

Consistent delay in recent timing of passerine autumn migration

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Climate change affects important biological processes, bird migration phenology being a particular well-documented one. While spring migration have been found to advance by numerous studies, autumn migration is less studied and show more variable change in timing. Few studies of autumn migration are based on data from after 2000, leaving the last two decades to be relatively less studied. Here, we investigate recent change in autumn migration phenology of European passerines. The most recent available bird ringing data from Denmark is used to analyse phenological change of median and late migration of 14 passerine migrants between 2003–2021. We find an overall delay of autumn migration, mainly driven by short-distance migrants. All short-distance migrants, one out of five medium-distance and three out of five long-distance migrants delay autumn migration. None of the included species advance autumn migration significantly. As climate change has continuously resulted in milder conditions in north-western Europe, we expect this to cause further effects on migration phenology also in recent decades. Our results provide novel insight into recent migration phenology trends, and the observed delay in long-distance migrants may illustrate a changed response to climate change.

1. Introduction

Climate change has profound and well documented effects on important ecological processes (Walther *et al.* 2002, Parmesan *et al.* 2013). One such process is the biannual bird migration of the northern hemisphere (Sparks *et al.* 2005). The effects of climate change on spring migration phenology have been thoroughly investigated (Thorup *et al.* 2007, Lehikoinen *et al.* 2019, Horton *et al.* 2020, Neate-Clegg & Tingley 2022) and studies of spring migration timing have found

migratory birds to adjust migration speed en route (Tøttrup *et al.* 2008), allowing an earlier onset of breeding and potentially an increase in breeding area residence time (Cotton 2003, Tøttrup *et al.* 2006b, Rubolini *et al.* 2007, van Buskirk *et al.* 2009). How these changes in spring migration phenology will affect population dynamics is highly dependent on the scale and direction of change of subsequent autumn migration phenology (Thorup *et al.* 2007). Unfortunately, less is known about the effects of climate change on autumn migration (Gallinat *et al.* 2015).

Earlier studies report both advancements and delays in migration timing, with results varying greatly between species (Jenni & Kéry 2003, Tøttrup *et al.* 2006a, van Buskirk *et al.* 2009, Neate-Clegg & Tingley 2022).

Most studies on autumn migration phenology are based on data prior to the 2000s while fewer studies based on recent data are available (Horton *et al.* 2020, Neate-Clegg & Tingley 2022). One of the recent studies found no over-all trend in timing of autumn migration of long-distance neotropical migrants in the period 1960–2019 because trends differed widely between species (Neate-Clegg & Tingley 2022) but the long time period of the study could mask recent trends. Another recent study generally found advancement of peak autumn migration of nocturnal migrants using remote-sensing data (Horton *et al.* 2020). The lack of studies of recent change is problematic because the rate of global temperature increase is accelerating and has never been higher (Smith *et al.* 2015). Studies based on the newest available data can therefore provide important and novel insight into the rate and direction of migration change, as temperature can be expected to have a larger impact on phenology in recent years than in the 1900s.

The aim of this study is to investigate most recent changes in bird migration phenology with specific focus on autumn, as a limited number

of studies have investigated this season. For our purpose, we use the most recent available bird ringing data from Denmark to analyse change in autumn migration phenology for 14 passerine bird species over 19 consecutive years.

2. Method

Standardized ringing was conducted in Blåvand, the westernmost point in Denmark (55°33'25.2"N 8°05'06.0"E) (Fig. 1). Here, all catches from the standardised autumn ringing season (from August 1st until November 15th) of the years 2003 to 2021 are included in the study. Standardized ringing is conducted from 30 minutes before sunrise and for the subsequent five hours. Ringing is conducted with fixed-position mist-nets, deploying a mean of 225 net meters per day in the period. Catch effort increased in the period (slope: 9.3 net-meter-hours per day per year, $p < 0.001$). However, there was no significant change in the number of birds trapped (N) (slope: $-27 N$ per year, $p = 0.465$) or the number of birds trapped corrected for catch effort (N') (slope: $-37 N'$ per year, $p = 0.242$). There was a slight negative relationship between N' and catch effort (net-meter-hours) (slope: $-0.06 N'$ per net-meter-hour, $p < 0.001$). This could be caused by closing of nets when birds were too numerous to handle responsibly.

