Adjustment to an advancement of spring by migratory birds: four possible solutions.

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Abstract: This review will look at the empirical evidence for each of four solutions migratory birds have to adjust to the advancement of spring. The four solutions are: (1) increased migration speed, (2) advanced departure from the wintering areas, (3) northward shift of the wintering areas and (4) prolonged northward spring migration. Empirical evidence was found for the first three of the solutions, but not for a prolonged northward spring migration. The effectiveness of the solutions and the type of solution however, varied greatly between species, populations and geographical areas. This review also shows that there are constraints for each solution. Due to a lack of data en route and from the wintering areas, it not possible to fully understand the mechanisms behind these changes, phenotypic or evolutionary response, and to say which solutions are likely to be better, or if perhaps all are needed. So a lot more research on en route conditions and wintering areas needs to be done, to make future predictions of the adjustment of migratory birds to the advancement of spring.

Introduction

We live in an ever changing world, but the changes we see today are mostly by our own making. During the earth's history climates changed all the time, as it is doing today. Organisms had to show incredible flexibility in order to cope with these changes. Due to human impact however, the climate is changing more rapidly than it has before, too fast perhaps for organisms to adjust fast enough to keep up with these changes.

Migratory birds are adapted to take the best of different habitats. Using habitats with great food sources as breeding grounds and avoiding rough winters by moving to warmer regions. However, environmental conditions are not constant, so the optimal time for being in either the breeding habitat or wintering habitat is also not constant (Coppack & Both 2002). Due to ice ages and global warming, the migratory range of these birds decreased and increased dramatically. The birds thus had to be very flexible in their migration distance and timing of breeding and overwintering (Coppack & Both 2002).

It is shown that climate change has led to an advance in spring migration and arrival of migratory birds (DeLeon et al. 2011; Knudsen et al. 2011; Vegvari et al. 2010). The rate of these advancements, however varied greatly. This variation can be due to several factors such as species, life history traits and geographic region. Long-distance migrants for example are said to show a smaller phenological response to climate change than short-distance migrants (DeLeon et al. 2011). Though the evidence for this trend is not clear, it seems that such a trend is likely to exist (Knudsen et al. 2011). This variation tells us that there can be many ways these birds use to adjust to climate changes and that these solutions can differ across species (Knudsen et al. 2011; Vegvari et al. 2010).

Some migratory birds have adjusted to climate changes by advancing their spring migration and arrival, but how they do this might differ. Migratory birds have four options to achieve this advancement. (1) They can increase the speed of spring migration, thus decreasing the traveling time and arriving earlier. (2) They can advance the start of the migration, thus leaving earlier to arrive earlier. (3) They can shorten the migration distance by overwintering on higher latitudes, thus decreasing the traveling time and arriving earlier. (4) The last thing they can do is to extend their migration north to higher latitudes, where the phenology matches their reproductive demands (Coppack & Both 2002). This does not mean that these four solutions have to exclude each other. It is possible that more than one solution is needed, to achieve an advancement of spring migration.

There are two ways migratory birds can achieve these solutions. The first way is that there is behavioral variation on the onset of spring migration which, would allow the bird to adjust to the new climate conditions. This would allow for a fast response on climate changes. The second way is that micro-evolution will occur. If there is any variation in the genes controlling the onset of spring migration, selection can act on this variation by selection for birds that depart earlier, migrate faster or winter at higher latitudes. This would mean these birds arrive earlier at the breading grounds and due to the advancement of spring these birds would have a fitness advantage over the birds that arrive later. However for this selection to occur there must be a selection pressure and there must be variation in the genes controlling the onset of spring migration. Although this variation is believed to be present, it is believed to be very small due to the severe fitness cost of arriving too early or too late (Coppack & Both 2002). So even if micro-evolution could occur and behavioral variation is present, the question if these changes are big enough still remains. Migratory birds may simply not be able to advance the onset of spring migration far enough and fast enough, to be able to adjust to present and future climate changes.

Migration timing is believed to be mostly controlled by endogenous cues (Coppack & Both 2002). So although climate change has mostly an effect on temperature, the timing of migration is not determined by temperature. Besides endogenous cues, the birds condition is also an imported factor in the onset of migration. The bird's condition is dependant on the conditions in the wintering areas. So there might be certain constraints on the four solutions mentioned before. A bird may not be able to advance spring migration, because the timing of moult is not able to advance. Or shift the wintering areas northward, because conditions more northward are not suitable.

