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Original Articles

Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration

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ABSTRACT

Climate change has been shown to shift the seasonal timing (i.e. phenology) and distribution of species. The phenological effects of climate change on living organisms have often been tested using first occurrence dates, which may be uninformative and biased. More rarely investigated is how different phases of a phenological sequence (e.g. beginning, central tendency and end) or its duration have changed over time. This type of analysis requires continuous observation throughout the phenological event over multiple years, and such data sets are rare. In this study we examined the impact of temperature on long-term change of passage timing and duration of the spring migration period in birds, and which species' traits explain species-specific variation. Data used covered 195 species from 21 European and Canadian bird observatories from which systematic daily sampling protocols were available. Migration dates were negatively associated with early spring temperature and timings had in general advanced in 57 years. Short-distance migrants advanced the beginning of their migration more than long-distance migrants when corrected for phylogenic relatedness, but such a difference was not found in other phases of migration. The advancement of migration has generally been greater for the beginning and median phases of migration relative to the end, leading to extended spring migration seasons. Duration of the migration season increased with increasing temperature. Phenological changes have also been less noticeable in Canada even when corrected for rate of change in temperature. To visualize long-term changes in phenology, we constructed the first multi-species spring migration phenology indicator to describe general changes in median migration dates in the northern hemisphere. The indicator showed an average advancement of one week during five decades across the continents (period 1959–2015). The indicator is easy to update with new data and we therefore encourage future research to investigate whether the trend towards longer periods of occurrence or emergence in spring is also evident in other migratory populations. Such phenological changes may influence detectability in monitoring schemes, and may have broader implications on population and community dynamics.

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1. Introduction

A rapidly changing climate is challenging some species which have to deal with altered environmental conditions (Walther et al., 2002; Parmesan, 2006; Penuelas et al., 2013; IPCC, 2014). Species have shown changes in their seasonal timing (i.e. phenology), distribution and abundance in response to climate change (Parmesan, 2006; Chen et al., 2011; Stephens et al., 2016). Probably the most prominent and widespread change observed in nature is advancement of spring phenology in seasonal habitats (Sparks and Menzel, 2002; Lehikoinen and Sparks, 2010). This applies to various taxonomic groups, such as plants (Menzel and Fabian, 1999; Cleland et al., 2007; Thackeray et al., 2010), invertebrates (Thackeray et al., 2010), and vertebrates both in terrestrial and aquatic ecosystems (Beebee, 1995; Crick et al., 1997; Thackeray et al., 2010).

Among all taxonomic groups, spring arrival phenology of migratory birds has been most intensively studied (Vähätalo et al., 2004; Rainio et al., 2006; Jonzén et al., 2006; Gordo, 2007; Pulido, 2007; Lehikoinen and Sparks, 2010; Knudsen et al., 2011; Tarka et al., 2015; Polakowski et al., 2018), due to large quantities of readily available citizen science data. However, a majority of the time series concern first arrival dates (FAD), which are known to be sensitive to variation in population size and observer effort, all difficult to control for in analyses (Mills, 2005; Miller-Rushing et al., 2008; Lindén, 2011). Moreover, FADs alone are cryptic measures for the start of migration, with no information about how far the start of migration has actually proceeded. A better, but also more data intensive approach – applied much more rarely – is to investigate changes in the distribution of migration (different phases such as beginning, median and end of migration period) (Lehikoinen and Sparks, 2010). Such analyses require data with continuous observation coverage throughout the entire season over multiple years.

Given that the early (beginning phase) and late (end phase) migrants within the same populations can respond differently to climate (Vähätalo et al., 2004; Rainio et al., 2006), it has been suggested that the duration of the migration season may change over time (Knudsen et al., 2011). For example, a recent case study from Scotland showed that 13 long-distance migrants (hereafter LDMs) have advanced the onset of their spring migration (10th percentile of the distribution) more than they had postponed the end of migration (90th percentile), leading to a longer duration of the total spring migration period (Miles et al., 2017). However, it is not well known how common or consistent such patterns are among other migratory species across the globe. Importantly, studies investigating how life-history traits explain between-species patterns in the distribution of migration have rarely controlled for phylogenetic relatedness – i.e., patterns may be more similar in closely related species (Burns and Strauss, 2011) and should not necessarily be treated as statistically independent observations.

