Arctic vegetation, hereafter referred to as “present-day” vegetation distributions. The map combines a potential natural vegetation map (Kaplan et al. 2003), the Circumpolar Arctic Vegetation Map (Walker et al. 2005), and the International-Geosphere-Biosphere-Program land cover dataset over the period 2000-2001 (Friedl et al. 2010).

Zhang et al. (2013) employed a version of the individual-based dynamic vegetation model LPJ-GUESS (Lund-Postdam-Jena General Ecosystem Simulator, Smith et al. 2001), which fine-tuned the model parameterizations of vegetation structure and dynamics associated
with arctic- and boreal-specific PFTs and soil types, to represent vegetation distributions for the present day and a future scenario of regional dynamical downscaling climate model. By using a similar model setup, we forced LPJ-GUESS with daily temperature, precipitation, incoming shortwave radiation, annual atmospheric CO$_2$ concentrations from the climatology of the CCSM4 CMIP5 simulations. Full details of the generation of present-day and future vegetation maps can be found in Zhang et al. (2013). The present-day and future vegetation maps have 0.5° spatial resolution, subsampled to match the climate layer resolution.

### 2.2.3 Songbird study species: description and present-day occurrence data

Our two study species were selected because they differ significantly in their geographic distributions and breeding habitat preferences and thus represent two groups of songbirds breeding at HNLs. Lapland Longspurs nest in very short vegetation communities only in arctic tundra ecosystems (Hussell et al. 2002). Their breeding distribution is restricted to coastal and alpine tundra along the coast of Alaska and in the Alaska and Brooks Ranges, as well as in coastal Yukon and Northwest Territories, the Canadian archipelago, along the southern shore of Hudson Bay, and northern Quebec (Hussel et al. 2002). White-crowned Sparrows nest exclusively at the base of tall woody shrubs in much of Alaska, Yukon, Northwest Territories, Nunavit, Newfoundland, and the northern extents of Alberta, Saskatchewan, Manitoba, and Ontario. Their breeding range also extends from non-coastal British Columbia and western Alberta into Idaho and Montana (Chilton et al. 1995, Boelman et al. 2015).

Occurrence data for both species was drawn from the Global Biodiversity Information Facility (GBIF, gbif.org). GBIF is an open-source, international data infrastructure comprising georeferenced species occurrence records with global coverage (Graham et al. 2004). Because this study is focused on suitable breeding territories in the HNLs of North America, occurrences
were restricted to those recorded in June or July (i.e. breeding season months) and above 45° N. This study used 1,482 Lapland Longspur and 2,441 White-Crowned Sparrow occurrence records. Occurrence records were collected from 2009-2015 by human observation, primarily reported through the Cornell Lab of Ornithology’s eBird Observation Dataset.

2.2.4 Ecological niche modeling

Ecological niche models were used to model present-day and future projected habitat suitability for both species on their breeding grounds. This study used Maxent - a general-purpose machine learning method - to assign each grid cell in the study domain a predicted habitat suitability. A relative measure of projected habitat suitability ranging from zero to one was generated per grid cell for both study species to facilitate comparison (Phillips et al. 2006).

Models for both species under present-day conditions were run with three regularization parameter values (1, 3, and 5), which determine how closely the expectation value of the probability distribution is required to match the observed value (where higher values allow for looser fitting models). We selected the regularization parameter that maximized the area under the receiver-operating curve (ROC). In this case, ROC curves plot the capability of a model to distinguish the presence of a species from random background distribution at all thresholds. The area under the curve (AUC) is the probability that the model correctly distinguished a random presence instance from a random background instance. AUC values range from 0.5, for random prediction, to one, for perfect prediction (Phillips et al. 2006). This resulted in selecting a regularization parameter of five for both species.

A series of four models were created for both species using subsets of the present-day climate variables to identify the appropriate combination of variables for inclusion in further analyses. The model’s dependence on input variables was determined by the percent contribution
of each variable to the model and the results of a jackknife test. The jackknife analysis built models excluding each variable in turn and built models based on each variable in isolation. (1) A model was created using the complete suite of 19 climate variables (Table 2.1). For both species, the variables identified by the jackknife analysis also fell into the top five by percent contribution. Additional models were created for both species as follows: (2) a model using only the five climate variables with the greatest percent contribution; (3) a model using five additional, randomly selected variables to include with the initial five variables included in (2); and, (4) a model using ten additional, randomly selected variables to include with the initial five variables included in (2). The process of random variable selection was repeated three times. For all models 20% of songbird occurrence records were randomly set aside to test model performance. Models built with the full suite of 19 variables maximized the AUC, and all climate variables were included in future analysis.

Present-day projected habitat suitability for both species was modeled using occurrence records from GBIF, the composite map of observed vegetation types developed by Zhang et al. (2013), and the complete suite of 19 climate variables. To project future projected habitat suitability for each species, the associations between their present-day occurrences and environmental covariates were mapped onto the projected future vegetation type and climate variables for 2051-2080 under future emission scenarios RCP4.5 and 8.5. We calculated the omission rate by generating binary predictions using a minimum threshold and used a binomial test to evaluate whether the observed omission rate was better than expected from random prediction (Anderson et al. 2002).

To test the influence of including vegetation distributions as a variable in niche models for the two study species, we built models based solely on the suite of 19 climate variables and
projected future habitat suitability under RCP4.5 and 8.5. Comparisons between present-day and future projected habitat suitability were found by finding the difference between values at each grid cell. Histograms of habitat suitability were generated for each projection.

2.2.5 Change in habitat characteristics: present-day to future

The extent of PFTs in the observed and modeled future projections was measured as the percentage of grid cells containing each type. Changes in climate variables over time were quantified by comparing means across the study domain.

2.3 Results

2.3.1 Influence of climate and vegetation on habitat suitability

Maxent models based on climate and vegetation data showed strong predictive ability of observed distributions for both study species, with AUC values of 0.82 for Lapland Longspurs and 0.74 for White-crowned Sparrows. The omission rates for Lapland Longspurs and White-crowned Sparrows were 0.003 and 0.006, respectively ($P < 0.0001$).

The three variables with the largest contribution to present-day projected habitat suitability for Lapland Longspurs were, in descending importance, PFT (40.9%), mean temperature of the warmest quarter (14.2%), and precipitation seasonality (9.8%). For White-crowned Sparrows, the three variables with the largest contribution, in descending importance, were mean temperature of the warmest quarter (43.6%), PFT (18.5%), and precipitation of the warmest quarter (9%). For both species, annual mean temperature had the greatest contribution to the model outputs when used in isolation and when removed, as identified by jackknife analysis.
Changes in climate and vegetation from present-day to future

Annual mean temperature across the study domain increased between 1960-1990 and 2051-2080 (mean of -4.9°C to -4°C (RCP4.5) and -1.6°C (RCP8.5), with the largest increases above 65°N (Fig. 2.1). Annual mean precipitation decreased from 498.9 mm to 474.4 mm
(RCP4.5) and 478.2 mm (RCP8.5). Mean temperature and precipitation of the warmest quarter both increased across the study domain (mean of 10.6°C to 12.4-13.9°C and 170.8 mm to 175.4-179.5 mm, respectively) (Fig. 2.1). Mean precipitation seasonality increased from 43.2% to 58.4-58%, with the largest increases in arctic Alaska and along the Alaskan-Canadian border (Fig. 2.1).

![Histograms of plant functional type frequency under present-day conditions and future projections based on RCP4.5 and 8.5. TED Forest = temperate broadleaf deciduous forest. BND Forest = boreal needleleaf deciduous forest. BNE forest = boreal needleleaf evergreen forest. Present-day vegetation distributions are adapted from a composite map of observations compiled by Zhang et al. (2013). Future vegetation distributions were adapted from output of a dynamic vegetation model presented by Zhang et al. (2013). Future vegetation distributions were simulated by LPJ-GUESS forced with the CCSM4 CMIP 5 products.](image-url)

The extent of several PFTs’ coverage differed greatly between present-day observations and future model projections (Fig. 2.1). Graminoid/forb and shrub tundra PFTs are currently dominant in 24% of the study domain but cover between 1% (RCP8.5) and 4% (RCP 4.5) by the late 21st century (Fig. 2.2). Much of this reduction was due to an increased dominance of temperate broadleaf deciduous forests, which increased from 1% to 19% (RCP4.5) and 24% (RCP8.5), and boreal needleleaf evergreen forests which increased from 38% to 45% (RCP4.5) and 44% (RCP8.5). The total amount of shrub cover increased under both future scenarios – by 26% (RCP4.5) and 31% (RCP8.5) - with much of this expansion coming from tall shrubs which increased from 13% to 16% (RCP4.5) and 21% (RCP8.5). Tall shrubs largely replaced tundra vegetation types in the high arctic.

2.3.3 Projected habitat suitability: present-day and future

Lapland Longspurs were found to have high habitat suitability under present-day climate and PFT distributions in arctic and sub-arctic tundra ecosystems (Fig. 2.3a). Under RCP4.5, future projections for the late 21st century predict regions of high habitat suitability to be farther north than present-day (Fig. 2.3b), with reduced suitability in 54% of the study domain and enhanced suitability in 46%. In contrast, under the RCP8.5 scenario, habitat suitability was reduced in 96% of the study domain, with the highest values at the northernmost latitudes (Fig2.3c). Histograms of habitat suitability were skewed right under present-day and future scenarios. However, values were more uniformly distributed under present-day conditions and more heavily skewed towards low values under RCP8.5 (Fig. 2.4a). Maximum habitat suitability values across the study domain were equivalent for the present-day and RCP4.5 (0.99) and lower under RCP8.5 (0.6). In contrast, high habitat suitability for White-crowned Sparrows was found primarily within the present-day boreal zone, with lower values in tundra ecosystems (Fig. 2.3d).
Fig. 2.3 Breeding habitat suitability for Lapland Longspurs (a-c) and White-crowned Sparrows (d-f) as determined by ecological niche models based on climate and plant functional type distributions. Results for present-day conditions are shown for both species in (a) and (d). Habitat suitability for the late 21st century (2051-2080) is shown for projections of climate and vegetation distributions based on two emission scenarios, RCP4.5 and 8.5 (b,e and c,f, respectively).