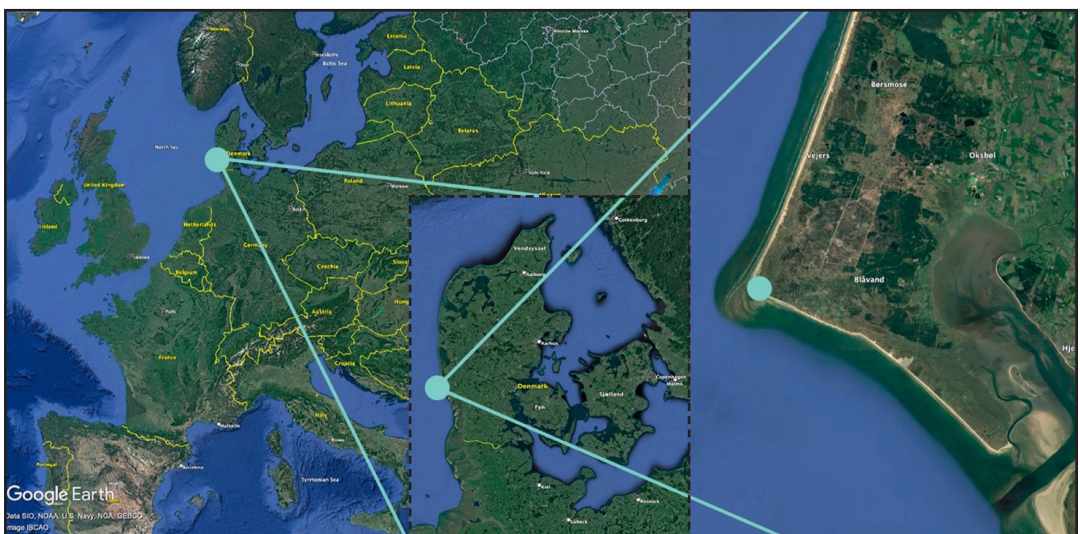


Fig.1. Location of Blåvand Ringing Station. The station is situated on the tip of an angled stretch of coastline.

Conditions are kept constant by keeping nets in fixed positions and vegetation in constant height and thickness. A Helgoland trap was installed in 2017 in close proximity to a number of the nets. To test whether the trap affected the number of birds caught, the number of birds caught per day as a function of catch effort (net-meter-hours) were modelled as a generalized linear model. Results show a small but significant negative effect of the trap on the number of birds caught (approx. 7 birds per season). Therefore, we do not consider the effects of the trap large enough to influence results of this study.

2.2. Data material

A total of 52,939 individual birds of 112 species have been ringed in the autumn seasons of the period. We included all migrant species exceeding a minimum of 10 individuals ringed in a season, for a minimum of 18 out of 19 years (after correcting for catch effort). A few species with migration periods ending after the ringing season was also excluded after visual inspection of the dataset. The final dataset consists of 34,134 individuals distributed on 14 species, with the mean number of individuals per species being 2438, ranging from 510 (Redwing, *Turdus iliacus*) to 6,937 (Goldcrest, *Regulus regulus*). Of the 14 species included, four of these are short-distance migrants, five are medium-distance and five are long-distance (following Tøttrup *et al.* 2006a). Migration distance was defined by location of wintering grounds, with short-distance migrants wintering mainly in northern and central Europe, medium-distance wintering in southern Europe and North Africa, and long-distance wintering in sub-Saharan Africa. The Danish bird migration atlas was used for data on wintering grounds (Bønløkke *et al.* 2006). The majority of birds ringed in Blåvand have breeding territories on the Scandinavian Peninsula or in Finland (Bønløkke *et al.* 2006).

