Interannual consistency of migration phenology is season- and breeding region-specific in North American Golden Eagles

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Interannual consistency of migration phenology is season- and breeding region-specific in North American Golden Eagles

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ABSTRACT

Interannual consistency (an indicator of the strength of adjustments) in migration phenology of Golden Eagles (*Aquila chrysaetos*) in North America is most strongly associated with breeding region, the season, and with late season temperature on breeding and wintering grounds. Consistency was greatest in boreal spring migration and the breeding regions of eastern Canada. Using multi-year GPS tracks of 83 adults breeding in 3 spatially distant regions (Alaska, northeast Canada, and southeast Canada), we quantified the interannual consistency of migration phenology and wintering latitude within and among individuals tracked across multiple years and the repeatability (r) by breeding regions and seasons. By comparing regions and seasons, we found that consistency was highest ($r > 0.85$) for boreal spring migration in eastern Canada while Alaska had the lowest value ($r < 0.15$). Because seasonal consistency of migration phenology was only detected in eastern Canada, we conclude that seasonal features are not a primary constraint. While regional differences in consistency were not related to differences in migratory distances, they could be the result of genetic or habitat differences. We also found that temperatures warmer than the decadal average at the region of departure delayed the start of boreal spring migration by ~10 days and advanced boreal autumn migration by ~20 days. These results suggest that warmer temperatures would reduce residence time on breeding grounds, contrary to expectations and trends found in other studies. Wide variations in migratory strategies across a species distribution can add to the lists of challenges for conservation but may give migrants the capacity to acclimate to environmental changes.

Keywords: Alaska, Canada, consistency, Golden Eagle, GPS tracking, migration phenology

LAY SUMMARY

- Avian migrants can adjust migration phenology with environmental conditions, seasons, and migration distance.
- We studied seasonal, regional, and environmental relationships with the consistency of Golden Eagle migration.
- To measure consistency, we quantified within- and among-individual variations and repeatability in migration timing and duration.
- Consistency and among-individual variation were highest for boreal spring migration and in eastern Canada eagles.
- We found that warmer temperatures delayed departures for boreal spring migration by ~10 days and advanced boreal autumn migration by ~20 days.
- We show that consistency differs among seasons and regions, suggesting that migration phenology in Golden Eagles is shaped by environmental factors.
- Wide variations in consistency of migration phenology across breeding regions and seasons can add to the challenge of species conservation by redefining the impact of breeding or wintering conditions on migratory strategies.

La constance interannuelle de la phénologie de la migration est spécifique à la saison et la région de reproduction chez l'aigle royal en Amérique du Nord

RÉSUMÉ

La constance interannuelle de la phénologie de la migration (indicateur de la force d'ajustement) chez l'aigle royal (*Aquila chrysaetos*) en Amérique du Nord est fortement associée à la région de production, la saison la température en fin de saisons sur l'aire de reproduction et d'hivernage. La constance était la plus élevée pour le départ et la fin de la migration du printemps boréal et pour les régions de reproduction de l'est du Canada. En utilisant des données GPS de 83 adultes provenant de trois régions de reproduction distinctes (Alaska, nord-est du Canada et sud-est du Canada) la constance de migration a été quantifié avec la variation intra-individuelle (individus suivis sur plusieurs années) and interindividuelle et la répétabilité (r) de la phénologie et de la durée de la migration ainsi que celle de la latitude d'hivernage par région de reproduction et par saison. En comparant les régions et les saisons, nos résultats montrent que la répétabilité de la phénologie de la migration du printemps boréal était la plus élevée ($r > 0.85$) dans l'est du Canada, alors que l'Alaska avait la plus basse valeur ($r < 0.15$). La tendance prédite où la constance de migration diffère entre saisons n'était présente que pour l'est du Canada, ce qui suggère que les facteurs saisonniers ne sont pas les contraintes principales sur la constance migratoire. Indépendamment de la distance de migration, les caractéristiques de l'habitat et la différence entre les populations peuvent expliquer le contraste régional de constance de la phénologie de la migration observée. De plus, les oiseaux ont migré 10 jours plus tôt en pré-reproduction et 20 jours plus tard en post-reproduction lorsque les températures locales étaient plus chaudes que la moyenne de la décennie. Ces résultats suggèrent que des températures plus chaudes induisent un temps de résidence plus court dans la région de reproduction, ce qui va à l'encontre de nos attentes et des tendances rapportées dans d'autres études. Une telle variation des stratégies de migration peut rendre difficile la conservation d'une espèce mais peut aussi donner aux populations la capacité de s'acclimater aux changements de son environnement.

Mots-clés : constance, migration, rapace, phénologie, aigle royal.

INTRODUCTION

The ability to move allows animals to find resources necessary for survival and reproduction, and avoid unsuitable conditions (Nathan et al. 2008, Shaw 2020). Large-scale movements, such as avian migration, likely evolved in response to seasonal depletion of resources and to increase chances of survival until the next reproductive season (Dingle and Drake 2007, Zúñiga et al. 2017, Winger et al. 2019). To avoid compromising survival and reproduction, the phenology of migration (i.e., start and end dates and duration) must be timed precisely, neither too early nor too late (Winger et al. 2019). Birds rely on variations in environmental conditions such as daylight, resource availability or air temperature (Studds and Marra 2011, Duerr et al. 2015, Curk et al. 2020), as cues to identify the optimal timing for migration.

While some studies have identified a behavioral response tailored to environmental conditions, the strength of the response varies among species (Rubolini et al. 2007, Therrien et al. 2017, Usui et al. 2017) and even among individuals (Bêty et al., 2004, Gill et al. 2013, Tedeschi et al. 2019). Some individuals can show highly consistent behavior (i.e., individuals departing at similar dates from year to year; Lourenço et al. 2011, Vardanis et al. 2011), whereas others are highly flexible in their phenology (e.g., wide ranges of departure dates across years; Hasselquist et al. 2017, Tedeschi et al. 2019). To measure the strength of individual responses within a population, behavioral ecologists quantify their consistency (Vardanis et al. 2016, Fraser et al. 2019). Such an approach allows the estimation of the adaptative capacity of both populations and individuals to cope with environmental changes (Vardanis et al. 2016, McCrary et al. 2019, Sugasawa and Higuchi 2020). To disentangle what dictates consistency levels within a species, studies comparing the consistency of migration phenology among regions or different populations are useful (e.g., seabirds Brown et al. 2021), but such work has yet to be implemented for many migratory species. The present study aims to fill such a gap for the birds of prey. Here, we examined seasonal and geographic variation of consistency of two different populations of Golden Eagle (*Aquila chrysaetos*) originating from three different breeding regions.

A consistent migratory phenology might be beneficial in various contexts (McNamara et al. 1998, Alerstam et al. 2006) such as migration prior to the reproductive season. While an early arrival to breeding location (end of boreal spring northward migration) increases chances of successful breeding (Bêty et al. 2004, Lourenço et al. 2011, Morrison et al. 2019), if that same arrival is too early, it can affect the survival of migrants with unsuitable prey or weather conditions (McNamara et al. 1998). A consistent strategy may reduce both risks for survival and reproduction for boreal spring migration (Winger et al. 2019). Conversely, boreal autumn migration (southward and post-breeding season) is influenced by survival linked to changing prey resources (Studds and Marra 2011, Curk et al. 2020) and the release from reproductive duties (Maynard and Davoren 2018, Sur et al. 2019). A flexible strategy might then be beneficial for boreal autumn migration to adjust for resource availability and breeding outcome. Because boreal autumn and spring migrations are influenced differently by survival and reproduction, individual responses to environmental conditions may vary seasonally, and affect consistency in migration schedule (McNamara et al. 1998, Alerstam et al. 2006, Conklin et al. 2013) especially in breeding adults.

