

Bachelor thesis

# The Annual Cycle of Long-Distance Migratory Birds in Relation to Climate Change

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## Abstract

Long-distance migratory birds are extensively studied, and appear to be especially vulnerable to climate change due to their large ranges. This makes them potential sentinel species for the effects of climate change. In order to interpret observations regarding long-distance migrants, understanding their annual cycle is key. Here I will describe the role played by three important aspects of the annual cycle of long-distance migrants: wintering, migration and breeding. Evidence for the effects climate change may have on each of these stages will be examined. Wintering has been shown to be of crucial importance to the rest of the cycle, and can function as a survival bottleneck, especially if climate change tends to harshen conditions on wintering grounds. Adaptation via a shift in wintering location may be a solution, and has in various forms been observed in several species. Migration timing is an important and heavily debated area of research. Many observations have been made regarding the way birds can time the onset of migration and their ability to change timing through plasticity and/or selection. The importance of migration timing and the pace of current climate change leads me to believe that birds may be forced to change through every mechanism available to them, decreasing the predictive properties of our knowledge from responses to past events. Breeding, finally, is another crucial stage for population survival and selection. A strong recent decline in many long-distance migrants is an indication of the negative effects global climate change may have. Decreased synchrony with food peaks is one of the mechanisms at play. The effect of increased competitor levels is also looked into, and may interestingly enough provide migrants with the ability to breed earlier and more successfully. The need for earlier onset of breeding is often insufficiently followed by changed behavior, resulting in declining populations. Observing and understanding the annual cycle of long-distance migratory birds and the (cascading) effects of climate change is crucial, as it can provide us with clues to future trends over a much broader spectrum of species and ecosystems.

## Introduction

Long-distance migratory birds exhibit a fascinating annual cycle in which huge distances are covered with impressive speed and efficiency. They have adopted a lifestyle in which they winter in remote parts of the world, such as Sub-Saharan Africa, and breed on the other side of the world, as far north as northern Scandinavia. In order to do so they undertake a well timed *en masse* demanding journey each spring and autumn. This highly visible and large scale phenomenon has aroused the fascination of human observers throughout the centuries, making it one of the most extensively studied fields of nature research.

Depending on conditions in different areas at different stages in their annual cycle for

survival and reproduction, long-distance migrants are especially sensitive to deteriorating conditions both globally and locally. This vulnerability, combined with the many long term records kept of their behavior throughout the years, renders them excellent study species, and their performance is regarded as a telltale indicator of the stability for nature areas and ecosystems over longer periods.

As the evidence of global climate change and its effects unfolds around us and is rapidly becoming part of the scientific consensus, scientists around the world closely watch migratory birds to better understand how global climate change has and will continue to change the environments in which long-distance migrants winter, migrate and breed, their ability to cope with such change and the adaptations observed.

This paper aims to give an overview of three important stages in the annual cycle of migratory birds: wintering, migration and breeding. I will describe these different stages, the challenges they pose and the ways they influence the rest of the cycle. Available evidence for climate change driven responses in studied species will be discussed.

## Wintering

### Sub-Saharan wintering grounds

During the wintering period, birds need to acquire sufficient body mass for survival and spring migration. In order to do so, they migrate to regions where food availability is high, and select the best available habitat in that region. For many long-distance migrants breeding in Europe, the wintering ground is situated in Sub-Saharan Africa. Rainfall and temperature are the primary governing factors in the sub Saharan ecosystem [1], and determine food availability to wintering birds.

In recent years climate change has brought higher temperatures in these regions, possibly causing conditions to deteriorate. Any deterioration would add to the standard deterioration of conditions in wintering areas within the wintering period. An increase in rainfall has however also been observed, which may moderate the deterioration of wintering habitats, or even improve conditions. It remains subject of debate whether long-distance migrants are confronted with harsher conditions due to climate change [2,3]. In the wintering areas human population has strongly increased, causing habitat loss through desertification, agriculture and wildfires caused by slash-and-burn agriculture. These factors combined, regardless of the exact extent of the positive effect of increased rainfall, are likely to confront wintering birds with increasingly tough wintering conditions.

