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Can migratory birds keep up with climate change by shifting their wintering- and breeding ranges?

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Abstract

The past decades, climate change has forced species to adapt to warming temperatures. Because of milder winters and springs, vegetation recovers earlier, allowing for advanced emerging of caterpillars and other insects. This leads to an advance in the food peak of those species depending on these resources during breeding. An earlier onset of breeding is required to avoid a mismatch with the hatching of offspring and the peak of food availability. Migratory birds are constrained in their start of breeding by the timing and duration of their migration. In 2002, Coppack & Both suggested four hypotheses about how migratory birds can achieve earlier arrival at the breeding grounds. Two of these are related to dispersal: 1) individuals can shift their wintering grounds northward, thereby decreasing migration distance, or 2) individuals can shift their breeding grounds northward, thereby 'delaying' the onset of spring in their breeding area. In this essay, I aim to review the recent literature for support of northward range shifts of the breeding- and wintering areas, and to see if the link has been made with advanced breeding. A literature search resulted in an overview of studies on range shifts of many different migratory species in different locations on the northern hemisphere. From this I conclude that the dominant shift in both the breeding- and wintering ranges was northward, and the mean velocity of the shift of the breeding grounds was slower, often resulting in reduced migration distances. However, there was still substantial variation between species, which may be explained by factors in the local environment. Research about the fitness consequences of these range shifts is scarce. I was therefore unable to draw conclusions about whether these shifts had positive or negative effects on the breeding timing of species or individuals. I suggest that future research should focus on the dispersal of individuals, and link this to their breeding phenology and fitness. This could help us understand the mechanisms migratory birds use to cope with climate change.

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Introduction

In the past decades, climate change has been characterized by an increase of the mean global temperature of around 1.0 °C, which is expected to increase even further in the future (IPCC, AR5). This seemingly minor change already has an impact on the ecology of a wide variety of species (Parmesan & Yohe, 2003; Root et al., 2003). Because of milder winters, spring events start earlier in the year, or in other words: spring phenology is advancing. Plants now shoot and flower earlier (Fitter & Fitter, 2002), and butterflies and other insects appear earlier (Roy & Sparks, 2000). This change in spring phenology can affect the timing of reproductive events. When the peak of prey availability advances, the hatching of offspring has to advance as well to avoid a mismatch. Some species have been able to respond to these changes: amphibians advanced their start of breeding (Li et al., 2013; Walther et al., 2002), and the same has been found for several bird species (Hällfors et al., 2020; McDermott & DeGroot, 2016).

For migratory species it may be harder to adjust the timing of breeding, because they have to migrate from their wintering grounds to their breeding grounds first. So, an advanced start of breeding is constrained by the timing of migration (Both & Visser, 2001). Besides, several fitness trade-offs are associated with the timing of arrival. Arriving too late may reduce chances of finding a suitable partner, and when chicks hatch the food peak may already be over. However, arriving too early may result in low food availability for yourself, and/or adverse weather conditions (Kokko, 1999). These factors indicate that there is probably strong selection for arriving at the breeding grounds at the right moment (Alerstam, 2011). Therefore, to keep up with climate change, birds need to advance their timing of migration. Many species already arrive earlier than in the past (Jonzén et al., 2007; Newson et al., 2016; Usui et al., 2017). Species that did not advance their arrival faced a decline in the past 30 years, possibly because of a mismatch with the peak of food availability (Møller et al., 2008; Saino et al., 2011).

There are different ways in which migrating birds can achieve earlier arrival at the breeding grounds. Four hypotheses have been suggested in Coppack & Both (2002), which are schematically shown in figure 1. Two of these are associated with the overall timing of migration. First of all, birds may increase the speed of their migration (fig. 1A). This can mainly be done by reducing stop-over duration and/or to increase fuelling efficiency, as flight speed may be hard to increase (Lindström et al., 2019; Schmaljohann & Both, 2017). Secondly, birds can advance the onset of their migration (fig. 1B): with an earlier departure from the wintering grounds, arrival at the breeding grounds will also be earlier. The other two hypotheses are associated with dispersal, either from the wintering- or the breeding grounds. So, thirdly, birds can shorten overall migration by wintering closer to the breeding grounds, which means wintering more northward when breeding happens in the northern hemisphere (fig. 1C). Finally, birds may prolong their migration and breed more northward. This is a way to catch up on the start of spring, as this happens later more to the north (fig. 1D). These proposed hypotheses are not mutually exclusive, a combination of two or more is also likely.