Consistency in migration phenology might also be affected by the distance traveled between the breeding and wintering grounds. Longer migrations increase travelling costs (Conklin et al. 2017) and prevent birds from forecasting the suitability of environmental conditions at their destination (Newton 2008). Individuals breeding at higher latitudes are also exposed to increased fluctuations of abiotic (e.g., temperature, precipitation) and biotic (e.g., food availability, parasitism, predation risk) conditions (Cannone et al. 2008, Comita 2017); such exposure can exacerbate the risks of timing mismatch with optimal conditions (Møller et al. 2008, Saino et al. 2011, Machín et al. 2018). Therefore, migrants breeding in higher latitudes and travelling over longer distances benefit from a consistent migration phenology more than individuals breeding farther from the poles and migrating over shorter distances (Pulido and Widmer 2005, Rubolini et al. 2007). Individuals travelling different distances, although originating from the same geographic or genetic population, can thus benefit from distinct migration strategies (Brown et al. 2017, Phipps et al. 2019) that affect population-level consistency in migration phenology (Supplementary Material Figure S1).

The Golden Eagle is an apex Holarctic predator and a facultative migrant that exhibits sedentary and migratory strategies across its range (Bildstein 2006, Watson 2010, Newton 2012). In North America, Golden Eagles are separated into western and eastern populations (Katzner et al. 2020) that are to some degree genetically distinct (Doyle et al. 2016). The western population includes migratory individuals breeding in Alaska and Canada and non-migratory residents in the U.S. and Mexico, whereas the eastern population currently only breeds in Canada and is considered predominantly migratory (Brodeur 1994, Katzner et al. 2020). The wide latitudinal breeding distribution (~30° latitude) creates a broad range of migratory distances traveled and environmental conditions encountered on the eastern breeding grounds (i.e., sub-arctic vs. boreal; Katzner et al. 2020). The flexibility in migratory strategies (i.e., resident and migratory) and the wide latitudinal gradient and range of environmental conditions make the Golden Eagle an interesting model species for the study of migratory consistency.

The goal of this study was to evaluate the interannual consistency of phenology of avian migration at the population level as a response to seasonal features (e.g., survival and reproduction), regional differences (e.g., breeding latitude and distance traveled) and variation in environmental conditions (e.g., temperature and resource availability via precipitation and snow cover). To do so, we measured the consistency of migration phenology (i.e., start and end dates and duration) from migratory tracks of adult Golden Eagles at a continental scale over multi-year migratory bouts in boreal spring and autumn. By focusing only on adults, we remove the effects of stage-related differences in drivers of migration (i.e., subadult eagles generally do not breed). We first hypothesized that consistency of migration timing (i.e., dates of migration start and end) and duration would be seasonally distinct because migration is influenced differently by survival and reproduction. Because a timely return to breeding ground for boreal spring migration is linked to increased potential for breeding success (Bêty et al. 2004, Lourenço et al. 2011, Morrison et al. 2019), we predicted that migration timing and duration would be more consistent for boreal spring than for boreal autumn migration. We further hypothesized that consistency of migration phenology would increase with longer migratory distances (Pulido and Widmer 2005). We predicted eagles returning to breed in northern breeding regions (Alaska and northeast Canada) would have higher consistency in migration phenology than the southernmost breeders (southeast Canada). Finally, we hypothesized that eagles would delay boreal autumn migration and advanced boreal spring migration and migrate faster when environmental conditions were optimal for survival and/or reproduction prior to and during migration. We thus predicted that eagles would depart earlier in boreal spring and later in boreal autumn when experiencing optimal conditions than when conditions were poorer. We also predicted migrations would also take less total time when environmental conditions are favorable. We define environmental conditions as poor with higher snow cover (Curk et al. 2020), lower temperatures (Tøttrup et al. 2010), and higher precipitation (Studds and Marra 2011) than the decadal average. Overall, this paper aims to elucidate the migratory strategies used by Golden

Eagles across North America.

METHODS

Telemetry Data

Telemetry data from eagles were gathered from 3 data sources: the Alaska Department of Fish and Game (AKDFG; *n* = 35 individuals; 2014–2019); the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP; *n* = 21 individuals; 2007–2020); and an eastern United States collaborative network: the Eastern Golden Eagle Working Group (*n* = 37 individuals; 2008–2020), which included Alabama Department of Conservation and Natural Resources, U.S. Forest Service–Talladega National Forest, North Carolina Wildlife Resources Commission, Delaware-Otsego Audubon Society, Virginia Department of Wildlife Resources, Georgia Department of Natural Resources, Tennessee Wildlife Resources Agency, and Conservation Science Global.

Eagles were captured on their respective breeding grounds or during late migration near the breeding area (*n* = 56; Alaska and Québec) or wintering grounds (*n* = 37; eastern USA) between 2007 and 2019. Eagles in Québec were targeted with a bownet or a net trap at baiting sites located near (~300 m) known nests before the breeding season (February 5 to April 5), before fall migration (October 2–25), or 3–4 weeks following hatching (June 17 to August 8). Following capture, standard morphometric measurements were taken, and each bird was banded with a United States Geological Survey (USGS and Canada Bird Banding Office band). Sex was identified with DNA from blood samples (Craig et al. 2009) or with a formula considering mass, wing chord, hallux length, and head length (Harmata and Montopoli 2013). Age (adult ≥ 4 years vs. subadult <4 years) was determined by the molting stages of flight feathers (Bloom and Clark 2001, Liguori 2004). Telemetry units were attached to eagles with a body harness made of Teflon ribbon of 6.5–8.5 mm thick. Capture and tagging methods used for Alaska and eastern U.S. eagles were very similar to the method described above (details can be found in Eisaguirre et al. [2019] and Miller et al. [2017], respectively).

Telemetry units used across all datasets were made by 3 companies (Cellular Tracking Technologies CTT-ES150, 70 g, Rio Grande, New Jersey, USA; Microwave Telemetry PTT-100, 30 g and PTT-100, 70 g, Columbia, Maryland, USA; and North Star Science and Technology, 55–65 g, solar GPS PTT, Oakton, Virginia, USA). Telemetry units recorded GPS and/or ARGOS locations (latitude and longitude) every 15 min or 1 hr. Telemetry units deployed from Alaska recorded both GPS and ARGOS locations (see Data Management below). Telemetry units deployed in Quebec and eastern USA collected only GPS data. Telemetry units were always <3% of the eagle's total mass (45–100 g). We had insufficient data to test if differences in tag size influenced migration schedule. However, we are confident that effects were minimal given little effect found in other studies (Sergio et al. 2015, Perkins et al. 2019) and the several weeks of acclimatization to the tag prior to migration (Weiser et al. 2016).

Data Management

We standardized the temporal resolution between individual tracks. To do so, we subsampled data recorded every 15 min to hourly intervals by extracting the first locations recorded at the start of each nominal hour. We also filtered out recorded speed >100 km hr^{-1} to delete erroneous data. To test our hypotheses, we only included adult birds (>4 years old) because preadults rarely breed and face different selective pressures than do adults. Because our approach requires accurate measurement of start, end, and duration of migration, we also excluded migratory tracks with gaps exceeding 3 days within 50 km of the wintering or breeding grounds. We then assigned the remaining telemetry tracks to 3 breeding regions (Figure 1): southern Alaska (later referred as Alaska), northeast Canada, and southeast Canada. Southeast Canada corresponds to eagles nesting south of the Saint Lawrence River in the Gaspé Peninsula, whereas northeast Canada refers to eagles breeding north of the river. These breeding regions also differ in bioclimatic conditions, with northeast Canada belonging to both the boreal and polar bioclimates dominated by taiga and tundra; whereas Alaska and southeast Canada both are part of the boreal bioclimate, dominated by temperate deciduous and mixed forests in southeast Canada and by temperate shrubland in Alaska (Rivas-Martínez et al. 2011; Figure 1). Unless otherwise noted, all data management and statisccal analyses were performed in R v 4.0.3 (R Core Development Team 2022) and QGIS v 3.16.2 (QGIS Development Team 2021). Results are reported as mean and standard error (mean ± SE) otherwise indicated.

