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Bird migration in a warming world: A review of challenges and potential adaptations

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Abstract: Migratory bird species are expected to be heavily affected by climate change as they experience and need to keep in tune with a great variety of environmental factors during their migration cycle spanning an often-large geographical range. At high latitudes, climate change is advancing the onset of spring changing the phenology of different trophic levels, affecting the timing of food peaks on which migrants rely when breeding, but also aspects like the phenology of their predators. In terms of maximizing fitness, migratory birds heavily rely on timing their migration right and are expected to be affected by these changes in phenology. In this essay, I investigate 1) how migratory birds are affected during different stages of their migration and 2) if there is any evidence that they are adapting to a warming world and by what mechanisms they can do so? Based on a literature survey, I found that climate change has different effects along the flyway of migrating birds. At wintering grounds and on stop-over sites, unpredictable changes in weather, such as droughts and periods of high precipitation, are reported to affect food abundance. Droughts can make it difficult for migratory birds to gain enough energy to fuel their migration and can affect survival during migration. In flight, changes in weather patterns and extremes, are expected to increase mortality but could also increase flight speed. At breeding grounds, the well-studied trophic mismatch between bird migration and food peaks affects food abundance during the breeding season, leading to decreased fitness. Four hypotheses have been stated by which migratory birds may adapt their migration to keep up with advancing breeding seasons. Based on a literature review I conclude that increasing migration speed is not likely an effective adaptation to arrive earlier at breeding grounds as this is very dependent on stop-over duration, flight speed and migration distance. Other adaptations, such as an earlier onset of migration are already widely reported in several species. The same is observed in terms of shifts of wintering and breeding grounds, where species winter closer to breeding grounds to reduce migration distance or breed further poleward to compensate for an earlier onset of spring. Two other currently less well-studied hypothesized adaptations have been observed in some species: altitudinal shifts and becoming resident. From this essay, I conclude that to gain a full comprehension of the effect of climate change on bird migration, research should focus on the combined effects during the whole migration cycle. Previous research mainly focussed on documenting the effects of climate warming on the breeding grounds whereas environmental changes in the wintering and staging areas and during migration flights should not be neglected. To gain a complete understanding of the effects of climate change, research should focus as well on documenting the influence of indirect effects of climate change, such as human-induced changes in land use, on migratory birds. Adaptations have been observed, sometimes multiple adaptations in one species. To gain a full insight into the potential and success of adaptations for migrants more experimental research is needed. This could aid in creating conservation strategies to protect critically endangered species.

Keywords: Avian migration, climate change, phenology, adaptations, conservation, HIREC.

CONTENTS

1. Introduction

Climate change and loss of biodiversity have been proceeding rapidly in the recent past and are strongly intertwined (Butchart *et al.* 2010; Bellard *et al.* 2012; Habibullah *et al.* 2022). Worrying predictions of temperature rise show an expected average 2º C rise globally with higher temperature rises closer to the poles (*IPCC* 2021). Climate change at high latitudes is expected to result in a later beginning of winter and earlier onset of spring (Parmesan 2006; Trenberth 2011). Climate change has already negatively affected many organisms, varying from vertebrates, to whole ecosystems such as coral reefs and mangroves (Parmesan 2006; Butchart *et al.* 2010). One major obstacle species have to cope with is the change in timing of resources, especially species occurring in areas with high seasonality (Visser & Both 2005; Bradshaw & Holzapfel 2008; Pulido & Berthold 2010). Migratory birds are a group of species which are highly dependent on seasonal timing or phenology. Migration from wintering to breeding grounds should be timed right to assure maximal food abundance while breeding (Brown & Sherry 2006; Newton & Brockie 2008; Seward *et al.* 2013).

Bird migration is an annual, occurring movement where birds move to lower latitudes during non-breeding periods and high latitudes during their breeding season (Newton & Brockie 2008). For migratory behaviour to evolve it is generally expected that such behaviour involves an overall higher fitness relative to staying year-round at either the higher or lower latitudes (Alerstam & Enckell 1979; Møller & Szép 2011). Seasonal changes in environmental conditions at high latitudes are considered to be one of the main drivers of migration, but seasonality is also present near the equator in terms of, for example, dry and wet seasons (Varpe 2017). Such changes in environmental conditions result in periods of low and higher habitat quality. Seasonal changes in food availability, for example in temperate regions, are considered one of the most important drivers of annual bird migration (Visser *et al.* 2012; Reed *et al.* 2013). Seasonal food availability plays an important role in migration, for example in fuelling up before migration and in the timing of breeding. Migratory birds need to fuel up before and during migration to have enough energy to fly long distances (Brown & Sherry 2006; Newton & Brockie 2008). In addition, migratory birds need to arrive at their breeding grounds when vegetation starts growing to match breeding with the food peak (Both & Marvelde 2007). Migratory birds need to be adapted to anticipate these periodic differences in habitat quality. In addition, there is strong evidence that bird migration from tropical to arctic habitats evolved to escape from a great diversity of pathogens found in tropical habitats (Piersma 1997; Poulin & de Angeli Dutra 2021). However, migrating birds are also more likely to be exposed to a broader parasite richness along their flyway (Gutiérrez *et al.* 2019). Besides tracking food peaks or mitigating the impact of pathogens, higher trophic levels can as well be a driver for migration as migrating birds try to minimise predation risk by birds of prey (Charmantier & Gienapp 2014). Predation is seen as a potentially important factor affecting bird migration, several aspects of migration could be influenced such as timing of migration and site selection at wintering, stop-over and breeding sites (Alerstam 2011).