These four hypotheses were proposed in 2002, and sparse evidence was available at that time. This essay will focus on the final two hypotheses, and discuss the more recent literature published in the past 20 years associated with

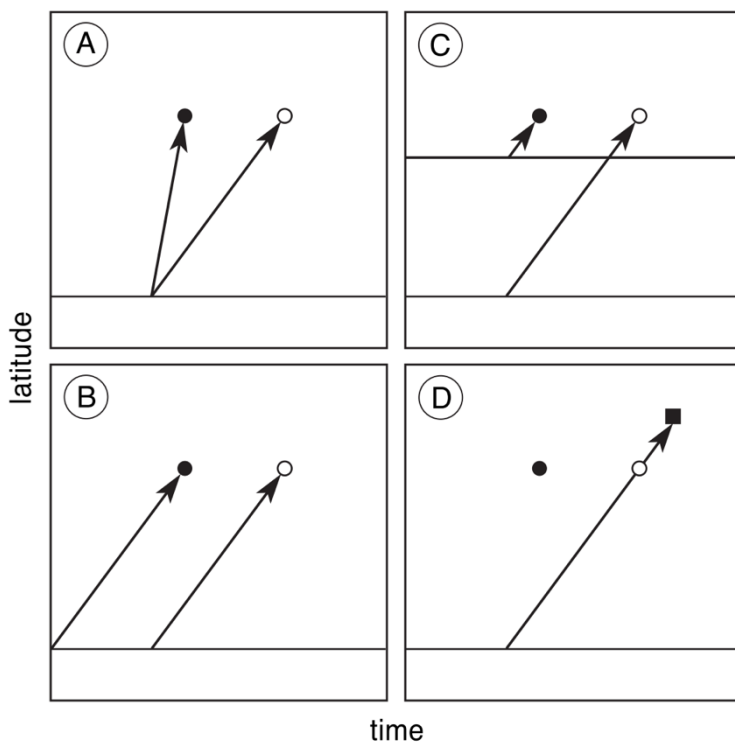


Figure 1: A schematic representation of four options for migratory birds to advance arrival at the breeding grounds, following advanced spring phenology. Open circles represent the existing arrival date, and filled circles indicate the required earlier arrival for earlier breeding at the same latitude. Arrows show the timing and distance of migration starting from a given wintering latitude (horizontal lines). (A) Birds increase the speed of spring migration. (B) Birds leave the wintering grounds earlier and migrate at the same speed. (C) Birds winter closer to the breeding area (horizontal bold line) and migrate for a shorter period. (D) Birds prolong northward spring migration and move towards improving breeding conditions (square). Figure taken from Coppack & Both (2002).

dispersal from the wintering- and breeding grounds. The main goal is to find out whether these are plausible mechanisms that help migratory birds adapt to climate change.

Dispersal: finding a suitable habitat

One way to define dispersal is the movement of an individual between breeding- and/or wintering locations in successive years, which is common in many species. Dispersal can be a useful behaviour in changing environments: if individuals are able to recognize, find, and settle in suitable habitats, this may significantly increase their fitness (directed dispersal). Most individuals only disperse over relatively short distances and are called “philopatric”, whereas some other individuals disperse over quite long distances, and are therefore classified as “long-distance dispersers” (Nathan et al., 2003). An example of a migratory bird species that disperses to match the best suitable habitat, comes from American redstarts (*Setophaga ruticilla*). It has been shown that, depending on the quality of the wintering territory, individuals dispersed relatively more towards the north or south of their natal area (Studds et al., 2008). Individuals from high quality wintering territories could depart earlier, and dispersed to breeding areas south of their natal area, because spring phenology matches best at that location at that moment. On the other hand, individuals from the wintering territories of poorer quality migrated to breeding areas north of their natal area, again, to best match the spring food peak with the hatching of the offspring. Besides, this example illustrates that not only conditions in the “dispersal location” are important, also the conditions prior to dispersal play a role. They may affect the direction and length of dispersal, but importantly, also the timing of migration. Without these dispersal strategies, which depend on local conditions, individuals may have faced mismatches and hence reduced breeding opportunities. Therefore, dispersal can

play an important role in the adaptation to changing environments (Jacob et al., 2017), and it could even be important in the current race against climate change (Boeye et al., 2013).

Shortening migration: wintering more northward

As discussed in Coppack & Both (2002), one of the hypotheses about how migratory birds can achieve an advanced arrival on the breeding grounds, is by dispersing northward during winter. If the breeding location does not change (or at a slower rate), the overall migration is shortened, because wintering happens closer to the breeding grounds. When individuals depart the wintering area at the same moment but from a more northern location, they will arrive at their breeding grounds earlier than without dispersal. With advanced spring phenology this would lead to a better-timed arrival and consequently a better-timed start of breeding. Besides, wintering closer to the breeding areas may provide more reliable information about the local breeding conditions, and choosing the right timing to migrate can become easier.