In this review I will look at how much evidence there is for each of the four solutions and which are more likely to be used. I will do so by discussing each solution separately and looking at how much evidence there is for each solution and if the bird's life-history-traits make the solution even possible.

Migration speed

Increasing migration speed can be a good solution for advancing spring migration. By increasing flight speed and shortening stopover time, they can shorten their total migration time and thus arrive earlier in their breeding grounds. However due to the high energy cost, birds may simply not be able to increase their flight speed. So for some species the flight speed may already be at the optimum (Coppack & Both 2002; Hedenström 2007). Climate change however does not only influence the breeding grounds but also influences the weather and food availability in the stopover sites. Climate change can thus potentially positively influence the stopover conditions, causing better weather conditions and earlier food peaks, which may allow for an increase in migration speed (Coppack & Both 2002; Hedenström et al. 2007)

In a North American study, the median capture dates of 15 Nearctic-Neotropical migratory bird species between a ringing station in the Gulf Coast of Louisiana (GCL) and two stations 2500 km north, Long Point Bird Observatory (LPBO) and Powdermill Nature Reserve (PNR), were compared (Marra et al. 2005). All of these species showed a trend of arriving earlier in the breeding grounds in warmer years and arriving later in colder years: -1 day/°C spring temperature averaged across the species. Of the 15 species studied, 13 species showed a decrease in traveling time between either GCL and LPBO or GCL and PNR (see table 1). The study showed that the interval between the medium capture dates in the south and northern ringing stations was inversely correlated with temperature. The average interval of 22 days decreased by 0,8 days per 1 °C increase in spring temperature, thus the birds are adjusting their migration rate to temperature increase.

It is unlikely that they would change winter departure dates by using changes in spring climate conditions in the breeding areas as cues, due to the assumption that most long-distance migrants primarily use endogenous cues to trigger migration. One possibility is that migratory birds use correlated environmental changes en route as cues to either delay or advance departure. However no such correlation was found in this study among eastern North American migratory birds. Instead it found that the birds adjust their migration rate to match annual variation in temperatures, making use of the improved conditions en route.

The idea that migration rate can be increased by improved conditions en route was also suggested by Both, who commented on a study done in Italy (Jonzén et al 2006). The study found an advancement in spring migration time through Italy and southern Fennoscandia in African-Palearctic long-distance migratory birds and argued this was due to evolutionary changes. This can however not be possible due to the lack of selection pressure (Both 2007). Instead, Both argued that phenotypic responses are more likely to be responsible. Increased rainfall in the Sahel probably improved migration conditions (Both 2007; Both 2010; Hedenström et al. 2007). These improved conditions could lead to an increase in migration speed by increasing fuelling rates and decreasing stopover time (Coppack & Both 2002).

The effect of the Sahel rainfall was shown for the pied flycatcher that arrived earlier in years with more rainfall in the preceding winter (Both 2010). The future predictions for Sahel rainfall are however negative (Both 2010), which means that African-Palearctic long-distance migratory birds can no longer profit from improved conditions en thus speeds up their migration. Both also showed that the migration dates through Northern Africa of the pied flycatcher have advanced with about 10 days. The arrival date in the breeding grounds in Central and in Western Europe however did not change accordingly, suggestion that certain factors en route from North Africa to the breeding grounds impose certain constraints on the migration speed. It is shown that migration speed can be greatly influenced by temperature (Both 2010). Though the spring temperatures have increased, the temperatures the birds encounter during their migration through Europe have not (Both 2010). This means that the migration speed of the pied flycatcher has been slowed down by unfavorable conditions en route from North Africa. Future predictions of the Sahel rainfall, makes it also likely that in the future the conditions en route to North Africa will worsen. These unfavorable conditions in Europe and the predicted unfavorable conditions in Africa make it unlikely the pied flycatcher will be able to speed up its migration speed.

A recent study however found completely the opposite result, arguing that migration speed to Europe has speed up and the passage of the Sahara Desert is delayed (Tøttrup et al. 2008). The study used ringing data from five long-distance migratory birds trapped en route from their wintering areas in Africa through the Middle East to their breeding grounds in Northern Europe. The study showed that improved conditions in the wintering areas delayed the onset of spring migration, suggestion that they make use of these improved conditions to optimize the chance of passing the Sahara Desert (Tøttrup et al. 2008). The birds did however advance their arrival in the North European breeding grounds. This means they had to speed up their migration through Europe to be able to achieve this. The only way they can speed up their European migration is if the conditions en route had improved, and they did indeed improve (Tøttrup et al. 2008).