After standardizing telemetry data, we used tracks to calculate migration characteristics. To distinguish migratory behavior from local movement, we calculated the residence distance and time for consecutive points along a track with a radius of 5 km with the function *residenceCalc* in R v 4.0.3 (R Core Development Team 2022; see also supplementary material of Torres et al. 2017). Using the difference between residence distance and residence time, we identified 3 behaviors: (1) transit (null values), (2) area-restricted search (positive values), and (3) rest (negative values; Torres et al. 2017). To ensure homogeneity across datasets, we determined the start of migration as occurring when there were at least 3 consecutive days of transit behavior paired with a long and linear trajectory and increased daily distance traveled (more than twice the daily mean distance during the breeding season; Miller 2012). We determined the end of migration as daily periods of transit behavior with rest and/or area-restricted search behaviors and a decrease in daily distance traveled (less than half the daily mean distance during migration). We considered every recorded location between migration start and end as migratory locations. We verified the accuracy of this approach by comparing, for 10 different tracks from Québec birds, these results with the migration start and end dates determined by the net square displacement (Nilsson 2014, Singh et al. 2016). Mean difference between the 2 approaches was <4 days of difference (Soriano- Redondo et al. 2020).

We then calculated characteristics of migratory tracks (i.e., migration departure date, arrival date, duration, and wintering latitude). We determined latitudes (breeding and wintering), start and end dates (ordinal dates) from the first and last recorded GPS locations of migration. In Alaska, telemetry units also recorded ARGOS locations, which were used only to retrieve schedule and duration data, when necessary, that is when GPS locations were not recorded in enough numbers (i.e., at least once a day) due to power or unit issues. In this case, start or end dates were determined as the first or last recorded ARGOS location of migration. However, for breeding and wintering latitudes, we always used the earliest recorded GPS locations at wintering or breeding sites. We calculated the duration of migration as the number of days between start and end of migration. We then measured the minimal migration distance as the sum of the Euclidean distance between consecutive points recorded during the migration (Freitas 2015).

Statistical Analyses

We estimated the consistency of migration phenology by calculating the measure of repeatability I for each of the three populations to test our first and second hypotheses (seasonal and regional consistency). Repeatability represents the proportion of the total variance attributed to the variance among individuals (Bell et al. 2009, Wolak et al. 2012). Thus, repeatability is calculated by dividing the variance among individuals by the sum of the variances within and among individuals (total variance; Wolak et al. 2012). It is a unitless linear index that ranges from 0 (flexible) to 1 (consistent) (Wolak et al. 2012, Stoffel et al. 2017), and is only calculated for the whole population. Therefore, no individual measure of consistency can be estimated with this metric (Bell et al. 2009, Wolak et al. 2012). A population with high within-individual variation and low among-individual variation results in low repeatability value ($r < 0.5$; Supplementary Material Figure S1). In this situation, individuals are behaving more similarly to each other across years than within themselves (Supplementary Material Figure S1). In contrast, a population with low within-individual variation and high among-individual variation results in high repeatability value ($r > 0.5$). Under that scenario, individuals behave more closely to themselves across years than to other individuals in the population (Supplementary Material Figure S1).

We built separate general linear mixed models (Zuur et al. 2009) for each migration characteristic. In the 7 models we built, response variables were duration for both seasons, start and end dates for both seasons, and winter latitude with sex as a fixed effect and individual ID as a random effect (intercept). Sex was added as a fixed factor so that the variance due to differences in morphology (Harmata and Montopoli 2013) or behavior (Kjellén 1994) would be differentiated from the variance within individuals. Each migration characteristic was modeled by breeding region (i.e., Alaska, southeast Canada, and northeast Canada) and migratory seasons (i.e., boreal spring and autumn migrations) separately, resulting in 21 models. Additionally, because some eagles in southeast Canada occasionally did not migrate, we used a one-sample *t*-test to test whether air temperatures and precipitation were different in non-migratory years compared to the decadal average. Linearity and homoscedasticity were checked before running the *t*-test.

From the variances estimated by these models, we calculated the measure of repeatability, resulting in a single repeatability value for each migration characteristic by season and by region. We estimated the variance among individuals as random effect (individual; intercept), the variance within individuals using the residuals, and finally calculated repeatability. To estimate a value of precision for repeatability (Nakagawa and Schielzeth 2010), we estimated confidence intervals and standard errors of the repeatability parameter using parametric bootstrapping with 3 permutations of 100,000 bootstrap samples using the package *rptR* 0.9.21 (Stoffel et al. 2017). Additionally, we used a likelihood ratio test with the function *rpt* from *rptR* 0.9.21 (Stoffel et al. 2017) to detect whether the value of repeatability was different from 0. We considered within-individual and among-individual variation and repeatability values as significantly different from each other if the 95% confidence intervals (CIs) did not overlap (Conklin et al. 2013).

To quantify whether environmental conditions relate to the start and end of migration and whether pre-migration environmental conditions were related to the duration of migration (hypothesis 3), we evaluated response of migratory timing and duration to 3 predictors. These predictors have the potential to be local environmental triggers of migration: maximum snow depth (a proxy for food resource availability; Curk et al. 2020), precipitation, and air temperature (indicating migratory and survival conditions or increase in primary productivity in spring; Newton 2008, Sur et al. 2019). These measures are correlated with the North Atlantic and Southern Oscillation Indexes, which are measures often used in long-term migration studies for large-scale weather conditions (e.g., Sullivan et al. 2016). Using the Env-DATA system on movebank.org, we extracted daily temperature (°C, spatial resolution 0.7°), total daily precipitation (kg m^2-1, spatial resolution of 32 km) and daily snow depth (m, spatial resolution 0.7°) for the 30 days preceding migration departure and arrival for each individual migration track (Li and Heap 2011, Dodge et al. 2013) to reflect the average conditions to which eagles were exposed when a migration decision was made. Environmental data were bilinearly interpolated (Dodge et al. 2013) to the start or end locations of each migration track. We then calculated average temperature, total precipitation, and maximum snow depth during the 30 days preceding a migration event. To identify cooler and warmer years and to correct for the natural differences in environmental conditions among regions, we calculated the *z*-score (the difference between the observation and decadal average divided by the decadal standard deviation; Quinn and Keough 2002) between the observed temperature, precipitation, and snow depth and the decadal average (2007 to 2020) of each one.

We modeled the effect of these pre-migration environmental conditions on migration phenology to test our third hypothesis. We used a generalized additive mixed model (Wood 2006, Zuur et al. 2014) framework with sex and breeding region as parametric fixed effects, individual eagles as a random effect (intercept), and pre-migration environmental predictors as smoothed predictors (i.e., residual snow depth, temperature, and precipitation). We built seven models with migration characteristics (i.e., duration for both seasons, start and end dates for both seasons, and winter latitude) as response variables. Before analyzing the output of our models, we verified the relevance of smoothing the predictors. We did so by calculating the Akaike Information Criteria (AIC; Burnham and Anderson 2002) of models where (1) all predictors were smoothed; (2) one predictor was linear, and others were smoothed (predictors were switched one at a time); and (3) all predictors were linear terms. We chose the model with the lowest AIC. To detect under- or over-smoothing of our models, we examined the estimated degrees of freedom (edf) and the number of knots (*k*; Wood 2006). We tested our models with several numbers of *k* per predictor (i.e., five, 10, 15, and 20). When *k* was higher than the edf by 2 units and no change in the relationship (based on variance explained) was seen between 2 *k* increments; we chose the model with the lowest number of *k*. For instance, if the relationship at 5 and 10 *k* was similar, we chose the model with 5 *k*. Finally, we verified model assumptions through plots of residuals against fitted values and histograms. When the normality assumption failed, we log10-transformed the response variable. To identify pairwise differences between breeding regions, we used a Tukey test (Quinn and Keough 2002).