## Wintering habitat quality

Conditions in the wintering area are of crucial importance to physical condition and thus performance during the rest of the cycle. Occupation of a better habitat during wintering allows migrants to start spring migration earlier and to breed more successfully. Also the returning rate to the wintering grounds is significantly higher [4]. These benefits are not the result of existing differences in quality, as is illustrated by Studds and Mara [5]. In an upgrade experiment they carried out, American Redstarts, *Setophaga ruticilla*, were removed from high quality wintering habitats, allowing these habitats to be occupied by birds that previously occupied habitats of less quality. It was shown that these individuals did start spring migration at an earlier date. A strong correlation was found in early spring migration and both breeding success and return rate, but whether this applies to upgraded birds as well can, although suggested by Studds and Mara [5], not be verified.

First-year birds that occupy a better habitat will be in better condition and migrate earlier, and have the opportunity to breed on average further south than their natal area, since they arrive in time to benefit from the food peaks in the south, that occur earlier in the year than in more northern regions. This shorter migration distance in spring and autumn means an added advantage. Adult birds are more site faithful in both breeding and wintering grounds. To them it is most beneficial to keep their timing synchronized for wintering and breeding habitats and latitudes [4]. Obviously this synchrony is self sustaining when conditions in both areas continue to match. I think that a loss of this inherent synchrony due to a shift in conditions in wintering and/or breeding grounds may well reduce the beneficial effect of such reduced plasticity, and result in selection towards higher plasticity in adult birds than observed thus far.

## Shifting wintering grounds

As wintering grounds become less permitting, survival chances are decreased. In order to improve survival chances during the winter, migrants need to alter their behavior. This can be done by adopting a nomadic lifestyle, or a slight shift in wintering ground. Birds may by means of plasticity and/or mutation reduce the migration distance by wintering nearer to the breeding grounds [6] or by breeding in closer proximity to the wintering grounds [6]. Ultimately, migratory birds may even abandon migration completely and become sedentary, often aided by food provisioning by householders [6]. Especially (but not exclusively) species with a high body mass are likely to shorten migration routes or become residents, due to their higher cost of travel [7]. Even though migration requires adaptations making migratory birds specialized for a migratory annual cycle, they are able to express or suppress sets of adaptations to such an extent that they can change migratory behavior within a few generations if required [8].

A drastic shift in the location of wintering grounds is observed in a number of species [6] among which a Blackcap population, *Sylvia atricapilla*, now wintering on the British Isles as well as on the Iberian Peninsula due to a genetic mutation [9]. Climate change may have caused more permitting circumstances on the British Isles, making this region an increasingly suitable wintering area, while in Iberia circumstances may have worsened or stayed unchanged. Feeding by humans in their gardens in and around rural areas in a situation with increased urbanization further accommodates birds to winter in such areas. The shorter distance from the breeding grounds in Central Europe allows birds to make more accurate predictions of weather conditions on the migration route and breeding grounds. Especially with a changing and increasingly unpredictable weather system this advantage over the traditional situation can be of crucial importance. Together with an overall shorter migration distance and possibly faster travel due to better physical conditions, they arrive earlier in the breeding areas and can occupy the better habitats. It has been shown that assortative mating occurs, causing the formation of separate breeding populations within one breeding area [9]. This separation may ultimately lead to speciation if assortative mating persists or selection against the offspring of hybrid pairings occurs. If birds wintering on the British Isles have a relative fitness advantage over their Iberian counterparts, an increasing portion of the group may come to consist of shorter-distance migrants. When conditions continue to change in a way that directional selection for closer or more northbound migration takes place, the new genotype may ultimately replace the old one.

It has been suggested that birds wintering on the British Isles may be tougher due to the harsher conditions on the British Isles [9], making them superior over their Iberian counterparts. I find this unlikely, as selection towards higher fitness due to toughness would already have taken place regardless of wintering area. It is well possible that certain similarities between wintering areas on the British Isles and breeding grounds in the east, not present between Iberia and the breeding grounds, allow for a more specialized approach to some challenges, as selection is allowed to become more unidirectional. Traits that are advantageous on the British Isles as well as in the breeding areas, but disadvantageous in Iberia, would now be selected for. If more, or more important traits are unidirectionally selected for in the new situation, a relative fitness advantage over their Iberian conspecifics is to be expected for those individuals. In my view the notion of higher fitness simply caused by deterioration of conditions is too simplistic and implausible in itself.