Thus, timing plays an important role in migration, but how does a migrating bird know when to leave to arrive at the right time? Change in day-length, or photoperiod, is considered as one of the most important environmental cues to time seasonal life-history events (Bradshaw & Holzapfel 2007; Visser *et al.* 2010). For birds, concerning the timing of events such as moulting, breeding, and migration, this is no different. Internal circannual rhythms are triggered by external cues such as photoperiod to assure the right timing in these life-history events (Helm *et al.* 2013). External changes such as changes in the length of daylight in temperate zones or changes in temperature trigger migratory species to migrate to higher latitudes (Sokolov & Tsvey 2016). Short-distance migratory birds are more likely to be well informed as local environmental changes could present information on conditions on the breeding grounds. Near the equator, where changes in photoperiod or temperature are low, the timing of migration is more likely regulated by internal time-keeping (Helm *et al.* 2013; Sokolov & Tsvey 2016). Such circannual rhythms are needed near the equator as, for example, photoperiod is more or less constant throughout the seasons and therefore life-history events are more genetically wired (Gwinner 1996, 2003; Helm *et al.* 2013). Long-distance migratory birds are less likely to adjust the timing of migration based on environmental conditions as information on the wintering grounds does not give information on environmental conditions on the breeding grounds (Both *et al.* 2006). Hence, climate change-induced changes in environmental conditions could impose a phenological mismatch, especially in long-distant migratory species. This is thought to be one of the causes of the decline in, for example, Afro-Palearctic (hereafter A-P) migrants (Vickery *et al.* 2014).

Previous research on the effect of climate change on bird migration has predominantly focussed on the relationship between the timing of migration and shifts in food abundance on the breeding grounds (Miller-Rushing *et al.* 2008; Charmantier & Gienapp 2014). Adaptations of migratory birds to shifts in food abundance have been reviewed on several occasions [for example: Charmantier & Gienapp (2014); Zhemchuzhnikov *et al.* (2021)]. However, climate change affects migrating birds at different stages of migration, such as at the wintering grounds, and staging sites but also during migration. For example, global increasing temperatures are expected to cause more droughts and more intense storms with heavy rainfall (Trenberth 2011). Such weather changes could have adverse effects on different stages of migration. In addition, adaptations of migratory birds to climate change might not be dependent on just one effect of climate change, such as an earlier onset of spring on the breeding grounds but be influenced by multiple effects experienced by birds throughout their whole migration cycle. Besides differences during migration, there is evidence that climate change does not affect all migratory birds equally. For example, migratory birds of different flyways, face different environmental alterations due to climate change (Askeyev *et al.* 2010; Harris *et al.* 2013). In previous studies, research has mainly focused on American and European species. Causes of declines in Afro-Palaearctic migrants have been reviewed by Vickery *et al.* (2014) who looked at the most important factors causing the decline. To my knowledge, no review has yet been made on how climate change affects migratory birds globally specifically focussing on the different stages of migration, and how much evidence on adaptations to climate change there is.

In this essay I will attempt to somewhat close this gap, using a similar structure as Vickery *et al.* (2014). I provide a literature overview, on how climate change affects migrating birds during different stages of their migration (chapter 2). By doing so, I intend to answer the question: (1) *"How does climate change affect bird migration along their flyway?"*. In addition, using a previous study by Coppack & Both (2002) as a baseline, I aim to find out how much evidence there is for different hypotheses on how migratory birds could adjust their spring migration to cope with climate change (chapter 3). I will attempt to answer: (2) *"Is evidence found for these hypotheses, and will the observed adaptation be sufficient for migratory bird species to cope in a warming world?"*.

2. Climate change along the flyway

Climate change is expected to affect migratory birds differently during the various stages of their migration cycle. Birds face multiple challenges during migration. Birds need to fuel up before migration, face various weather conditions during migration and need to arrive at the right time on the breeding grounds after migration (Newton & Brockie 2008; Alerstam 2011). In this chapter, I will investigate how climate change affects different stages of migration based on illustrative case studies. As migration is a complex phenomenon, I will only scratch the surface of what is known. However, by showing several case studies I aim to illustrate the complexity of the problem.

2.1. *Wintering grounds*

Barbet-Massin *et al.* (2009) predicts that by 2100 37 A-P migrant passerines will have undergone range reduction in their wintering grounds. These predictions have been made based on IPCC climate simulations of temperature and precipitation changes in wintering grounds. A-P migrants heavily rely on rainfall in the Sahel zone of Africa, as this provides good food resources needed to migrate (Vickery *et al.* 2014; Mondain-Monval *et al.* 2020). There is strong evidence that precipitation in the Sahel is an important driver for populations wintering in the Sahel (Ockendon *et al.* 2014). After a period of drought around the 1980s rainfall has recovered but the continuation of this trend is highly uncertain with droughts still occurring and various model predictions predicting either increasing drought or increasing precipitation (Chappell & Agnew 2004; Ben Mohamed 2011; Vickery *et al.* 2014; Biasutti 2019). Hence, it is difficult to predict how species wintering in the Sahel will be affected by climate change.

Migratory species from American continents, breeding in North America and wintering in the tropics, show a similar trend. Lack of precipitation and drought negatively affects the annual survival of migratory birds wintering in central America (McKinnon *et al.* 2015; La Sorte *et al.* 2017; Rockwell *et al.* 2017). Drought reduces food availability and in turn, has a negative effect on body condition and lowers the energy intake needed to migrate to breeding grounds (McKinnon *et al.* 2015). As droughts are expected to become more frequent in central America, populations wintering here are expected to decrease (Hidalgo *et al.* 2013).