Wintering further north does require flexibility or adaptation of endogenous rhythms, that are entrained to the changing of the daylength (Gwinner, 1996). Not only departure decisions, but also pre-migratory activities like moult and gonadal maturation largely rely on these endogenous rhythms, so their functioning is crucial for a timely onset of migration. Wintering at higher latitudes means that daylength increases faster, and endogenous systems related to the timing of migration have to respond to this change in increasing daylength. In other words: wintering more to the north requires alterations in the spatio-temporal programme of the birds. In three migratory species it was shown that individuals exposed to a more 'northern' photo-cycle advanced their migratory activity compared to individuals with a 'normal/southern' photo-cycle (Coppack et al., 2003; Coppack & Both, 2002). This is an indication of the flexibility in the response to changing photo-periods that may also exist in other species, which is crucial for these species to keep up with climate change (Kronfeld-Schor et al., 2017). However, this may also result in a superfluous advance: when individuals that already winter further north also advance their onset of migration, they may arrive too early at the breeding grounds. Flexibility in the spatio-temporal programme therefore needs to be 'at the right scale', to ensure a well-timed arrival at the breeding grounds.

Wintering more northward can also have consequences for the quality of the wintering area. Especially for trans-Saharan migrants who winter south of the Sahara, wintering more to the north means coming closer to the very dry areas, possibly resulting in lower food availability because of low precipitation levels (Ambrosini et al., 2011). Wintering north of the Sahara, in the Mediterranean area, might then also be favourable, which has been observed for the white stork (*Ciconia ciconia*), a long distance migrant (Gordo et al., 2007; Rotics et al., 2017). In cases like this, wintering more northward may increase the quality of the area, often up to certain temperature/weather limits. But in extreme cases, it may even be more beneficial to be a resident than a migrant (Lemoine & Böhning-Gaese, 2003). These notions can be important, because, as illustrated by the example of the American redstarts (Studds et al., 2008), the quality of your wintering area can

also affect the timing of your migration. The same has been shown by other studies (Both, 2010; Haest et al., 2020; McKellar et al., 2013, but see: Bussière et al., 2015).

Prolong migration northward

The other hypothesis about how migratory birds can use dispersal to achieve earlier arrival at the breeding grounds, is by prolonging the migration and to breed more to the north (also called “breeding dispersal”). In years with an early spring, individuals may choose to keep migrating, and to stop further north. Thereby they catch up on the progress of spring, because its peak will be later more northward. Also, then they adjust their relative timing of breeding, and avoid the mismatch they would have had further to the south. It was already found that some individuals move relatively large distances while in their breeding range, possibly to explore dispersal possibilities (Cooper & Marra, 2020).

When prolonged migration to the breeding areas provides a fitness benefit for these individuals, this could have evolutionary consequences on a population level. In that case, long distance dispersal could boost non-random gene flow between populations (Edelaar & Bolnick, 2012). When individuals from more southern regions disperse northwards in the breeding range, they bring the genetic elements needed for breeding in their southern location, which are relatively early for this northern population. If this results in increased fitness, these early genes can mix in the more northern population. This fitness benefit may contribute towards stronger selection for earlier breeding, which will boost evolution in this direction. Only one study to date has found experimental evidence for a fitness increase of individuals that bred further north compared to their ‘natural’ breeding location (Lamers et al., 2021). In this study, female pied flycatchers were translocated from their natural breeding grounds in the Netherlands to a population that breeds further to the north in Sweden, where spring generally starts around 15 days later. Earlier timing of breeding of the translocated individuals led to a fitness that was 2.5 times higher than their Swedish conspecifics. The study also showed that even hybrids (half Swedish, half Dutch) showed an advanced laying date, indicating that there is a genetic effect. This is important, because in that case the increased fitness can be a very strong driver of selection for earlier breeding (and breeding dispersal northward) (Tarka et al., 2015).

Research question

The main question that I aim to answer in this essay is whether migratory birds can use dispersal in their wintering- or breeding ranges to prevent breeding mismatches due to a warming climate. This question will be split up into two different sections. The most important data I need is long term dispersal data, across many different migratory species, which in the literature mostly translates to range shifts of species over the past decades. The first goal therefore is to discuss and evaluate studies that found breeding- and wintering range shifts of migratory bird species over the past few years, and how fast and in which direction the shifts happened. The important second part is, if I am able to conclude that individuals disperse as a consequence of climate change. What is often missing from studies linking breeding- or wintering dispersal to a response to climate change, is the connection with timing of breeding and potential fitness consequences. Hence, the

second goal is to evaluate whether the observed range shifts are associated with an advance in breeding timing and if this has any fitness benefits.

In the past few years, did we generate new evidence that range shifts of the breeding- or wintering range are a potential tool for birds to cope with climate change?