In the late 21st century, under both emission scenarios, high habitat suitability for White-crowned Sparrows was found in arctic and sub-arctic regions of Alaska and Canada (Fig. 2.3e,f). Habitat suitability values were reduced in 69% and enhanced in 31% of the study domain under both future scenarios. The largest decreases occurred in two regions: (1) the mountainous regions of the Yukon Territory, British Columbia, and the southern coast of Alaska, and; (2) the tundra-
boreal ecotone region extending north westward from Hudson Bay (Fig. 2.3d-f). Histograms of habitat suitability scores were skewed towards lower values for both future scenarios, as compared to the present-day distribution (Fig 4b). However, histograms of both future scenarios appeared bimodal, with a lesser secondary peak at higher habitat suitability scores. The maximum habitat suitability score across the study domain was largely equivalent across all scenarios (0.91-0.99).

![Histograms of breeding habitat suitability scores for Lapland Longspurs and White-crowned Sparrows for the present-day and two future emission scenarios for 2051-2080 (RCP 4.5 and 8.5). Panels (c) and (d) show results from ecological niche models based solely on climate variables.](image)

**Fig. 2.4** Histograms of breeding habitat suitability scores for Lapland Longspurs ((a) and (c)) and White-crowned Sparrows ((b) and (d)) for the present-day and two future emission scenarios for 2051-2080 (RCP 4.5 and 8.5). Panels (a) and (b) show results from ecological niche models based on climate and plant functional type distributions. Panels (c) and (d) show results from ecological niche models based solely on climate variables.

More widespread declines in habitat suitability were predicted for both species by the late 21st century in model runs that included only climate variables, as compared to those which
included vegetation (Supplemental Fig. B.1). For Lapland Longspurs, nearly all grid cells (~100 %) decreased in habitat suitability between present-day and both future scenarios without vegetation. The maximum habitat suitability scores decreased from 0.97 for present-day to 0.68 (RCP4.5 ) and 0.26 (RCP8.5), and the proportion of low suitability scores increased markedly (Fig. 2.4c). Similarly, habitat suitability values decreased in a majority (80-83%) of grid cells for White-crowned Sparrows between present-day and future scenarios without vegetation. Maximum habitat suitability scores for White-crowned Sparrows decreased from 0.91 in the present-day to 0.79 in both future projections. Histograms of habitat suitability scores were skewed right, with a higher proportion of grid cells with low scores (Fig. 2.4d).

2.4 Discussion

2.4.1 Future songbird habitat in North America: Temperate-boreal declines and arctic expansion

In agreement with our first expectation, the model projects widespread declines in suitable habitat for a tundra specialist species by the end of the 21st century, especially under the higher emissions scenario (RCP8.5), due to changes in both climate and vegetation distributions. Under the more moderate emission scenario (RCP4.5) our model projects declines in habitat suitability in the majority of the study domain (54%), and a northward shift in highly suitable habitat into high arctic regions that are largely unsuitable for breeding in the present-day. Under RCP8.5, habitat suitability declined in nearly all (96%) of the study domain, with moderately suitable habitats occurring in high arctic regions. This is likely due to large reductions in the extent of graminoid/forb and shrub tundra PFTs (from 24% to < 4 %) which are critical to Lapland Longspur nesting, and replacement by tall shrubs (from 13% to 16-21%) and deciduous
trees (from 1% to 19-24%). Lapland Longspurs build nests almost exclusively in areas with sparsely distributed deciduous shrubs that are less than 20 cm tall (Boelman et al. 2015), thus the projected changes in vegetation distributions had a large influence on the future availability of their suitable habitats.

In disagreement with our first expectation, the model also projects widespread declines in suitable habitat for a habitat generalists which breed over a wide range of latitudes by the late 21st century. Under both emissions scenarios, habitat suitability declined in 69% of the study domain - primarily in British Columbia, southern Alaska, and the southern shore of the Hudson Bay. Although habitat suitability declined in the majority of the study domain, currently unsuitable habitats in northern Canada and Alaska are projected to provide suitable breeding habitat in the future. White-crowned Sparrows are known to rely on tall shrubs for nesting, which could explain their northward expansion into the high arctic (Chilton et al. 1995, Boelman et al. 2015). However, continental-scale declines in suitable breeding habitats, despite the expansion of tall shrubs, suggests that coincident changes in climate appear to have constrained expansion of suitable habitat for White-crowned Sparrows in the southern portion of the domain.

Overall, our findings are consistent with Stralberg et al.’s (2015) prediction that North American boreal bird species with more northerly distributions (e.g. Lapland Longspurs) will fare worse than those with more southerly distributions (e.g. White-crowned Sparrows) in the future. Our findings are partially consistent with Boelman et al.’s (2015) projections for the arctic foothill regions of Alaska by 2050. Their results predicted a significant decrease in extent of suitable nesting habitat for Lapland Longspurs, with a concurrent increase for that of White-crowned Sparrows. While our results for Lapland Longspurs agree with those of Boelman et al. (2015), they differ from those for White-crowned Sparrows. This discrepancy can be attributed
to the fact that Boelman et al. (2015) considered a much smaller geographic area compared to the current study which is of continental scale. Although the current study indeed predicts that the highest values of habitat suitability for White-crowned Sparrows will be in the northern foothills region, the small gain we found in this region is greatly outweighed by losses predicted across our much broader study domain. Additionally, Boelman et al.’s (2015) projections are based solely on vegetation change, whereas the current study also considers change in a suite of climatic variables that were found to be important in defining the birds’ breeding habitats. In agreement with Huang et al. (2017) we found multi-directional shifts in habitat suitability for both species in the future, primarily north or northeastward, suggesting that avian distributions may be susceptible to environmental change along longitudinal as well as latitudinal gradients.

We point out that future projections of habitat suitability assume species conserve their niches over time and that extinction rates outpace adaptation (Pearson and Dawson 2003). These assumptions may be acceptable in that species often shift their ranges in response to disruptions to their ecological niche (Parmesan and Yohe 2003, Sexton et al. 2009) and the speed of habitat changes may outpace these species’ ability to adapt.

2.4.2 Future shifts in vegetation are critical to determining suitable habitat

In agreement with our second expectation, ecological niche models that included only climate predicted a harsher fate for both specialist and generalist species compared to those that included both climate and plant functional type distributions. Lapland Longspur and White-crowned Sparrow habitat suitability decreased in ~100% and ~80% of the study domain, respectively, by the late 21st century based solely on climate. Our findings are consistent with those of Matthews et al. (2011) which projected more extreme future declines in suitable breeding habitat for avian species in temperate forests of the eastern United States when using
models based solely on climate and elevation, as compared to models which also included changes in suitable habitat for tree species.

Differences in our climate-only versus climate-and-vegetation niche model projections are attributable to two main factors. First, in addition to temperature variables, plant functional type was found to strongly control present-day distributions of both species when included in niche models (19-40%) due to the importance of vegetation characteristics to songbird breeding habitat suitability. Changes in the dominant plant functional type represents shifts in the species composition and often in the physical structure of vegetation communities. Both vertical and horizontal vegetation structure have long been identified as important drivers of songbird habitat usage (MacArthur and MacArthur 1961, Rotenberry and Wiens 1980) due to the importance of structure in providing foraging platforms, perch sites, shelter from predators, as well as influencing microclimate (Holmes and Sherry 2001). Vegetation structure and density may also serve as proxies for the abundance and variety of food resources (Holmes and Sherry 2001, Boelman et al. 2015). Given the indisputable importance of vegetation characteristics to songbird breeding habitat suitability, it is not surprising that our future projections are heavily influenced by the significant changes in vegetation predicted by the vegetation model employed in this study.

A second reason for differences in our climate-only versus climate-and-vegetation niche model projections, is that in order to capture transient dynamics in vegetation distributions, the dynamic vegetation model used does not require vegetation to be in equilibrium with climate forcings (Chapin et al. 1996). Therefore, projections of plant functional type distributions may show a delayed response to changes in climate (Chapin et al. 1996) that moderates our habitat suitability projections. This inherent property of dynamic vegetation models likely renders them
superior to static vegetation models for projecting future habitat suitability which typically, unrealistically assume that shifts in vegetation types occur in synchrony with shifts in climate (Pearson and Dawson 2003, Botkin et al. 2007).

The fact that our future projections of habitat suitability differed greatly with and without plant functional type projections demonstrates the importance of including vegetation – in addition to climate - in the development of wildlife habitat models to predict future habitat suitability. The marked differences in results we found in doing so highlight limitations of species forecasts that do not include biotic interactions. Our findings complement those of Araújo and Luoto (2007) and Matthews et al. (2011) which found that biotic interactions can influence species distributional responses to climate change at macroecological scales. In addition, our results reinforce a growing sentiment within the ecological niche modeling community that unlinked biotic interactions should be included as predictor variables in correlative niche models (Anderson 2017). Biotic interactions will likely influence species’ responses to global climate change, and thus should be considered in predictions of future outcomes (Gilman et al. 2010).