The difference between these two studies may be the result of the monitoring of different populations, which may have different migratory strategies. Another reason could be that the conditions in western flyway have improved and thus allowing for faster migration. This may not be the case in the eastern flyway (Tøttrup et al. 2008).

That migratory birds can speed up their migration was also shown in a theoretical study, in which they compared recent trends among migratory bird species, having either summer or winter moult (Hedenström et al. 2007). It found that the species from both moult scenarios advanced their spring migration, but only the species from the summer moult scenario advanced their departure from the winter areas. The species with the winter moult did not advance their departure, thus to achieve the advance in spring arrival they had to speed up their migration.

That species differ in their adjustment of migration speed becomes clear in the case of the Pink-footed Goose. The geese have advanced their departure from the wintering grounds in Denmark due to improved local conditions. Their departure from stopover sites in Mid Norway and North Norway however did not advance and neither did their arrival at the breeding grounds (Bauer et al. 2008). This means that the conditions en route were not suitable enough to continue the advancement along the whole route and thus the Pink-footed Geese had to slow down their migration northward (see table 1).

Species	Migrant type	Spring arrival	Wintering area data	Summer area data	migration speed	Source
Swainson's Thrush	Long-distance	-1 day/C averaged across the species		Powdermill Nature Reserve	-3,95 days/year	Marra et al. 2004
Red-Eyed Vireo	Long-distance	-1 day/C averaged across the species		Powdermill Nature Reserve	-3,66 days/year	Marra et al. 2004
White-eyed Vireo	Long-distance	-1 day/C averaged across the species		Powdermill Nature Reserve	-2.98 days/year	Marra et al. 2004
Tennessee Warbler	Long-distance	-1 day/C averaged across the species		Powdermill Nature Reserve	-2,01 days/year	Marra et al. 2004
Hooded Warbler	Long-distance	-1 day/C averaged across the species		Powdermill Nature Reserve	-0,46 days/year	Marra et al. 2004
Common Yellowthroat	Long-distance	-1 day/C averaged across the species		Powdermill Nature Reserve	-1,19 days/year	Marra et al. 2004
Northern Waterthrush	Long-distance	-1 day/C averaged across the species		Powdermill Nature Reserve	-0.63 days/year	Marra et al. 2004
Indigo Bunting	Long-distance	-1 day/C averaged across the species		Powdermill Nature Reserve	-0,34 days/year	Marra et al. 2004
Grey Catbird	Long-distance	-1 day/C averaged across the species		Long Point Bird Observatory	-0,74 days/year	Marra et al. 2004
Swainson's Thrush	Long-distance	-1 day/C averaged across the species		Long Point Bird Observatory	-0,14 days/year	Marra et al. 2004
Wood Thrush	Long-distance	-1 day/C averaged across the species		Long Point Bird Observatory	-1,40 days/year	Marra et al. 2004
Red-Eyed Vireo	Long-distance	-1 day/C averaged across the species		Long Point Bird Observatory	-6,70 days/year	Marra et al. 2004
Magnolia Warbler	Long-distance	-1 day/C averaged across the species		Long Point Bird Observatory	-0,80 days/year	Marra et al. 2004
Common Yellowthroat	Long-distance	-1 day/C averaged across the species		Long Point Bird Observatory	-1,81 days/year	Marra et al. 2004
Ovenbird	Long-distance	-1 day/C averaged across the species		Long Point Bird Observatory	-0,39 days/year	Marra et al. 2004
Indigo Bunting	Long-distance	-1 day/C averaged across the species		Long Point Bird Observatory	-1,30 days/year	Marra et al. 2004
Rose-breasted Grosbeak	Long-distance	-1 day/C averaged across the species		Long Point Bird Observatory	-0,90 days/year	Marra et al. 2004
pink-footed Geese	Long-distance	0 days ?	denmark		longer stopover in Norway	Bauer et al. 2008

Table 1 Shifts in migration speed and spring arrival for several long-distance migratory bird species. Spring arrival is averaged for all species studied by Mara et al.