However, climate change on the wintering grounds does not always affect migratory birds negatively. For example, Higuchi (2012) found a positive correlation between breeding success of whistling swans *Cygnus columbianus* and higher temperatures along the flyway and reduced snowfall in the wintering sites in Japan. Higuchi hypothesised that, with reduced snowfall, whistling swans can more easily forage in wintering grounds, increasing their survival (Higuchi 2012). However, it is important to note that this correlation is mainly based on population trends in relation to temperature. The causality between temperature and breeding success needs to be experimentally tested, if possible. Nevertheless, this is not the only case where climate change is expected to have a positive effect on a migrating bird population. Reduced precipitation on the wintering grounds and earlier onset of spring on the breeding grounds positively affected the survival of burrowing owls *Athene cunicularia* and barnacle geese *Branta leucopsis* respectively [for further reading see: Wellicome *et al.* (2014); Layton-Matthews *et al.* (2020)].

2.2. *During migration and staging sites*

During migration, migratory birds are exposed to several environmental factors which could complicate their journey. Body condition during migration, stopover site quality and weather conditions all potentially affect population levels of migratory birds [for an in-depth review see Newton (2006)]. For stopover sites, similar problems occur as for wintering grounds. Increasing droughts decrease food quality and abundance threatening the energy intake of migratory birds, needed for further migration. For example, the Sahel region is not only used as a wintering ground but also as a stopover site for migratory birds travelling from areas in southern African countries (Jenni-Eiermann *et al.* 2011; Tøttrup *et al.* 2012). Hence, the previously mentioned threats, such as the potential increase of droughts in the Sahel, could limit food intake during a stopover, making further migration more difficult.

The mortality in migratory raptor species such as osprey *Pandion haliaetus*, Montagu's harrier *Circus pygargus* and marsh harrier *Circus aeruginosus*, is highest during migration (Klaassen *et al.* 2014). Despite uncertainty on the reason for this high mortality, it is hypothesized that mortality is linked to weather conditions, such as adverse wind conditions, and climatic extremes are known causes of mass mortality in migratory birds (Newton 2007; Klaassen *et al.* 2014; Haest *et al.* 2019; Loonstra *et al.* 2019). In line with this hypothesis, authors working on burrowing owls found a negative relation between spring and autumn storm events and survival, suggesting an important role of weather extremes during migration on population dynamics (Wellicome *et al.* 2014). There is still limited actual data on how a change in weather patterns due to climate change can affect migratory bird species. Changes in weather patterns can vary locally and thus the effect could be highly species- and region-specific. La Sorte & Fink (2017), found that, under climate change, wind strengths are expected to decrease during autumn migration within the transatlantic flyway. However, it is unclear if this will affect migratory birds positively or negatively. In another study done by La Sorte *et al.* (2019), nocturnal migrants were found to experience stronger headwind resistance during autumn migration and tailwind support during spring. As wind plays an important role in the optimization of migration, climate change-induced changes in atmospheric circulations could affect the efficiency of migration (Newton & Brockie 2008; Alerstam 2011; Loonstra *et al.* 2019).

2.3. *Breeding grounds*

Higher latitudes, such as temperate and arctic zones, have been greatly affected by climate change (Parmesan 2006; Trenberth 2011; Hodgkins 2014). Different trophic levels in ecosystems respond at different rates to climate change (Helm *et al.* 2013). In a recent review, tree budburst was shown to advance three to eight days per degree Celsius increase, as a response, insects hatched earlier either directly as a response to budburst or as a response to increasing temperatures (Renner & Zohner 2018). Thus, as climate change is increasing temperatures, causing an earlier onset of spring, the timing and shape of food peaks are affected (Vatka *et al.* 2016). If long-distance migratory birds use external cues not linked to climate, such as photoperiod, to time migration, the phenology of their arrival is most likely not advancing with warmer springs (Both & Visser 2001). Hence, long-distance migratory birds, who do not use cues about environmental conditions in breeding grounds, could mismatch their timing of breeding with food abundance (fig. 1) (Visser *et al.* 2012; Vatka *et al.* 2016; Zhemchuzhnikov *et al.* 2021). As a result, with climate change, resources are becoming more limited for parents to raise chicks, causing higher mortality and population declines (Ross *et al.* 2018; Zhemchuzhnikov *et al.* 2021). This has been well studied in pied flycatcher *Ficedula hypoleuca* populations in Europe but is also observed globally, for example in North America, and in many other migratory bird species, for example, arctic shorebirds (Kwon *et al.* 2019; McGuire *et al.* 2020).

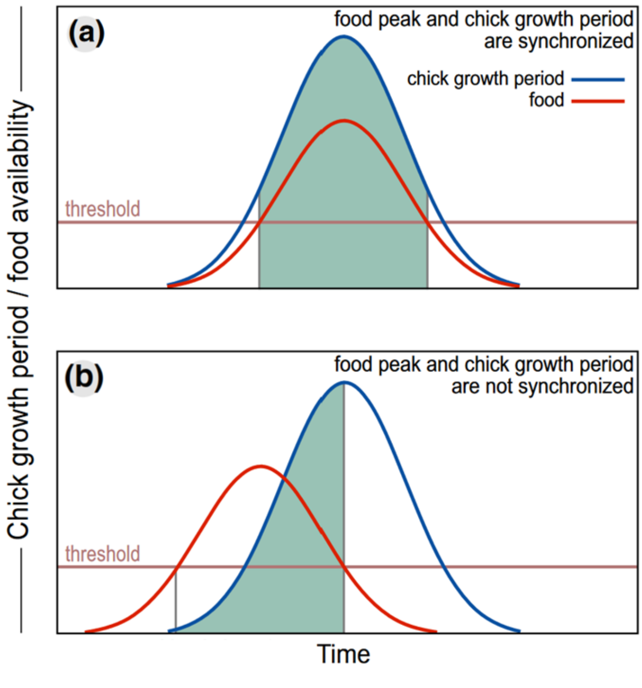

Figure 1: a) Hatching of chicks (blue) and food abundance (red) are synchronised, assuring plenty of food for raising of offspring. b) Food abundance starts earlier than the peak in chick growth, causing a partial mismatch. Adapted from Zhemchuzhnikov *et al*. (2021).