2.3. Statistical analyses

Analytical approach broadly follows a study of autumn migration phenology in Denmark

from 1976 to 1997 (Tøttrup *et al.* 2006a) to allow direct comparison of the time periods. Analyses of phenology was performed on two measures of migration timing: median and late migration departure. Median and late migration departure is defined as the Julian date when 50% and 5% of the total catch remains to be caught, respectively, calculated for each autumn season. Early migration departure (95% remaining to be caught) was initially included in analyses (in accordance with Tøttrup *et al.* 2006a), but showed on visual inspection to be greatly influenced by local breeding birds. This was evident in a large number of catches and re-catches of resident individuals, which far outnumbered migrating individuals of the same species during the onset of the migration period. The measure for early departure was therefore excluded.

Two types of statistical analysis were performed: mixed-effect linear models (MELM) and quantile regression (QR). MELM was used to analyze departure of the whole group and migration groups, while QR was used to analyze departure of single species.

MELM allows species to be included as a random effect, taking into consideration the different migration timing of each species, and is therefore used to analyze groups of several species. For MELM, the total daily catch (N) of each species was corrected for catch effort by standardizing to 900 net-meter-hours (N') per day. N' was used to calculate the date when 50% and 5% of the total yearly catch remained to be caught, corresponding to the date for the median and late passage of the migration. Figure 2 illustrates how the dates for median and late migration passage are calculated from the dataset. Regression was then performed as the Julian date when 50% and 5% remained to be trapped as a function of year, using slope as the phenological change (days per year change in departure). MELM results are presented in table 1.

MELM for median migration:
 Julian date at 50% ~ year + (1|species)

MELM for late migration:
 Julian date at 5% ~ year + (1|species)

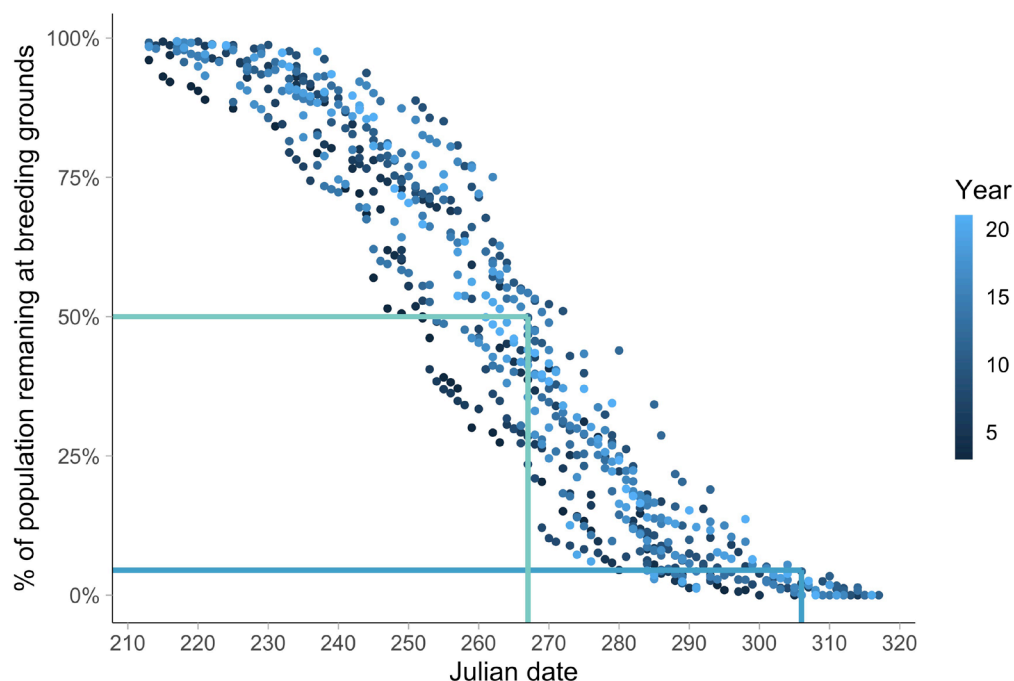


Fig. 2. Percentage of dunnoek population remaining at breeding grounds for the years 2003–2021. Lines represents the dates when 50% of the population (light blue) and 5% (dark blue) remained in 2011 representing median and late migration, respectively.