Concerning various life-history traits, there has been a long ongoing debate about potential differences in between tropical LDMs and short-distance migratory species (hereafter SDMs). Some studies have suggested that SDMs would have advanced their timing of migration more than LDMs (Rubolini et al., 2007; Usui et al., 2017), whereas other studies have not found such pattern (Jonzén et al., 2006; Knudsen et al., 2010). SDMs may be better able to predict the conditions in the breeding areas than LDMs, since they winter much closer to the breeding grounds (Usui et al., 2017). Climate change may increase the need for additional stop-overs in LDMs, which can lead to delayed timing of spring migration (Howard et al., 2018). Furthermore, the potential of advancing spring migration can also be limited in LDMs because of shorter stop-over durations compared to SDMs (Schmaljohann and Both, 2017).

Bird populations are considered as good indicators of environmental change (Gregory et al., 2005; Gregory, 2006; Stephens et al., 2016), which also applies to phenology. The majority of bird species are migratory, which allow for investigations of the timing in their seasonal movements (Newton, 2008). For instance, such investigations can be based on (relatively standardized) bird migration data collected on a regular basis at bird observatories located in different parts of the world (Lehikoinen and Sparks, 2010).

The aim of this study is to examine general patterns of change in the different phases of avian spring migration. We combined long-term datasets from 21 bird observatories in northern Europe and Canada of 195 species. First, we investigate the dependence of phenological changes on temperature and whether a potential rate of change varies throughout the migration season (start, median and end phase of the migration, hereafter early, median and late phases, respectively), which could ultimately translate into changes in the overall duration of the spring migration period. We hypothesize that the early and median phases would show stronger response to temperature and faster advances in phenology than the late phase (Rainio et al., 2006; Jonzén

Table 1
Study sites, study periods, number of study species, data collection methods and reference describing data collection methods. In addition, rate of spring temperature change (mean ± SE; °C) is reported for each observatory site. Significant temperature changes according to linear regression analyses during the study periods of the observatories are shown in bold. Variation in monitored number of species depends on protocol of the observatory (e.g. method and monitoring period) and local conditions. Stations including both ringing and daily counts combine numbers using standardized methodology.

Observatory	Years	N	Methods	Reference	Temp change
Beaverhill, Canada	1992–2013	2	trapping, counts	Hussell and Ralph (2005)	−0.102 ± 0.087
Bruce Peninsula, Canada	2000–2014	16	trapping, counts	Hussell and Ralph (2005)	−0.047 ± 0.139
Calf of Man, UK	2005–2014	8	trapping	Archer et al. (2010)	−0.020 ± 0.146
Falsterbo, Sweden	1980–2015	21	trapping	Roos and Karlsson (1980)	**0.060 ± 0.023**
Gedser, Denmark	2007–2015	9	trapping	www.Gedserfuglestation.dk	−0.118 ± 0.225
Gibraltar Point, UK	1975–2014	2	trapping	Archer et al. (2010)	**0.054 ± 0.013**
Hanko, Finland	1979–2012	112	trapping, counts	Vähätalo et al. (2004)	**0.061 ± 0.025**
Holme, UK	2005–2014	10	trapping, counts	Archer et al. (2010)	0.031 ± 0.176
Innis Point, Canada	1997–2014	8	trapping, counts	Hussell and Ralph (2005)	−0.008 ± 0.086
Jomfruland, Norway	1979–2014	60	trapping, counts	Ranke et al. (2011)	**0.060 ± 0.021**
Jurmo, Finland	1970–2015	46	trapping, counts	Vähätalo et al. (2004)	**0.049 ± 0.016**
Lista, Norway	1990–2015	66	trapping, counts	Ranke et al. (2011)	0.023 ± 0.035
Long Point, Canada	1961–2014	39	trapping, counts	Hussell and Ralph (2005)	**0.026 ± 0.013**
Lesser Slave Lake, Canada	1994–2014	5	trapping, counts	Hussell and Ralph (2005)	−0.075 ± 0.104
Ottenby, Sweden	1959–2015	30	trapping	Stervander et al. (2005)	**0.038 ± 0.011**
Pelee Island, Canada	2003–2013	31	trapping, counts	Hussell and Ralph (2005)	0.064 ± 0.141
Prince Edward Point, Canada	1995–2013	21	trapping, counts	Hussell and Ralph (2005)	0.099 ± 0.052
Ruthven Park, Canada	1998–2013	8	trapping, counts	Hussell and Ralph (2005)	0.055 ± 0.069
Rybachy Courish Spit, Russia	1959–2014	23	trapping	Sokolov (2006)	**0.044 ± 0.013**
Sundre, Sweden	1999–2014	8	trapping	Mellroth and Steinholtz (2013)	−0.001 ± 0.076
Thunder Cape, Canada	1995–2014	22	trapping, counts	Hussell and Ralph (2005)	0.024 ± 0.091