- a. Did birds shift their wintering ranges northward? And how fast? Did this result in shortened overall migration? And does it relate to the timing of breeding?
- b. Did birds shift their breeding ranges northward? And how fast? And does it relate to the timing of breeding?

Methods

This study is based on the available literature published after the paper of Coppack & Both (2002), discussing range shifts of migratory birds. A literature search was conducted using literature search engine Web of Science (v. 5.35). First, I searched for all literature after 2002 using the keywords “climate change” and “range” or “distribution” and “bird”. With the output list set to “most relevant”, I searched the first 20 pages. Additionally, I searched the list of literature that had cited a study by Thomas & Lennon (1999), on birds that extend their ranges northward. Finally, I went through all the selected literature, to search for relevant references within these papers.

I only selected studies that either calculated a range shift in kilometers or degrees latitude per year, or studies that provided an indication of the most frequently found directions in which the range of a species shifted. I did not include studies that were performed over less than five years of data. Studies on multiple species are preferred, but studies on single species are also included. This is done because usually the data is more specific, and may describe more local details. This literature search and selection resulted in a total of 27 relevant studies.

If available, I first extracted the mean shift of the breeding- and/or wintering range from the studies. If necessary, I calculated the mean velocity of the shift across all species included in the study. The shift could be measured at the northern edge, southern edge, or as a ‘centroid shift’. I always extracted the centroid shift as the latitudinal shift if available – otherwise I took the northern range shift (but only if the study corrected for an overall range expansion). Secondly, if available, I extracted the *dominant direction* in which the breeding- and/or wintering range shifted. This is the direction that was most frequently found to be the direction a species or individuals shifted in, per study. Finally, I extracted whether, and how much the total length of migration had shortened, again averaged over all species in the study. I also noted the number of species included in the study, which species or species group it was about, for how many years they were studied, the location of the study and the sampling method. Because of the difference in sampling, it was not possible to extract comparable sample sizes from the literature. The different sampling methods are discussed in

more detail later on in this essay. All studies are summarized in a table, and based on this, the available literature is discussed below.

Individual fitness consequences of range shifts were rarely addressed in the studies taken up in the analysis. Therefore, to draw conclusions about fitness effects, I also extracted information about the increase or decrease in abundance of species after they shifted their ranges, if this information is available in the study.

Results

Shift breeding and wintering ranges

From the 27 studies, 24 reported a shift in the breeding (n=13) or the wintering ranges (n=13) of migratory bird species (table 1). In the wintering range, species mostly shifted towards the north (n=6). This can be concluded when looking at both the dominant shift direction and the mean latitudinal shift. Another shift that was often found is towards the north-east (n=5). Mean range shift of the wintering ranges over all relevant studies, weighted for the number of species included, is 1.497 km/year northward, which ranged between 0.84 km/yr to 6.31 km/yr northward. Results for the shifts in breeding range are similar, but are more variable in their dominant shift direction. Species again mostly shifted towards the north (n=8), but shifts towards the south are also observed (n=2). Mean range shift of the breeding ranges over all relevant studies, again weighted for the number of species, is 1.212 km/year northward, and it ranged between 3.314 km/yr southward to 3.58 km/yr northward. Although the direction of the latitudinal shift for both the breeding- and wintering area appear similar (showing a shift towards the north), the 'share' of the most dominant shift direction out of all shifted species or individuals indicate that there is still much variation between and within species.

I did not find clear patterns that show that these results differ between species or species groups. A wide variety of species (groups) are represented, but most of the studies were performed using a mix of species groups, which do not allow for such distinctions. Also, between the different sampling methods or study locations there are no clear differences to be observed in the results.

Shortening of migration

Studies on a change in migration length were harder to find (n=7), but all of them indicated a shortening of total migration distance. The mean shortening of migration distance across all relevant studies, weighted for the number of species, was -2.155 km/yr, ranging from 0.62 km/year to 13.2 km/year shortening. As indicated above, I also found that on average, wintering ranges shift slightly faster northwards than breeding ranges (1.497 vs. 1.212 km/yr), which corresponds to the studies finding shortening of migration distances. In one of the studies, most species shortened their migration, but the mean change in migration length was positive. This indicates that some species had a prolonged migration that was

longer than the shortening of the migration of the majority of the species (Potvin et al., 2016).

Fitness consequences

Many of the studies use a large number of species to draw conclusions about range shifts. As a result, fitness consequences of range shifts are often not measured. Some studies show whether species that shift their ranges increase or decrease in numbers. Although it is merely an indication of a fitness effect, in declining species, the shift may have had a negative fitness impact, whereas for species that increase in numbers, the shift may be beneficial and increase their fitness. In three of the five studies that took this into account, species with increasing numbers were also the ones that shifted their distributions northward. Another study did not find any relationship between range shifts and population increases/decreases (McCaslin & Heath, 2020). In barn swallows (*Hirundo rustica*), a population decline is associated with a range shift into less favourable wintering habitats, characterized by a drier and warmer climate (Ambrosini et al., 2011).