QR does not incorporate species as random effects but can utilize a bigger dataset (date of all individual catches instead of dates for median and late migration). QR was performed on the actual Julian dates of all individual catches for each species as a function of year, on 50% and 5% quantiles. Slope of QR describe phenological change in days per year. QR is illustrated for dunnoek in figure 4. As QR is based on more datapoints, it is statistically stronger than MELM when analyzing responses of single species instead of multiple-species groups. QR results can be found in table 2.

QR for median migration:

Julian date of catch \sim year of catch, $\tau=0.5$

QR for late migration:

Julian date of catch \sim year of catch, $\tau=0.05$

Testing across all species and quantiles introduces repetitions of tests. To control for

family-wise error rate, p-values are Holm-Bonferroni corrected (Rice 1989). Reported p-values are non-corrected, while significance codes for results in table 1 and 2 are marked with parentheses when results are non-significant after correction.

All data work and statistical tests were performed with R, version 4.2.1 (R Core Team, 2022), using the packages “tidyverse” (Wickham *et al.*, 2019), “Quantreg” (Koenker 2022) and “Stats” (R Core Team 2022).

3. Results

3.1. Whole group and migration group analyses

Overall, migrants delayed median autumn departure with 0.19 days per year (95% CI of slope=0.05–0.33, $p=0.008$) and 0.30 days per year for late population departure (95% CI=0.14–0.46, $p<0.001$).

This change in migration timing is mostly driven by short-distance migrants which are found to delay the most. See table 1 for details.

Short-distance migrants show the greatest change in departure, with 0.28 days per year (95% CI=0.05–0.51, $p=0.017$) and 0.39 days per year (95% CI=0.16–0.62, $p<0.001$) for mean and late population parts, respectively (Fig. 3).

Medium-distance migrants show no over-all significant change in departure timing, though one medium-distance migrant have the longest delay of all species.

Long-distance migrants showed no significant change in departure for mean population parts but a tendency for delayed departure of late population parts (0.33 days per year, $p=0.032$, nonsignificant after correction) (Table 1).

Table 1. Change in timing of autumn migration for all species combined and by migration strategy over 19 years (2003–2021) as results of mixed effects models. Slope represents days pr. year change for median (50% of population remaining to be caught) and late (5% of the population remaining) population departure. Positive values correspond to delayed departure. Significance level: 0.05 *; 0.01 **; 0.001 ***; 0. (*) indicates non-significant results after Holm-Bonferroni correction of p-values.

Group	Median migration (50%)		Late migration (5%)	
	Slope	Conditional R ²	Slope	Conditional R ²
All species	0.19**	0.93	0.30***	0.90
Short-distance migrants	0.28*	0.74	0.39***	0.39
Medium-distance migrants	0.20	0.74	0.19	0.53
Long-distance migrants	0.10	0.88	0.33(*)	0.86

Table 2. Change in timing of autumn migration in 15 species of passerine birds over 19 years (2003–2021) as results of quantile regression (QR). Slope represents days pr. year change for median (50% of population remaining to be caught) and late (5% of the population remaining) population departure. Positive values correspond to delayed departure. Significance level: 0.05 *; 0.01 **; 0.001 ***; 0. (*) indicates non-significant results after Holm-Bonferroni correction of p-values.

Common name	Scientific name	Migration distance	Median migration (50%)	Late migration (5%)
			QR slope	QR slope
Blackbird	<i>Turdus merula</i>	Short	0.32***	0.24***
Common Chaffinch	<i>Fringilla coelebs</i>	Short	0.25(**)	0.54***
Eurasian Wren	<i>Troglodytes troglodytes</i>	Short	0.25***	0.29(*)
Goldcrest	<i>Regulus regulus</i>	Short	0.27***	0.61***
Common Chiffchaff	<i>Phylloscopus collybita</i>	Medium	−0.01	−0.01
Dunnoek	<i>Prunella modularis</i>	Medium	0.47***	0.69***
European Robin	<i>Erithacus rubecula</i>	Medium	0.05	−0.06
Redwing	<i>Turdus iliacus</i>	Medium	0.08	0.20
Song Thrush	<i>Turdus philomelos</i>	Medium	−0.13	0.33(*)
Eurasian blackcap	<i>Sylvia atricapilla</i>	Long	0.42***	0.42***
Common Whitethroat	<i>Curruca communis</i>	Long	0.28(*)	0.51(*)
Garden Warbler	<i>Sylvia borin</i>	Long	0.07	0
Pied Flycatcher	<i>Ficedula hypoleuca</i>	Long	0.32***	−0.28
Willow Warbler	<i>Phylloscopus trochilus</i>	Long	0.26***	0.21