et al., 2006; Knudsen et al., 2011). This would also imply that the spring migration period would increase with increasing temperatures and be expanded overall (Miles et al., 2017). Second, we study whether there are differences in migration onset and duration. We hypothesize that short-distance migrants have advanced their phenology more than LDMs, since LDMs are more constrained to respond to changes in the breeding grounds. Third, if this is supported, we expect to observe a stronger increase in the duration of migration, especially in SDMs. Fourth, we point out any consistencies and spatial differences in the patterns of change in Europe and Canada. We predict that changes in the phenology are related to regional changes in temperature. Areas with a higher temperature increase are likely to have larger shifts in phenology. Fifth, we control for phylogeny in the trait analyses, since we predict that the patterns of change are not phylogenetically independent (Usui et al., 2017), acknowledging that existing evidence is controversial (Knudsen et al., 2011). Our final aim is to publish the first state indicator for bird migration phenology, which can be related to climatic changes in the environment, in particular climate change in the boreal and temperature zone of the northern hemisphere.

2. Material and methods

2.1. Phenology data

The data were collected at 21 bird observatories in northern Europe (12) and Canada (9), which had at least eight years of available data (Table 1, Table S1). The observatories were situated in the boreal and temperate climatic zones (Fig. 1). Because of the relatively northern location of the sites, individuals of a given species at a site are more likely to belong to the same population (Lehikoinen et al., 2017). At these observatories bird abundance data were systematically collected on a daily basis for at least eight years throughout spring migration, using either mist-net trapping (ringing data) and/or counts of migrating and staging birds. The data collection methodology used by each observatory is shown in Table 1.

We selected those species for analyses that had at least eight years of data and a minimum of 20 individuals per year (Vähätalo et al. 2004). Furthermore, we included only years for the species with a minimum observation coverage of 90% of the full migration season of the species i.e. 10% of observation days (count or ringing) could be missed (e.g. due to poor weather conditions or lack of observers). We calculated 5%, 50% (median) and 95% arrival dates (percentiles; Vähätalo et al. 2004) expressed as Julian dates (e.g., 1 = 1st January, 32 = 1st February) for each study species and each study year.

Altogether 195 species fulfilled the requirements and were included in the analyses. For each species, we report in Table S1 the migratory strategy (temperate SDM or tropical LDM; see Cramp et al., 1977–1994; Partners in Flight, 2017), the number of study years, and their phylogenetic structure (order, family and genus based on taxonomy of IOC version 7.3; Gill and Donsker, 2017).