2.5 Conclusions

In conclusion, our three main model projections for future of songbird breeding habitat at high northern latitudes of North America by the late 21st century are: (1) widespread decline of suitable breeding habitat, (2) countered by a small northward shift of the most suitable breeding habitats, and; (3) a large dependence of future breeding habitat on both temperature and distributional changes in vegetation, suggesting that species responses to changing climate in northern ecosystems may be moderated by transient dynamics in the vegetation they rely on for
nutrition and shelter. Finally, the disparities between our modeled projections for the late 21st century point to the large role that even relatively straightforward biotic interactions may play in forecasting ecological responses to global change.
CHAPTER 3:

Earlier arctic-boreal spring advances American robin (*Turdus migratorius*) migration

Abstract

Global climate change is causing major disruption to the synchrony of seasonal activities of a wide variety of taxa, which may be especially acute at high northern latitudes where the advancement of spring has been most pronounced. Millions of songbirds migrate to breed in arctic and boreal ecosystems, timing their arrival and subsequent phenological events to maximize their reproductive success. We investigated (1) whether the most common songbird in North America, the American robin (*Turdus migratorius*), has advanced its migration timing through the Canadian boreal forest in response to the advancement in spring conditions and (2) how multiple metrics of migration phenology -- timing of arrival to stopover site, migration movement rate, and timing of arrival to breeding grounds-- were influenced by environmental dynamics. We found that American robins migrating through Slave Lake, Alberta have advanced the timing of their spring migration through the region over the past quarter-century in response to the concurrent winter warming (-0.51 days per year, p < 0.05). Robins were delayed in arriving to a boreal stopover site in years with persistent snow cover, although once in the region, individuals are more likely to stopover during periods of inclement weather and are delayed in arriving to breeding grounds in years with later snow-free dates and deeper snow depths. We discovered that robins accelerate their migration movement rates once west of the Rocky Mountains (85.3 vs. 136.8 km/day, p < 0.1). Our findings indicate that robins adjust their migration phenology at various points *en route* to their breeding grounds in response to environmental dynamics.
3.1 Introduction

One of the major consequences of recent anthropogenic climate change is a modification to seasonal dynamics. In particular, much of the northern hemisphere has seen a decrease in winter precipitation along with rising winter and spring temperatures, which have altered the timing of seasonal transitions to spring growing seasons (Ault et al. 2015, Badeck et al. 2004, Piao et al. 2008, Santer et al. 2018). These changes in seasonality have caused tremendous alarm over the potential disruption of synchrony between abiotic conditions and biota because of the critical links between growing season conditions, reproductive success, and overall population health for many species (Meller et al. 2018, Møller et al. 2008). A wide body of work has emerged documenting the presence, or absence, of shifts in timing of life history events, known as phenology, in a wide range of taxa as a potential indicator of a species ability adapt to global climate change (Parmesan & Yohe 2003, Root 2003).

Temperatures at high northern latitudes are rising nearly twice as fast as the increase seen globally (Trenberth et al. 2007, Stocker et al. 2014), with acute impacts to arctic and boreal ecosystems particularly during the winter and spring seasons (Solomon 2007). Along with rising winter and spring temperatures, sea-ice and terrestrial snow cover extent and duration have declined in recent decades (Callaghan et al. 2011, Comiso et al. 2008, Serreze et al. 2000, Simmonds 2015), fundamentally changing the progression of spring at high latitudes (Ernakovich et al. 2014). At the pan-arctic scale, earlier snowmelt and warmer spring temperatures have caused an advance in onset of the growing season of vegetation by approximately 1.6 days per decade (Park et al. 2016).

Many studies have investigated whether the phenology of animal species residing in arctic-boreal regions, either as year-round residents or seasonal migrants, has been able to keep
pace with shifts in spring environmental conditions or phenology of primary producers. Høye et al. (2007) found significant trends towards earlier emergence of arthropods and clutch initiation dates of birds in Greenland. Similarly, North American red squirrels in the Canadian Yukon advanced their timing of reproduction by about 18 days between 1989-2002 in step with increases in spring temperatures and white spruce cone abundance, their primary food source (Réale et al. 2003). Le Corre et al. (2017) found that the spring migration of caribou herds in northern Quebec and Labrador advanced between 2000-2011, but that arrival to breeding grounds when caribou encountered higher spring snowfall and colder temperatures during migration. In the absence of long-term datasets, numerous studies have investigated the capacity of species to keep pace with climate change by examining their responses to inter-annual variability in environmental conditions. For example, Lameris et al. (2018) found that arctic-breeding migratory geese accelerated their migration northward in response to earlier spring. Although animals that rely on arctic and boreal ecosystems are well adapted to the inter-annual variability in environmental conditions characteristic of these regions (Finch & Rose 1995, Martin 2001, Boonstra 2004, Beaumont et al. 2011), it is largely unknown how they will cope with more extreme shifts that may become persistent or frequent in nature.

Millions of birds migrate from around the world to breed at high northern latitudes to take advantage of the large pulse in food resources and lower predatory pressure compared to more temperate ecosystems. Studies have shown that their timing of arrival to their breeding grounds and subsequent phenological events are related to the timing of onset of spring conditions or dynamics of environmental conditions throughout the breeding season (e.g. Boelman et al. 2017, Grabowski et al. 2013, Liebezeit et al. 2014, Smith et al. 2010, Ward et al. 2016). Timing of arrival to breeding grounds is critically important to birds breeding at high
northern latitudes, because they must establish territories and initiate clutches as early as possible to ensure young have sufficient time to develop before the onset of fall.

Despite an increasing understanding of the magnitude and variability in phenological responses in arrival timing within and among species, we lack a mechanistic understanding of how migratory birds are adjusting their arrival timing or not in response to changing spring conditions (Chmura et al. 2018). Although initiation of migration is largely cued by photoperiod and local environmental conditions (Farner & Follett 1966, Dawson et al. 2001, Ramenofsky & Wingfield 2007), the high energetic costs of migration, pressure to breed, and subsequent consequences for reproductive success (Gill et al. 2001, Norris et al. 2004, Paxton & Moore 2015) force migrants to make numerous decisions as they travel to their breeding grounds (Alerstam 2011). Migration rates and whether or not individuals choose to refuel at stopover sites control the arrival timing of individuals to their breeding grounds. Our lack of understanding of how these decisions relate to environmental conditions limits our ability to predict potential constraints on birds’ ability to shift arrival timing in response to ongoing and future change.

Our limited understanding of the mechanisms underlying shifts in arrival timing stem primarily from methodological limitations in how avian migratory phenological datasets are collected. The majority of studies rely on site-specific information, which is limited in spatiotemporal coverage, especially at high northern latitudes (Gordo 2007). This is particularly true for migratory songbirds because up until recently there were not tracking devices small enough to be worn by most species with high location accuracy that did not need to be recovered (Kays et al. 2015). However, recent advances in GPS technology have generated units small enough to be placed on songbird species. Without being able to track migratory songbirds in
space and time we have been limited in our ability to understand their migrations and have been largely unable to link their movements to spatiotemporal dynamics in environmental conditions in the same detail as has been done in larger species (Kays et al. 2015). Doing so would allow us to understand how migratory songbirds respond to spatiotemporal variation in environmental and ecological conditions within their migratory routes, stopover sites, and breeding grounds.

Our first goal was to determine if and how the well-documented advance in spring environmental conditions in arctic-boreal North America over the past quarter-century has altered the timing of spring migration of the most common songbird in North America, the American robin (*Turdus migratorius*). Our second goal was to qualitatively characterize the spring migratory routes and breeding grounds of American robins that stopover in Slave Lake, Alberta and gain a quantitative understanding of how environmental dynamics control spring migration phenology. To address these goals we used a long-term dataset (1994-2018) of robin migration timing in Slave Lake, Alberta and tracked robins as they migrated through the Canadian boreal forest to their breeding grounds. We predicted that the earlier onset of spring environmental conditions in arctic-boreal North America over the past 25 years caused earlier migration of American robins to Slave Lake, Alberta. We also predicted that multiple metrics of American robin spring migration phenology -- timing of arrival to stopover site, migration movement rate, and timing of arrival to breeding grounds -- are positively influenced by favorable spring environmental conditions. Based on existing understanding of migratory routes and known robin habitat preferences, we predicted robins migrating through Slave Lake, Alberta will use the Central or Pacific Flyways and will breed primarily in forested habitat, as opposed to sparsely vegetated ecosystems.
3.2 Methods

3.2.1 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. Vegetation in the park consists mostly of mixed boreal forest dominated by trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), and white birch (*Betula papyrifera*).

3.2.2 Study species

American robins are the most abundant and broadly distributed thrush species in North America (Vanderhoff et al. 2016). 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 (Vanderhoff et al. 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 1995, Vanderhoff et al. 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. Banding data from Fairbanks, Alaska shows that robins typically arrive between the beginning of May and mid-June (Benson and Winker 2001).
3.2.3 Field methods and robin location data

Daily estimates of migratory individuals from the Lesser Slave Lake Bird Observatory (LSLBO) were based on daily constant effort mist netting, visual migration counts, census, and casual observations. The number of probable known residents individuals were subtracted from the daily estimated total to estimate the number of probable known migrants for each day during spring migration.

American robins were captured in mist-nets from 2016-2018 at the LSLBO and Boreal Centre for Bird Conservation (BCBC). Mist-netting occurred between April 15 and May 1 each year. The LSLBO is a part of the Canadian Migration Monitoring Network and deploys twelve mist nets (12 m x 3 m) which are opened daily for 7 hours beginning 30 minutes before sunrise. In order to increase opportunities for capturing robins, we deployed on average six additional mist nets which were opened daily beginning 30 minutes before sunrise. Each individual was weighed and sex and age were determined based on plumage before being 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 grams were fitted on individuals weighing greater than 70 or 80 grams, respectively. GPS units were scheduled to acquire and store their location every 48 hours 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.

3.2.4 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.
Daily surface wind velocity data are provided by the European Centre for Medium-Range Weather Forecasts (ECMWF) 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, 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 (USGS) 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.

3.2.5 Long-term robin arrival timing to Slave Lake (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 arrival timing using a generalized least squares approach taking into account temporal autocorrelation. We tested for presence of trends and the influence of the following suite of environmental variables on arrival timing: annual snow-free date, mean monthly air temperature, snow depth, and precipitation for January through April, and the mean strength of the PDO from the 12 months preceding arrival (May of the previous year through April). To test for the presence of long-term trends, we used a generalized least squares approach taking into account temporal autocorrelation for each environmental variable in isolation. To test for the influence of environmental variables, we performed model selection of linear models based on all possible combinations of environmental variables and year, restricting the inclusion of environmental variables which were highly correlated (R > 0.7). We ranked candidate models based on Akaike’s information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002), where the number of individuals observed at Slave Lake was considered the sample size. We considered models with ΔAICc < 2 to have strong empirical support.

3.3.6 Stopover and breeding grounds arrival timing

We modeled robin arrival to our tagging site in Slave Lake, Alberta and their breeding grounds, and investigated factors influencing arrival timing using the Anderson-Gill (AG) extension to the Cox proportional hazards (Cox PH) regression modeling (Therneau and Grambsch 2000). We tested the proportional hazards assumption of Cox PH using the formula test recommended by Therneau and Grambsch (2000) and only included predictor variables which did not have significant violations of the proportionality (P > 0.05). We used a 365-day, 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 timing, we used the date on which we captured an individual at Slave Lake as a stopover event because all individuals were captured while foraging. We generated daily records for each individual starting on January 1 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). 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 $\beta$ coefficients) of included year variables did not overlap.