Another way to infer fitness consequences of a range shift is to look at individual fitness consequences, but there were no studies that specifically investigated this.

Striking results: a few highlighted studies

When compared among the other studies collected for this essay, some show remarkable results that I wanted to discuss in more detail. First of all, Zuckerberg et al. (2009) find an average shift of the breeding range of 3.58 km/yr north, across a total of 129 species. This seems a quite big shift, considering that there were few other studies finding a comparable shift, even when considering studies on single species. In fact, most of the studies on breeding range shifts of a single species find either no shift (Ambrosini et al., 2016; Lacy et al., 2015) or a southward shift (Marion & Bergerot, 2018). One explanation could be that the location of this study is more confined compared to other studies using a large number of different species, which may result in describing a more local (and therefore more pronounced) pattern. The only study that has shown a similar range shift is Hitch & Leberg (2007) (2.35 km/yr northward). The differences are that this study was performed with only 26 species, and uses a preferred sampling method (see discussion), but on a much larger scale.

Secondly, Lehtikoinen & Virkkala (2016) show that birds in Finland have shifted their breeding ranges northward in 40 years, but also document the longitudinal shift, and the direction of the 'temperature shift'. They find that the dominant shift is towards the north-northeast direction, and this coincides with the temperature shift in Finland in that same period (fig. 2). Other studies have also found that the shift of the species range is related to warming temperatures (Ambrosini et al., 2016; Coristine & Kerr, 2015; Maclean et al., 2008; Smallegange et al., 2010; Visser et al., 2009), but not as specifically as shown in figure 2.

Table 1: 28 studies resulting from the literature search about shifting breeding- or wintering range and shortening of migration. The dominant direction shift is the direction that was most frequently observed in the study. In brackets the percentage of species/individuals is shown that was observed to (significantly) shift its ranges in the dominant direction (if available). Remaining species/individuals did not shift or shifted in a different direction. Positive mean latitudinal shifts indicate northward movement, negative latitudinal shifts indicate southward movement. Whether overall migration length had shortened is indicated with the direction (shortened/lengthened), and again if available, the percentage of species/individuals that was observed changing its migration in that way. Crosses indicate that this specific parameter was not measured/mentioned in the study.

Study						Breeding range shift	Wintering range shift		Migration length		
	Publication	Location	Species or species group	Number of species	Number of years studied	Sampling method	Dominant direction shift (% of species or individuals)	Mean latitudinal shift in km/yr	Dominant direction shift (% of species or individuals)	Mean latitudinal shift in km/yr	Direction of change (% of species or individuals)
Ambrosini et al., 2016	Northern Europe	European robin	1	65	Ring recoveries	None	NA	NE (53.6)	4.42	Shortened (46.4)	x
Lacy et al., 2015	North America	Greater Sandhill cranes	1	47	CBC and BBS	None	NA	NW	13.17	x	x
Thomas & Lennon, 1999	UK	Various	59	20	Bird atlases	N	0.945	x	x	x	x
Coristine & Kerr, 2015	North America	Passerines	34	19	BBS	N	0.305	x	x	x	x
Brommer, 2004	Finland	Various	116	12	Bird atlas	N	1.56	x	x	x	x
Virkkala & Lehikoinen, 2014	Finland	Various	94	40	Counts	N	1.24	x	x	x	x
Hitch & Leberg, 2007	North America	Various	26	26	BBS	N (23.6)	2.35	x	x	x	x
McCaslin & Heath, 2020	North America	Various	73	23	BBS	N (33.8)	0.475	x	x	x	x
Hovick et al., 2016	North America	Various	277	43	BBS	N (52)	0.651	x	x	x	x
Zuckerberg et al., 2009	New York	Various	129	20	Bird atlases	N (57)	3.58	x	-	x	x
Lehikoinen & Virkkala, 2016	Finland	Various	128	25	Counts	NNE (75)	1.436	x	x	x	x
Gillings et al., 2015	UK	Various	122	22	Bird atlases	NNW (?)	0.66	x	x	x	x
Curley et al., 2020	North America	Short distance migrants	77	26	CBC and BBS	NW (14.2)	-0.003	N (29.8)	3.09	Shortened	-2.985
Potvin et al., 2016	Finland	Various	29	55	Ring recoveries	S (20.1)	1.717	x	0.841	Shortened	0.88
Marion & Bergerot, 2018	France	Great cormorant	1	33	Counts	SSE	-3.314	NNE	2.44	Shortened	-5.754
Ambrosini et al., 2011	Europe & Sub-Saharan	Barn swallow	1	97	Ring recoveries	x	x	N	6.31	x	x
La Sorte & Thompson, 2007	North America	Various	254	30	CBC	x	x	N	1.03	x	x
Paprocki et al., 2014	North America	Raptors	6	37	CBC	x	x	N (100)	5.13	x	x
Fiedler et al. 2004	Germany	Various	30	average 25	Ring recoveries	x	x	N (33.3)	x	x	x
Niven et al., 2009	North America	Various	305	40	CBC	x	x	N (68.2)	1.408	x	x
Pavón-Jordán et al., 2015	Europe	Smew	1	22	Counts	x	x	NE	x	x	x
Lehikoinen et al., 2013	Northern Europe	Waterbirds	3	30	Counts	x	x	NE	x	x	x
Maclean et al., 2008	Northern Europe	Waders	7	20	Counts	x	x	NE (85.7)	x	x	x
Pavón-Jordán et al., 2019	Europe	Waterbirds	25	24	Counts	x	x	None	NA	x	x
Visser et al., 2009	Netherlands	Short distance migrants	24	73	Ring recoveries	x	x	x	x	Shortened (50)	x
Heath et al., 2012	North America	American kestrel	1	49	Ring recoveries	x	x	x	x	Shortened	-0.616
Smallegange et al., 2010	Germany	Blue tit/Great tit	2	5	Ring recoveries	x	x	x	x	Shortened	-13.2

