Effects of climate change on avian life history and fitness

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Introductory Research Essay No. 04
Department of Ecology
SLU Uppsala 2008

Contents

Abstract

Evidence for the impact of the recent climate change on ecological systems has rapidly accumulated for a variety of biota. In avian communities the documented responses to a changing climate (i.e. mainly changes related to temperature) are primarily range shifts, changes in breeding time, and the difficulty to synchronise offspring and food phenology. In this review I summarise the key changes and responses of bird communities and populations to changing temperatures. First, short- and long-distance migrants adjust their migratory phenology by advancing their arrival at the breeding grounds and starting to breed earlier. Whereas resident species and short-distance migrants, however, might profit from a milder climate long-distance migrants are predicted to face growing disadvantages and population declines. Second, insectivorous bird species try to synchronise the timing of their broods with the successively earlier occurrence of the peak in prey abundance. The fitness related responses to changes in the phenology of food for nestlings, however, vary between studies, ranging from earlier breeding, shorter incubation and changes in clutch size to the reduction of second broods, parental survival and reproductive prospects. So far, the majority of studies supports that birds are not fully able to synchronise their broods with the peak of food abundance, thus reducing reproductive success. The repercussions of global warming on life history traits and fitness correlates of avian populations depend on the adaptive potential of the population. Documented examples of evolutionary responses are rare, especially at the microevolutionary level. While breeding time seems to display great phenotypic plasticity, thus causing individuals to be able to adaptively track changes in spring temperatures; it nonetheless remains unclear whether the degree of phenotypic plasticity observed is enough to cope with future changes in annual temperatures. Furthermore, most current studies are based on insectivorous hole-nesting bird species breeding in broad-leaved woodlands that rely on the abundance of winter moths’ larvae. The generality of these studies for other bird species breeding in other habitats therefore is questionable.

Keywords: arrival time, climate change, evolutionary change, fitness parameters, long- and short distance migrants, migration phenology, mismatch hypothesis, North Atlantic Oscillation, phenotypic plasticity

1 Introduction

Over the last 100 years the average global temperature has increased between 0.5 and 0.9 ºC, primarily through an increase in average spring and winter temperatures (IPCC 2007). A number of studies indicate that climate change has already influenced the phenology and distribution of a great variety of taxa (Walther et al. 2002). For bird populations in particular, three general trends have been identified: (i) many northern-latitude bird species have expanded their range northwards (Thomas & Lennon 1999), (ii) breeding dates have advanced, and (iii) the fitness consequences of increased temperatures may depend on the species' ability to shift their breeding to match the phenology of their prey (Visser et al. 1998). Populations that are unable to adjust their timing of reproduction to warmer temperatures during the breeding season may experience reduced reproductive success, either due to physiological constraints in the timing of egg production (Visser et al. 1998, Thomas et al. 2001), or due to the decupling of cues that initiate migration from the wintering habitats with temperatures at the breeding grounds (Both & Visser 2001).

In this review I will especially focus on the effects of recent climatic changes on migratory bird species. For migrant birds, the timing of their arrival and their physical condition on the breeding grounds are important determinants of reproductive success and fitness (Both & Visser 2001, Marra et al. 1998). Long-distance migrants in particular, may be more vulnerable as they are constrained in their plastic responses to climate change by endogenous mechanisms controlling migration (Møller 1994, Visser et al. 1998). I will review how the arrival distribution of migratory bird species has shifted du to altered large scale climatic patterns and the potential changes in life history and fitness for species with different migratory strategies. Furthermore, I will discuss avian fitness declines induced by the increasing mismatch between prey phenology and breeding time observed for great tits (*Parus major*), blue tits (*Parus caeruleus*), and pied flycatchers (*Ficedula hypoleuca*; Visser et al. 1998, Thomas et al. 2001, Both et al. 2004). Finally, I will examine the current available data on the evolutionary potential of bird species to respond to and adapt to climatically induced changes of their environment.

2 Climate change and migration phenology

2.1 Arrival at the breeding grounds

The majority of migratory bird species has shown an overall tendency to arrive earlier at or close to their breeding grounds towards the end of the 20th century (Lehikoinen et al. 2004). The earlier arrival to the breeding grounds may be caused in three different ways: (i) the wintering area has moved closer to the breeding grounds, (ii) migration speed has increased, and (iii) migration starts earlier (Lehikoinen et al. 2004). Changes of climate variables at different scales (of regional temperatures or at the dimension of the North Atlantic Oscillation; see Box 1) can affect migration phenology in general, and species with different migratory strategies in particular, differently.