Advanced departure

Another possible way migratory birds can advance their spring migration is by earlier departure from wintering areas (Coppack & Both 2002). It looks like a good solution, leaving earlier to arrive earlier, but it is not that simple. The onset of spring migration is believed to mostly controlled by endogenous cues, so a change in onset of spring migration would require a change in the birds circannual rhythm (Coppack & Both 2002). This would require either genetic variation or behavioral variation to be present, to allow for plasticity in the onset of spring migration. This variation however is believed to be low, due to the server fitness cost of being too early or too late (Coppack & Both 2002). Besides this variation in the onset of spring migration, it should also be possible for the bird to depart earlier. Fattening up and moult could prevent the bird from leaving the wintering grounds earlier.

This constraint becomes clear in the case of the barn swallow. The barn swallow has advanced its spring migration by four to eight days. A recent study has shown that the barn swallow might achieve this by earlier departure from their wintering areas in South Africa (Altwegg et al. 2011). This study showed that barn swallows wintering in Gauteng (northernmost South African province) have advanced their departure by four to eight days, which corresponds nicely with their earlier arrival in the breeding grounds. However the other regions studied, Western Cape and KwaZulu-Natal, did not show this advancement. The birds that winter in the KwaZulu-Natal region showed no sign of earlier departure and the birds wintering in the Western Cape region even showed a delay of six days (see table 2). It can be that there are constraints on leaving earlier from KwaZulu-Natal and the Western Cape. Barn swallows need to complete their moult before they start their migration. The full completion of this moult would takes at least 135 days, which is close to the time spent in the Western Cape region, which is 140 days (Altwegg et al. 2011). The Western Cape is the southernmost wintering region and has thus the shortest residence time. The other two regions are more northward and thus have a longer residence time, which thus allow for more flexibility in departure date. This can explain why the birds wintering in Gauteng did advance their departure and the birds wintering in KwaZulu-Natal and the Western Cape did not.

Another study, which investigated the advancement of spring arrival in nine long-distance migratory bird species, showed that these birds had advanced their arrival in northern Europe in all stages of migration (Jonzén et al. 2006). It argued that this is due to climate-driven evolutionary changes in the timing of spring migration. They say that it cannot be a phenotypic response, because increasing African temperatures should delay the departure from the wintering areas, and can thus not be responsible for the earlier arrival dates. Even though the onset of migration is under endogenous control, there is variation in the onset of spring migration between different individuals (Jonzén et al. 2006). This variation would allow for selection on earlier departure dates. As mentioned before, Both did not agree with the conclusions of this study. He found it more likely that phenotypic response were responsible (Both 2007).

A study done in Oxfordshire (U.K.), on the arrival dates of 20 long-distance migratory bird species, found that the arrival dates in Oxfordshire had advanced eight days (Cotton 2003). No effects of the NAOI (North Atlantic Oscillation Index, an index of air pressure over the North Atlantic Ocean) on arrival dates were found, instead a negative correlation of sub-Saharan African temperatures on arrival dates was found. This suggested that the departure dates from the wintering areas have advanced. Arrival in the European breeding grounds is thus not affected by climate conditions in the breeding ground but by conditions in the wintering areas. Improved conditions in the wintering areas can therefore allow for an advancement in the onset of spring migration. This strong relationship between sub-Saharan African temperatures and arrival dates in the breeding grounds, suggests that a phenotypic response is responsible for the changes and not evolutionary changes (Cotton 2003).

So conditions in wintering grounds affect the arrival dates in the breeding grounds. So if birds use local climate changes as cues, how can they predict the climate changes in the breeding grounds, which are thousands of miles north of their wintering areas. A recent study showed that they possibly can predict the condition in the breeding grounds (Saino and Ambrosini 2008). It showed that temperature anomalies in sub-Saharan Africa north of the Equator in the late wintering season can predict temperature anomalies in Europe during the next two months, when the earliest migrants arrive. So by reacting to local changes in the wintering area they can indirectly react to changes in their breeding area. This would allow the birds to fine tune their migration in terms of departure date and migration speed (Saino & Ambrosini 2008). Being able to predict possible improved environmental conditions further on in the migration schedule would allow them to leave the wintering areas as soon as possible, without the cost of encountering unfavorable weather conditions en route. This means that migratory birds are able to advance their departure from the winter grounds to adjust for the advancement of spring in the breeding grounds.

As mentioned before the Pink-footed Goose has advanced its departure from wintering areas in Denmark, due to improved local conditions, only to be slowed down by unfavorable conditions en route (Bauer et al. 2008). This shows that birds wintering in Europe, are also able to advance departure from wintering areas (see table 2).