3. Adaptations in migration

In 2002, Coppack & Both (2002) hypothesised four ways by which long-distance migratory birds could advance their arrival at breeding sites to reduce the phenological mismatch between breeding and food abundance. The first hypothesis states that migration speed could be increased, shortening migration duration, either by minimizing stop-over time or by increasing flight speed (migration speed, fig. 2a). Second, an obvious solution to reduce phenological mismatch is to simply leave the wintering grounds earlier, however, this might be limited by environmental cues informing migratory birds about when to leave (migration timing, fig. 2b). Alternatively, birds could winter at higher latitudes to reduce the distance between wintering and breeding grounds (migration distance, fig. 2c). Lastly, migratory birds could migrate to breeding grounds at higher latitudes to compensate for the earlier onset of spring in their original breeding sites (latitudinal shifts, fig. 2d). In this chapter, I will see how much evidence, if there is any, there is for each hypothesis using a literature search on Web of Science™. Per hypothesis, I searched literature using the following keywords: "*Bird [hypothesis] climate change"* and sorting by relevance. From the first 10 studies I selected the 5 most relevant studies, in addition, I looked at whether the studies investigated different species to get a broad picture of the hypothesis. From this, I tried to determine if evidence for these hypotheses has been observed in literature and which hypothesis would be the most promising way for migratory birds to adapt. It is important to note that some hypotheses are intertwined and non-exclusive. Therefore, multiple hypotheses are sometimes studied within the same study.

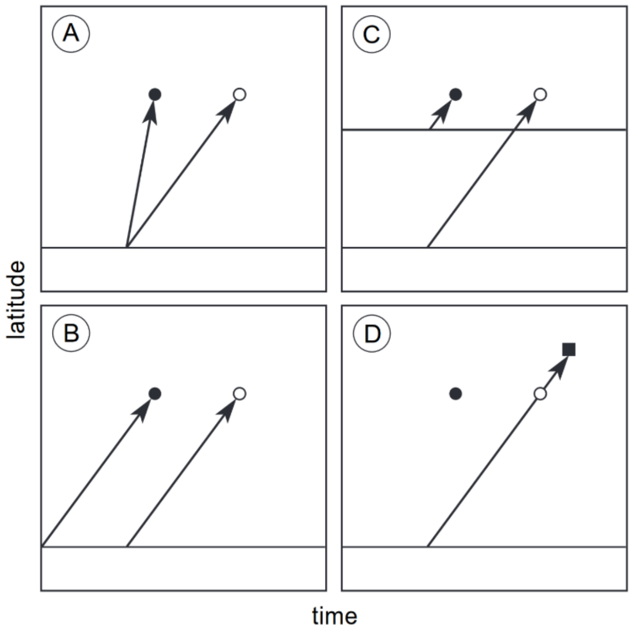

Figure 2: Schematic illustration of the four hypotheses of how migratory birds could advance in time to reduce phenological mismatch. Arrows with open circles represent migration without change, and arrows with closed circles represent adaptations. The four hypotheses consist of a) faster migration speed, b) earlier onset of migration, c) wintering closer to breeding grounds, and d) shifting breeding ground poleward (black square) Figure obtained from Coppack & Both (2002).

3.1. *Migration speed*

The definition of the term 'migration speed' differs per study. Where some studies look at stop-over time or flight speed, other studies focus on the total time of migration, making it somewhat difficult to compare studies. Here, I will use migration speed as a collective name for all three definitions. From five studies, studying migration speed, migration speed seems flexible and adaptable to various conditions (Table 1). Migration speed appears to be mainly determined by stop-over duration and frequency and less by flight speed, potentially because flight speed is weather-dependent (Alerstam 2011; Schmaljohann *et al.* 2017). Péron *et al.* (2007) found that stop-over duration and therefore migration speed was mainly related to food intake and not to temperature. Thus, one could argue that migration speed is depending partially on the need of migratory birds to stop and refuel, as found in snow buntings (McKinnon *et al.* 2016). As a result, migratory birds that need to refuel more often, for example when increasing their migration distance poleward, decrease their migration speed (Howard *et al.* 2018). In a pied flycatchers population from the Netherlands, individual variation in arrival time is mainly determined by differences in departure time and not migration speed as this appeared constant (Ouwehand & Both 2017). A study using data on multiple species from observatories found an advancement in the timing of migration between the period 1959-2015 but no shortening of migration duration (Lehikoinen *et al.* 2019). This suggests that migration speed is not progressing over time. There is a potential advantage of decreasing migration speed. At a population level, decreasing migration speed can spread out individuals over time causing lower densities at stop-over sites, lowering competition and potentially increasing food intake (Moore & Yong 1991; Lehikoinen *et al.* 2019).

Migration speed appears to be flexible in some species, with increases and decreases in migration duration as result. Schmaljohann & Both (2017) found that stop-over reduction could potentially increase migration speed, but this would not be sufficient to keep up with climate change-induced trophic mismatches. Thus, despite the flexibility of migration speed and duration, there does not seem to be a consensus if migration speed is an effective way to cope with climate change.