Warmer temperatures along the migration route and especially within Europe have been shown to facilitate the birds' northward migration (Ahola et al. 2004, Both et al. 2005). Temperatures along the migratory route thereby affect especially the first arrival dates but also the mean arrival dates of species (Hüppop & Hüppop 2003, MacMynowski & Root 2007; but see Box 2 for analytical problems).

Winter migrants arrive earlier at their breeding grounds in years with high North Atlantic Oscillation (NAO) indices (Forchhammer et al. 2002, Hüppop & Hüppop 2003, Sparks et al. 2005; see Box 1). Since vegetation productivity in Sub-Saharan Africa is positively influenced during high NAO years (Oba et al. 2001), long-distance migrants (i.e. tropical migrants) will experience improved foraging conditions that lead to earlier departures and a faster migration through Africa (Marra et al. 1998, Cotton 2003, Jonzén et al. 2006, Gordo & Sanz 2008). While many studies document the effect of the NAO on advancing arrival times, it is, however, not agreed upon whether long- or short-distance migrants should display the strongest response. The earlier arrival of long-distance migrants has consecutively found to be strongly correlated to NAO indices (e.g. Hüppop & Hüppop 2003, MacMynowski & Root 2007), while nonetheless, this has also been shown to apply to short-distance migrants (Forchhammer et al. 2002). Although the majority of studies support that long-distance migrants respond strongest to the NAO in advancing their arrival time, the argument should not be ignored that migrants wintering further away from the action centre of the NAO in the northern hemisphere will be less influenced by it in their timing of spring-time arrival.

Apart from the above argumentation, short- and long-distance migrants differ in their arrival distributions and their expected response to climate change. The spring and autumn migratory phenology of the two groups are conspicuously different. Short-distance migrants have advanced their arrival date in spring more than long-distance migrants, and in England these did so on average by 4.7 (± 0.8 SE) days in the period from 1951-1993 (Butler 2003).

Box 1. The North Atlantic Oscillation (NAO)

The NAO is a large-scale atmospheric oscillation centred between the Arctic and the subtropical Atlantic (Hurrell et al. 2001, Visbeck et al. 2001). Its winter index (December - March) is defined by the sea-level pressure gradient between the Icelandic low-pressure centre and the high-pressure system over the Azores. In years with negative or low NAO indices weak west winds lead to a stronger influence of continental winter high-pressures resulting in colder and drier conditions in north-western Europe. Positive NAO indices, by contrast, are associated with greater pressure differences in the Icelandic Low and the Azores High, producing stronger westerly winds that induce warmer and wetter weather condition (Ottersen et al. 2001).

During the last 30 years the NAO has shown a trend towards a more positive phase (Figure 1), with Europe experiencing milder winters and earlier spring phenological occurrences of plants and insects (Post et al. 2001). Thus the NAO has a major influence on European weather patterns that affects habitat conditions (e.g. new growth of trees) and food availability (e.g. insect quantity) of resident and migratory bird species at their breeding grounds (Hüppop & Hüppop 2003).

Box 1. (continued)

While north-western Europe experiences warmer and wetter winters during high NAO indices, these winters are followed by decreased vegetation productivity in the African Sahel Zone and increased productivity in Southern Africa (Oba et al. 2001). The latter is likely to improve feeding conditions of long-distance migrants and lead to earlier departures (Marra et al. 1998), while the former might lead to adverse migratory fuelling conditions at important stop-over sites (Bairlein & Hüppop 2004).

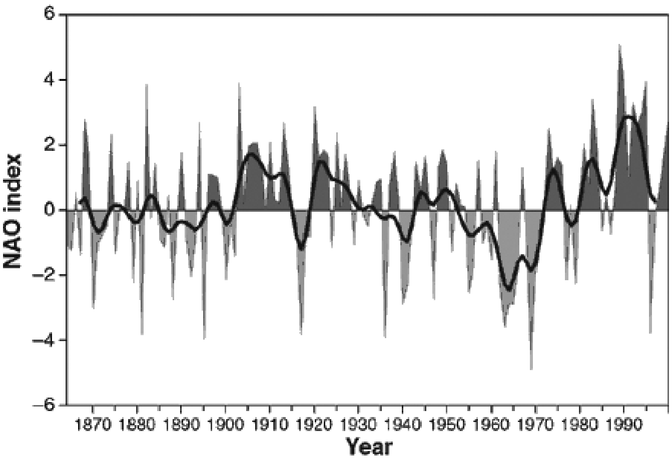

Figure 1. Upward trend of the winter NAO index based on the differences between the normalized pressures between Lisbon, Portugal, and Reykjavik, Iceland from 1864 to 2000. The bold black line represents the meridional pressure gradient smoothed to remove fluctuations with periods less than 4 years (Hurrell et al. 2001).