2.2. Temperature data

We used HadCRUT4 temperature data available at http://www.cru.uea.ac.uk/data/ to calculate change in spring temperatures at each monitoring site during the years for which each site contributed data. The HadCRUT4 includes global monthly temperatures in 5° × 5° grids. We used the grid-point closest to each observatory and calculated site-specific temperature changes during the early spring months (March–April), using linear regression. Although the 5° grids are relatively coarse, we think that this describes the general climatic conditions in the observatory area since temperature is spatially strongly autocorrelated (e.g. Halkka et al., 2011; Lehikoinen et al., 2013) and arrival dates are rather influenced by large scale climatic patterns than local weather conditions (Pakanen, 2018). We also calculated the mean annual anomaly of temperatures (difference from the mean) for each site and year, and correlated those values with the annual migration dates of species.

Fig. 1. Locations of the study bird observatories in Europe and Canada.

2.3. Statistical analyses

We used linear mixed effects models with migration date quantile (5%, 50% or 95%) or duration of migration (95% quantile minus 5% quantile) as response variable. For each response variable, we used the following explanatory variables: i) temperature anomaly in a given area (Temp; a continuous variable), ii) centralized year (Year; a continuous variable to account for long-term trend, year 1987 set to 0), iii) migratory behaviour (Mig; categorical variable with two levels: SDM = 1 or LDM = 0; centralized by subtracting mean value of the variable from each observation) and iv) continent (Con; categorical variable with two levels: Europe = 1 or Canada = 0; also centralized), using both their main effects and their interactions. Centralizing all explanatory variables (including the categorical ones) facilitates the interpretation of general effects in presence of interactions (Schielzeth, 2010). In our case, the intercept, as well as the main effects of year, continent and migration represent general average effects for the whole data, rather than for a particular comparison group. There were no problems with collinearity between variables (Pearson's correlation coefficients were all below 0.5, e.g. temperature and year r = 0.34; Booth et al., 1994). All models included random effects to allow for site-specific intercepts, as well as species-specific intercepts and temporal trends (slopes of year). In addition, we tested for possible phylogenetic correlation in responses among species by comparing eight models with different combinations of random effects of phylogeny, using nested random effects of genus, family and order of the focal species. We first ran the full model with all potential phylogeny combinations (see Table S1), using REML as the objective function. Second, we ranked the models based on AIC (Burnham and Anderson, 2004) and used the random effect structure of the top ranked model for all further analyses. Third, we conducted separate analyses for different phases of migration (5%, 50% and 95% arrival dates) and the length of the migration period. For this third step we built 14 model combinations based on combinations of the fixed effects of year, migratory behaviour, continent and their interactions, and temperature without interactions (Tables S3–S6), again using the top ranked random effects structure. Last, we ranked these models based on AICc, using ML as the objective function. We did not consider more complex models within 2 ΔAIC values that were otherwise similar to a simpler but higher ranked model, but included uninformative parameter(s) sensu Arnold (2010). In these models the additional uninformative parameter(s) make the model more complex without adding any information to the model. In case of multiple competing models, we performed model averaging (Burnham and Anderson, 2004) using MuMIn package in R (Bartoń, 2018).

For the main analysis we used the functions lmer (package lme4; Bates et al., 2015) and lmerTest (package lmerTest; Kuznetsova et al., 2017) in R (version 3.4.1; R Core Team, 2017). The analysis were conducted separately for different phases of migration (5%, 50% and 95% arrival dates) and the length of the migration period. For all LMMs, visual inspection of residuals plots did not reveal obvious deviations from normality.

Last, we produced a phenology indicator by combining the information of the median arrival dates from all the observatories as a single index. We selected the median, as this is most robust to noisy data and best describes the trend of the overall population (i.e. how average individual in the populations are behaving). The index was constructed using a mixed effect model with annual arrival dates from 1959 onwards explained by year (as a factor variable to show the annual variation in the indicator), migration strategy and continent plus the interaction term between migration strategy and continent. Site and the top ranked structure for phylogeny were included as random effects. The fitted annual values of the model were standardized so that the year 1959 had value 0. We tested whether the trend of the indicator had any significant breakpoints using R function breakpoints (package strucchange; Zeileis et al., 2003), to test whether an increase in data towards the end of the study period resulted in a detectable change in trend.