# Migration

## Importance of appropriate timing

It is crucial for each individual to be at the right place at the right time. In order to do so, migration has to be timed in accordance with conditions at departure site, the flyway, possible stopover sites and destination. In autumn migration, departure can only take place after nestlings fledge, but before the strong reduction in food availability and temperature drop take their toll. This decision can however not be made on short notice, since birds have to moult before the onset of the demanding journey ahead [6]. The process of moulting brings considerable costs to the individual, forming gaps in its wings, reducing agility and energy efficiency in flight. Thus breeding birds have to anticipate on the migration at hand by changing feathers beforehand, while doing so too early may be too large of a handicap if still provisioning for nestlings.

Spring migration to the breeding grounds comes with its own challenges, as an early arrival may accommodate acquiring better habitats at the breeding site, advancing the timing of the onset of breeding and increase overall breeding success. In order to successfully migrate, birds need to build fat reserves so they are in sufficient condition to survive the demanding journey with as little delay as possible. Moreover they depend on cues that indicate the right time to migrate, such as daylength. Too early and they will be faced with delays elsewhere on the route and increased mortality due to harsh conditions on their way northwards, as temperatures may still be too low to allow traveling through [10]. Too late and the best habitats are taken, resulting in lower breeding success and later breeding, which will in turn mean less food for nestlings and adults, deteriorated conditions during fall migration and the need to delay fall migration in order to prevent overlap in moulting with breeding and/or migration.

## Timing mechanisms

The timing of migration is a complex task, as it requires birds to predict weather conditions for the subsequent two months in areas up to thousands of kilometers away. Short-distance migrants do not have to do this over such a large distance and timespan, and are therefore better able to predict the right timing. It has been shown that a shorter distance does in fact lead to better adaptation to local weather conditions of the breeding site [11]. In captivity, migration restlessness has been shown to increase with day length, but direct heritability has not been shown thus far.

Jonzen et al observed a change in arrival times in both Italy and Scandinavia, and propose that this has to be an evolutionary response. They reason that birds have no way of predicting weather conditions and can therefore not advance their departure date

through a response to their environment, and since conditions on the migration route have become harsher over recent years, faster migration due to weather events accommodating faster travel is also dismissed [2, 12]. The validity of such claims and the conclusion that follows are questionable [3]. Earlier arrival in Scandinavia is not selected for, as spring has not significantly advanced there. Weather conditions *en route* are not decisively worse, as rainfall in the Sahel has increased over the past decades, possibly accommodating faster travel [3].

Although the possibility that birds may be able to predict future weather conditions over a long distance is often dismissed, Saino and Ambrosini provided statistical evidence for a link between weather conditions in Sub-Saharan Africa in February and that in Europe (especially in the north and east, where the climate is continental and more crucial to predict) two months later, when migrants arrive [13]. While presenting an interesting theoretical possibility, it remains doubtful if birds really use this information. While global climate change requires birds to take such available information into account as much as possible, it also causes the link between conditions in Sub-Saharan Africa in February and that in Europe two months later to be weakening [13].

### **Advancing migration and arrival**

Earlier arrival in North Africa has been observed in species such as the Pied Flycatcher, *Ficedula hypoleuca*. In the case of the Pied Flycatcher this does however not result in earlier arrival on the breeding grounds. Since weather in Europe over the period preceding breeding in Western Europe does not seem to permit earlier arrival [10], birds breeding there need to spend longer time in North Africa and Southern Europe. By the time they can migrate, they may have to migrate more northwards in order to take advantage of the food peaks that have advanced less there. If waiting in North Africa and Southern Europe does not reduce fitness, it may well provide these species with the possibility to suddenly advance breeding (in the south) if climate change causes the period preceding breeding to become less hostile against migrants.

Earlier onset of migration, due to plasticity or otherwise, may be masked by the impossibility of earlier travel through Europe, delaying the birds to such an extent that arrival date in fact does not advance. Evidence for such plasticity has been found, as the photoperiodic cue for migrating seems to be depending on daylength at the time of hatching [10]: early-born birds in the south tend to migrate earlier. This would provide a mechanism of inherent passing on of timing from parents to their offspring, as birds migrating early will also breed early and have chicks that will migrate early themselves. Interestingly, birds born in the north, after the summer solstice, display a reversed pattern, migrating earlier as they were born later, supporting the notion that

daylength at birth is at least in part determining migration timing. As birds advance breeding as much as possible after arrival, an advancement in migration onset is to be expected in following generations.