RESULTS

Telemetry units lasted from one complete migration track to nine consecutive years of migration tracks from 2007 to 2020 (Supplementary Material Table 1). We removed 53 migratory tracks from 10 subadult individuals and another 72 migratory tracks with gaps exceeding 3 days at the start or at the end. Of the 83 tracked Golden Eagles included in the analysis, we had a total of 174 migratory tracks for boreal spring and 147 for boreal autumn. Alaska included *n* = 28 individuals (number of tracks = 85), whereas northeast Canada included *n* = 44 individuals (no. tracks = 165), and southeast Canada *n* = 11 individuals (no. tracks = 71; Supplementary Material Table S1; Figure 1). From these individual eagles, 83% had ≥2 years of migratory tracks and 61% had ≥3 years (Supplementary Material Table S2).

Three Golden Eagles (2 males and 1 female) breeding in southeast Canada (representing 27% of eagles tracked in that region) skipped boreal autumn migration for 1–5 years (not necessarily consecutively) and spent winter in their breeding area. All 3 eagles also migrated at least 1 year while tracked. In 2015, 2 of these individuals skipped migration simultaneously. Years of residency were not significantly warmer (mean difference: 0.62 ±

1.31°C, $t = –1.41$, df = 3.26, $P = 0.2$) or wetter (mean difference: 3.69 ± 18.15 mm, $t = 0.61$, df = 1.11, $P = 0.55$) than the decadal average. For the years they migrated, the among-individual variation in migration start dates for these flexible individuals was 4.2 times higher (variation for flexible individuals: 565.5 days^2, 57.0 ± 1.4 days in difference among years; variation for other individuals 134.7 days^2 with 24.7 ± 13.4 days in difference among years) than southeast Canada migrants that never skipped migration while tracked.

Breeding latitudes differed among regions by an average of 8.9° (± 4.1°, $F = 379.7$, df = 2 and 171, $P < 0.001$). Alaska eagles bred at an average of 61.5 ± 0.1°; the northeast Canada eagles at 56.0 ± 0.3°; and the southeast Canada eagles at 48.1 ± 0.1° (Figure 1). Migration distance for southeast Canada eagles (1,133 ± 108 km) was three times shorter on average than both Alaska and northeast Canada eagles (3,303 ± 94.4 km, $F = 21.64$, df = 2 and 314, $P < 0.001$).

Seasonal and Regional Differences in Migration

Of the mean migration characteristics, only the end date for boreal autumn migration, did not differ among regions (Table 1). Southeastern eagles had the shortest boreal spring migration duration (15.4 days shorter on average) and also started and ended migration 10.4 and 25.8 days earlier than in other regions (Figure 1, Table 1). Southeastern eagles started and ended boreal autumn migration 19.5 days later, on average, than did eagles from the other regions (Figure 1, Table 1). Boreal spring migration of northeastern Canada eagles was the longest (13.2 more days, on average), started and ended the latest (11 and 24.3 days later on average) relative to other regions. Northeastern Canada eagles also ended boreal autumn migration the earliest with 25.5 days earlier on average relative to other regions (Figure 1, Table 1). Duration of both migration for Alaskan eagles (21.5 days on average) was intermediate between that of southeast and northeast Canada eagles (Figure 1, Table 1).

Within-individual and among-individual variation, repeatability of migration start and end dates, and duration differed between seasons (Figure 2). Among-individual variation in the start and end of boreal autumn migration was 2–8 times greater than for boreal spring migration, depending on the region (Figure 2). Repeatability of boreal autumn migration start date in northeast Canada (0.33) was half the average for boreal spring start date and end date in the same region (0.76 and 0.78, respectively; Figure 2). Within-individual variation was 2–4 times higher but not significantly different for boreal autumn migration (within-individual variation departure date: 60.8 ordinal date^2) than for boreal spring migration (within-individual variation departure: 129.7 ordinal date^2; within-individual variation arrival: 241.4 ordinal date^2; Figure 2A). In southeast Canada, the repeatability of start and end dates of boreal spring migration appeared higher ($r = 0.79$, 0.85, respectively) than start and end dates of boreal autumn migration ($r = 0.34$, 0.41, respectively), but these differences were not significant different across seasons (Figure 2). Within-individual variation in southeast Canada was 7–11 times higher for boreal autumn migration (within-individual variation departure: 268 ordinal dates^2; within-individual variation arrival: 244 ordinal dates^2) than boreal spring migration (within-individual variation departure: 22.98 ordinal dates^2; within-individual variation arrival: 34.91 ordinal dates^2) creating this significant difference in within-individual variation between seasons (Figure 2A).

In Alaska, the trend was opposite, with repeatability of boreal autumn migration dates four times higher than repeatability of the end date of boreal spring migration (Figure 2). Among-individual variation in the end of boreal spring migration was low relative to the other regions (Alaska among-individual variation: 9.16; Figure 2B). Repeatability of boreal spring migration end date was also 5 times lower for Alaskan eagles than eagles from both eastern regions (Figure 2C; Supplementary Material Table 1). However, among- and within-individual variation of Alaskan boreal spring migration dates fell between 9.16 and 49.76 ordinal date^2, substantially lower than that of eastern eagles (northeastern: 60.77–412.5 ordinal date^2; southeastern: 132.82–412.5 ordinal date^2; Figure 2A-B; Supplementary Material Table 1). For wintering latitudes, repeatability values were high for all breeding regions, with r = 0.94 (95% CI: 0.86–0.98) for Alaska, r = 0.88 (95% CI: 0.61–0.96) for southeast Canada, and r = 0.92 (95% CI: 0.84–0.96) for northeast Canada (Supplementary Material Table 1). For the duration of migration, repeatability values averaged in the middle range from 0.21 to 0.65 with no significant differences across seasons or regions (Figure 2D).

Environmental Conditions

Eagles responded to variation in the average temperatures and maximum snow depths by changing when and where they migrated. Eagles departed from their wintering grounds ~10 days later when the average temperature was warmer and snow depth was deeper than the decadal average at the wintering grounds (Table 1 and Figure 3). Eagles also arrived ~10 days earlier at the breeding grounds when temperatures were colder than the decadal average at the breeding grounds (Table 1 and Figure 3). Eagles left the breeding grounds ~20 days earlier when average temperatures were warmer and snow depth on the breeding grounds was higher than the decade average at the breeding ground (Table 1 and Figure 4). Wintering latitude was ~1° lower in years with the warmer temperatures on the wintering grounds (Table 1).

DISCUSSION

Consistency is a useful indicator of the capacity of populations to cope with environmental changes (Wolak et al. 2012). While previous migration consistency studies on raptor species have focused on the population or individual levels (Vardanis et al. 2016, McCrary et al. 2019, Sugasawa and Higuchi 2020), we show that, among Golden Eagles in 3 different regions of North America (i.e., potential subpopulations), consistency of migration phenology changes with seasons and regional conditions. Our measures of consistency (i.e., repeatability and within- and among-individual variations) showed a wide range of values among regions and seasons, indicating differences in migratory strategies. Our results support our first hypothesis that migration phenology in Golden Eagles is seasonally consistent. Specifically, boreal spring migrants showed the lowest within-individual variation in timing and the highest consistency for eagles breeding in 2 regions: northeast and southeast Canada. We rejected our second hypothesis that regional consistency of migration phenology increased with migratory distances and breeding latitudes. Consistency differed between Alaskan and eastern Canadian eagles, but not between northern breeders and southeastern Canadian eagles, as expected. Additionally, seasonal and regional differences were present only in migration start and end dates, not in duration or with wintering latitude. Our results also did not support our third hypothesis that the timing and duration of migration would be correlated with optimal environmental conditions. Instead, we found the opposite pattern: warmer temperatures at the wintering or breeding grounds delayed the start and end of boreal spring migration and advanced the start of boreal autumn migration. We did find, however, that greater snow depth on the wintering grounds delayed migration start date. Overall, Golden Eagles in North America exhibited a diversity of migratory strategies at both regional and seasonal levels. In the following section, we discuss potential features and correlates of the observed differences.