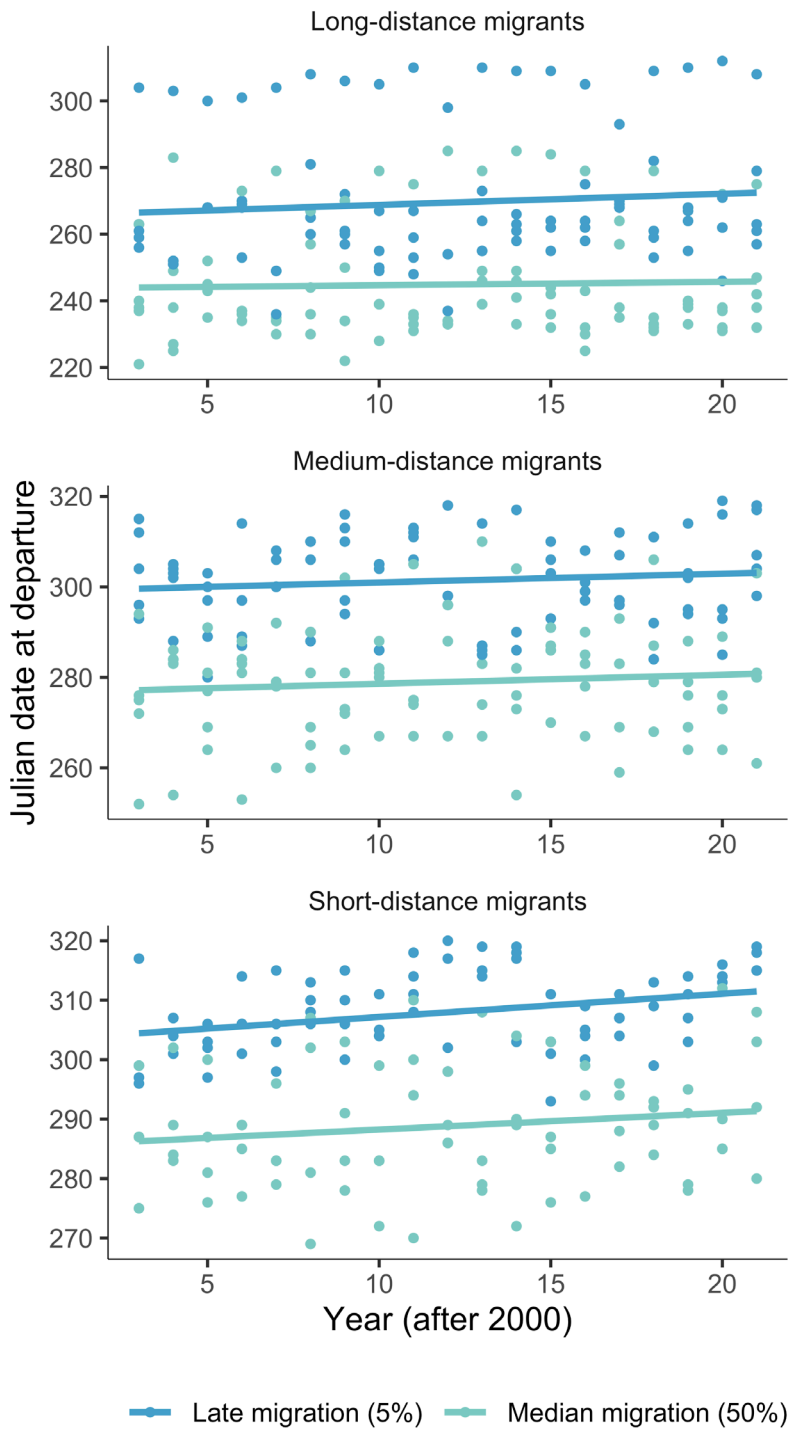


Fig. 3. Change in autumn migration for migration groups. Dark blue points represent dates when 5% of the population remains at breeding grounds (median population departure), light blue points represent dates when 50% remains (late population departure). Trends are illustrated by linear regression lines.