Long-distance migrants not only arrive later in spring but also depart earlier in autumn. Short-distance migrants, on the contrary, do delay their autumn passage (Jenni & Kéry 2003, MacMynowski & Root 2007). It has been suggested that short-distance migrants may benefit from a warming climate in several respects: shortening of migration distance, earlier start of reproduction, increased reproductive output owing to a prolonged breeding season, and better conditions in the breeding area after the breeding season (Jenni & Kéry 2003). A warmer climate at the breeding grounds may even facilitate that some species of short-distance migrants eventually stay over winter. This has already been observed both in the United Kingdom (blackcap *Sylvia atricapilla*, chiffchaff *Phylloscopus collybita*) and in the north-eastern United States (eastern bluebird *Sialia sialis*, yellow-rumped warbler *Dendroica coronata*, white-throated sparrow *Zonotrichia albicollis*, field sparrow *Spizella pusilla* and brown-headed cowbird *Molothrus ater*; Butler 2003). Long-distance migrants, however, may not obtain the same benefits from global warming. The start of their reproduction is constrained by a less plastic spring arrival date, controlled by an endogenous rhythm (Both & Visser 2001), and their autumn migration is probably constrained by the onset of the dry season in the Sahel rather than by conditions at the breeding grounds (Jenni & Kéry 2003). Consequently, their breeding season may not be prolonged. Recent climate changes therefore are likely to cause a considerable asymmetry in the effects on long- and short-distance migrants, with an increasing advantage for short-distance migrants (Jenni & Kéry 2003). Investigations on population declines of European breeding birds have shown that long-distance migrants already have declined more severely than short-distance migrants or resident birds for several reasons including climate change (Sanderson et al. 2006).

Box 2. The accuracy of measuring arrival times

Most research on the timing of arrival has examined the first arrival dates of species. First arrival observations, however, are only a single point in the migration distribution and only tell how this end of the distribution responds to weather or climate (Lehikoinen et al. 2004). First arrival dates may be influenced by individual birds responding independently to external stimuli and, particularly in species with sex-differences in migratory phenology, are likely to capture only the arrival of males (Sparks et al. 2005, MacMynowski & Root 2007). While sensitive to changes, first arrival dates will tell little about changes in the arrival distribution of a species.

Mean or median dates of arrival are more reliable by showing how the larger proportion of the population is responding to climatic changes (Lehikoinen et al. 2004, Sparks et al. 2005). Mean arrival dates will thus be less influenced by records of rogue birds or the size of the population. Albeit the advantages to look at mean arrival times this measurement has been argued to be more susceptible to biases from inconsistent data collection effort and to be a less good indicator of species' responses to changes early in the migratory period (MacMynowski & Root 2007).

2.2 Effects on breeding time

Good conditions at wintering habitats as well as higher temperatures along the migration route and on the breeding grounds influence the timing of breeding (Both et al. 2005, Both at al. 2006a). While female collared flycatchers (*Ficedula albicollis*) and pied flycatchers both breed earlier in years with positive NAO indices, the effect on clutch size varies substantially. Collared flycatchers responded with the initiation of larger clutches whereas pied flycatchers reduced their clutch size (Przybylo et al. 2000, Sanz 2003). Clearly, responses to changed breeding time may vary markedly, even between closely related species or between populations of the same species at different geographic locations (e.g. clutch size reductions of pied flycatchers in Spain and clutch size increases in the Netherlands; Sanz 2003, Both et al. 2004).

The overall timing of breeding shows large scale geographical patterns. In general, western European populations breed earlier and yet further advance their breeding date in years with more vegetation growth on their wintering grounds and North African staging sites. Northern and eastern European populations, in contrast, do generally breed later and just advance their breeding dates when the ecological conditions in Europe are more advanced following positive NAO winters (Both et al. 2006a).