Seasonal Differences

Seasonal differences in migratory behavior are common for many raptor species (Bildstein 2006, López-López et al. 2014, Watson et al. 2018, Phipps et al. 2019, Sugasawa and Higuchi 2020) and often are thought to be due to the different drivers (reproduction and survival) during the boreal spring vs. boreal autumn (McNamara et al. 1998). We expected consistency of migration phenology in Golden Eagles to reflect these relationships (Newton 2008, Dingle 2014) as observed in many empirical studies (e.g., McNamara et al. 1998, Alerstam et al. 2006, Conklin et al. 2013). We found a higher consistency in the timing of boreal spring migration than in boreal autumn migration for eastern Canada breeders. We also observed among-individual variation in boreal autumn migration phenology that was two and sometimes eight times greater than for boreal spring migration. For raptors, seasonal differences in consistency of migration phenology have previously been reported for Osprey (*Pandion haliaetus*; Alerstam et al. 2006) and Oriental Honey Buzzard (*Pernis ptilorhynchus*; Sugasawa and Higuchi 2020), while two other studies did not find such a pattern for Eurasian Marsh Harriers (*Circus aeruginosus*) and Egyptian Vultures (*Neophron percnopterus*; López-López et al. 2014, Vardanis et al. 2016). Osprey showed higher variation in migration phenology in boreal autumn compared to boreal spring (Alerstam et al. 2006), but this was not reflected in repeatability values (Vardanis et al. 2016). In fact, consistency of migration phenology does not seem to follow a seasonal pattern across raptor species from similar breeding regions. Most of these studies, including ours, did not monitor breeding success. Breeding phenology and success affects migration phenology as the ending of the breeding season varies among individuals (Maynard and Davoren 2018, Sur et al. 2019). With this information included, other studies may find trends similar to those we found when assessing seasonal consistency. Yet, the conflicting results found in the literature and the fact that, in our study, the expected trend was only observable in eastern Canada suggests that the effects of seasonal features (i.e., survival and/or reproduction) might change across breeding region and populations. Following the breeding effort and success of tracked individuals could be a future avenue to determine how breeding effort and success modulate consistency of migration phenology.

Regional Differences

The regional differences in consistency of Alaskan and eastern Canadian eagles did not, however, follow our hypothesis on regional consistency of migration timing and duration. We expected northern breeders to have lower consistency than breeders from southeast Canada because of their longer distance migration. However, southeastern Canadian eagles had repeatability values that were not significantly lower than either Alaskan or northeastern Canadian eagles. Both eastern regions had repeatability values significantly higher than Alaska for boreal spring migration. Our results suggest that migration distance is not a primary factor determining consistency in migration phenology as measured at a continental scale. Short-distance migration is not considered costly (e.g., Conklin et al. 2017, Brown et al. 2021) and Golden Eagles use many strategies to lower those costs (Duerr et al. 2012, Katzner et al. 2015). Therefore, the difference in energetic costs of migration implied with migratory distance might not be high enough to affect migratory consistency for Golden

Eagles.

Breeding region was also related to differences in migration phenology. Eagles from both eastern regions followed our prediction of seasonal consistency, while Alaskan eagles showed an opposite trend. Similar patterns in migration consistency have been observed in passerines such as Hoopoes (*Upupa epops*; van Wijk et al. 2016), Eurasian Woodcock (*Scolopax rusticola*; Tedeschi et al. 2019), and Great Reed Warbler (*Acrocephalus arundinaceus*; Hasselquist et al. 2017). Van Wijk et al. (2016) suggested that Hoopoes respond to environmental conditions dictating food availability in boreal spring, resulting in high consistency. In North America, eastern Golden Eagles are thought to breed in poorer quality habitats relative to western populations (Miller et al. 2017). In Alaska, Golden Eagles breed in habitats with a variety of prey, such as Arctic ground squirrels (*Urocitellus parryii*), ptarmigans (*Lagopus* ssp.), and snowshoe hares (*Lepus americanus*). These last two prey exhibit strong population cycles and Arctic ground squirrels are not present in eastern Canada (McIntyre and Adams 1999, McIntyre and Schmidt 2012, Herzog et al. 2019). While diet studies in eastern Canada are rare and mostly based on observations, Golden Eagles in this region are believed to forage more heavily on birds (Herzog et al. 2019), although they also prey on caribou calves (Anctil et al. 2019), carrion (Fitzgerald et al. 2013), and potentially snowshoe hares (Katzner et al. 2020). Tracking these differences in prey availability may be a research avenue to decipher how the consistency of migration schedule is tailored with environmental conditions in breeding regions.

Golden Eagles in Alaska and eastern Canada might also differ genetically. Eagles breeding in Alaska are part of the North American western population, a geographically and genetically distinct population from eastern Canada (Kochert et al. 2002a, Doyle et al. 2016, Katzner et al. 2020). Because differences in consistency could ultimately be genetically driven (Nussey et al. 2007, Danchin et al. 2012), we hypothesize that this can be the case for the observed differences between eastern and western populations. This could also support the lower among- and within-individual variations, sometimes tenfold lower observed in Alaskan eagles, which suggest that overall Alaskan eagles are more consistent as a population than eastern eagles. Plasticity is the result of environmental and genetic interactions (Nussey et al. 2007, Danchin et al. 2012) and to fully untangle their involvement in consistency levels, further studies against other genetically distinct population from similar habitats would be necessary.

Flexible Migratory Strategies

We observed differences not only in consistency of migratory characteristics, but also in migratory decisions. Indeed, three individuals in southeast Canada (27% of tracked eagles in the region) used a flexible migratory strategy by switching from residents to migrants from year to year. These eagles wintered within their breeding territory on several separate years, while migrating to northeast USA (e.g., Maine, Vermont, New York, and Pennsylvania) in other years. Yet, the eastern North American population is considered entirely migratory (Katzner et al. 2020). A few observations of Golden Eagles have been previously reported in southern Québec and central Ontario during the winter (Todd 2000, ebird 2017), but distinction between a local breeder or a northern migrant could not be confirmed.

As a facultative migrant species, individual Golden Eagles can choose a life-long residency strategy, which is observed in western North America (Watson 2010, Katzner et al. 2020). Reported occurrences of flexible individual migrants on a year-to-year basis by

Golden Eagles or other raptors are rare (Holte et al. 2016, Watson et al. 2018, McCrary et al. 2019). In North America, a flexible migration strategy was observed recently by resident Red-tailed Hawks (*Buteo jamaicensis*) that migrated in a particularly dry year (McCrary et al. 2019) and for Ferruginous Hawks (*B. regalis*), where 2% of the population did not migrate for 1 or 2 winters with a peak abundance in prey in the breeding region (Watson et al. 2018). In Finland, most adult Golden Eagles winter in the breeding region, whereas subadults migrate south (Watson 2010), suggesting that residency in this population is based on social dominance over resources. In southeast Canada, habitats thought to be of lower quality (Miller et al. 2017) may only support a few individuals capable of covering the costs of residency in certain years (Watson 2010, Winger et al. 2019). In late fall, eagles in southeast Canada feed on carrion from hunting and trapping (Katzner et al. 2012, Fitzgerald et al. 2013), which could account for the variability in residency between years. Evidence of flexible migration strategy does confirm that, conditions allowing, staying in the breeding area is more advantageous for reproduction than migrating, and that individual eagles have the potential to become complete residents if winter conditions were to change to provide more food (Watson 2010, Shaw and Couzin 2013, Zúñiga et al. 2017).

Influences of Environmental Conditions

Most studies of raptor migration report a delay in boreal autumn migration and an advance in boreal spring migration with warmer air temperatures at breeding sites or migration flyways (Gienapp et al. 2007, Jaffré et al. 2013, Sullivan et al. 2016, Therrien et al. 2017). Although mostly based on migratory counts (and hence without individual monitoring), such response to changing temperatures would result in a longer breeding area residency time in warm years, a trend even more pronounced for short-distance migrants (Tøttrup et al. 2010, Usui et al. 2017). In contrast, our results suggest an opposite trend, whereby eagles arrived earlier to the breeding grounds when air temperatures at arrival were colder and left the breeding grounds earlier when air temperatures at departure were warmer than the decadal average. Such eagle behavior suggests that warmer years would lead to shorter breeding area residency time.