3.2. Single species analysis

Results show that all short-distance migrants have significantly delayed departure (Table 2). Goldcrests (*Regulus regulus*) show the largest overall change for the group, delaying median population departure with 0.27 days per year ($p < 0.001$) and 0.61 days per year for late population departure ($p < 0.001$).

Blackbirds (*Turdus merula*) delayed departure with 0.32 days per year ($p < 0.001$) and 0.24 days per year ($p < 0.001$) for median and late population departure, respectively. Common Chaffinch (*Fringilla coelebs*) shows a tendency for delayed departure for median population (0.25 days per year, $p = 0.008$, non-significant after correction), while late population departure is significantly delayed by 0.54 days per year ($p < 0.001$).

Eurasian Wren (*Troglodytes troglodytes*) show significantly later departure of 0.25 days per year

($p < 0.001$) for median population parts, and a tendency for delayed departure of late population parts (0.29 days per year, $p = 0.015$, non-significant after correction).

The Dunnock (*Prunella modularis*) is the only medium distance migrant to show significant change in autumn migration timing with the largest departure delay of all species in the study. Median population departure is found to delay with 0.47 days per year ($p < 0.001$) and with 0.69 days per year ($p < 0.001$) for late population departure (Fig. 4).

We found significant delay in departure for three long-distance migrants: Eurasian Blackcap (*Sylvia atricapilla*), Pied Flycatcher (*Ficedula hypoleuca*) and Willow Warbler (*Phylloscopus trochilus*). Departure of Eurasian Blackcap is significantly delayed with 0.42 days per year ($p < 0.001$) for both median and late population departure. Pied Flycatcher departure has been

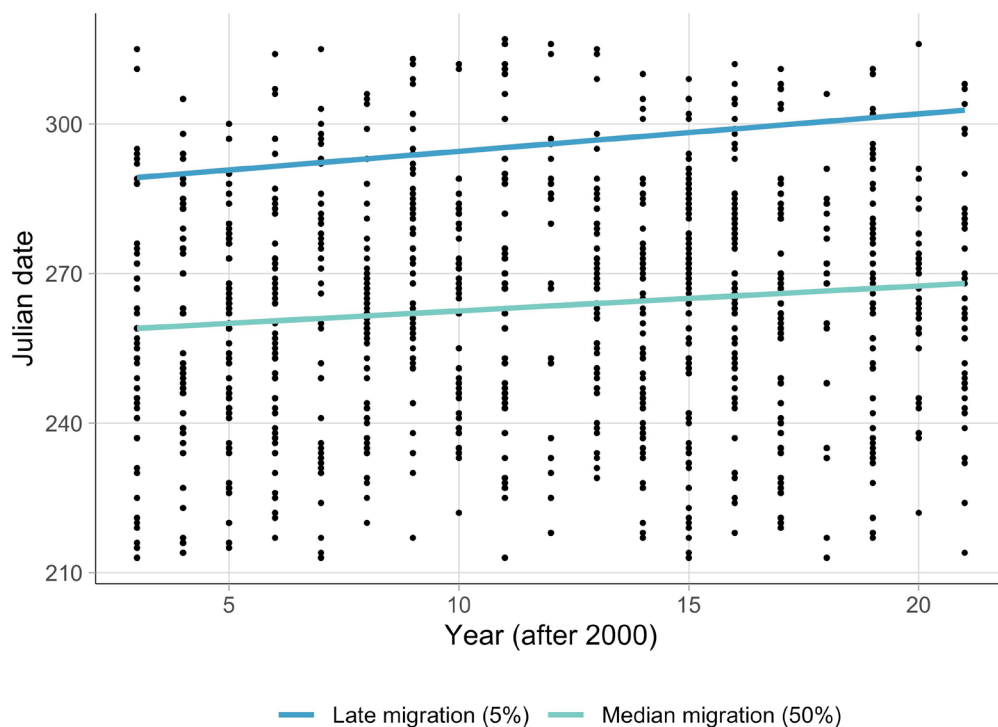


Fig. 4. Change in migration phenology of dunnock. Points represent individual captures. Lines represent quantile regression of 5% and 50% quantiles.

significantly delayed by 0.32 days per year ($p < 0.001$) for median population departure. Willow Warbler show a significant delay in median population departure of 0.26 days per year ($p < 0.001$).