To test for the influence environmental and demographic variables on stopover timing based on capture data, we performed model selection of Cox proportional hazards models of all individuals. We generated candidate models based on all possible combinations of variable. However, we restricted the inclusion of snow depth and air temperature as predictor variables in the same model based on a high correlation ($R^2 > 0.6$). We ranked candidate models based on Akaike’s information criterion corrected for small sample sizes ($\text{AIC}_c$; Burnham and Anderson 2002), where the number of individuals observed at Slave Lake was considered the sample size. We considered models with $\Delta\text{AIC}_c < 2$ to have strong empirical support. We assessed significance of variables with robust $z$ tests and 95% confidence intervals for odd ratios (Therneau and Grambsch 2000). 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.

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 and identified as being at an individual’s breeding grounds based on the proximity to the final GPS location (> 80% of total distance traveled) and the movement rate (< 10 km/day). 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 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 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.

3.2.7 Migration movement rate

We investigated environmental, demographic, and morphological 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 km/day). To standardize our analysis we sub-sampled to only include sequential locations, hereafter referred to as steps, that were acquired 48 hours 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 territories on throughout northwestern Canada and Alaska. The northern Rocky Mountains represent a significant geographic barrier that 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 t-tests. We also tested differences in mean environmental conditions experienced at the locations selected by these two regions using t-tests, such as snow free date, snow depth, number of days before/after the snow free date, proportion of locations with snow present, and wind speeds. We repeated the same procedure to test for differences in

We tested for differences in movement rates between sexes and age classes using t-tests and tested for the influence of mass and wing lengths using linear regression. We summarized environmental conditions along each step by averaging conditions at each start and end location. We tested for the influence of snow depth, air temperature, precipitation, and wind speeds on movement rates using linear regression.

For all individuals that were tracked entirely to their breeding grounds we estimated total migration rates based on distance traveled and number of days between capture at Slave Lake and arrival to breeding grounds. We investigated differences in total migration rates between sexes, age classes, and years using t-tests. We tested how mass and wing length related to total migration rate using linear regression.
3.3 Results

Figure 3.1: Arrival timing of American robins to Slave Lake, Alberta over the previous 25 years (1994-2018) as measured by the dates on which 5, 50, 95% of total observed individuals for a given year were observed.

3.3.1 Long-term trend in arrival timing to Slave Lake (1994-2018)

We found significant trends in American robin arrival timing to Slave Lake, Alberta over the 25-year period from 1994-2018, with all three phases of migration arriving approximately 0.5 days earlier per year (Fig. 3.1; 5% arrival date: coefficient = -0.48, p < 0.05; 50% arrival date: coefficient = -0.36, p < 0.1; 95% arrival date: coefficient = -0.51, p < 0.01). We found significant trends in mean January air temperature (coefficient = 0.26, p < 0.1) and mean February and March precipitation (February: coefficient = 0.002, p < 0.05; March: coefficient = 0.003, p < 0.05) at Slave Lake over the same time period. The following abiotic variables were found to significantly relate to the 5% arrival date of American robins to Slave Lake: mean April precipitation, mean January, March, and April snow depths, mean annual strength of the PDO, and year (Fig. 3.1b, Tables 3.1 and C.1). The following abiotic variables were found to relate to the 50% arrival date: mean January and April precipitation, mean monthly snow depth in January...
Table 3.1: Influence of abiotic variables on American robin arrival timing to Slave Lake, Alberta (1994-2018). All variables reported were retained in top ranked linear models.

<table>
<thead>
<tr>
<th></th>
<th>Coefficient</th>
<th>SE</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>5% arrival</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation (April)</td>
<td>+1.38</td>
<td>0.91</td>
<td>&lt; 0.14</td>
</tr>
<tr>
<td>Snow depth (January)</td>
<td>+2.01</td>
<td>0.86</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Snow depth (March)</td>
<td>+1.17</td>
<td>0.86</td>
<td>0.19</td>
</tr>
<tr>
<td>Snow depth (April)</td>
<td>+1.4</td>
<td>0.84</td>
<td>0.11</td>
</tr>
<tr>
<td>PDO</td>
<td>+1.2</td>
<td>0.86</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Year</td>
<td>-2.42</td>
<td>0.86</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td><strong>50% arrival</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation (January)</td>
<td>+1.49</td>
<td>0.79</td>
<td>&lt; 0.1</td>
</tr>
<tr>
<td>Precipitation (April)</td>
<td>+1.77</td>
<td>0.84</td>
<td>&lt; 0.1</td>
</tr>
<tr>
<td>Snow depth (January)</td>
<td>+1.39</td>
<td>0.85</td>
<td>0.12</td>
</tr>
<tr>
<td>Snow depth (February)</td>
<td>+1.5</td>
<td>0.89</td>
<td>0.1</td>
</tr>
<tr>
<td>Snow depth (March)</td>
<td>+1.5</td>
<td>0.84</td>
<td>&lt; 0.1</td>
</tr>
<tr>
<td>Snow depth (April)</td>
<td>+1.39</td>
<td>0.85</td>
<td>0.12</td>
</tr>
<tr>
<td>Snow free date</td>
<td>+1.64</td>
<td>0.78</td>
<td>&lt; 0.1</td>
</tr>
<tr>
<td>Air temperature (January)</td>
<td>-2.21</td>
<td>0.87</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Air temperature (February)</td>
<td>+1.86</td>
<td>0.83</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Air temperature (April)</td>
<td>+1.86</td>
<td>0.83</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>PDO</td>
<td>+1.2</td>
<td>0.84</td>
<td>0.15</td>
</tr>
<tr>
<td>Year</td>
<td>-2.3</td>
<td>0.77</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td><strong>95% arrival</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation (February)</td>
<td>-1.79</td>
<td>0.82</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Precipitation (March)</td>
<td>-2.69</td>
<td>0.82</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Snow depth (January)</td>
<td>+2.46</td>
<td>0.78</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Air temperature (January)</td>
<td>-2.37</td>
<td>0.89</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Air temperature (March)</td>
<td>-1.28</td>
<td>0.91</td>
<td>0.18</td>
</tr>
<tr>
<td>PDO</td>
<td>+2.46</td>
<td>0.78</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Year</td>
<td>-2.67</td>
<td>0.79</td>
<td>&lt; 0.01</td>
</tr>
</tbody>
</table>

through April, snow-free date, mean January, February, and April air temperature, mean annual strength of the PDO, and year (Table 3.1 and C.2). The following abiotic variables were found to relate to the 95% arrival date: mean February and March precipitation, mean January snow
depth, mean January and March air temperature, mean annual strength of the PDO, and year (Table 3.1 and C.3).

3.3.2 Migration route

American robins captured at Slave Lake, Alberta continued their migration traveling on average 753 km (median = 187.8 km) between Slave Lake and their breeding grounds, with one individual traveling 3206.6 km. Several individuals traveled to locations at the northern limit of known American robin breeding ranges (Fig. 3.2a). Individuals captured at Slave Lake traveled in a prevailing north-west direction towards the Yukon Territory and Alaska in all three study years (2016-2018), following the Pacific Flyway (Fig. 3.2b). Distances traveled between Slave Lake and breeding grounds was not related to wing length and did not differ between sexes or age classes, but was significantly related to the mass of the individual (coefficient = 66.7, se = 24.83, p < 0.05).

![Figure 3.2: American robin GPS locations with (a) breeding and overwintering range extents (adapted from Birds of North America, Vanderhoff et al. 2016) and (b) general migratory flyways (adapted from the United States Fish and Wildlife Service).](image-url)
3.3.3 Stopover timing at Slave Lake (2016-2018)

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.

Over the study period (2016-2018) 77 robins were captured at Slave Lake in connection with our tagging effort. Arrival timing differed significantly in 2018 compared to 2016 and 2017 (Fig. 3.4, Table C.4). The top supported models ($\Delta AIC_C < 2$) predicting arrival to Slave Lake based on tagging data retained 2018, snow-free date, snow depth, precipitation, sex, age, mass, and wing length variables (Table 3.2; Table C.5). 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. Arrival timing to Slave Lake was delayed in 2018 relative to 2016 and 2017 ($z = -3.91$, $P < 0.01$, odds ratio = 0.03, 95% CI = [0.01-0.18]). Later seasonal snowmelt delayed arrival timing ($z = -3.96$, $P < 0.01$, odds ratio = 0.86, CI = [0.79-0.92]). However, deeper snow and higher total precipitation increased odds of stopover (Table 3.2). Younger individuals (second year) were delayed in arrival compared to older individuals (after second year) (Table 3.2). Individuals with longer wings arrived earlier than individuals with shorter wings (Table 3.2). Older individuals (after second year) had, on average, significantly longer wings than younger individuals (after second year: mean = 129.7 cm, second year: 126.7 cm, $t = 36.9$, $p < 0.001$). We do not consider the effects of sex and mass to be significant because the 95% confidence interval of the arrival odds ratio overlapped one.
Figure 3.3: Snow-free dates and American robin locations across three study years (2016-2018)
Table 3.2: Results for variables in all models with ∆AIC_c < 2 in analysis of stopover timing for individuals captures at Slave Lake (n = 77). For each variable z scores, P values, odds ratios, and 95% confidence intervals values from the top model in which the variable was retained. Sex variables are referenced to female. Age variables are a binary age class and referenced to individuals in their second year.