3.2. *Migration timing*

All studies regarding the timing of migration found an advancement of migration in terms of spring departure to breeding grounds (Table 1). Both year and temperature had a negative effect on migration departure, showing that, with increasing temperature over time, birds migrate earlier to cope with climate change. Two trans-Saharan migratory birds: the Sedge warbler *Acrocephalus schoenobaenus* and reed warbler *A. scirpaceus*, advanced their spring migration date by 0.73 ± 0.086 d yr^{-1} (Péron *et al.* 2007). Palaearctic migrants wintering in south Africa advanced their spring departure with 0.17 d y^{-1} but intra-African species delayed their migration by 0.03 d y^{-1} (Bussière *et al.* 2015). These migrants breed in the arctic at high latitudes where seasonality has been advancing the strongest (Parmesan 2006). This explains why intra-African species did not advance their arrival time as climate change near the equator is not advancing as rapidly. Two studies found a negative correlation between departure date and temperature. Together the studies covered 195 species from Canada and Europe and 6 species from Japan. The Canadian and European species showed an average 0.5-day departure advancement per ºC and the Japanese Black-faced bunting *Emberiza spodocephala* and Hawfinch *Coccothraustes coccothraustes* -5.3 and -8.0 days/1ºC respectively (Kobori *et al.* 2012; Lehikoinen *et al.* 2019). These studies show a global trend of migratory bird species using temperature as a cue to depart earlier. In addition, these studies combined with similar observations from Australia, show that earlier spring migration is a global pattern (Chambers 2005; Kobori *et al.* 2012; Lehikoinen *et al.* 2019).

Thus, there seems a substantial amount of evidence for the hypothesis that the timing of migration is advancing over time to cope with climate change. However, it is important to note that timing might be limited to factors such as the possibility and speed at which migrants can fully fuel up on their wintering grounds. Cooper *et al.* (2015), found that American Redstart *Setophaga ruticilla* which experimentally had reduced food intake departed later (day 30 ± 6) than control birds (day 24.0 ± 15.8).

3.3. *Migration distance*

Migratory birds have been observed wintering closer to breeding grounds over time (table 1). Multiple species, such as several raptors, spread out over several flyways, have been observed shifting their wintering grounds more poleward (Paprocki *et al.* 2014; Gu *et al.* 2021). These results are in line with previous research done on American kestrels *Falco sparverius*, showing a decrease in migration distance over time with increasing winter temperatures (Heath *et al.* 2012). The same study found that kestrel nesting phenology advanced with warm winters (Heath *et al.* 2012). Shortening of migration distance, or 'short-stopping', is a term broadly studied in the northern hemisphere and is mainly used to describe changes in migration distance by shifting wintering grounds northward (Elmberg *et al.* 2014). There appears to be a broad consensus that short-stopping is mainly caused by climate change although wintering ground degradation and energy constraints are also mentioned as possible causes (Heath *et al.* 2012).

Two studies, focussing on whooping cranes *Grus americana* and greylag goose *Anser anser*, concluded that short-stopping is based on individual decisions to winter closer to breeding grounds (Teitelbaum *et al.* 2016; Podhrázský *et al.* 2017). In small groups of migrating whooping cranes, the group follows older cranes that learned to winter closer to breeding grounds. Hence, the older the oldest individual in a migratory group, the closer this group winters to breeding grounds (Teitelbaum *et al.* 2016). A similar pattern was found in Bewick's swan *Cygnus columbianus bewickii*, where an increase in short-stopping was accounted as an individual response to climate change but also a generational effect (Nuijten *et al.* 2020). Evidence for a generational effect has been found in peregrine falcons *Falco peregrinus*, where genetic differences between long-distance and short-distance migrating populations suggest a cause for changes in migration distance (Gu *et al.* 2021).

These results show that a change in migration distance is a possible adaptation that migratory birds can apply to arrive earlier at breeding grounds. Plasticity in short-stopping makes it a potentially effective method to adapt to yearly changes in temperature and potentially also in changes in land use or habitat degradation.

3.4. *Latitudinal shifts*

In several cases, migratory birds have been observed shifting their breeding ground more poleward to reduce a phenological mismatch at their breeding ground (table 1). In this adaptation, variation is found between long-distance migratory, short-distance migratory, and resident birds. Rushing *et al.* (2020), found in 32 bird species (resident, temperate, and neotropical migrant) an average poleward shift of 0.003º /y. When separated in winter geography, different patterns in range shifts were found (fig. 3). No evidence was found for latitudinal shifts in northern margins of neotropical migrants and southern margins of temperate migrants and residents (Rushing *et al.* 2020). A similar study found only a latitudinal shift in short-distance migrants but not in residents or long-distance migrants (Hovick *et al.* 2016). A possible explanation for differences between residents, long-, and short-distance migrants is that short-distance migrants are not limited by a lack of information about breeding grounds like long-distance migrants (Both & Visser 2001; Hovick *et al.* 2016). However, that does not explain the results of Rushing *et al.* (2020). The capability of species to shift their breeding range poleward can experimentally be tested. Translocation experiments where breeding output has been measured have been successful and could prove as a method to test if a species is capable to shift poleward and what the effect would be on its reproductive success (Burger & Both 2011).

Under future ecological niche simulations, peregrine falcons are expected to shift breeding grounds with 2.08º by 2070 (Gu *et al.* 2021). Such projections are based on how climate change affects ecological niches. Despite such projections, observations of shifts in the past have not been sufficient to cope with temperature changes over latitudes (Hovick *et al.* 2016). This could explain why some species have not shown any latitudinal shifts as this adaptation could be futile (Visser *et al.* 2009). In addition, when wintering grounds are not shifting, migration duration will increase with poleward shifts (Howard *et al.* 2018). If the increase in fitness by shifting poleward is equal to the loss in fitness due to longer migration, then a latitudinal shift might not evolve as an adaptation to cope with climate change.