3 Constraints on fitness

3.1 General seasonal fitness declines

In avian life-history the timing of reproduction is a pivotal factor affecting fitness (e.g. Verhulst & Tinbergen 1991, Verhulst et al. 1995). Seasonal declines in reproductive success, like reduced clutch size and lower fledgling recruitment, have long been recognised in studies of birds (e.g. Perrins 1970). This seasonal decline in reproductive performance could be caused by (i) deteriorating food conditions, (ii) correlations between breeding time and territory quality, and (iii) correlations between breeding time and individual quality (van Noordwijk et al. 1995, Verhulst et al. 1995).

The time of season when favourable conditions for reproduction exist is commonly limited by a time-window of sufficient food supply (van Noordwijk et al. 1995). For many sedentary and migratory insectivorous birds for example, it is essential to have chicks in their nests during the peak of caterpillar biomass. Studies on great tits and pied flycatchers have shown that differences in nesting success of later breeding birds towards earlier breeding birds are at least partly attributable to deteriorating food conditions (van Noordwijk et al. 1995, Siikamäki 1998).

The quality of the environment can act as a constraint through the availability of high quality breeding territories or overwintering habitats (Verhulst & Tinbergen 1991, Wiggins et al. 1994, Marra et al. 1998). This is especially likely for migratory species where early arriving individuals have access to the best breeding habitats and partners (Marra et al. 1998). Furthermore, early arriving individuals may be in better physical condition and thus able to reproduce more successfully (Marra et al. 1998, Both & Visser 2001).

3.2 Climate change induced fitness declines: the mismatch hypothesis

A growing number of studies show that the phenological patterns of many species have advanced under the climatic changes of the last decades (Forchhammer et al. 1998, Post et al. 2001, Walther et al. 2002). The progression of spring averaged 2.3 days per decade (Parmesan & Yohe 2003) and warmer temperatures have lead to earlier plant and insect occurrences (Visser et al. 1998, Post et al. 2001).

As already indicated above, the successful reproduction of many sedentary and migratory insectivorous birds is determined by the abundance of prey biomass. The simplified trophic structure of the food chain can be represented by oak trees (*Quercus robur*), winter moth (*Operophtera brumata*) caterpillars, and insectivorous birds (e.g. Visser et al. 1998, Visser & Holleman 2001). Winter moth caterpillars first appear with the budding of oak trees and are just available until they start to pupate and move into the soil. These processes are strongly temperature related, as caterpillar growth and pupation proceed more rapidly during warmer weather condition, such that caterpillars not only occur earlier but are also available for a shorter time period (Both & Visser 2005). Investigations of long-term population trends in pied flycatchers, great tits, and blue tits have documented an advancement in the caterpillar biomass peak (approximately nine days since the 1970s; Visser et al. 1998) and the resulting often negative implications for avian fitness correlates (e.g. breeding time, brood size, and adult survival; Visser et al. 1998, Thomas et al. 2001, Laaksonen et al. 2006). Since the reproductive success of these insectivorous species strongly depends on synchronising the peak in their offspring’s food demand with the peak occurrence of prey items they face the need to adapt to the changes in their environment. This synchronisation, however, is seldom fully achieved so that there is an observable mismatch between food supply and nestling demand (mismatch hypothesis; Visser et al. 1998).

Alterations in avian life history and fitness in correlation to food peak shifts have been documented for a variety of factors:

(i) The interval between the arrival time of migratory birds and the initiation of clutches has decreased. In pied flycatchers the selection for early egg laying has become stronger (Figure 2; Both & Visser 2001). This response to warmer temperatures and changes in food availability is nonetheless limited by the arrival date of the flycatchers, which has not advanced, so that large parts of the population are laying too late for an optimal exploitation of the food peak (Both & Visser 2001).

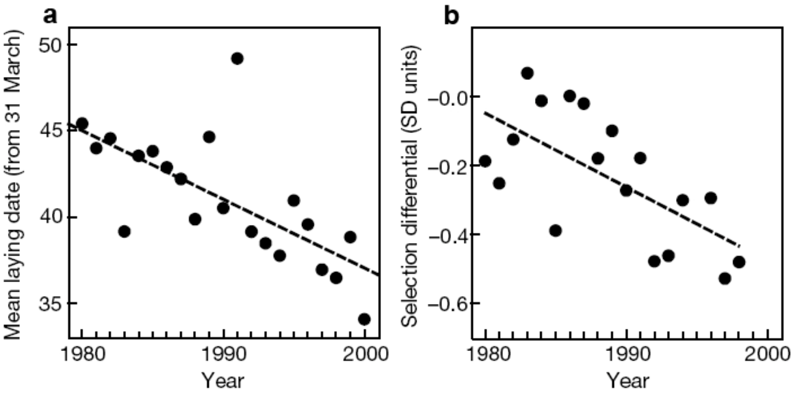

Figure 2. Breeding date of a pied flycatcher population in the Netherlands from 1980 to 2000, with (a) the advancement of the mean laying date, and (b) the standardized selection differential for laying date decreasing with year over this period (Both & Visser 2001).