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>z</th>
<th>P</th>
<th>Odds ratio</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snow free date</td>
<td>-3.96</td>
<td>&lt; 0.01</td>
<td>0.86</td>
<td>[0.79-0.92]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>2.49</td>
<td>&lt; 0.05</td>
<td>1.15</td>
<td>[1.03-1.29]</td>
</tr>
<tr>
<td>Precipitation</td>
<td>1.25</td>
<td>0.21</td>
<td>2.06</td>
<td>[0.67-6.37]</td>
</tr>
<tr>
<td>Age (&lt; 2 years)</td>
<td>-2.39</td>
<td>&lt; 0.05</td>
<td>0.55</td>
<td>[0.33-0.9]</td>
</tr>
<tr>
<td>Sex (female)</td>
<td>-1.41</td>
<td>0.16</td>
<td>0.72</td>
<td>[0.45-1.14]</td>
</tr>
<tr>
<td>Mass</td>
<td>-1.86</td>
<td>&lt; 0.05</td>
<td>0.96</td>
<td>[0.92-1.002]</td>
</tr>
<tr>
<td>Wing length</td>
<td>2.4</td>
<td>&lt; 0.05</td>
<td>1.08</td>
<td>[1.01-1.16]</td>
</tr>
<tr>
<td>Year 2018</td>
<td>-3.91</td>
<td>&lt; 0.01</td>
<td>0.03</td>
<td>[0.01-0.18]</td>
</tr>
</tbody>
</table>

3.3.4 Migration movement rate

Movement rates along the migratory route were positively related to distance from Slave Lake, Alberta (coefficient = 0.1, se = 0.01, p < 0.001) and negatively related to snow depth (coefficient = -0.77, se = 0.36, p < 0.05). Individuals which were found to transverse 130°W longitude, hereafter referred to as Alaskan-breeding individuals, traveled faster west, as compared to east, of 130°W (Fig. 3.4a,b Table 3.4). Snow-free dates at locations selected by Alaskan-breeding individuals were significantly later west of 130°W than at locations east and had deeper snow, despite reaching these locations later in their migration (Table 3.3). Alaskan-breeding individuals arrived to locations west of 130°W sooner after the snow-free date than at locations east of 130°W (Fig. 3.4c; west: mean = 1.7 days; east: mean = 15 days, t = 2.07, p < 0.05). However, the proportion of locations selected by Alaskan-breeding individuals was not significantly different in the two regions (Table 3.3). Although meridional wind speeds did not
differ between at locations selected by Alaska-breeding individuals, zonal wind speeds were, on average, more favorable east of $130^\circ$W, as compared to locations west of $130^\circ$W (Table 3.3).

Movement rates of Alaskan-breeding individuals in the region east of $130^\circ$W were significantly, positively related to snow depth (coef = 1.89, se = 0.93, p < 0.05) and negatively related to zonal wind speed (coef = -13.86, se = 5.95, p < 0.05). We found no significant relationships between environmental covariates and movement rates of Alaskan-breeding individuals in the region west of $130^\circ$W.

<table>
<thead>
<tr>
<th>Variable</th>
<th>East</th>
<th>West</th>
<th>P-value</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rate (km/day)</td>
<td>85.34</td>
<td>136.82</td>
<td>&lt; 0.1</td>
<td>-1.82</td>
</tr>
<tr>
<td>Snow free date (day of year)</td>
<td>111.8</td>
<td>137.1</td>
<td>&lt; 0.01</td>
<td>-3.91</td>
</tr>
<tr>
<td>Number of days before/after snow-free date (-/+/days)</td>
<td>15</td>
<td>1.7</td>
<td>&lt; 0.05</td>
<td>2.07</td>
</tr>
<tr>
<td>Snow depth (cm)</td>
<td>8.82</td>
<td>44.1</td>
<td>&lt; 0.1</td>
<td>-1.77</td>
</tr>
<tr>
<td>Percent in snow (%)</td>
<td>32.8</td>
<td>44.4</td>
<td>&gt; 0.1</td>
<td>-0.86</td>
</tr>
<tr>
<td>Zonal wind speed (m/s)</td>
<td>0.59</td>
<td>-0.22</td>
<td>&lt; 0.1</td>
<td>1.72</td>
</tr>
<tr>
<td>Meridional wind speed (m/s)</td>
<td>0.66</td>
<td>0.47</td>
<td>&gt; 0.1</td>
<td>0.41</td>
</tr>
</tbody>
</table>

### 3.3.5 Arrival to breeding grounds

Over the study period (2016-2018), 55 individuals were tracked using GPS units. Of these, 41 individuals are presumed to have been tracked entirely to their breeding grounds. American robins selected breeding grounds throughout northwest Canada and Alaska in a range of habitat types (Fig. 3.5a). Individuals bred over a wide range of latitudes between $54.6$-$68.3^\circ$N (Fig. 3.5b). Although the majority of individuals bred in forested ecosystems, robins were also found to breed in ecosystems with mosaic vegetation, shrublands, grasslands, and sparsely vegetated ecosystems (Fig. 3.5c).
Arrival timing to breeding grounds was not found to differ significantly between study years (2016-2018) (Table C.6). The top models ($\Delta$AIC$_c < 2$) predicting arrival to breeding grounds retained distance traveled from Slave Lake, snow-free date, snow depth, sex, age, and interaction terms between sex and distance and distance and snow-free date (Table 3.4 and Table C.7). For variables that were retained in multiple top models, responses were similar among top models, so we report the response from the model with the lowest AIC$_c$ value. Longer distances traveled from Slave Lake to breeding grounds delayed arrival timing to breeding grounds (Table 3.4). Later snowmelt and deeper snow depths delayed arrival timing to breeding grounds (Table 3.4). Males were delayed in arriving to breeding grounds compared to females (Table 3.4). However, the significant interaction between sex and distance traveled from Slave Lake ($z = -2.56, P < 0.05$) to breeding grounds suggests that differences in arrival timing to breeding grounds between
Figure 3.5 (a) American robin breeding ground locations and habitat types. Distribution of breeding sites by (b) latitude and (c) habitat type.
sexes were smaller further from Slave Lake. The significant interaction between snow-free date and distance traveled suggests that the effect of snow-free date becomes more pronounced further from Slave Lake (Table 3.4). We do not consider the effects of age to be significant because the 95% confidence intervals of the arrival odds ratio overlapped one.

Table 3.4. Results for variables in all models with ΔAIC < 2 in analysis of arrival timing to breeding grounds (n = 41). For each variable z scores, P values, odds ratios, and 95% confidence intervals values from the top model in which the variable was retained. Sex variables are referenced to female. Age variables are a binary age class and referenced to individuals in their second year. Distance variables are distance traveled between Slave Lake and final GPS fix.

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>z</th>
<th>P</th>
<th>Odds ratio</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance</td>
<td>-2.95</td>
<td>&lt; 0.01</td>
<td>0.98</td>
<td>[0.97-0.99]</td>
</tr>
<tr>
<td>Snow free date</td>
<td>-2.27</td>
<td>&lt; 0.05</td>
<td>0.96</td>
<td>[0.92-0.99]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>-1.45</td>
<td>0.15</td>
<td>0.61</td>
<td>[0.31-1.19]</td>
</tr>
<tr>
<td>Sex (female)</td>
<td>2.18</td>
<td>&lt; 0.05</td>
<td>5.63</td>
<td>[1.19-26.62]</td>
</tr>
<tr>
<td>Age (&lt; 2 years)</td>
<td>1.5</td>
<td>0.13</td>
<td>2.55</td>
<td>[0.76-8.53]</td>
</tr>
<tr>
<td>Distance*female</td>
<td>-2.15</td>
<td>&lt; 0.05</td>
<td>0.998</td>
<td>[0.997-0.999]</td>
</tr>
<tr>
<td>Distance*snow free date</td>
<td>2.954</td>
<td>&lt; 0.01</td>
<td>1.0001</td>
<td>[1.00-1.0002]</td>
</tr>
</tbody>
</table>

On average, the total migration rate was 23.9 km/day (median = 4.74 km/day). Total migration rate was significantly related to distance traveled between Slave Lake and breeding grounds (coefficient = 0.04, se = 0.002, p < 0.001). Migration rate was positively related to mass of individual (coef = 2.37, se = 0.92, p < 0.05), but not to wing length and did not differ significantly between age classes. Mean migration rates differed significantly between sexes, with females, on average, traveling faster (females: mean = 35.2 km/day, males: mean = 13.1 km/day, t = -2.17, p < 0.05). Females and males did not travel significantly different distances and or have significantly different masses. However, females did have significantly shorter wings than males (females: mean = 125.9 cm, males: mean = 131.1 cm, t = 4.01, p < 0.01). Total
migration rates and distances did not differ significantly between years. Total migration rate was not explained by date of arrival to Slave Lake.

3.4 Discussion

3.4.1 Robins advance spring migration through Canadian boreal forest over last quarter-century

Our findings strongly suggest that the timing of American robin migration through the Canadian boreal forest has trended earlier in response to the well-documented advance in spring environmental conditions at high latitudes in North America over the past quarter-century (Parmesan & Yohe, Menzel et al. 2006, Park et al. 2016). Specifically, we found that migration over Slave Lake, Alberta advanced by approximately 0.5 days per year over the time period 1994-2018, concurrent with a local winter warming trend. This is consistent with the findings of Ward et al. (2016) who found that first arrival dates of 16 migrant shorebird and passerine species to a site in arctic Alaska advanced by approximately 0.12 days per year over a fifty year period (1964-2013). Avian arrival timing at this site advanced by approximately one day per 1°C annual change in air temperature (Ward et al. 2016). Our findings also agree with those of Inouye et al. (2000) who found American robins advanced their arrival timing to a high altitude site in the Rocky Mountains by 14 days over a 25-year period from 1974-1999. Although phenological shifts are among the most widely documented responses to climate change (Root et al. 2003) - with many studies reporting earlier migration of birds in the spring consistent with rising temperatures (e.g. Ahola et al. 2004, Marra et al. 2005, Tøttrup et al. 2006) - our study is an important contribution since very few are focused at high northern latitudes despite their rapid pace of warming (Gordo 2007, Høye et al. 2007).
We found that robin spring migration timing to the Canadian boreal forest is influenced by local winter and spring environmental conditions, as well as large-scale climate oscillations. Specifically, we found that robins migrate earlier over Slave Lake when winter and spring snowpack is shallower, and spring precipitation is lower. This is consistent with previous studies at high northern latitudes which suggest that migration timing of arctic-breeding birds can be advanced or delayed in response to the favorability of spring environmental conditions (e.g. Boelman et al. 2017, Fox et al. 1987, Grabowski et al. 2013, Morton 1978, Senner et al. 2015). Migratory birds may delay arrival in response to unfavorable conditions because persistent snow cover limits access to food resources and adverse weather conditions cause birds to expend additional energy (Custer & Pitelka 1977, Krause et al. 2016, Norment & Fuller 1997, Wikelski et al. 2003), both of which can impact reproductive success (Alerstam et al. 2003, Hua et al. 2013, Smith & Moore 2003, Newton 2004, Wingfield et al. 2004). Birds typically travel over long distances to breeding ground and fine-tune migration rates depending on conditions along the route (Tøttrup et al. 2010), which are typically correlated with those across the region (Åkesson et al. 2017, Halkka et al. 2011).