Harsher wintering conditions increase the time needed to gain enough physical condition to successfully migrate if birds are unable to compensate by altered wintering behavior or location. Later onset of migration also forces birds to migrate further north, where the food peaks that breeding success heavily depends on occur later. This may cause these populations to shift their breeding grounds northwards [4]. This enhances the overall tendency for more northern breeding caused by the lesser extent of general spring advancement in these regions.

The needed advancement in arrival time is not observed in every species, and the underlying mechanisms for advancement are not easy to pinpoint. In my opinion the pace at which climate change is causing mistimed breeding is so high that in many species every possibility to advance breeding, both through plasticity and evolutionary response is called upon. Due to the unique combination of rapid climate change and a world in which human activities cause habitats to decline, knowledge of past events and responses offer no reliable insight into the future.

## Breeding

### Importance of breeding

Animals go to great lengths to breed, putting in tremendous effort and risking own survival. While demanding for the individual, reproduction is the driving force behind the entire biological process. The extent to which an individual is able to pass its genes to generations to come is the very definition of its fitness. Although it is meaningless to describe such a mechanism in terms of goals and directives, its importance gives the dangerous and stressful breeding period its meaning, as the populations and ultimately the species depend on it for both survival and selection processes.

### Decline of long-distance migrants

Long-distance migrants decline in seasonal habitats, suggesting an impact of climate change. The decline is mostly observed in long-distance migrants breeding in seasonal, western European breeding grounds. In northern regions, where spring advancement is less, the decline is not as strong. Seasonality of habitats in areas where spring has advanced significantly is causing food peaks to come to lie out of temporal reach for those long-distance migrants that are unable to sufficiently advance their arrival date. Such a mismatch between breeding and maximal food availability has been shown to

play a role in population declines in Pied Flycatchers, *Ficedula hypoleuca* [14]. In the meantime residents and short-distance migrants, experiencing milder winters and able to respond to more direct cues, appear to do relatively well in all areas [15].

Although the residents benefit from warmer winters in Europe and human feeding, the vulnerability of long-distance migrants to climate change does not seem to be caused by increased competition from thriving residents, as residents have increased in the north as well as in the west. Moreover, no correlation between the decline of long-distance migratory birds and increased competition from residents has been found there. Similarity in trends within long-distance migratory species and a correlation with weather conditions in the wintering area supports the notion that this vulnerability to climate change is most likely a direct result of deteriorating conditions in wintering areas [15].

Especially long-distance migrants that arrive relatively late perform worse in terms of breeding success. Decades ago, migrants arriving late were probably able to, to some extent, benefit from late seasonal food peaks. With an advanced spring in the breeding area, they may be simply too late even for those latest of food peaks. These late food peaks probably have become more important for earlier arriving birds, while the earliest food peaks that used to be exploited by early arriving long-distance migrants may now be out of reach. This may further increase the chances of resident birds, that still feed on those peaks. As discussed earlier, this general mistiming of long-distance migrants would lead to selection on earlier arrival (if at all possible), but this evolutionary response has not been convincingly documented thus far [15].

Short-distance migrants and residents are better able to advance breeding since they can better predict weather conditions [11] and are faced with fewer limiting factors as encountered in migration over long distances. This causes them to thrive, even in seasonal habitats where timing is crucial. This discrepancy in the success of long-distance migrants and their competitors may lead to increased competition, which could further reduce the chances of the long-distance migrants.

### **Effects of competitor levels**

The presence of competitors does not only result in increased competition. It has been shown that long-distance migrants prefer to breed in areas with competitive residents such as titmice rather than areas depleted of such competitors [16], even though titmice are superior in direct competition. Areas with titmice present are occupied first, and time before laying is shorter in such areas [17]. Migrant flycatchers have even been shown to prefer breeding in close proximity to a titmouse, probably in order to better be able to copy behavior and reduce vigilance costs [17]. Moreover they copy even arbitrary traits of nesting sites chosen by titmice [18]. In a situation in which immediate decisions and early

onset of breeding are called for, as is increasingly the case, higher numbers of resident competitors may also provide more opportunities to observe resident competitor density and nesting behavior. This may mean that arriving migrants can more easily benefit from the good predictive properties of resident birds in terms of site quality and nesting behavior, and are thereby enabled to make better decisions in a shorter timeframe.

Competitor densities need to be intermediate however, as the success of long-distance migrants does suffer from too much competition [16,17]. Now that urbanization and agriculture cause breeding habitats in many species to get increasingly scarce, the threshold above which migrants experience mostly negative effects of migrant numbers is likely to be lowered accordingly.