We used start and end dates at the individual level, rather than standardized counts of migrating birds. Counts are designed to evaluate population-level patterns (e.g., Therrien et al. 2017), often include immature animals that usually migrate later than adults (Kjellén 1994, Mueller et al. 2003, Miller et al. 2016), and could lead to different inferences about migration phenology. Indeed, Gill et al. (2013) found that changes in migration phenology in shorebirds were explained by first time migrants whereas, similar to our results, adults were highly consistent. Other external conditions, such as wind (Calvert et al. 2009, Eisaguirre et al. 2018), competition for food (Watson et al. 2018), body condition (Bearhop et al. 2004), and breeding effort (Sur et al. 2019) could also influence the timing of adult migration in adults. In our system, snow precipitation can increase in warm springs and suggests that Golden Eagles delay start of boreal spring migration when maximum snow depth is higher than the decadal average on their winter grounds. Collecting phenology data from individuals is therefore essential for understanding how environmental and ecological factors shape migration strategies.

Conclusion

The consistency of migration phenology in Golden Eagles varies across North America and with temperature prior to the start of spring and autumn migration. We could, therefore, expect changes in migratory phenology to environmental change to vary across those gradients. For instances, populations with lower repeatability values such as in Alaska will likely respond faster than the Eastern North American population to an increase in temperatures. Because the eastern North American population of Golden Eagles is endangered or of conservation concern in several provinces and states (Katzner et al. 2012), changes in migration phenology and longer breeding area residency time may increase the ecological importance of breeding ground habitat for this population, especially with an increased residency behavior. Our study emphasizes how variation in migration phenology and consistency across breeding regions and seasons adds to the challenge of species conservation and also suggests that such variations can give populations and individuals the capacity to acclimate to environmental changes.

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Ethics statement: Use of Golden Eagles for this research was approved by the West Virginia University Institutional Animal Care and Use Committee (IACUC): protocol #11-0304 for eagles in the eastern USA, by the MFFP: CPA-FAUNE 20-08; CPA-FAUNE 19-05; CPA-FAUNE 18-05; CPA-FAUNE 2017-08; CPA-FAUNE 14-35, for eagles in Québec, Canada and by the ADFG IACUC (approval number is 2013-036) with USGS banding permit is 22395 for Alaska.

Author contributions: L.D.M. conceived the study. L.D.M. drafted the manuscript and analysed the data with feedback from N.L.; J.F.T, J. L., and N. L. supervised the work and research. J.L, T.B, T.A.M., T.K., S. S., R. S., and J. C. collected and provided data and gave feedbacks on the study and the manuscript. All authors approved the submission of the manuscript.

Data availability statement: Additional information and figures supporting this article have been uploaded as part of the Supplementary Material. However, the Golden Eagles we study are both protected and persecuted, within the USA and globally. Nest locations are one of the primary sites of persecution of eagles, and the raw biotelemetry data we analyzed show those nest locations. The Québec Government prohibits the release of sensitive wildlife data including locations of the Golden Eagle that is protected under the Act respecting threatened or vulnerable species (E-12.01). The State of Alaska also prohibits the release of sensitive wildlife locations including eagle nests and territories per Alaska Statute 16.05.815(d). Consequently, we do not make data publicly available. Data is available for research upon request to authors. Computer code is available at Maynard et al. (2022).

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Figure 1. Spatial and temporal extent of 321 Golden Eagle migration tracks from 2007 to 2020 in North America with mean wintering latitudes (bottom right), breeding latitudes (middle right), and migration distance (top right) by breeding regions. For migration schedule (top), lines each side of the mean date is the standard error.

Figure 2. Within-individual variation (**A**), among-individual variation (**B**), and repeatability values (*r*) ([**C**] start and end ordinal dates, [**D**] duration) by breeding regions and seasons. Whiskers show 95% confidence intervals and violon plot of parametric bootstraps for three migration characteristics. The earliest day is the ordinal date of the earliest departure among migrants. Asterisks indicate significant difference at $\alpha = 0.05$ (no overlap between 95% CI) between 2 regions or migration characteristics.

Figure 3. Boreal spring migratory phenology and weather/abiotic conditions at the departure/arrival site. Significant smoothed relationships between snow depth (mm) and temperature (°C) and boreal spring migration start **(A, B)** and end **(C)** dates derived from general additive mixed models (see Table 1).

Figure 4. Boreal autumn migratory phenology and weather conditions at the departure/arrival site. Significant smoothed relationships between temperature (°C) and boreal autumn migration start **(A)** and end **(B)** dates derived from general additive mixed models (see Table 1).

Table 1. Generalized additive models with gaussian distribution of the migration characteristics by seasons from 83 Golden Eagles in North America, 2007-2020 (n=321 tracks). Fixed predictors are the sex, breeding region, and smoothed predictors are total precipitation, average temperature, and snow cover at departure; edf = estimated degree of freedom. Bold indicates significant predictors.

Model		Parametric fixed effect					Approximate significance of smooth terms				R^2	*N*
Season			Estimate	SE	*F*	*P* value		edf	F	*P* value		
Winter	Wintering latitude	Intercept	39.3	0.82		<0.001	Precipitation	3	3.01	0.11	0.56	132
		Sex	–1.90	0.88	4.70	0.03	**Max snow depth**	**1**	**5.54**	**0.02**		
		Breeding regions	**9.96**	**0.89**	**62.090**	**<0.001**	Average temperature	1	0.120	0.73		
Boreal spring Migration	Departure date	Intercept	77.75	2.53		<0.001	**Average temperature**	**4.47**	**4.07**	**0.003**	0.19	1369
		Sex	–3.86	2.68	2.88	0.06	**Max snow depth**	**1**	**4.76**	**0.03**		
		Breeding regions	**–12.22**	**3.8**	**6.13**	**0.003**						
		Precipitation	0.76	0.97	0.62	0.43						
	Duration	Intercept	3.4	0.11		<0.001	**Max snow depth**	**2.1**	**2.82**	**0.05**	0.4	169
		Sex	–0.18	0.11	1.52	0.22						
		Breeding regions	**–1.15**	**0.16**	**26.52**	**<0.001**						
		Precipitation	0.00	0.05	0.01	0.94						
		Average temperature	–0.03	0.03	0.55	0.46						
	Arrival date	Intercept	109	3.68		<0.001	**Average temperature**	**3.4**	**14.96**	**<0.001**	0.47	168
		Sex	–5.84	3.52	1.38	0.21						
		Breeding regions	**–34.10**	**5.06**	**25.28**	**<0.001**						
		Precipitation	0.1	1.26	0.01	0.94						
		Max snow depth	0.07	0.07	1.2	0.27						

Boreal autumn Migration	Departure date	Intercept	284.6	4.33		**<0.001**	0.59	132
		Sex	2.58	3.49	0.55	0.46		
		Breeding regions	**34.5**	**4.42**	**35.67**	**<0.001**		
		Precipitation	–1.2	1.66	0.5	0.48		
		Average temperature	**–4.7**	**0.60**	**61.0**	**<0.001**		
		Max snow depth	**–0.1**	**0.06**	**5.0**	**0.03**		
	Duration	Intercept	49.1	5.59			0.2	132
		Sex	4.15	4.54	0.84	0.36		
		Breeding regions	**–25.29**	**5.78**	**10.33**	**<0.001**		
		Precipitation	2.99	2.12	1.98	0.16		
		Average temperature	1.32	0.76	3.04	0.08		
		Max snow depth	–0.01	0.07	0.02	0.90		
	Arrival date	Intercept	333.0	5.97		<0.001	0.11	132
		Sex	4.58	6.15	5.6E–01	0.46		
		Breeding regions	–11.42	6.26	3.02	0.05		
		Precipitation	0.29	2.33	0.02	0.90		
		Average Temperature	**–3.52**	**0.67**	**27.26**	**<0.001**		
		Max Snow Depth	1.45	1.91	0.58	0.45		