We also found that the timing of robin spring migration to the Canadian boreal forest was strongly related to the strength of the PDO, with robins migrating earlier in years with more negative PDO values. Since negative phases of the PDO are associated with warm and dry winters in continental North America (Gedalof et al. 2002), this is consistent with our second hypothesis. Numerous studies have found that migration timing is related both to local environmental conditions and large-scale climate oscillations (e.g. Marra et al. 2005, MacMynowski et al. 2007, Palm et al. 2009, Tøttrup et al. 2010). For example, Rainio et al. (2006) found that the majority of 75 species investigated migrated earlier to sites in northern
Europe after winters in which the North Atlantic Oscillation (NAO) was higher. This likely due to the fact that the annual strength of the NAO influences climate in Europe (Hurrell et al. 2003) and so may capture changes in phenology along avian migratory routes more broadly than local environmental conditions (Hallett et al. 2004). Similarly, the PDO describes climate variability in North America at interannual to interdecadal timescales (Mantua et al. 1997, Zhang et al. 1997) with similar spatial structure and implications for North American climate as the the El Nino/Southern Oscillation (ENSO), but has a higher amplitude at high latitudes (Gedalof et al. 2002).

In agreement with both our first and second hypotheses, we found that robin migration timing through the Canadian boreal forest has shifted earlier over the past quarter-century and is positively influenced by favorable spring environmental conditions. Shifts in the timing of migration as measured at a single location along a migratory pathway are often considered an important barometer of a species’ ability to adapt to climate change (Both et al. 2006, Møller et al. 2008). However, this represents an indicator of migration timing at single point in time and space, which may be overly simplistic given that migration is an integration of a series of events that occur in disparate ecosystems (Åkesson et al. 2017, Franks et al. 2018). Therefore variation in the timing of a single migration metric may not fully capture the complex processes involved as birds adjust their phenology in navigating an increasingly dynamic mosaic of stopover ecosystems en route to their breeding grounds. While it is well established that photoperiod and local environmental conditions cue initiation of migration (Farner & Follet 1966, Dawson et al. 2001, Ramenofsky & Wingfield 2007), very little is known about the factors influencing migration movement rates and decisions (Lindström et al. 2014) which ultimately determine arrival timing to breeding grounds.
3.4.2 Snow conditions trigger migratory stopover events and control timing of arrival to breeding grounds

We found that although annual arrival times of robins to their stopover site is delayed by the persistent snow cover, once in the region, individuals are more likely to stopover during periods of inclement weather (i.e. snowfall or rain). These multi-directional responses to snow conditions are likely tied to the high energetic demands of migration and the risks associated with migrating in or into adverse weather conditions. Songbirds breeding at high northern latitudes are under immense pressure to reach their breeding grounds because of the shorter snow-free season compared to more temperate ecosystems (Park et al. 2016). However, migratory individuals must balance this pressure against the costs of migration which include high metabolic and energy demands to sustain flight (Wikelski et al. 2003), exposure to extreme events (Butler 2000, Morrison et al. 2007), and high mortality risk (Ydenberg et al. 2004, Baker et al. 2004). These tradeoffs are critical because time spent and energy expended during migration can influence subsequent breeding success (Gill et al. 2001, Norris et al. 2004, Paxton & Moore 2015). Therefore, migratory individuals are expected to maximize their fitness through behavioral modifications during migration (Alerstam 2011), and as such have been shown to respond to environmental conditions en route to breeding grounds (Tøttrup et al. 2008). For example, Briedis et al. (2017) found that although semi-collared flycatchers departed from their overwintering grounds in Eastern-Central Africa on approximately the same dates in two consecutive years, a persistent cold snap caused them to spend twice as long in the Mediterranean Basin in one year before continuing on to their breeding grounds.

Similarly, we found that later snow-free dates and deeper snow depths delayed robin arrival timing to breeding grounds. This is consistent with other studies which have found that
passerine arrival timing and breeding phenology was delayed or advanced in response to spring snow dynamics (e.g. Meltofte et al. 2007, Troy 1996). Boelman et al. (2017) found that two passerine species delayed their arrival timing to breeding grounds in arctic Alaska in a year with unusually late snow melt. In addition, Liebezeit et al. (2014) found that timing of snowmelt was the best predictor of arctic-breeding shorebird and passerine breeding phenology. Birds breeding at high northern latitudes are highly sensitive to snow conditions because of elevated energetic demands and limited access to food resources, both of which impact reproductive success (Alerstam et al. 2003, Hua et al. 2013, Smith & Moore 2003, Newton 2004, Wingfield et al. 2004).

3.4.3 Robins breeding in habitats with a short snow-free season accelerate migration movement rates west of the rockies

We found that Alaskan-breeding robins nearly doubled their migration movements rates after they transversed the Rocky Mountains. We suggest this acceleration could be partly attributable to more favorable wind conditions experienced by robins west of the rockies as compared to east. As predicted by theories of flight mechanics, birds have been shown prefer calm or tailwind conditions over headwinds (Hedenström et al. 2002, Liechti 2006). However, we found that Alaskan-breeding individuals arrived to locations west of the rockies approximately two weeks sooner after snowmelt as compared to east of the rockies, suggesting an increased tolerance for less favorable environmental conditions. This could reflect the immense pressure to reach breeding grounds at high northern latitudes. For example, the nesting season for robins is approximately 30 days in Fairbanks, Alaska, compared to about 60-80 days in much of the conterminous United States (James & Shugart 1974). The compressed breeding season at high northern latitudes means that passerines must lay eggs as soon as possible to
ensure that there is sufficient time for young to develop and adults to moult before embarking on fall migration (Martin 1987, Verhulst & Nilsson 2008). Timing may be especially tight for robins, which may attempt to rear a second set of fledglings in a single breeding season (Young 1951).

### 3.4.4 Robins breed primarily in mixed broadleaf and needle-leaved forests

In agreement with our third hypothesis, robins migrating through Slave Lake bred primarily in mixed broadleaf and needle leaved forests, but also took advantage of ecosystems with mosaics of forests, shrubs and grasses. This is consistent with previous work showing robins are habitat generalists and are known to take advantage of many different habitat types throughout their breeding range, including urban or agricultural areas (Tewksbury et al. 2002). Robins typically breed in forested and woodland habitats with areas of shorter grasses interspersed for foraging opportunities (Vanderhoff et al. 2016), placing nests within tree foliage (Savard & Falls 1981). They are often found in edge habitats, and many studies shown that robins prefer early-successional forests which have been cleared or recently burned (Martin 1973, Hutto 1995, Sallabanks 1995).

Robins migrating through Slave Lake continued their migration in a general northwest direction towards Alaska, indicating that populations stopping over at Slave Lake use the Pacific Flyway, as opposed to the adjacent Central Flyway (see Fig. 3.2). Songbird migration routes are thought to be at least partially genetically encoded and reflect colonization routes of past range expansions (Alerstam et al. 2003). Modern migratory pathways are influenced by glacial retreat and expansion during the Pleistocene (Rappole 1995, Berthold 2001) and the colonization of northern areas as they became available (Hewitt 2000, Taberlet et al. 1998).
3.5 Conclusions

Our main findings are that American robins migrating through Slave Lake, Alberta: (1) have advanced the timing of their spring migration through the region by one half day per year over the past quarter-century in response to the concurrent winter warming; (2) migrate through the region earlier in years with more negative PDO values, which correspond to warmer, drier local winter conditions; (3) are delayed in arriving to a boreal stopover site in years with persistent snow cover, although once in the region, individuals are more likely to stopover during periods of inclement weather; (4) are delayed in arriving to breeding grounds in years with later snow-free dates and deeper snow depths, and; (5) use the Pacific Flyway, and breed primarily in mixed broadleaf and needle leaved forests, but also take advantage of ecosystems with mosaics of forests, shrubs and grasses. Further, and to our surprise, we discovered that robins accelerate their migration movement rates once west of the Rocky Mountains, perhaps in response to the immense pressure they face to reach breeding grounds in time to ensure that there is sufficient time for young to develop and adults to molt before embarking on fall migration (Martin 1987, Verhulst & Nilsson 2008).

From these findings, we conclude that migratory American robins migrating through the Canadian boreal forest adjust their migration phenology at various points along their migration in response to environmental conditions, primarily snowmelt dynamics, and respond to environmental controls operating at local to continental scales. This strongly suggests that as arctic-boreal regions continue to warm, and spring conditions continue to advance American robins will continue to advance their migration. If robins are able to take advantage of lengthening breeding seasons they may be able to rear a second brood per season (Vanderhoff et al. 2016). However, changes in seasonality at high northern latitudes are outpacing those in other
regions which may result in an uncoupling of the environmental cues robins use along their migratory route (Åkesson et al. 2017). Continued warming, and the well-documented expansion of shrubs into tundra ecosystems could expand currently suitable breeding habitat for robins (Boelman et al. 2015).

To our knowledge, our study is the first to conduct an in depth, quantitative analysis of the factors influencing migration movement rates and decisions of small, long distance migratory birds. In this way, we demonstrate that advances in tracking technology revolutionize migration research by providing unprecedented understanding of how environmental dynamics affect migration behavior, which provides predictive insight into phenological responses to climate change. Our study is particularly timely, given the August 2018 installation of the ICARUS (International Cooperation for Animal Research Using Space) tracker aboard the International Space Station (ISSO). ICARUS will track the movements of small organisms, eventually including insects, using miniaturized, autonomously powered GPS units with the hopes of unlocking previously unanswered questions about Earth and life on it.
CONCLUSIONS

The high northern latitudes of North America are undergoing rapid climatic change with significant impacts to the ecosystems in which millions of long distance migratory songbirds breed. Concurrent changes in climate and vegetation are altering the composition, structure and seasonality of their critical breeding and migratory habitats. The phenological responses and changes in suitable breeding ranges for songbirds breeding at high northern latitudes are largely unknown. Further, gaining mechanistic understanding of phenological responses has proven nearly impossible. These unknowns are due in large part to the remote nature of Arctic-boreal ecosystems, and the lack of suitable means by which to observe small and broadly distributed organisms that migrate over large distances. In turn, we have been unable to integrate songbird phenology datasets with existing, ground-based networks and remotely sensed observations of environmental conditions and vegetation that would enhance mechanistic understanding. Together, my thesis chapters explore ongoing and future responses of songbird habitat and phenology in Arctic-boreal habitats using novel observational, modeling and analytical approaches.