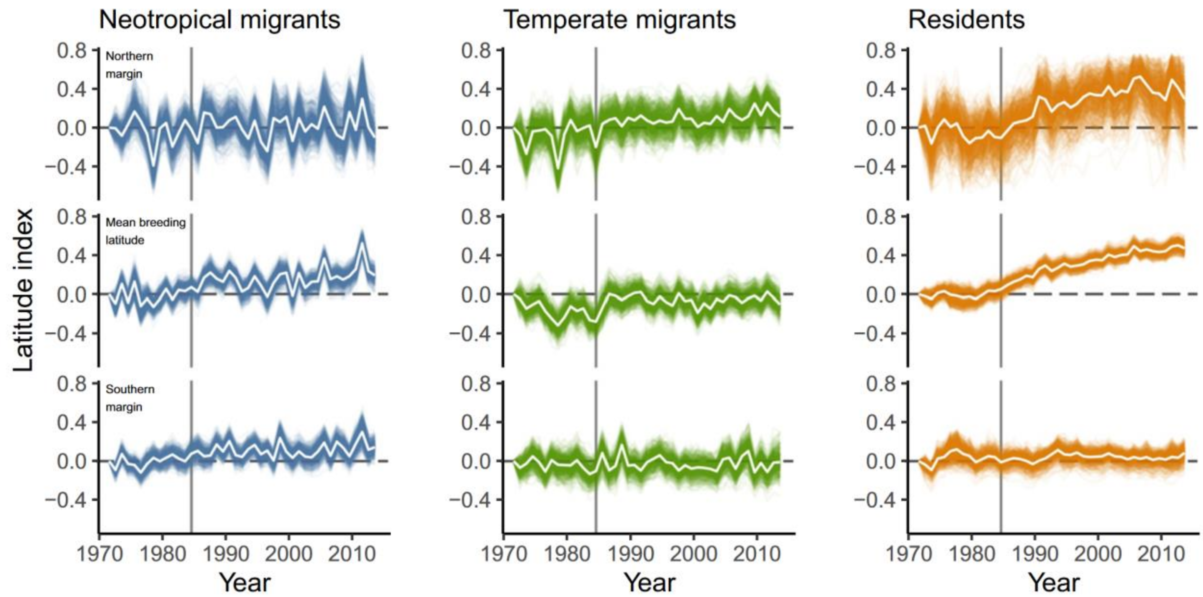

Figure 3: Range shift of neotropical migrants (n = 19), temperate migrants (n = 6), and resident species (n = 7). Before 1985 (vertical grey line) no significant changes in directional shifts were found [obtained form and for further reading see *Rushing* et al. *(2020)*].

3.5. *Alternative adaptations*

In addition to the four hypotheses formulated by Coppack & Both (2002), there have been additional ways described in literature by which migratory birds can cope with climate change. Some migratory species perform annual altitudinal shifts where they migrate from wintering to breeding grounds at different elevations (Barçante *et al.* 2017; Hsiung *et al.* 2018). Some hypotheses state that altitudinal migration has evolved due to seasonal food limitations that differ along an altitudinal gradient, or different weather conditions at different altitudes (Hsiung *et al.* 2018). Besides the form of migration, an altitudinal shift could be an adaptation for migratory birds in general, where, as a response to keep up with climate change-induced food peaks or avoid adverse weather changes, animals shift their geographical distribution to higher altitudes (Scridel *et al.* 2018). This phenomenon has been observed in Southeast Asia but has been rarely studied in migratory birds (Peh 2007; La Sorte & Jetz 2010). Nevertheless, projections have been made that migratory birds will shift to breeding at higher altitudes where their habitat is more suitable (Pacifici *et al.* 2017; Liang *et al.* 2021). A problem with altitude shifts is that warming is expected to occur at a faster rate at higher altitudes, which potentially makes altitudinal shifts, not an effective adaptation (Rangwala *et al.* 2013). In addition, in contrast to long-distance migration, altitudinal migration is often based on individual decisions to migrate based on year-to-year environmental conditions (Hsiung *et al.* 2018). This could explain why currently there is little evidence reported for altitudinal shifts by migratory bird species as a response to climate change, though currently this adaptation is also understudied.

Last, skipping migration altogether could be a way to adapt to the negative changes faced during migration as a consequence of climate change. Common buzzard *Buteo buteo* populations in Europe have been observed reducing their migration as a response to temperature changes, resulting in increasing resident populations that were previously migratory (Martín *et al.* 2014). This has been experimentally tested in captive-bred blackcaps *Sylvia atricapilla*, where simulated selection resulted in favouring decreased migratory activity which in the long term is expected to result in residency (Pulido & Berthold 2010). With the loss of Arctic Ocean ice, sea birds are also expected to lose their migratory behaviour and become residents (Clairbaux *et al.* 2019). However, it is suggested that such rapid occurring adaptations are effective only for short- to moderate-distance migratory species and less so for long-distance migratory species as increasing poor habitat between wintering and breeding grounds limits the shortening of migration (Coppack *et al.* 2008; Pulido & Berthold 2010). Hence, loss of migratory behaviour could be very species specific.

Table 1: An overview of case studies supporting one of the hypotheses as stated by *Coppack & Both (2002)*. Studies were obtained via Web of Science™ using search terms such as: *"Bird [hypothesis] climate change"*. Per hypothesis, a minimum of 5 papers were selected and their most important findings regarding this hypothesis were summarised under "effect".