3. Results

3.1. Temperature changes

Spring temperature (March through May) increased significantly at seven out of 12 European observatories since the early 1980s, but only one Canadian observatory showed a significant temperature change (Table 1). Canadian sites showed a significantly smaller temperature change than European sites (mean changes 0.004 and 0.024 °C per year for Canada and Europe, respectively, *t*-test, $P < 0.001$).

3.2. Migration dynamics

In all 5%, 50% and 95% arrival date models, the best phylogeny structure included family, genus and species, but not order (ΔAICs > 2; Table S2). This random structure was also used for duration models.

In the model selection of fixed effects, two models explaining the 5% arrival dates were within 2 ΔAIC units, but the second best and more complex model was omitted due to uninformative parameters (Arnold, 2010; Table S3). According to the best model, temperature advanced start of migration about -0.7 days $°C^{-1}$ and there was an additional significant advancement in time of -1.3 days in a decade. This advancement was c. 0.07 days in a decade greater in SDMs compared to LDMs (Table 2, Fig. 2). We found hardly any difference in the rate of advancement between Europe and Canada ($P = 0.09$). In general, SDMs migrated c. 3 days earlier than LDMs, and European SDMs migrated about 10 days earlier than Canadian SDMs (Table 2).

Two models ranged within 2 AICc units in both model selections explaining both median and 95% arrival dates. In both cases the second best and more complex model was omitted due to uninformative parameters (Arnold, 2010; Tables S4 and S5). Median migration dates were significantly negatively associated with temperature (-0.5 days $°C^{-1}$) and there was also a general advancement of ca -1.2 days in a decade. European migrants advanced their median dates -0.8 days in a decade faster than Canadian migrants. Short-distance migrants had on average 5 days earlier migration dates, but there was no difference in rate of advancement over time (Tables 3 and S4).

95% dates showed weakest, although still significant, responses to temperature (-0.2 days $°C^{-1}$) among all three migration phases, and there was also weak advancing trend in time (-0.4 days in a decade). 95% arrival dates have advanced faster among European species compared to Canadian species (-0.8 days in a decade; Tables 4 and S5, Fig. 2). In all 5%, 50% and 95% arrival dates, SDMs migrated in general earlier than LDMs in Europe, but not in Canada (Tables 3–5).

Five models were within 2 ΔAIC units explaining the duration of the migration period (Table S6). After model averaging, migration duration was significantly associated with temperature, year, continent and migration strategy. The spring migration period became longer with increasing temperature ($+0.45$ days $°C^{-1}$) and with time ($+1.1$ days in a decade). Migration periods were on average 12 days longer in Europe compared to Canada and 4 days longer in SDMs compared to LDMs (Table 5).

3.3. Migration phenology indicator

The spring migration phenology indicator showed that median migration dates in Europe and Canada have on average advanced about one week during five decades (Fig. 3). The trend is clear throughout the study period 1959–2015 without obvious breakpoints.

4. Discussion

Our results highlight the impact of temperature on spring migration phenology and shows that the strongest advances has occurred during the early and median phases of migration. In comparison, other similar studies found evidence of the strongest advances during the early phase of spring migration (Jonzén et al., 2006; Miles et al., 2017). Using the median as the input data is methodologically more robust and less noisy, and shows that a large part of the population is changing its migratory timing. This emphasizes the ecological implications of these changes.

All phases of the migration were negatively associated with the temperature supporting the idea that temperature change is a key driver of spring migration phenology. Furthermore, the indicator showed that median migration dates have advanced about one week in five decades. The phenology indicator currently covers sites mainly from the boreal and temperate zones in Northern Europe and Canada, and hence expanding spatial coverage of the study sites would enhance spatial representation (both latitudinal and longitudinal).