In Chapter 1, I successfully devised an automated signal processing and machine learning approaches to estimate dates on which songbird communities arrived to arctic breeding grounds from landscapes level bioacoustic recordings collected in northern Alaska. My novel approaches demonstrate that variation in avian migratory arrival can be detected autonomously. Large-scale deployment of this innovation in wildlife monitoring would enable the coverage necessary to assess and forecast changes in bird migration in the face of climate change.

In Chapter 2, I used ecological niche models that include not only climate, but also vegetation distribution, to make spatially explicit projections of future habitat suitability for
songbirds breeding throughout North America’s high northern latitudes by the late 21st century. My most important conclusion is that improved forecasts of species’ responses to global change will depend on the inclusion of vegetation projections into habitat suitability models.

In Chapter 3, I investigated whether the American robin (Turdus migratorius), has advanced the timing of its spring migration through the Canadian boreal forest in response to the advance of spring environmental conditions over the past 25 years. In addition, I used GPS tracking technology to quantify how multiple metrics of robin migration phenology are influenced by a suite of environmental dynamics. My overall conclusion is that migratory American robins migrating through the Canadian boreal forest adjust their migration phenology at various points along their migration in response to environmental conditions, primarily snowmelt dynamics, and respond to environmental controls operating at local to continental scales. This strongly suggests that as arctic-boreal regions continue to warm, and spring conditions continue to advance American robins have the capability to advance their migration. Further, my results suggest that as the well-documented expansion of shrubs into tundra ecosystems continues, suitable breeding habitat for robins is likely to expand.

I suggest that future work focus on incorporating the new observational datasets that I have developed in Chapter 1 (i.e. automated bioacoustics) and used in Chapter 3 (i.e. miniaturized GPS tracking) to develop more sophisticated ecological niche models that the one I used in Chapter 2. Integrating more spatially and temporally dynamic, expansive, and distributed datasets than are typically used in niche modeling frameworks will yield a more mechanistic understanding of species responses to ongoing and future climate change.


GBIF.org (23rd March 2015) GBIF Occurrence Download http://doi.org/10.15468/dl.r7goxp

GBIF.org (23rd March 2015) GBIF Occurrence Download http://doi.org/10.15468/dl.dxd4i4


Halkka, A., Lehikoinen, A., & Velmala, W. (2011). Do long-distance migrants use temperature variations along the migration route in Europe to adjust the timing of their spring arrival?.


A.1 Supplemental Text

A.1.1 Identifying songbird vocalizations and arrival date to breeding grounds

(1) Supervised classification. We selected the decision threshold with a resulting false positive rate of 30.3% and the true positive rate of 69.7%. The AUC was 0.78. The linear classifier described 65% of the variance ($R^2 = 0.65$) of the proportion of songbird vocalizations in recordings as determined by manual listening of the training dataset and had a root-mean-square-error of 0.19 (Supplemental Fig. A.2). Discrepancies between the VAI and the listener scores may be caused by the sample size over which these values are calculated. In this case the VAI is the proportion of clips containing songbird vocalizations in a thirty-minute recording. In contrast, the listener scores are found only for 10 clips per recording (20 seconds).

Time series of the vocal activity index (VAI) for 2010-2014 at all sites show large daily and inter-annual variability in songbird vocalizations (Fig. 2 and Supplemental Figs. A.3-A.5).

Arrival date estimates were largely insensitive to the threshold used. Arrival dates estimated using thresholds of 30-70% of the maximum value in the VAI differed from the arrival dates estimated using a 50% threshold by less than a day on average (Fig. S7).

(2) Unsupervised classification. The first five principal components, on average, explained 70% of the variance ($R^2 = 0.7$) in the VAI (Supplemental Fig. A.2). The weighted sum of the first five principal components, using the linear model coefficients, and the VAI had a root-mean-square of 0.11 (Supplemental Fig. A.2).

Time series of the weighted sum of the first five principal components for 2010-2014 at all sites show large daily and inter-annual variability in songbird vocalizations (Fig. 2 and Supplemental Figs. A.3-A.5).

A.1.2 The influence of environmental conditions and songbird phenology on the VAI

Statistically significant linear relationships ($p < 0.1$) were found between the VAI and environmental covariates for all twenty thirty-day recording periods as measured by a F-test. Snow cover, temperature, wind speed, atmospheric pressure, and precipitation were found to have statistically significant relationships with the VAI in the following number of cases: eight, eleven, six, seven, and one, respectively. The relationships between the VAI and environmental covariates over the thirty-day period, as measured by the mean $R^2$ for a model type, were stronger for the significant multivariable models than the single variable models (multivariable: 0.52 +/- 0.06; snow cover: 0.33 +/- 0.07; temperature: 0.23 +/- 0.05; wind speed: 0.07 +/- 0.02; atmospheric pressure: 0.47 +/- 0.01; precipitation: 0.03 +/- 0.01) (Fig. 3 and Supplemental Fig. A.6). In all cases mean $R^2$ values were higher, or equivalent, when considering the period prior to clutch initiation as compared to the entire thirty-day period. Conversely, mean $R^2$ values were lower when considering the period after clutch initiation, with the exception of models based on wind speed data (Fig. 3).
A.2 Supplemental figures

Fig. A.1. Map of Alaska (inset) and Toolik Field Station with approximate locations of acoustic recording units.
Fig. A.2. Performance of supervised and unsupervised classification approaches. (a) Performance of classification of acoustic data based on presence/absence of songbird vocalizations compared to listener scores. Each point represents the proportion of clips in a thirty-minute recording containing songbird vocalizations as determined by the linear classifier (VAI) and listener scores. The dashed line represents the one-to-one showing perfect agreement between the VAI and listener scores. The solid line is the least squares regression line. (b) Proportion of variance in the VAI explained ($R^2$) by the top principal components (from the unsupervised approach), measured by a linear regression, as a function of the number of components used. Linear models were built for each thirty-day recording period independently and principal components were added in succession. Mean $R^2$ values represent means across all study sites and years. (c) Comparison of the VAI to the weighted sum of the first five principal components fit by a multivariable linear model (b).
Fig. A.3. Songbird community vocal activity estimated by supervised and unsupervised approaches near Imnaviat Creek.

(a)-(e) Songbird daily Vocal Activity Index (VAI), snow cover (blue), and air temperature (red) near Imnaviat Creek (IMVT) between 2010-2014. (f)-(j) Weighted sums of the first five principal components at the same site and time. Grey boxes identify the available recording period for acoustic data.
Fig. A.4. Songbird community vocal activity estimated by supervised and unsupervised approaches near Roche Mountonee Creek.

(a)-(e) Songbird daily Vocal Activity Index (VAI), snow cover (blue), and air temperature (red) near Roche Mountonee Creek (ROMO) between 2010-2014. (f)-(j) Weighted sums of the first five principal components at the same site and time. Grey boxes identify the available recording period for acoustic data.
Fig. A.5. Songbird community vocal activity estimated by supervised and unsupervised approaches near Sagavanirtok Department of Transportation.

(A)-(E) Songbird daily Vocal Activity Index (VAI), snow cover (blue), and air temperature (red) near Sagavanirtok Department of Transportation (SDOT) between 2010-2014. (F)-(J) Weighted sums of the first five principal components at the same site and time. Grey boxes identify the available recording period for acoustic data.
Fig. A.6. Comparison of the VAI to linear model predictions using only environmental covariates found to be statistically significant.
Fig. A.7. Threshold sensitivity of arrival date estimates from supervised approach.

Sensitivity of arrival date estimates to various thresholds. Under the supervised approach, songbird arrival date estimated as the first date that had a VAI that exceeded 50% of the maximum value over the thirty-day recording period. Grey lines show the difference in the arrival date estimate for each year under a range of thresholds as compared to the estimate using a 50% threshold. The black shows the mean difference across years.
APPENDIX B

Supplemental material for Chapter Two
B.1 Supplemental figures

Fig. B.1 Breeding habitat suitability for Lapland Longspurs (a-c) and White-crowned Sparrows (d-f) as determined by ecological niche models solely based on climate. Results for present-day conditions are shown for both species in (a) and (d). Habitat suitability for the late 21st century (2051-2080) is shown for projections of climate and vegetation distributions based on two emission scenarios, RCP4.5 and 8.5 (b,e and c,f, respectively).
APPENDIX C

Supplemental material for Chapter 3
Table C.1 Ranked candidate linear models of the influence of abiotic variables on American robin 5% arrival timing to Slave Lake, Alberta (1994-2018).

<table>
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<td>Snow depth (January) + PDO + Year</td>
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<tr>
<td>Precipitation (April) + Snow depth (March) + Year</td>
<td>138.35</td>
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Table C.2 Ranked candidate linear models of the influence of abiotic variables on American robin 50% arrival timing to Slave Lake, Alberta (1994-2018).

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**Table C.3** Ranked candidate linear models of the influence of abiotic variables on American robin 95% arrival timing to Slave Lake, Alberta (1994-2018).
Table C.4 Results from candidate models testing differences between study years (2016-2018) for arrival timing to Slave Lake based on tagging data. Shown are model specific 95% confidence intervals of odds ratios for each variable.

<table>
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<th>2017 reference</th>
<th>2018 reference</th>
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<tr>
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<td>1.14-2.03</td>
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<td>32.7-55.5</td>
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<tr>
<td>2018</td>
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<td>NA</td>
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</table>

Table C.5 Results for variables in all models with ΔAIC < 2 in analysis of stop-over timing for individuals captures at Slave Lake (n = 77). For each model AICc values are presented as well as z scores, P values, odds ratios, and 95% confidence intervals values for each variable. Sex variables are referenced to female. Age variables are a binary age class and referenced to individuals in their second year.