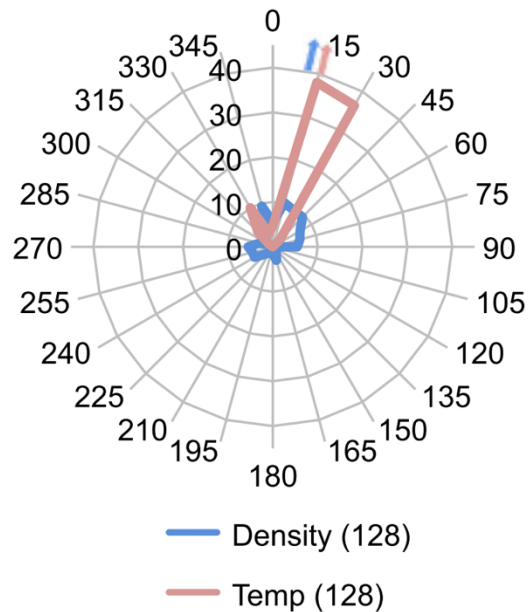


Figure 2: The distribution of density and temperature shifts across all species ($n=128$) taken up in the analysis by Lehikoinen & Virkkala (2016). The colour lines show the distribution of directions in 15° intervals. Blue represents the density shifts of all species (95% c. i. of the mean direction $358-30^\circ$); red represents the shift of temperature (95% c. i. $8-17^\circ$) in their same breeding range. Arrows in corresponding colours show the mean direction of the particular distribution.

Discussion

The main purpose of this essay is to review the recent literature about dispersal as a tool for migratory birds to cope with advancing spring phenology, because of climate change. The first part of the research question is whether, and in which direction individuals have dispersed in the past decades, and specifically, if this resulted in a range shift of species in their wintering- and breeding ranges. From the collected literature, it seems that most of the shifts of species in both the breeding and wintering range happened towards the north, although there was variation. For the wintering range the direction of the shift is more consistent, and the average shift per year is larger, when compared to the shifting of the breeding range. In several studies, it was concluded that this (difference in) range shift in both locations led to a shortening of the total migration length, which seems to be the dominant finding in literature. The second part of the research question was related to the fitness effects of these range shifts. This is important to consider, because it can indicate whether dispersal can lead to an advanced start of breeding (and therefore increased breeding success), which is needed for migratory birds to cope with the advancing start of spring. Some studies indicate that species that have shifted their ranges, also show an increase in population size, which can be an indirect measurement of the fitness consequences of range shifts. If dispersing individuals have a fitness benefit and dispersal is consequently selected for, this may eventually result in population growth. So, in the case of a growing population, one could suggest that the range shift had a positive fitness effect. On the other hand, some populations remained stable, or even declined. However, this does not necessarily mean that the range shifts had no or negative effects: in some cases, populations may have declined even more if they had not shifted their ranges (and the other way around). Unfortunately, very little research has been done on individual fitness effects of dispersal. Because of this and contrasting

results, I cannot conclude with certainty that the observed range shifts have led to an advanced start of breeding.

There is one study however, that presents relevant findings, but could not be included in the table, because it did not provide compatible results. Black tailed godwits (*Limosa limosa islandica*) have shown to winter increasingly more to the north, and also arrive increasingly earlier (Gill et al., 2019). With changing spring phenology, wintering more to the north may thus have fitness benefits for early arriving individuals. However, this shifting pattern is only shown across generations – individuals seem to be very consistent in their wintering locations and migration timing. This potential fitness benefit therefore is not based on phenotypic plasticity, but on long term changes that only occur between generations: an important observation in predicting the evolutionary response of migratory birds to warming temperatures.