Figure 1

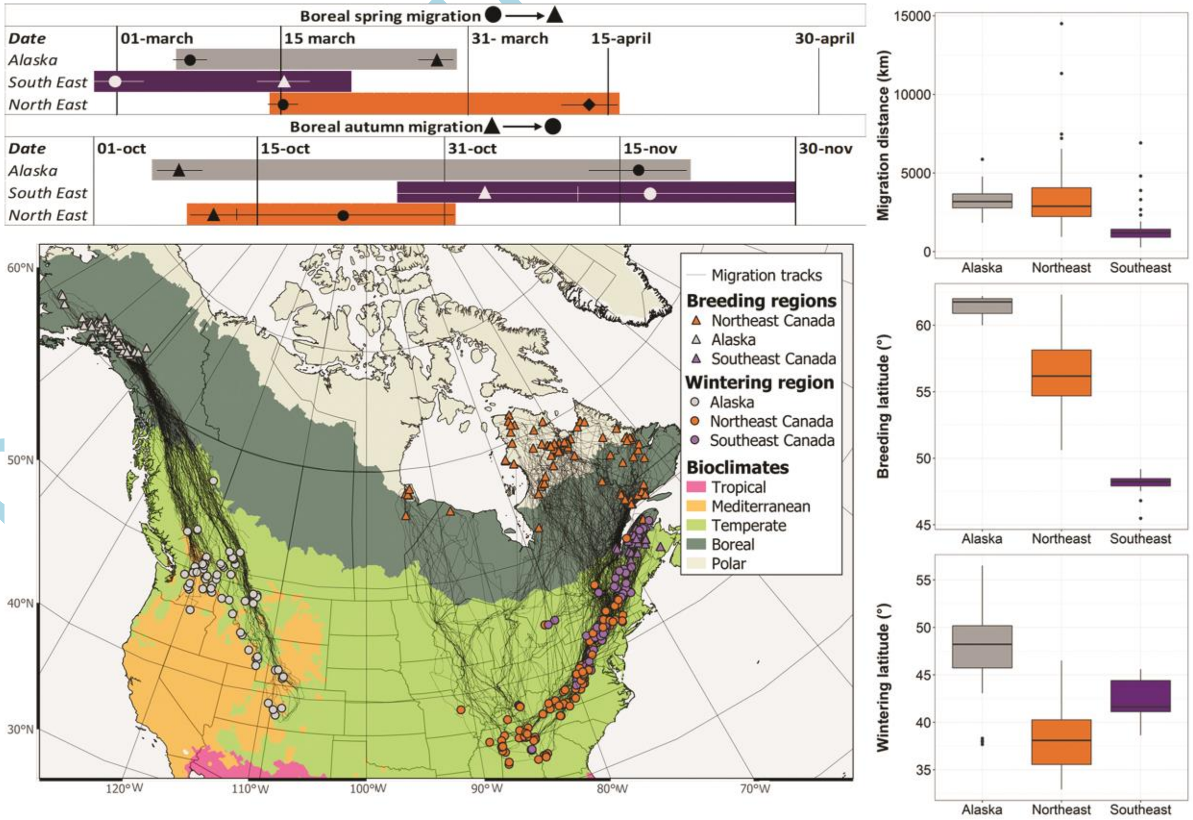

Boreal spring migration ● ⟶ ▲
Date
01-march
15 march
31- march
15-april
30-april
Alaska
South East
North East
Boreal autumn migration ▲ ⟶ ●
Date
01-oct
15-oct
31-oct
15-nov
30-nov
Alaska
South East
North East
60°N
50°N
40°N
30°N
120°W
110°W
100°W
90° W
80°W
70°W
Migration tracks
Breeding regions
Northeast Canada
Alaska
Southeast Canada
Wintering region
Alaska
Northeast Canada
Southeast Canada
Bioclimates
Tropical
Mediterranean
Temperate
Boreal
Polar
Migration distance (km)
15000
10000
5000
0
Alaska
Northeast
Southeast
Breeding latitude (°)
60
55
50
45
Alaska
Northeast
Southeast
Wintering latitude (°)
55
50
45
40
35
Alaska
Northeast
Southeast

Figure 2

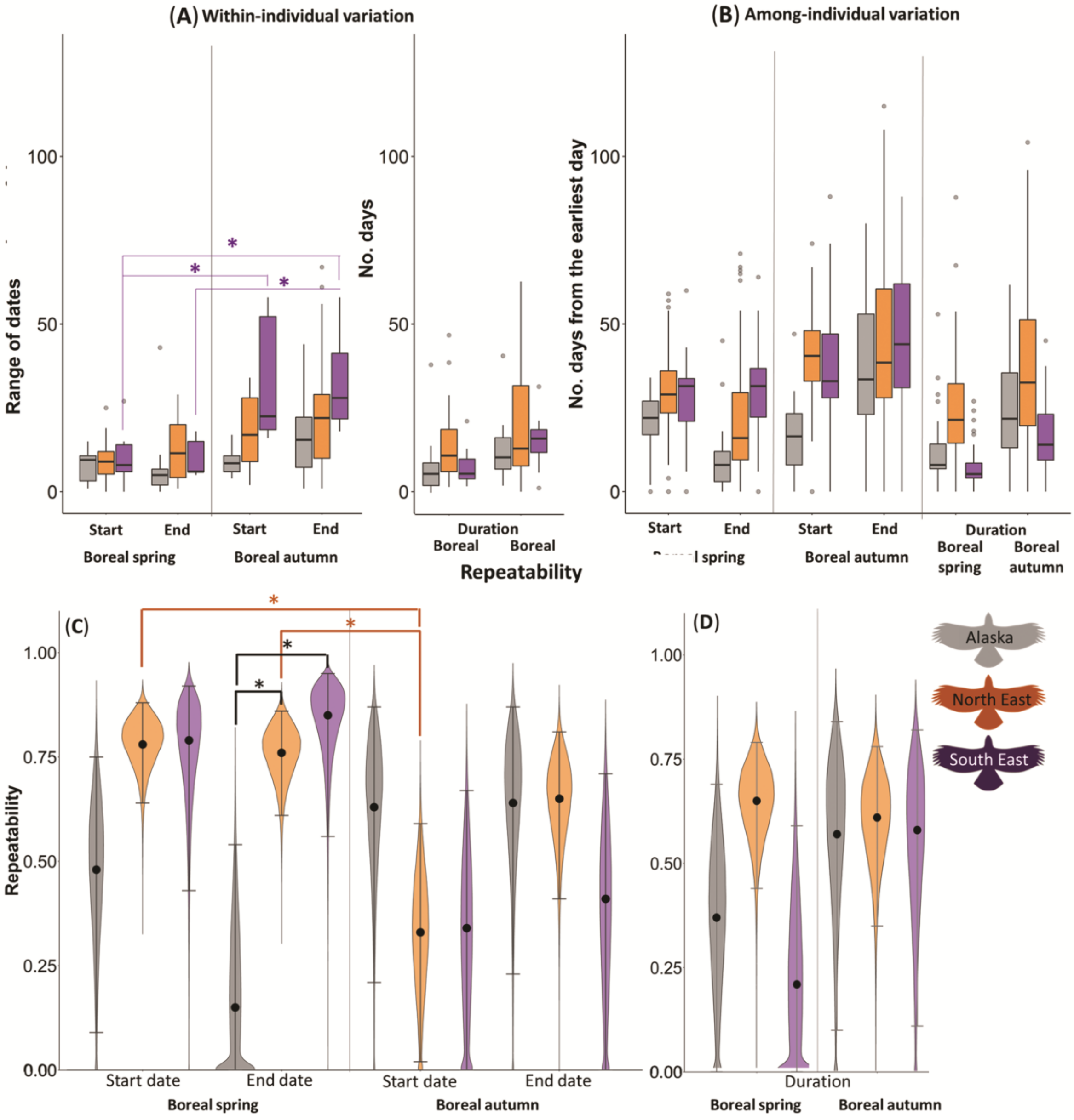

(A) Within-individual variation
(B) Among-individual variation
Range of dates
No. days
No. days from the earliest day
100
50
0
*
*
*
Start
End
Start
End
Boreal spring
Boreal autumn
Duration
Boreal
Boreal
Repeatability
Start
End
Start
End
Boreal spring
Boreal autumn
Duration
Boreal spring
Boreal autumn
(C)
Repeatability
1.00
0.75
0.50
0.25
0.00
*
*
*
*
Start date
End date
Start date
End date
Boreal spring
Boreal autumn
(D)
1.00
0.75
0.50
0.25
0.00
Duration
Boreal spring
Boreal autumn
Alaska
North East
South East