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<th>z</th>
<th>P</th>
<th>Odds ratio</th>
<th>95% CI</th>
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<tr>
<td>Snow free date</td>
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<td>[1.03-1.29]</td>
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<td>[0.33-0.9]</td>
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Model 2 (AICc = 477.47)

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<tbody>
<tr>
<td>Snow free date</td>
<td>-3.98</td>
<td>&lt; 0.01</td>
<td>0.85</td>
<td>[0.79-0.92]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>2.5</td>
<td>&lt; 0.05</td>
<td>1.15</td>
<td>[1.03-1.28]</td>
</tr>
<tr>
<td>Sex (female)</td>
<td>-1.41</td>
<td>0.16</td>
<td>0.72</td>
<td>[0.45-1.14]</td>
</tr>
<tr>
<td>Age (&lt; 2 years)</td>
<td>-2.38</td>
<td>&lt; 0.05</td>
<td>0.54</td>
<td>[0.33-0.9]</td>
</tr>
</tbody>
</table>

Model 3 (AICc = 477.81)

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>z</th>
<th>P</th>
<th>Odds ratio</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Precipitation</td>
<td>1.25</td>
<td>0.21</td>
<td>2.06</td>
<td>[0.67-6.37]</td>
</tr>
<tr>
<td>Snow free date</td>
<td>-4.03</td>
<td>&lt; 0.01</td>
<td>0.86</td>
<td>[0.8-0.93]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>2.4</td>
<td>&lt; 0.05</td>
<td>1.14</td>
<td>[1.03-1.27]</td>
</tr>
<tr>
<td>Age (&lt; 2 years)</td>
<td>-2.3</td>
<td>&lt; 0.05</td>
<td>0.56</td>
<td>[0.34-0.92]</td>
</tr>
</tbody>
</table>

Model 4 (AICc = 478.17)
<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>Std. Error</th>
<th>z value</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snow free date</td>
<td>-4.22</td>
<td>&lt; 0.1</td>
<td>0.85</td>
<td>[0.79-0.92]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>2.48</td>
<td>&lt; 0.01</td>
<td>1.15</td>
<td>[1.03-1.28]</td>
</tr>
<tr>
<td>Mass</td>
<td>-1.86</td>
<td>&lt; 0.05</td>
<td>0.96</td>
<td>[0.92-1.002]</td>
</tr>
<tr>
<td>Wing length</td>
<td>2.4</td>
<td>&lt; 0.05</td>
<td>1.08</td>
<td>[1.01-1.16]</td>
</tr>
<tr>
<td><strong>Model 5</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snow free date</td>
<td>-4.01</td>
<td>&lt; 0.001</td>
<td>0.86</td>
<td>[0.8-0.92]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>2.46</td>
<td>&lt; 0.05</td>
<td>1.03</td>
<td>[1.03-1.28]</td>
</tr>
<tr>
<td>Wing length</td>
<td>1.13</td>
<td>0.26</td>
<td>0.97</td>
<td>[0.97-1.11]</td>
</tr>
<tr>
<td>Age (&lt; 2 years)</td>
<td>-1.86</td>
<td>&lt; 0.1</td>
<td>0.36</td>
<td>[0.36-1.03]</td>
</tr>
<tr>
<td><strong>Model 6</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snow free date</td>
<td>-4.02</td>
<td>&lt; 0.01</td>
<td>0.86</td>
<td>[0.79-0.92]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>2.54</td>
<td>&lt; 0.05</td>
<td>1.15</td>
<td>[1.03-1.29]</td>
</tr>
<tr>
<td>Mass</td>
<td>-1.24</td>
<td>0.22</td>
<td>0.97</td>
<td>[0.93-1.02]</td>
</tr>
<tr>
<td>Sex (female)</td>
<td>1.71</td>
<td>&lt; 0.1</td>
<td>0.65</td>
<td>[0.4-1.06]</td>
</tr>
<tr>
<td>Age (&lt; 2 years)</td>
<td>-2.11</td>
<td>&lt; 0.05</td>
<td>0.58</td>
<td>[0.35-0.96]</td>
</tr>
<tr>
<td><strong>Model 7</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>1.18</td>
<td>0.24</td>
<td>1.97</td>
<td>[0.64-6.09]</td>
</tr>
<tr>
<td>Snow free date</td>
<td>-4.04</td>
<td>&lt; 0.01</td>
<td>0.86</td>
<td>[0.8-0.93]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>2.43</td>
<td>&lt; 0.05</td>
<td>1.14</td>
<td>[1.03-1.27]</td>
</tr>
<tr>
<td>Sex (female)</td>
<td>-1.33</td>
<td>0.18</td>
<td>0.73</td>
<td>[0.46-1.16]</td>
</tr>
<tr>
<td>Age (&lt; 2 years)</td>
<td>-2.27</td>
<td>&lt; 0.05</td>
<td>0.56</td>
<td>[0.34-0.92]</td>
</tr>
<tr>
<td><strong>Model 8</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>1.89</td>
<td>&lt; 0.1</td>
<td>2.99</td>
<td>[0.96-9.32]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>2.38</td>
<td>&lt; 0.05</td>
<td>1.14</td>
<td>[1.02-1.27]</td>
</tr>
<tr>
<td>Year 2018</td>
<td>-3.91</td>
<td>&lt; 0.01</td>
<td>0.03</td>
<td>[0.01-0.18]</td>
</tr>
</tbody>
</table>

Model 5 (AIC<sub>c</sub> = 478.18)

Model 6 (AIC<sub>c</sub> = 478.24)

Model 7 (AIC<sub>c</sub> = 478.32)

Model 8 (AIC<sub>c</sub> = 478.41)
<table>
<thead>
<tr>
<th>Model 9 (AIC\textsubscript{c} = 478.58)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (&lt; 2 years)</td>
</tr>
<tr>
<td>Precipitation</td>
</tr>
<tr>
<td>Snow depth</td>
</tr>
<tr>
<td>Year 2018</td>
</tr>
<tr>
<td>Age (&lt; 2 years)</td>
</tr>
<tr>
<td>Sex (female)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model 10 (AIC\textsubscript{c} = 478.64)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snow free date</td>
</tr>
<tr>
<td>Snow depth</td>
</tr>
<tr>
<td>Mass</td>
</tr>
<tr>
<td>Wing length</td>
</tr>
<tr>
<td>Age (&lt; 2 years)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model 11 (AIC\textsubscript{c} = 478.89)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snow free date</td>
</tr>
<tr>
<td>Snow depth</td>
</tr>
<tr>
<td>Mass</td>
</tr>
<tr>
<td>Age (&lt; 2 years)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model 12 (AIC\textsubscript{c} = 478.92)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snow free date</td>
</tr>
<tr>
<td>Snow depth</td>
</tr>
</tbody>
</table>
Table C.6 Results from candidate models testing differences between study years (2016-2018) for arrival timing to breeding grounds based on tagging data. Shown are model specific 95% confidence intervals of odds ratios for each variable.

<table>
<thead>
<tr>
<th>Year</th>
<th>2016 reference</th>
<th>2017 reference</th>
<th>2018 reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016</td>
<td>NA</td>
<td>0.36 - 2.1</td>
<td>0.79 - 1.76</td>
</tr>
<tr>
<td>2017</td>
<td>0.48 - 2.75</td>
<td>NA</td>
<td>0.84 - 2.18</td>
</tr>
<tr>
<td>2018</td>
<td>0.57 - 1.26</td>
<td>0.46 - 1.19</td>
<td>NA</td>
</tr>
</tbody>
</table>
Table C.7 Results for variables in all models with ΔAICc < 2 in analysis of arrival timing breeding grounds based on GPS data (41 individuals). For each model AICc values are presented as well as z scores, P values, odds ratios, and 95% confidence intervals values for each variable. Sex variables are referenced to female. Age variables are a binary age class and referenced to individuals in their second year. Distance variables are distance traveled between Slave Lake and final GPS fix.

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>z</th>
<th>P</th>
<th>Odds ratio</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Model 1 (AICc = 113.22)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance</td>
<td>-2.95</td>
<td>&lt; 0.01</td>
<td>0.98</td>
<td>[0.97-0.99]</td>
</tr>
<tr>
<td>Female</td>
<td>2.18</td>
<td>&lt; 0.05</td>
<td>5.63</td>
<td>[1.19-26.62]</td>
</tr>
<tr>
<td>Snow free date</td>
<td>-2.27</td>
<td>&lt; 0.05</td>
<td>0.96</td>
<td>[0.92-0.99]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>-1.45</td>
<td>0.15</td>
<td>0.61</td>
<td>[0.31-1.19]</td>
</tr>
<tr>
<td>Distance*female</td>
<td>-2.15</td>
<td>&lt; 0.05</td>
<td>0.998</td>
<td>[0.997-0.999]</td>
</tr>
<tr>
<td>Distance*snow free date</td>
<td>2.954</td>
<td>&lt; 0.01</td>
<td>1.0001</td>
<td>[1.00 - 1.0002]</td>
</tr>
<tr>
<td><strong>Model 2 (AICc = 113.41)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance</td>
<td>-3.02</td>
<td>&lt; 0.01</td>
<td>0.989</td>
<td>[0.982-0.996]</td>
</tr>
<tr>
<td>Snow free date</td>
<td>-1.75</td>
<td>0.08</td>
<td>0.97</td>
<td>[0.95-1.00]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>-1.31</td>
<td>0.19</td>
<td>0.69</td>
<td>[0.41-1.19]</td>
</tr>
<tr>
<td>Distance*snow free date</td>
<td>2.918</td>
<td>&lt; 0.01</td>
<td>1.0001</td>
<td>[1.000-1.0001]</td>
</tr>
<tr>
<td><strong>Model 3 (AICc = 113.60)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance</td>
<td>-3.04</td>
<td>&lt; 0.01</td>
<td>0.98</td>
<td>[0.97-0.99]</td>
</tr>
<tr>
<td>Snow free date</td>
<td>-2.02</td>
<td>&lt; 0.05</td>
<td>0.97</td>
<td>[0.93-0.99]</td>
</tr>
<tr>
<td>Snow depth</td>
<td>-1.33</td>
<td>0.18</td>
<td>0.68</td>
<td>[0.38-1.2]</td>
</tr>
<tr>
<td>Young</td>
<td>1.5</td>
<td>0.13</td>
<td>2.55</td>
<td>[0.76-8.53]</td>
</tr>
<tr>
<td>Distance*snow free date</td>
<td>2.98</td>
<td>&lt; 0.01</td>
<td>1.0001</td>
<td>[1.000-1.0002]</td>
</tr>
<tr>
<td><strong>Null model (AICc = 153.62)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>