Although it is not yet possible to confidently draw conclusions about fitness effects of range shifts, I think it is likely that the shifts in species distributions have occurred as a result of climate warming. Eight of the 27 studies describe that the shift of the wintering- or breeding range coincided with a change in temperature. Species generally move away from an area when temperatures become higher. In the breeding areas in Europe, this shift mainly occurs towards the North-East (Lehikoinen & Virkkala, 2016).

Measurements of fitness consequences

There are a few explanations why research on individual fitness consequences of dispersal are so scarce. First of all, to gather information on dispersal of individuals, birds need to be tracked individually. Especially in small birds this can be a challenge (Nathan et al., 2003). Satellite transmitters can be used to track birds in real time, while on the move, but are relatively large. Most of the current studies using these devices are therefore done with bigger birds (raptors, water birds), although I could not find relevant studies on these species either. Fortunately, with advancing technology, it will soon be more accessible to also track small passerines. This can for example be done by using geolocators, which are small and light, and can therefore also be used on relatively small birds. The downside of this method, is that tagged individuals need to be recaptured to be able to collect the data from the devices. When the whereabouts of these individuals in a big population are unknown, the detection of (long distance) dispersal of individuals becomes even harder. An alternative to ‘track’ smaller birds without using geolocators, is by using stable isotopes extracted from feathers, for example. This allows you to trace the latitude of the ‘origin’ of migration, without having to follow the individual (Rushing et al., 2015).

Besides tracking data, breeding data also needs to be collected for these individuals to calculate fitness effects. To be able to look at the long-term effects of climate change, both the tracking- and breeding monitoring effort need to be repeated multiple years, which is a big time- and financial investment.

A different way to look for fitness benefits of dispersal, is by comparing immigrants in a breeding population with residents. If immigrants have higher breeding success than residents, this may suggest that dispersing in the breeding area provides fitness benefits. A selective advantage for immigrants has been found for different species (Ebert et al., 2002; Gliwicz, 1993), and may also be sex-

specific (Martinig et al., 2020; Pärn et al., 2009). Similar studies could be performed in migratory bird species, to determine the success of dispersing individuals. A problem with this method is that it is often unknown which direction the immigrants came from, so conditions of that location are also unknown. This makes it harder to estimate the connection with climate change.

Variation in range shifts: movement in other directions

The results of this literature review are mostly consistent with the hypothesis that shifts in species breeding- and wintering areas are related to warming temperatures. Species ranges generally move to the north, away from areas that are slowly becoming too warm. However, northward is not the only shift direction that was observed in the studies collected here. Therefore, I would like to explore other reasons for species ranges to shift in other directions, which may explain some of the variation that is observed (Hovick et al., 2016). As mentioned before, most of the studies are performed with multiple species. This allows them to look at general dispersal patterns across migratory systems, and general climate trends. However, when looking at a single species, reasons for dispersal may occur on a local scale as well, and may be unrelated to climate change.

An example of an important factor that may drive dispersal in any direction is habitat loss (Zitske et al., 2011). Because of development of agriculture and urbanization, suitable habitats change and become progressively less available. This can be a reason for species/populations to shift their wintering- or breeding location, away from these anthropogenic factors (Liu et al., 2020). Other local changes in habitat may also play a role, like changes in vegetation composition or food availability (Archaux, 2004), human disturbance, or predation pressure (Lenoir et al., 2010). Changes can happen at any location in the species range (north, east, south, west), and may drive the population away from that location. Movement in one general direction is in that case hard to predict on a larger scale.

An explanation for a lack of movement in some species is that climate change is not extreme enough for species to respond to warming. Local conditions may deviate from the global trend, and are actually cooling instead of warming (VanDerWal et al., 2012). Dispersal will therefore be less likely, as the urge for it does not become evident from local conditions. Another possibility is that species may be unable to respond to the climate warming, and are bound to their wintering- and breeding ranges as they are now. This could be because they do not respond to the changes, or because there is no area available to shift towards.