That species may differ in their reaction on climate change, is shown in the case of the Barnacle goose. Recently Barnacle Geese breeding in the Russian Arctic have delayed their departure from wintering areas in the Netherland by a month (Jonker et al. 2010) (see table 2). It was found that an advanced onset of spring could not explain such a delay. This is logical because an advanced onset of spring would predict an advanced departure, not a delayed departure. Instead simulations made it likely that it could be better explained by either decreased potential intake rates or increased predation danger in the Baltic stopover site. Although this delay of departure is likely not caused by an advanced spring, it does show there is flexibility in departure dates from wintering areas. This flexibility may be useful to adjust to future climate changes.

Species	Migrant type	Spring arrival	Wintering area data	Departure wintering area	Source
barn swallow	Long-distance	- 4-8 days	Gauteng	- 4-8 days	Altwegg et al. 2011
barn swallow	Long-distance		KwaZulu-Natal	0 days (perhaps constraint by moult)	Altwegg et al. 2011
barn swallow	Long-distance		Western Cape	+ 6 days (perhaps constraint by moult)	Altwegg et al. 2011
pink-footed Geese	Long-distance	0 days ?	denmark	advanced	Bauer et al. 2008
barnacle geese	Long-distance	0 days?	Netherlands	Delayed one month	Jonker et al. 2010

Table 2 Shifts in departure from the wintering areas and spring arrival for several long-distance migratory bird species

Northward shift of the wintering areas

Another way, besides speeding up their migration and advancing departure, for migratory birds to arrive earlier at their breeding grounds, would be by shortening migration distance (Coppack & Both 2002). By shifting their wintering areas northward, they shorten their migration distance and can thus arrive earlier at the breeding grounds. Another reason why a northward shift of the wintering areas would be favorable is that they may be able to better predict the onset of spring in their breeding grounds (Visser et al. 2009).

A problem with this solution is that the birds wintering higher north will experience very different photoperiodic conditions than they encounter on their current wintering areas (Coppack & Both 2002). However during their evolutionary history, long-distance migratory birds may have wintered higher north before, so adaptive responses to photoperiodic variation may still be present (Coppack & Both 2002). This was recently tested in a indoor experiment on Pied Flycatchers. The results suggested that Pied Flycatchers wintering higher north will be able to advance pre-breeding moult, the onset of spring migration activity, and gonadal maturation (Coppack et al. 2008; Coppack & Both 2002). However wintering much higher north did not show more advancement, suggestion the Pied Flycatcher is only able to shift their wintering areas northward to a certain point (Coppack et al. 2008).

That migratory birds can indeed shift their wintering grounds, is shown in a study done on short-distance migrants (Visser et al. 2009). It showed that winter recovery distances have reduced over the past seven decades, for birds ringed during the breeding season in the Netherlands. Of the 24 bird species studied, 21 showed a decrease in migration distance. Of these 21 species, 12 showed a significant decrease in migration distance (see table 3). This decrease in migration distance could partially be explained by variation in local Dutch winter temperatures, with smaller migration distance in warmer winters (Visser et al. 2009). However a significant year effect was also found, which means there are unexplained variables that affect changes in migration distance.

Another study done on short-distance migratory birds, ringed in Germany, showed that birds breeding in Germany also reduced their migration distance (Fiedler et al. 2004). Of the 30 bird species studied, 18 showed a decrease in migration distance. Of these, 8 showed a significant decrease in migration distance (see table 3.). However the other 12 species studied showed an increase in migration distance, of which 5 showed a significant increase (see table 3.). The decrease of migration distance in 8 of the species corresponds nicely with the expectation that under warmer climate conditions birds are likely to winter closer to their breeding grounds (Fiedler et al. 2004). The increase in migration distance in 5 other species suggests, that maybe more is going one. However, the study stated that some of the detected increases in migration distance could be attributed to methodological problems.

Not only European birds are shown to have decreased their migration distance by shifting their wintering areas northward, also birds wintering in North America have shown to shift their wintering areas northward (La Sorte & Thompson 2007). 254 bird species (migratory and non migratory birds) were studied, using data from the North American Christmas Bird Count (1975-2004). The study showed that there was a trend of a northward shift of the wintering ranges, but the magnitude of this trend varied greatly among the different species.