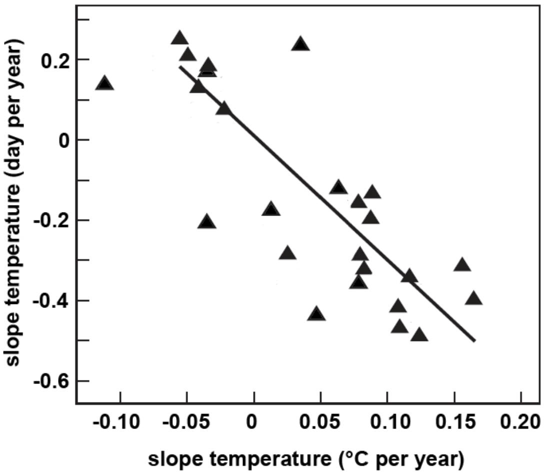

Figure 3. Responses in laying date of pied flycatcher populations in Europe from 1990 to 2002. Populations in areas with a stronger increase in temperature advanced their laying date more (each symbol representing one population; Both et al. 2004).

(ii) The first egg date of many species has advanced. Birds breeding in the United Kingdom have shown a general trend towards earlier laying since the 1980s (Crick & Sparks 1999) and long-term studies have shown that this is the case for resident and migratory species (i.e. great tits and pied flycatchers; Cresswell & McCleery 2003, Laaksonen 2006). The advancement of clutch initiation is strongly dependent on regional spring temperature patterns and earlier egg laying within the geographical breeding area of a species did just take place when regional temperatures increased (Figure 3; Both et al. 2004). This observation is in agreement with the trade-off between earlier egg laying and temperature-dependent constraints on egg production, as higher energetic costs and the risk of laying poor-quality eggs early in the season will impede the production of early clutches (van Noordwijk et al. 1995, Stevenson & Bryant 2000). Constraints during egg laying are also one explanation to why a population of great tits in the Netherlands shows no advancement in laying date, since only temperatures during the time of caterpillar growth increased while temperatures during egg laying have remained unchanged (Visser et al. 1998).

(iii) The laying - hatching interval has become shorter over the years, thus advancing hatching date. Birds that responded to the advancement of the food peak with earlier egg production mostly also fledged their young earlier (Figure 4; Cresswell & McCleery 2003, Both & Visser 2005). A shorter laying - hatching interval indicates a reduction of incubation time *per se* (i.e. by incubating the clutch earlier), with which the birds partly try to further compensate for their incomplete response to the caterpillar peak (Both & Visser 2005). Observations made on a great tit population in the United Kingdom, however, point out a decreasing variance in hatch date which indicates that the proportion of birds hatching during optimal food abundance has increased (Cresswell & McCleery 2003).

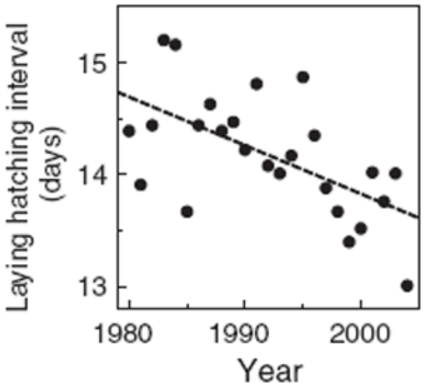

Figure 4. Changes in the interval between the laying of the last egg and hatching of the first egg from 1980 to 2000 in a pied flycatcher population in the Netherlands (Both & Visser 2005).