Common name (number of species)	*Scientific name*	*Location*	*Hypothesis*	*Method*	*Effect*	*Study*
Various (n = 37)	NA	Europe	Migration speed, latitudinal shifts	Species distribution	Increased migration time for long-distance migratory birds of 31.2 days (+11.6 days) by 2070.	Howard *et al.* (2018)
Sedge warbler, reed warbler	*Acrocephalus schoenobaenus, Acrocephalus scirpaceus*	Europe	Migration speed, migration timing	Capture-mark-recapture	Stop-over duration is positively correlated with body mass gain. Spring migration advanced in recent years (-0.73 ± 0.086 d yr^{-1}).	Péron *et al.* (2007)
Various (n = 6)	NA	Japan	Migration timing	Long-term observation	Birds departed 21 days earlier on average, two species departed earlier with increasing temperature.	Kobori *et al.* (2012)
Snow bunting	*Plectrophenax nivalis*	Canada	Migration speed, migration timing	Geolocators	The arrival date at both winter and breeding sites was predicted by departure date, stop-over days, and migration speed.	McKinnon *et al.* (2016)
Various (n = 195)	NA	Europe, Canada	Migration speed, migration timing	Long-term trapping and count dataset from 21 observatories	The median migration date decreased by 0.5 days/1°C, migration duration increased by 0.45 days/1°C.	Lehikoinen *et al.* (2019)
Various (n = 8)	NA	Australia	Migration timing	Long-term bird sighting observations	13 out of 16 arrival trends were negative per year.	Chambers (2005)
Northern wheatears	*Oenanthe oenanthe*	Alaska	Migration speed	Geolocators	Travel speed is flexible to environmental factors. Travel speed is negatively correlated with stop-over time.	Schmaljohann *et al.* (2017)
Various (n = 16, grouped in 3 categories: Palearctic terrestria migrants, Palearctic migratory waterbirds, intra-African migrants).	NA	South-Africa	Migration timing	Bird atlas data	Palearctic migrants advanced their departure by -0.17 d yr^{-1}. Intra-African migrants delayed departure with 0.03 d yr^{-1}	Bussière *et al.* (2015)
Various (n = 24)	NA	Netherlands	Migration distance, latitudinal shifts	Bird ring recoveries	12 of 24 species analysed showed a reduction in migration distance. No species showed an increase in migration distance.	Visser *et al.* (2009)

`Whooping cranes	*Grus americana*	US	Migration distance	Observation and telemetry	Small migratory groups established new wintering grounds 40 km closer to the breeding ground per year of age of the oldest bird.	Teitelbaum *et al.* (2016)
Greylag goose	*Anser anser*	Czech Republic	Migration distance	Capture-mark-recapture	In the period 1956 – 2015, greylag geese wintered closer to their breeding ground or became residents	Podhrázský *et al.* (2017)
Various (n = 6)	NA	US	Migration distance	Bird counts and observations	Six raptor species shifted their wintering distribution northwards over time. The fastest change was found in rough-legged hawks *Buteo lagopus*, 8.41 km y^{-1}.	Paprocki *et al.* (2014)
Various (n = 32)	NA	US	Latitudinal shifts	43-year monitoring data	All species increased their mean breeding latitude with an average of .007◦/y. Resident birds showed the strongest shift, followed by neotropical migrants and temperate migrants.	Rushing *et al.* (2020)
Various (n = 277)	NA	US	Latitudinal shifts	Breeding bird survey	Over 43-year, short-distance migrants (n = 130) shifted their breeding ground an average of 86 km poleward. Neotropical migrants (n = 99) and residents (n = 48) did not shift their breeding grounds.	Hovick *et al.* (2016)
Peregrine falcon	*Falco peregrinus*	Arctic Eurasia	Latitudinal shifts, Migration distance	GPS tracking, modelling	Ecological niche modelling predicts that by 2070 six populations will shift their breeding and wintering distribution by 2.08° and 1.47° respectively.	Gu *et al.* (2021)
Pied flycatcher	*Ficedula hypoleuca*	Netherlands	Migration timing, migration speed	Geolocators	Migration duration was the same for all tracked individuals (2 weeks). Arrival time at the breeding ground was positively correlated with departure from wintering ground.	Ouwehand & Both (2017)

4. Conclusion & Discussion

In this essay, I have provided an overview of the complex climate change-induced challenges migratory birds face during their migration. In addition, I have performed a small, but focused review of the evidence in current literature for the four hypotheses by which migrants may adapt to climate warming as stated by Coppack & Both (2002).

For my first research question: *"How does climate change affect bird migration along their flyway?"*, I found that migratory birds, especially long-distance migrants, experience a variety of challenges along their flyways due to climate change. At wintering grounds and on stop-over sites, unpredictable changes in weather, such as droughts and periods of high precipitation, affects food abundance (Vickery *et al.* 2014). For instance, increased droughts decrease food abundance, making it difficult for migratory birds to gain enough energy to fuel their migration (Jenni-Eiermann *et al.* 2011; Cooper *et al.* 2015; La Sorte *et al.* 2017). Such changes in food abundance affect survival during migration. In flight, changes in weather patterns and extremes, are expected to increase mortality but could also increase flight speed (Newton 2007; La Sorte & Fink 2017; Haest *et al.* 2019). At breeding grounds, the well-studied trophic mismatch between bird migration and food peaks affects food abundance during the breeding season, leading to decreased fitness (Ross *et al.* 2018; Zhemchuzhnikov *et al.* 2021).