Common Whitethroat (*Curruca communis*) show tendencies for delayed median and late population departure (0.28 days per year, $p = 0.036$, and 0.51 days per year, $p = 0.023$, respectively (both are non-significant after correction).

4. Discussion

Other studies have shown widely different direction and magnitude of change in migration timing between species (Tøttrup *et al.* 2006a, Thorup *et al.* 2007, van Buskirk *et al.* 2009, Neate-Clegg & Tingley 2022). Here, we report an overall delay of autumn migration. Short-distance migrants delay migration most evidently, which is in accordance with studies looking at earlier time periods (Jenni & Kéry 2003, van Buskirk *et al.* 2009, Lehikoinen 2011, Haest *et al.* 2019). We also find delayed migration of three long-distance migrants, a group that have previously been found to advance autumn migration (Jenni & Kéry 2003, Tøttrup *et al.* 2006a, Haest *et al.* 2019). None of the included species advanced autumn migration significantly.

In this study, data from the most recent 19 years have been analysed to gain insight in current phenological change. Our result suggests that long distance migrants may react differently to climate change in the last two decades than in the previous century. This could be the result of the accelerating rate of temperature rise, which is especially high in Europe (Smith *et al.* 2015). The acceleration has tripled since 1981 and Europe has experienced the ten warmest years during the last two decades (NOAA 2022). The effect of climate change on migration timing can therefore be expected to be most prominent during the 21st century, compared to other influencing factors. A recent study found that short-distance migrants have responded more to climate change in recent years, as observed species overwintered at breeding grounds more frequently during the latter half of the study (Bókonyi *et al.* 2019). It has also been shown that migration timing can shift

quickly in response to climate. A relationship has been observed between the North Atlantic Oscillation and the timing of spring migration timing (Forchhammer *et al.* 2002), demonstrating the short-term adaptive capabilities of migrant birds. We propose that long-distance migrants may have shifted from primarily advancing autumn migration during the 20th century to delaying autumn migration in recent decades due to the increasing effects of climate change. Our results support previous observed delay in autumn migration of short-distance migrants (Jenni & Kéry 2003, van Buskirk *et al.* 2009, Lehikoinen 2011, Haest *et al.* 2019).

Direct comparison of such phenological studies should be made with caution as ringing stations and observatories are recording birds from different geographical areas where regional climatic conditions may vary and potentially impact the results. Birds migrating over Christiansø and Blåvand are originating from the Scandinavian Peninsula and Finland, although Christiansø most likely receives more birds from Finland and Russia, and Blåvand receives more from Norway (Bønløkke *et al.* 2006). How comparable the populations of Blåvand and Christiansø are will most likely also differ between species. Some species show clear migration divides through Denmark, like White Wagtail (*Motacilla alba*) and Common Whitethroat, while the populations of south-west migrants can be expected to be more similar (Bønløkke *et al.* 2006).

We find stronger evidence for delayed autumn migration in short-distance compared to long-distance migrants. This difference could be the result of the controlling factors of migration timing (*e.g.*, Newton 2007). Short-distance migrants are more often facultative migrants, with timing and extent of autumn migration being controlled mostly by breeding ground conditions such as climate and food availability (Newton 2007). Long-distance migrants are considered obligate migrants, with migration timing being controlled in part by day length (Newton 2007). The timing of autumn migration could be expected to change as a product of micro-evolution, altering the endogenous control of migration timing. An evolutionary change such as this is expected to be a slower response than phenotypic plasticity. Thus, the difference in migration delay between short- and

long-distance migrants could be an expression of difference in the underlying mechanisms.