Figure 3

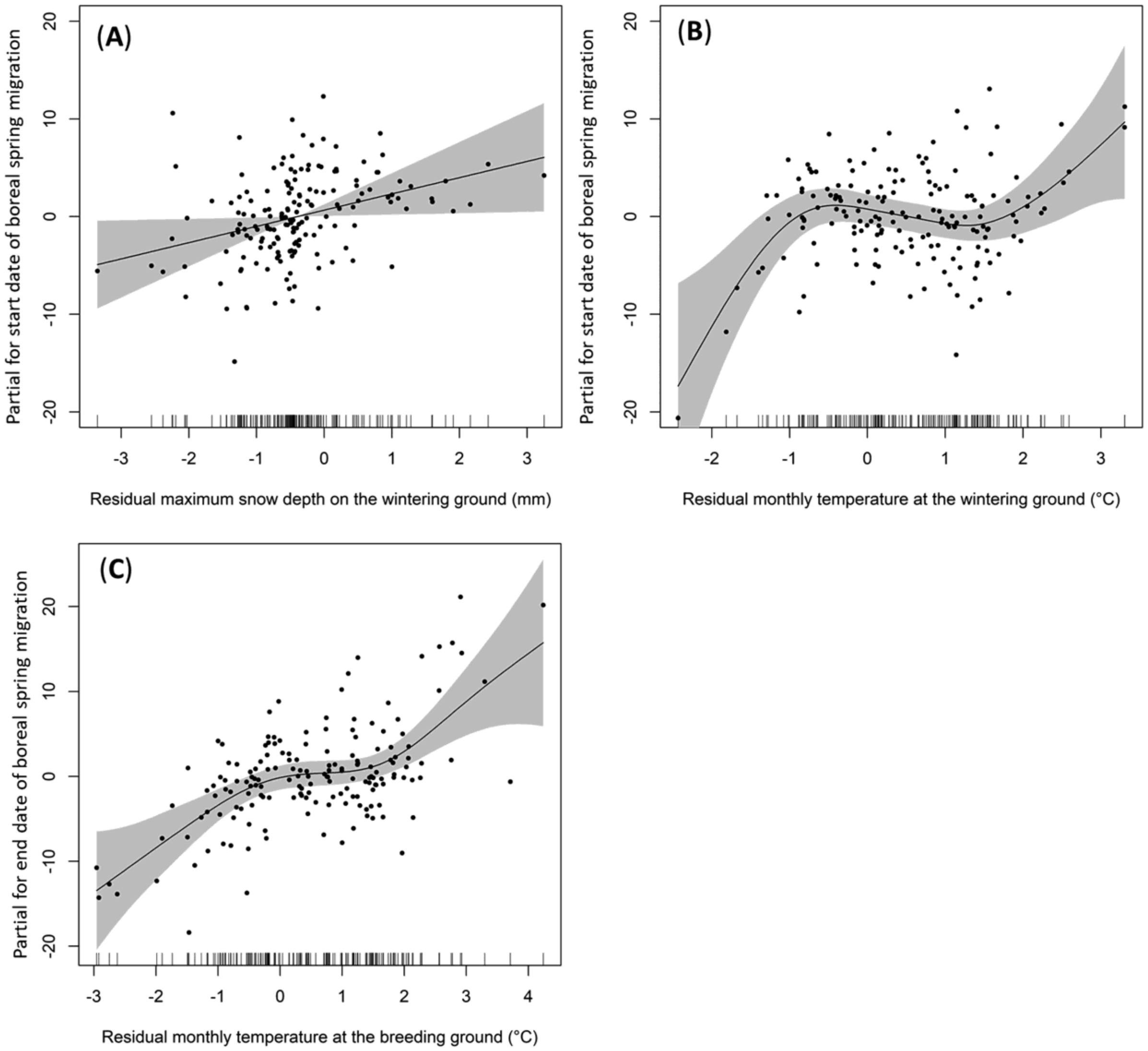
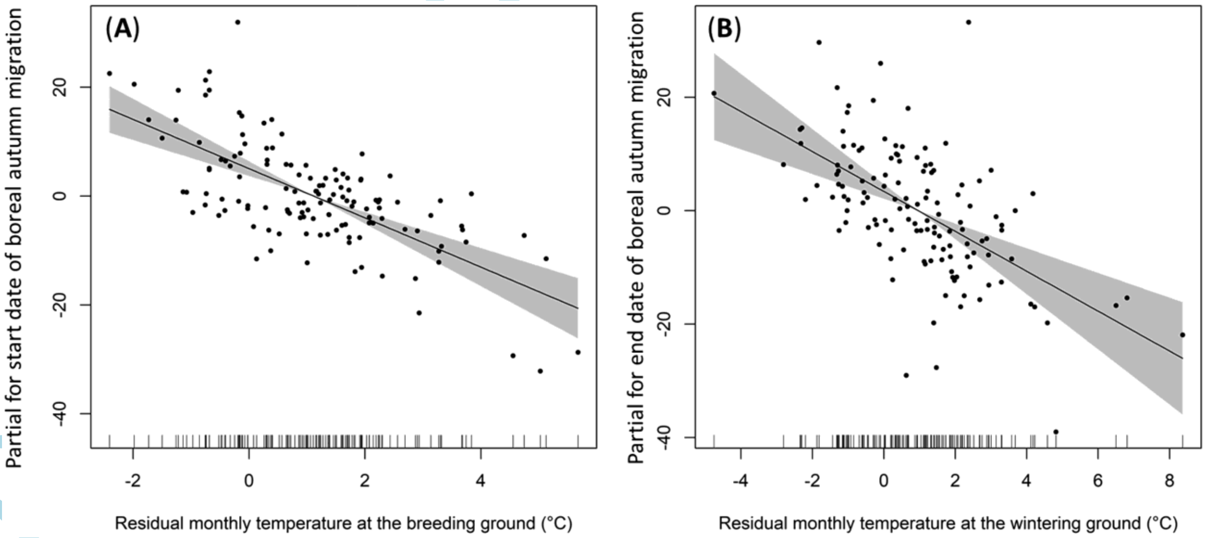

(A)
Partial for start date of boreal spring migration
20
10
0
-10
-20
-3
-2
-1
0
1
2
3
Residual maximum snow depth on the wintering ground (mm)
(B)
Partial for start date of boreal spring migration
20
10
0
-10
-20
-2
-1
0
1
2
3
Residual monthly temperature at the wintering ground (°C)
(C)
Partial for end date of boreal spring migration
20
10
0
-10
-20
-3
-2
-1
0
1
2
3
4
Residual monthly temperature at the breeding ground (°C)

Figure 4


(A)
Partial for start date of boreal autumn migration
20
0
-20
-40
-2
0
2
4
Residual monthly temperature at the breeding ground (°C)
(B)
Partial for end date of boreal autumn migration
20
0
-20
-40
-4
-2
0
2
4
6
8
Residual monthly temperature at the wintering ground (°C)