Low response to temperature and weak advancement of the latest migrants compared to early migrants have resulted in a general prolongation of the migration season, similar to the LDMs of the Scottish case study (Miles et al., 2017). Hence, extension of the migration period seems to be a consistent pattern for birds of the temperate and boreal zones in the northern hemisphere among both SDMs and LDMs. The results are well in line with earlier findings from North America showing that the whole winter-to-spring climate transition period has

Table 2
Parameter estimates (β ± SE) of the models explaining 5% migration dates based on the top ranked model (Table S3). SDMs and LDMs are short- and long-distance migrants, respectively. All explanatory variables were centralized to zero mean.

Variable	β ± SE	t	P
Intercept	110.7 ± 2.27	48.7	< 0.001
Temperature	−0.67 ± 0.02	−16.0	< 0.001
Year	−0.13 ± 0.02	−8.4	< 0.001
Continent (Europe compared to Canada)	−11.91 ± 3.27	−3.6	< 0.001
Migration (SDMs compared to LDMs)	−2.64 ± 1.42	−1.9	0.063
Year * Continent (Europe compared to Canada)	−0.05 ± 0.03	−1.7	0.087
Continent * Migration (European SDMs compared to others)	−10.32 ± 3.77	−2.7	0.007
Year * Migration (SDMs compared to LDMs)	−0.07 ± 0.03	−2.8	0.006

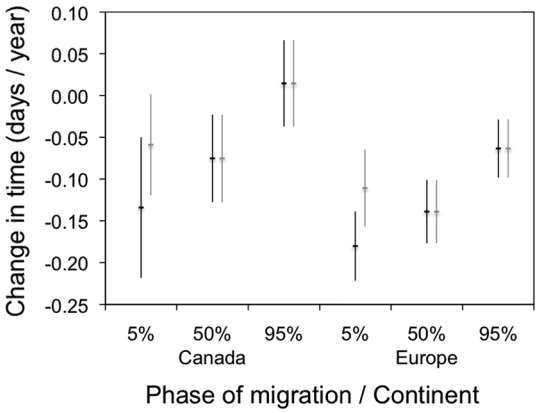

Fig. 2. Annual rates of change in 5%, 50% and 95% migration dates of short- (SDMs, in black) and long-distance migrants (LDMs in grey) in Canada and Europe based on the top ranked models. Vertical bars show the 95% confidence intervals.

Table 3
Parameter estimates (β ± SE) of the top model explaining annual 50% migration dates (Table S4). Year is study year, Con is continent and Mig is migration strategy of the species. All explanatory variables were centralized to zero mean.

Variable	β ± SE	t	P
Intercept	124.7 ± 1.90	65.5	< 0.001
Temperature	−0.46 ± 0.04	−10.5	< 0.001
Year	−0.12 ± 0.02	−7.2	< 0.001
Continent (Europe compared to Canada)	−8.64 ± 2.53	−3.4	0.001
Migration (SDMs compared to LDMs)	−4.70 ± 1.31	−3.6	< 0.001
Year * Continent (Europe compared to Canada)	−0.08 ± 0.03	−2.8	0.006
Continent * Migration (European SDMs compared to others)	−9.74 ± 3.27	−3.0	0.003

Table 4
Parameter estimates (β ± SE) of the top models explaining annual 95% migration dates (Table S5). Year is study year, Con is continent and Mig is migration strategy of the species. All explanatory variables were centralized to zero mean.

Variable	β ± SE	t	P
Intercept	143.1 ± 1.46	98.17	< 0.001
Temperature	−0.22 ± 0.05	−4.48	< 0.001
Year	−0.04 ± 0.02	−2.77	0.007
Continent (Europe compared to Canada)	−1.60 ± 2.05	−0.78	0.437
Migration (SDMs compared to LDMs)	−6.94 ± 1.24	−5.61	< 0.001
Year * Continent (Europe compared to Canada)	−0.08 ± 0.03	−2.60	0.011
Continent * Migration (European SDMs compared to others)	−7.77 ± 2.76	−2.82	0.005

Table 5
Parameter estimates (β ± SE) of the models explaining duration of the migration season after model averaging (Table S6). Y is study year, Con is continent and Mig is migration strategy of species. All explanatory variables were centralized to zero mean.