Related to this, is the fact that climate warming is not happening equally strongly everywhere. Warming happens faster at higher latitudes, and species that breed there will have to respond with bigger range shifts to keep up (La Sorte & Jetz, 2012; La Sorte & Thompson, 2007; Virkkala & Lehikoinen, 2014). This is especially challenging for species that already breed in the arctic, because shifting northwards becomes impossible when there is no space to disperse. This may explain part of the variation in both the velocity and direction of the range shifts. Species that breed at relatively low latitudes may not notice much temperature change and therefore do not need to shift their distributions. For species breeding at moderately high latitudes, temperatures are increasing faster and a faster shift northward is required (like the several studies in Finland included here have shown). Finally, as mentioned before, species breeding at very high latitudes may

not have space to disperse northwards, and range shifts will unlikely happen in that direction. Without room to shift northwards, the only way to cooler temperatures is to shift towards higher altitudes, which may be possible in any direction, depending on the breeding location. Altitudinal shifts (towards higher elevation) of breeding grounds have already been reported in several species (Tingley et al., 2012).

Strengths and limitations

With this essay, I was able to review a substantial amount of literature about range shifts in migratory bird species. I managed to create an overview of the direction and velocity of species range shifts. Unfortunately, it was not possible to draw conclusions about the fitness consequences. In part, this may be due to the methodology of most studies, but a more thorough review of the literature may have resulted in a few more relevant studies about this. Due to the time constraint, I was unable to look for more literature than I did here.

I summarized the literature into one table, that shows the mean shift direction and velocity of the wintering- and breeding ranges, across the entire study. This sometimes meant that, when many species were included, much of the variation was not accurately represented. I show some of the variation by including the percentages of species or individuals that displayed the dominant shift direction. However, this measurement was not always provided by the authors. Variation may have also been more representative if I was able to show standard errors (if possible), or by providing a more visual representation of the results, instead of this table.

Besides, the conclusion that a species shifted its range is not always based on the same information. Often, range shifts were described by a shift in the center of abundance of the species (the 'central' location where the species occurs most, so not the geographical center), which is the preferred method. Alternatively, in other studies, a change in the northern or southern edges of the distribution is used to describe the general shift of the species range. However, if the edge of the species' range moves north, this does not have to be a general shift northward; it may also indicate a general expansion of the species range. This is often corrected for by also reporting the change at the southern edge of the range: if this moves northward or stays constant, it can be considered a northward movement of the species range. These different ways of measuring range shifts may mean that they are not always fully comparable. Below, I will go into more detail about the different methods used in the studies to measure range shifts.

Different sampling methods

Species range shifts are not always measured in the same way, which sometimes makes them less comparable. Therefore, I would like to briefly discuss the different methods used by the studies included in this essay, and show what the main differences and possible pitfalls are.

The first methods that are used are the BBS (Breeding Bird Survey) and CBC (Christmas Bird Count), or similar long-term counting surveys outside of North America. These long-term programmes consist of many survey routes located across the country, that are used by participants to score the presence of

breeding (BBS) or wintering birds (CBC) at standardized locations and times. Participants score a species when it is seen or heard, so it is not completely certain that a bird is breeding/wintering in that location at that moment, or that it may still be migrating north/south. Secondly, a large proportion of studies uses ring recoveries to determine range shifts. Ring recoveries, like the survey data, can show population trends over long time periods. Because they depend on reading rings, wrong assignment of species is unlikely. However, also similar to the survey data, they depend on the visibility or catchability of birds. When the probability of finding a (dead) bird changes over time in different locations, the results are not a good representation of the true biology. The final main method of measuring range shifts is by using bird atlases. Whereas survey data and ring recoveries are based on continuous long-term data, bird atlases are generally used to compare two moments in time and measure the difference in species range between these two time points. These measurements provide valuable and more detailed information about the change between two time points, but lack the resolution to explain what happened in between.

In my opinion, the extra yearly ‘resolution’ provided by survey data and ring recoveries is important to be able to conclude whether species respond to climate change, and also whether these responses are phenotypic plasticity or evolutionary adaptation. If species respond to local changes in climate (temperature, precipitation, etc.), this may indicate phenotypic plasticity. Based on a comparison of only two time points, such conclusions cannot be drawn. Considering the large variation that is found between species in their range shifts, short-term combined with long-term measurements are important in learning about the way migratory birds respond to a changing climate.

Conclusion

To conclude, I think this essay provides a good overview of the studies on shifting wintering- and breeding ranges in migratory birds. The most observed shift in both sides of migration is northward, but mean shift velocity in the breeding ranges is lower, often resulting in shortened migration distances. But, shift directions are quite variable, especially in the breeding ranges. Species-specific conditions may be important in explaining this variation. Studies linking range shifts to breeding phenology are scarce, but very important for drawing conclusions about the ability of birds to adapt to climate warming. Advanced breeding is essential for migratory birds to keep up, and avoid a mismatch with the local food peak. I suggest that future research in this field focuses more on individual measurements of dispersal in the wintering- or breeding ranges, accompanied by measurements of timing of breeding and breeding success, such as Gill et al., (2019). This type of studies are not easily accomplished, but provide very important information, that we can use in our conservation efforts for migratory birds to aid in their battle with climate change.

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