That not only short-distance migratory birds can shift their wintering grounds northward is shown in a recent study, which looked at ringing recovery data (1912-2008) from a long-distance migratory passerine bird, the barn swallow (Ambrosini et al. 2011). It showed that the barn swallow shifted its wintering grounds northward at a rate of 3 to 9 km/year. The birds could be assigned to two clusters that segregated their wintering grounds approximately at 10° S. These clusters differ significantly in their shift of the wintering grounds. The southern cluster shifted northward 2 to 3 times stronger (8.89 ± 1.22 km/ year) than the northern cluster (3.45 ± 1.44 km/year) and the northern cluster showed a 4 to 5 times stronger eastward shift (0.118 ± 0.028°/year) than the southern cluster (0.023 ± 0.010°/year). The smaller shift northward by the northern cluster might be caused by the Sahara Desert bordering the north of the northern cluster, and thus constraining the northward shift. The southern cluster may thus have less constraints in their northward shift (Ambrosini et al. 2011). The eastern shift of the northern cluster may by a consequence of the expansion of the Sahara Desert, which forces the birds to winter farther to the east (Ambrosini et al. 2011).

Species	**Migrant type**	**Spring arrival**	**Wintering area data**	**Migration distance/Northward shift winter area**	**Source**
Eider	Short-distance			-0.028 (log distance versus year slope)	Visser et al. 2009
Hen Harrier	Short-distance			-0.005 (log distance versus year slope)	Visser et al. 2009
Buzzard	Short-distance			-0.004 (log distance versus year slope)	Visser et al. 2009
Kestrel	Short-distance			-0.006 (log distance versus year slope)	Visser et al. 2009
Oyste catcher	Short-distance			-0.009 (log distance versus year slope)	Visser et al. 2009

Lapwing	Short-distance			-0.007 (log distance versus year slope)	Visser et al. 2009
Black-headed Gull	Short-distance			-0.017 (log distance versus year slope)	Visser et al. 2009
Common Gull	Short-distance			-0.014 (log distance versus year slope)	Visser et al. 2009
Barn Owl	Short-distance			-0.009 (log distance versus year slope)	Visser et al. 2009
Long-eared Owl	Short-distance			-0.018 (log distance versus year slope)	Visser et al. 2009
Great Tit	Short-distance			-0.007 (log distance versus year slope)	Visser et al. 2009
Starling	Short-distance			-0.004 (log distance versus year slope)	Visser et al. 2009
Common Shelduck	Short-distance			-0.51 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Eurasian Sparrowhawk	Short-distance			-0.27 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Northern Lapwing	Short-distance			-0.27 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Common Gul	Short-distance			-0.11 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Black Redstart	Short-distance			-0.33 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Common Blackbird	Short-distance			-0.14 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
European Greenfinch	Short-distance			-0.67 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Eurasian Bullfinch	Short-distance			-0.28 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Stock Dove	Short-distance			0.202 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Common Wood Pigeon	Short-distance			0.348 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Song Thrush	Short-distance			0.234 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Common Starling	Short-distance			0.572 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
European Goldfinch	Short-distance			0.371 (regression coefficient (year of recovery/recovery distance(km)))	Fiedler et al. 2004
Barn Swallow	Long-distance	Advanced	North of 10° S	3.45 ± 1.44 km/year	Ambrosini et al. 2011
Barn Swallow	Long-distance	Advanced	South of 10° S	8.89 ± 1.22 km/year	Ambrosini et al. 2011

Table 3 Shifts migration distance for several short-distance and long-distance migratory bird species. From the studies from Visser et al. and Fiedler et al. only the birds that showed significant changes in migration distance are shown.

Northward shift of the breeding areas

The last way migratory birds can adjust to the advancement of spring is by prolonging their northward spring migration and thus shifting their breeding areas northward. By doing this they move to areas where the phenology matches their ecological and physiological requirements and avoid unsuitable breeding conditions in the south (Coppack & Both 2002).Global warming has indeed moved the northern margin of birds breeding in Europe further north (Coppack & Both 2002). I found however no empirical evidence that a trend of a prolonged northward spring migration is going on.

Discussion

It seems that there is a great amount of variation in the solutions migratory birds use to advance their spring migration. Increasing migration speed, advancing departure dates and wintering at higher latitudes all seem to be possible solutions. Only for a prolonged northward spring migration there was a lack of empirical evidence, but this does not mean that it cannot be a possible solution. Climate change is shifting the northern boundaries of many species further north, so it could be possible that in the future species will breed at higher latitudes.