For the second question: *"Is evidence found for these hypotheses, and will the observed adaptation be sufficient for migratory bird species to cope in a warming world?"*, I have found evidence confirming all of the four hypotheses stated by Coppack & Both (2002). Some adaptations are more likely to occur and appear to be more effective than others. Especially migration speed seems to be limited as it is highly dependent on other factors such as stop-over duration, weather conditions during flight and migration distance (Alerstam 2011; McKinnon *et al.* 2016; Schmaljohann & Both 2017; Howard *et al.* 2018; Lehikoinen *et al.* 2019). Other adaptations appear more likely to be effective adaptations. Several studies have found a negative effect between temperature and migration timing, causing migratory birds to depart earlier in warm years to reduce their trophic mismatch in breeding grounds (Péron *et al.* 2007; Kobori *et al.* 2012; Bussière *et al.* 2015). The same applies to wintering closer to breeding grounds, where multiple species have been observed to winter closer to breeding grounds over time (Visser *et al.* 2009; Paprocki *et al.* 2014; Podhrázský *et al.* 2017). Migration distance, both in terms of breeding at higher latitudes and wintering closer to breeding grounds, has a genetic basis but can also occur from individual plasticity (Teitelbaum *et al.* 2016; Gu *et al.* 2021). To determine if these adaptations will be sufficient to keep up with climate change is difficult as the impact of climate change is spatially highly variable and, as previously stated, has different (additive and perhaps interactive) effects along the flyway. A combination of different adaptations seems to be the most effective way to cope with climate change, for example, as seen in peregrine falcons who have been observed advancing their wintering site northward (migration distance) as well as their breeding grounds (latitudinal shifts) (Gu *et al.* 2021).

4.1. *Multiple challenges along the way*

Changes in temperature, precipitation and other weather variables due to climate change are contributing to declines in bird populations (Habibullah *et al.* 2022). Migratory bird species are expected to be strongly affected by climate change as they have to cope with a great scale of environmental factors along their geographical range (Newton & Brockie 2008; Zurell *et al.* 2018). Based on the literature reviewed here, I conclude that migratory birds, both long- and short-distance, are experiencing a broad scale of climate change-induced challenges along their flyway. Many studies have focussed on the phenology of migration in relation to a trophic mismatch at the breeding grounds. However, there are as well major challenges to be faced at wintering grounds and during migration op stop-over sites as well as in-flight. Therefore, future research should focus more on the effect of climate change on bird migration as a whole as these different stages are all affected and likely dependent on each other.

It is important to note the effects of climate change on migratory birds do not always need to be negative. In several cases, climate change has resulted in increased survival and breeding success

(Higuchi 2012; Layton-Matthews *et al.* 2020). This shows that the effect of climate change is highly species-specific and dependent on how climate change will regionally alter environmental conditions.

4.2. *Evidence for adaptations*

Migratory birds show a broad scale of adaptations to cope with changing environmental conditions. Different species show different adaptations in varying degrees. From chapter 2 it can be concluded that climate change affects species differently and at different stages of migration. Thus, species-specific adaptations are expected as not every species experiences the same level of change. Besides, species vary greatly in migratory behaviour (for example short- and long-distance), which likely results in different levels of adaptations needed to cope with environmental changes (Hovick *et al.* 2016; Rushing *et al.* 2020). In addition to the four hypotheses, I stated two more adaptations for migratory birds to cope with climate change have been reported in literature: altitudinal shifts and becoming resident. For both adaptations, I found some evidence, but more research on these topics is needed. It is important to note that these adaptations mainly focused on timing of arrival at breeding grounds. More insight into the adaptations at different stages of migration is needed to gain a comprehensive view of the ability of migratory birds to adapt.

I have found very few experimental studies on how migratory birds can adapt to climate change. Although it might be complex, it would be very insightful to test the adaptability of migratory birds. Burger & Both (2011), showed that translocation can be used to simulate a northward shift in the breeding grounds for pied flycatchers. It would be interesting to also test translocation of migratory birds on their wintering grounds. Coppack *et al.* (2008) experimentally tested this in pied flycatchers bred in captivity, however, to my knowledge this has not been tested in wild populations. Such a study could for example focus on translocation of first-time migratory and adult individuals to wintering grounds closer to breeding grounds. If such translocation studies result in higher breeding success, then translocation could be applied as a conservation method for critically endangered migratory bird species (Hoegh-Guldberg *et al.* 2008; Butt *et al.* 2021). The majority of the studies that I found on adaptations focused on birds migrating in or towards the northern hemisphere. To obtain a more complete picture of the adaptability of migratory birds, future research should also focus on migratory birds within the southern hemisphere. The variation observed in species from the southern hemisphere could provide more insight into migration in general and our understanding of adaptability (Dingle 2008).

4.3. *Additional challenges: indirect effects of climate change*

Climate change affects all species globally (Habibullah *et al.* 2022). We as humans change land use as a response to climate change [for in-depth detail see: Froese & Schilling (2019)]. Such changes in land use have a negative effect on biodiversity in general (de Chazal & Rounsevell 2009; Williams & Newbold 2020). Human-induced rapid environmental changes (or HIREC) are also proposed as a threat to migratory bird species and are an indirect effect of climate change. For example, droughts in the Sahel result in damming and exploitation of wetlands to irrigate crops, changing the habitat of migratory birds that use these wetlands (Zwarts *et al.* 2010; Vickery *et al.* 2014). A similar effect is found in Doñana National Park (SW Spain), an important wetland used by migratory birds such as the black-tailed godwit *Limosa limosa*. Groundwater extraction in nearby human settlements to irrigate crops causes wetlands in Doñana to decline (Dimitriou *et al.* 2017; Fernández-Ayuso *et al.* 2018). Such conflicts are not easily resolved as different parties, such as local farmers and nature conservationists, will have different interests. When studying the effect of climate change on bird migration it is needed to take such indirect consequences of climate change on the land use in wintering, stop-over, and breeding areas of migrant birds into account as well to gain a full picture of the challenges migrant birds face.

This is just one example of the additional challenges that migratory birds face as an indirect consequence of climate change. Migratory birds face multiple human-induced global change risks such as loss of winter and breeding habitat (Zurell *et al.* 2018). Humans depend on resources provided by the land that migratory birds use along their flyways. These lands are now changed by humans to keep using resources as a response to climate change. Therefore, future research should focus on how these resources can be utilized by humans in the future without degrading migratory bird habitats.

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