Currently mostly late arriving, younger birds learn from observing resident behavior, whereas older birds arrive earlier and have more time and experience available to them so that they can make decisions from more direct observations [18]. If resident species are better able to adapt to climate change, they may exhibit a stronger advancement in breeding time than migrants, their respective timing may come to lie apart even further. In this way certain behaviors exhibited by resident birds may take place before most young migrants arrive, depriving them of the opportunity to observe and thus learn from observed behavior of interspecifics in the future.

### **Breeding as early as possible**

Earlier breeding is required, but is limited by arrival after migration. Upon arrival birds can only breed as early as possible from that moment onward. Charmantier et al have found that a population of Great Tits, *Parus major*, in Wytham, England, has advanced breeding by a staggering 14 days, resulting in only a slight mismatch with food availability [19]. This mismatch is explained as the result of the changed conditions in the time between the onset of breeding and hatching, in which larvae development also takes place more rapidly. The observed response of Great Tits takes place within individual females, without delay and at such a rate that it can not be explained by microevolution and is therefore accredited to plasticity. Great Tits in the Netherlands do however not advance breeding date sufficiently. Plasticity does seem to increase in the Netherlands population, but not enough thus far [20]. No explanation for the high plasticity found in the Wytham population is given. I propose that, if these data are valid, earlier selection for plasticity has taken place in the Wytham population, whereas in the Netherlands possible unpredictability of weather conditions within a season has made the likelihood of mistimed breeding for individuals that are overly sensitive to environmental cues too high for such strong plasticity. It remains to be seen if emerging selection for higher plasticity will result in an adequate response fast enough to maintain a viable population.

## Discussion

In different parts of their annual cycle, long-distance migratory birds face specific challenges. Survival and success in one stage of the annual cycle can be decisive for that of subsequent stages. This is exemplified by the profound effect wintering habitat has on migration timing, which in turn is decisive for breeding success. In at least some species, an effect of climate change has been shown to be a factor in these challenges, more often than not adding to pre-existing difficulties. When global climate change affects several parts of the annual cycle of long-distance migrants, the effects may be additive. A cascade effect may be the result, in which minor changes, of little importance on their own, are amplified over time and can ultimately be the driving force behind selection, population success and ultimately extinction. These mechanisms are likely to take place in a much broader spectrum than only long-distance migratory birds, although sufficient data in other fields and less sensitivity of other species can cause the effects to go unnoticed at first.

In general, migratory species throughout the animal kingdom seem to decline, of which ample examples are described in literature [21]. The challenge for conservation of ecosystems is to keep abundance of animals, rather than just preventing extinction. Even in well studied species, such as migratory birds, the population dynamics are little understood. The effect of climate change on factors such as breeding habitat, wintering habitat, migration route and/or a combination of these are likely to be at least in part responsible for the observed decline in numbers and the collapse of ecosystems. Within each species different phenomena may or may not apply. Research on long-distance migratory birds learns that understanding the cues animals rely on for adaptation is of vital importance for understanding the consequences of climate change on migratory species. Effects are not always clear and convincingly pinpointed, but monitoring especially predictor species is crucial, since the effects of declining migrants can be extensive. This is illustrated by the observation that migratory birds, for example, are needed to keep down insect levels in certain areas [21]. In order to preserve species and ecosystems, the traditional approach of intervening when abundance of a species gets critically low is insufficient. Since migratory species often depend on sheer numbers for survival, a proactive approach is called for.

Better understanding of the life cycle of long-distance migrants in the future relies on development and application of new and/or improved methods of research. Recent studies on stable isotopes in feathers of long-distance migrants have shed more light on for example patterns of wintering locations. Due to the virtual impossibility of recapturing individuals at different stages in their cycle, such data offers a limited insight in the exact

locations and timing of examined individuals. Future research on small migratory birds would greatly benefit from the development of extremely light-weight tracking devices. A possible first step could be logging the daylength an individual is exposed to over time, from which an estimate of latitudinal movement could be deduced. The need for recapture and the relatively crude measurements this method would provide may eventually be replaced by devices that are locatable via radio signals, send out information rather than only logging it and/or provide a more exact method of location, for example via GPS. When these and other techniques are developed in the future, hopefully a more accurate and detailed understanding of migratory species can be obtained.

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