Variable	β ± SE	z	P
Intercept	31.19 ± 1.59	19.58	< 0.001
Temperature	0.45 ± 0.06	7.40	< 0.001
Year	0.11 ± 0.02	5.18	< 0.001
Continent (Europe compared to Canada)	11.91 ± 2.62	4.54	< 0.001
Migration (SDMs compared to LDMs)	3.68 ± 1.31	2.81	0.005
Year * Continent (Europe compared to Canada)	−0.05 ± 0.04	1.16	0.246
Continent * Migration (European SDMs compared to others)	2.13 ± 2.99	0.71	0.477
Year * Migration (SDMs compared to LDMs)	0.01 ± 0.02	0.41	0.674
Temperature	0.00 ± 0.02	0.06	0.954

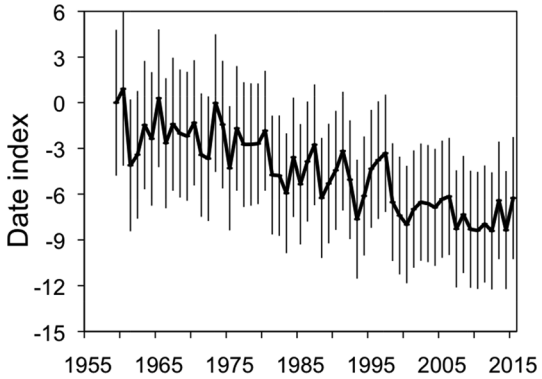

Fig. 3. The spring migration phenology indicator shows the median migration date of bird species in European and Canadian bird observatories according to LMM fit from 1959 to 2015. The year 1959 receives value 0 and annual bars represents 95% confidence intervals.

been prolonged due to longer lags between transition phases (Contosta et al., 2017). Notably, there were no significant differences between Europe and North America or between SDMs and LDMs in the extent of prolongation of the migration season.

The main reason why the first half of migrants have advanced their migration considerably more than late migrants of the same species could be that competition for suitable nesting habitat and potential mates is larger early in the season as birds arriving early are likely to have a larger breeding capacity (Rainio et al., 2006). Early breeders typically have the highest reproductive output (Daan and Tinbergen, 1997) whereas late migrants are more likely inexperienced young and/or low-quality individuals, that may not even necessarily breed (Newton, 2008). Especially in long-lived species, young non-breeding birds do not suffer obvious penalties by arriving late to the breeding areas (Newton, 2008).

The extended migration season can have several implications for biodiversity monitoring. Importantly, monitoring species' full migration season requires more resources as migration starts earlier, but the latest migrants do not necessarily change their migration dates. Furthermore, prolongation of the migration season may also, even for stable populations, act to reduce numbers during the peak migration season because the migration window is broader. This is a crucial point for population monitoring making use of migration passage data, as counting only during the migration peak may falsely indicate a population decrease. At the population level, longer migration seasons mean that migration of individuals is more spread out. This may reduce resource competition with conspecifics as fewer individuals may occupy the same stopover areas at the same time (Moore and Yong, 1991). Even though our results concern birds, the same prolongation of the (spring) occurrence season could equally well be evident in other taxa e.g. flowering of plants, periodic occurrence of insects or spawning of fish, which are all phenomena known to be influenced by climatic variation (Beebee, 1995; Crick et al., 1997; Menzel and Fabian, 1999; Cleland et al., 2007; Thackeray et al., 2010).

In Europe, SDMs migrated much earlier than LDMs wintering in the tropics, but this was not the case in Canada. This could be due to two reasons: First, wintering areas of European tropical migrants are likely situated further south because the Sahara Desert constitutes a highly unsuitable wintering area for most species (Alerstam, 1990). In North America, northern limits of many tropical migrants may be located in the southern United States, the Caribbean Islands and northern Mexico (Partners in Flight, 2017). Thus, some North American tropical LDMs

have shorter migration distances than European LDMs, which enables shorter differences in timing between North American SDMs and LDMs. Second, European study sites are situated in milder climate than Canadian sites, where winter is long and harsh and spring normally arrives rapidly (despite Contosta et al., 2017). Likely for the same reasons migration seasons are longer in Europe relative to Canada, as milder climate allows an earlier start of the migration in Europe (Vähätalo et al., 2004).