The increased temperature at breeding grounds in northern Europe leads to a longer growing season (Liu *et al.* 2016), and thereby prolonged resource availability. Delay in autumn migration of short-distance migrants could simply be driven by the benefit of exploiting these resources. It has been suggested by Jenni & Kéry (2003) that an evolutionary pressure to migrate before the dry season of the Sahel has driven phenological advancement of long-distance migrants in autumn (Jenni & Kéry 2003). Earlier onset of spring migration and breeding allowed autumn migration to advance, and thereby migrants to pass the Sahel when conditions were more favorable. This is supported by the results of Thorup *et al.* (2007) as they observe only a small increase in breeding-area residence time of long-distance migrants during the same period, suggesting that autumn migration had been advancing in the same magnitude as in spring. The delayed migration of long-distance migrants observed in this study, suggests that the benefit of migrating before the Sahel dry season has become less important compared to the benefits of delaying migration. Examples of these benefits are the possibility for migrants to exploit the extended resource availability on breeding grounds to achieve better physical conditions prior to autumn migration (Tøttrup *et al.* 2006a) and a longer post-breeding moult period for species that moult flight feathers allowing for better plumage quality. Both of these benefits could be expected to increase survival of long-distance migrants. It has also been proposed that delayed autumn migration could be due to an extended breeding period, allowing migrants to produce more offspring (Tøttrup *et al.* 2006a). It is likely that this is true for spring migration, as it has been found that multi-brooded species advance first arrival date of spring migration more than single-brooded species (Végvári *et al.* 2010). Whether delayed autumn migration is also the result of an extended breeding season, and thereby increased reproductive output, is less certain. A study of Reed Warbler (*Acrocephalus scirpaceus*) showed significantly earlier onset of the breeding season in the period 1970–2006, while the end of the breeding season did not shift (Halupka *et al.* 2008).

Whether delay in autumn migration has the potential to affect population dynamics, depends on the factors that drive this change. While delay of autumn migration may not necessarily influence reproductive output of migratory birds directly, it is very likely to affect survival. Understanding how survival is changing in different species and the dynamics that control autumn migration timing will shed light on future change and conservation issues.

Varpuslintujen syysmuuton ajoittumisen viivästyminen

Ilmastonmuutos vaikuttaa tärkeisiin biologisiin prosesseihin, joista lintujen muuttuva muuttofenologia on erityisen hyvin dokumentoitu. Vaikka lukuisat tutkimukset ovat osoittaneet kevätmuuton aikaistuvan, syysmuuttoa on tutkittu vähemmän. Sen ajoituksessa näkyy myös enemmän vaihtelua. Harvat syysmuuton tutkimukset perustuvat tuoreimpiin, vuoden 2000 jälkeisiin tietoihin, minkä vuoksi viimeisintä kahta vuosikymmentä on tutkittu suhteellisen vähän. Tässä tutkimuksessa selvittämmekin varpuslintujen syysmuutossa viime aikoina tapahtuneita muutoksia Euroopassa. Aineistomme koostuu Tanskan uusimmista saatavilla olevista rengastustiedoista. Niiden avulla analysoimme 14 varpuslinnun syysmuuttoon liittyviä muutoksia vuosina 2003–2021. Tutkimuksessa havaitsimme, että syysmuutto on yleisesti viivästynyt, mikä johtuu pääasiassa lyhyen matkan muuttolinnoista. Kaikki lyhyen matkan muuttajat, yksi viidestä keskimatkan muuttajasta ja kolme viidestä pitkän matkan muuttajasta viivyttivät syysmuuttoa. Yksikään tutkimuksessa mukana olleista lajeista ei aikaistanut syysmuuttoa merkittävästi. Koska leudommat olosuhteet ovat yhä yleisempiä luoteis-Euroopassa ilmastonmuutoksen seurauksena, odotamme muuttuvien olosuhteiden vaikuttavan muuttofenologiaan myös tulevana vuosikymmeninä. Tuloksemme tarjoavat uutta tietoa lintujen viimeaikaisista syysmuuton trendeistä ja osoittavat, että havaittu viive pitkän matkan muuttajissa voi kuvastaa muuttunutta reagointia ilmastonmuutokseen.

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