So a faster migration speed, advanced departure dates and wintering further north seem to be good solutions to be able to adjust to the advancement of spring. It can however not be said which solution is more likely to occur. There is a lot of variation in possible solutions between different species, different populations and different geographical regions. The barn swallow for example advanced departure dates in Northern South Africa but did not advance departure dates in South Africa (Altwegg et al. 2011). The southern population is probably constrained by the duration of moult, which prevents them to leave earlier. The northern population has not such a constraint and can thus advance departure dates. This means that the northern population has an advantage over the southern populations. So in the future, barn swallow populations might be wintering further north, in order to depart earlier. This also shows that one solution is perhaps not enough to adjust to climate changes, but that multiple solutions are needed to keep up with the changes.

Geographical regions also have an impact on which solution to use. Pied Flycatchers for example, have speed up their passage of the Sahara Desert, but slowed down their migration through Europe (Both 2010). Another study showed that birds using the eastern flyway (Pied Flycatchers use the western flyway), delayed their passage of the Sahara Desert and speed up migration through Europe (Tøttrup et al. 2008). In the western flyway conditions en route to northern Africa probably improved, and in the eastern flyway they have not. Better conditions en route would allow for a shorter stopover time and thus speed up migration. This shows that climate change differs per region. Different regions are affected differently, so differences in solutions are to be expected between different geographical regions.

Another difference is that between short-distance migrants and long-distance migrants. Short-distance migrants seem to adjust better to climate changes than long-distance migrants (Both & te Marvelde 2007). Due to their shorter migration distance short-distance migratory birds may be able to better predict conditions in the breeding areas. Trends in northward shifts of wintering areas are also found more in short-distance migrants than in long-distance migrants. However not much research is done on northward shifts in long-distance migrants, which could be responsible for the bias to short-distance migrants. The case of the barn swallow shows however that a long-distance migrant is also able to shift their wintering area northward. The case of the barn swallow showed also again the impact of geographical regions. Northern populations were limited in their northward shift by the Sahara Desert in the north.

So the solutions, if they are possible, are in many cases constrained by other life-history traits or specific geographical conditions. So besides the question if they can adjust to climate change, we should also ask the question if they can adjust enough. Faster migration speed is limited by conditions en route and stopover time. Due to climate change conditions en route will improve in certain areas and will thus allow for faster migration. But at a certain point migration cannot be speed up anymore and stopover time will be optimal. Northward shifts of wintering areas are limited by conditions up north and adaptive responses to photoperiodic variation. The advantage of wintering at higher latitudes is evened out by the disadvantage of worsening conditions in the northern winter areas. An advancement of departure days is possible, but only if other life-history traits allow for it. Fattening up and moult forces the bird to spend a minimum amount of time in the wintering areas and departure can thus only be advanced to a certain point.

Empirical evidence is thus present that migratory birds use three of the four solutions to advance spring migration. But if this response is a phenotypic response or a micro-evolutionary response is not known. It is likely that the changes in migration speed are due to improved conditions en route and not by micro-evolution. But for shifts in departure date and latitude of wintering areas it is not known. Improved conditions could be responsible for the shifts. It is however shown that some species show genetic variation in the timing of spring arrival and onset of spring migration (Coppack & Both 2002). And this may perhaps also be the case for wintering latitudes. However little is known about selection pressures en route and selection pressure in the breeding areas may not always be present (Both 2007). There is also little known about the wintering areas of different populations. So it is hard to determine which bird winters where and when it leaves, making it impossible to say if micro-evolution is going one. There is however little doubt that evolutionary changes will occur in the future (Both 2007), but how fast and with what magnitude cannot be said.

Migratory birds are able to adjust to the advancement of spring, be it by faster migration speed, advanced departure or more northern wintering areas. It seems that an increased migration speed is the easiest solution, because it is not constrained by geographical locations and other life-history events. But it is dependent on improved conditions en route. However the same can be said about the northward shift of the wintering areas, which can only be possible if conditions further north are suitable enough. Each solution has its advantages and disadvantages and a lot more research is needed to be able to fully understand these changes and to say if these adjustments will be fast enough and large enough to keep up with climate changes. Especially a lack of data of the wintering areas and en route conditions of migratory birds prevent a good understanding of what is going one. So future research should be focused on en route conditions and wintering areas to be able to make good predictions about the future of migratory birds.

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