We found a small difference in the rate of advancement between SDMs and LDMs only during the early phase of migration. There has been scientific debate about the potential differences in the advancing rates of spring migration in SDMs and LDMs for more than a decade. While Jonzén et al. (2006) suggested that LDMs were actually advancing their spring migration at least as much as SDMs in a set of European passerines, a larger meta-analysis on European data by Rubolini et al. (2007) suggested that SDMs advance their spring migration even more. While a recent publication further confirms that SDMs have a greater tendency to advance their migration than LDMs (Usui et al., 2017), this doesn't appear to apply universally (see Calvert et al., 2012; Knudsen et al., 2011). The pattern observed depends on the phase of the migration (excluding FADs) and taxonomic group of interest. Importantly, the SDM and LDM comparison can be influenced by phylogenetic relatedness as certain taxonomic groups have higher tendency to be SDMs or LDMs. For instance, many insectivorous warbler species are LDMs, whereas the majority of ducks and geese are SDMs (Cramp et al., 1977–1994, see also Table S2). Since we found that the model including family and genus of species was clearly better than models without phylogeny, some taxonomic groups are likely advancing their spring phenology faster than others. Because of this, we argue, that analyses investigating species traits and phenology should preferably be corrected for phylogenetic distance between species. It is certain, nonetheless, that both SDMs and LDMs have advanced the timing of their spring migration in both Europe and North America.

There can be several reasons for why LDMs have advanced their timing of migration less than SDMs. It could be because SDMs winter closer to their breeding grounds and thus experience cues of the advancing spring which make them start their migration earlier if needed according to climatic circumstances. In contrast, LDMs don't have this possibility while they are in their tropical wintering grounds which might be the reason why their arriving dates correlate positively with their departure dates from the wintering grounds (Ouwehand and Both, 2017). Furthermore, recent tracking data has also suggested that the potential for LDMs to advance their spring migration by reducing stopover periods is limited (Schmaljohann and Both, 2017) and climate change may actually increase the number of stop-overs in LDMs (Howard et al., 2018) resulting in a delay rather than in a advancement.

The spatial difference in advancement between Europe and Canada could be due to weaker temperature changes at Canadian sites (see also Wang et al., 2011). Even though we included temperature as a variable in the models, it may not capture the whole climatic signal due to the coarse nature of the monthly means in 5° grids. It remains challenging to identify the best climatic explanatory variables for such a large and diverse group of species as in this study. A significant and positive temporal trend in temperature was documented for more than half of the European sites with long time-series of climate data. This highlights the importance of long-term data sets to show changes in climate.

To conclude, spring migration phenology of birds has advanced due to increased spring temperatures, but advancing has been asymmetrical within species' migration seasons. This has led to a lengthened migration season, which may affect duration of the breeding season (Halupka and Halupka, 2017), population dynamics, and detectability in monitoring schemes (Lehikoinen, 2013; Newson et al., 2013). We call for future research investigating potential changes at the population level durations of species' seasonal activities and potential consequences for population dynamics. We also strongly encourage other research investigating the potential lengthening of spring occurrence periods in other taxa. Corresponding changes in other taxa could be linked with lengthening in winter-to-spring transition (Contosta et al., 2017) or result lead into lengthening of the spring-to-autumn period (Miles et al., 2017; Liu et al., 2017). The spring migration phenology indicator presented here can be used for various large-scale analyses on climate effects in biological systems, as well as to inform the general public about consequences of climate change. We encourage development of similar indices for other taxonomic groups. The index is easy to update with new data, including future years and more sites.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.01.083.

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