(iv) Clutch size followed no general within-year or between-year trend but largely depended on temperature and food availability at the time of egg-laying. Low temperatures in the month before laying lead to the initiation of larger clutches, since the peak in caterpillar biomass will probably be delayed (i.e. a strategic response). If temperatures, by contrast, are low a few days just before laying smaller clutches will be formed (i.e. possibly an energetic constraint; Cresswell & McCleery 2003). In pied flycatchers inter-annual temperature increases are associated with increases in clutch size (Figure 5a; Both et al. 2004). The formation of larger clutches, nonetheless, not automatically results in a higher reproductive success but rather amplifies the already existing mismatch with the food peak. In years with an early food peak (i.e. shorter food peak) clutch sizes showed a steeper within-year decline followed by declining recruitment rates (Both & Visser 2005). Brood survival and recruitment into the breeding population are highly dependent on the biomass peak. In a great tit population in the Netherlands broods raised before or after the food peak fledged fewer and lighter chicks whereas heavier and fitter offspring resulted from synchronised clutches (Figure 5b; Visser et al. 2006). As the phenology of the food has advanced more than the phenology of the birds, the interval between laying and the food peak has become shorter and most of the bird thus have their offspring too late to profit optimally from the peak in caterpillar biomass (Visser et al. 2006).

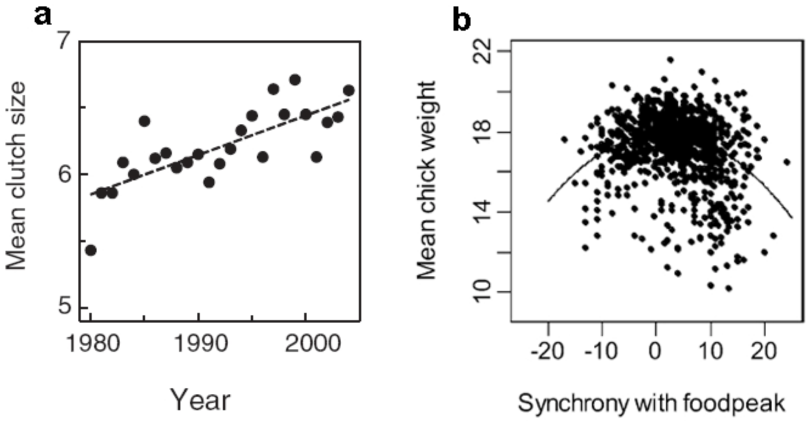

Figure 5. Annual reproductive parameters of (a) clutch size in pied flycatchers from 1980 to 2004 (Both & Visser 2005), and (b) mean chick weight of great tits in relation to the caterpillar peak (Visser et al. 2006).

(v) The frequency of second broods does decrease with rising annual spring temperatures. The shortened biomass peak has reduced the reproductive value of second clutches for facultatively double-brooded species over the years (i.e. great tits and blue tits) and hence decreased the frequency of second clutch production (Visser et al. 2003). If spring temperatures continue to increase, the number of second clutches will eventually decrease further, since only the first clutch will be timely enough to profit from adequate food resources. This will affect population dynamics, for once no second broods are produced the number of recruited offspring is going to decline (Visser et al. 2003).

(vi) Parental fitness and survival decrease with the degree of mismatch to the food peak. The metabolic effort of parents for rearing young rises when the offset between breeding date and caterpillar peak increases. The mismatch between nestling demand and prey abundance forces parents to increase foraging effort beyond their sustainable limit (i.e. decreasing the probability of future survival and reproductive prospects), resulting in a trade off between immediate metabolic effort and persistence in the breeding population (Thomas et al. 2001).

In summary, birds are trying to attain synchronisation with the climatically induced shift in their food resources by laying eggs earlier and reducing incubation time. The mismatch to the food peak may, however, seldom be fully compensated for. Bird populations not breeding at the optimum food availability face lower brood survival and fledgling recruitment, while parental birds are additionally confronted with lower future fitness and survival prospects. Population declines may be the consequence and are already observed in mistimed pied flycatcher populations in the Netherlands, Spain, and Sweden (Both et al. 2004, Both et al. 2006b).

Despite the striking implications and the large amount of evidence for the mismatch hypothesis within the above study systems (i.e. great tits, blue tits, pied flycatchers) the generality of the drawn conclusions remains questionable. Other insectivorous bird species that, however, not primarily depend on caterpillar prey or occur within different habitat types, such as open grasslands, might experience substantially different patterns of prey abundance. For this other habitats and species different “match-/mismatch-scenarios” in relation to prey availability might apply.

4 Evolutionary responses

A critical question to species long-term viability is whether they can adjust to climatic changes. Species may principally respond in three ways to the selection pressures imposed by climate change (Davies et al. 2005, Gienapp et al. 2008). First, they can evade the new conditions and shift their ranges in the direction to more suitable habitats (Hickling et al. 2006, Parmesan 2006). Second, they can remain within their current range and adapt to the changes by means of phenotypic plasticity or, third, evolve by selection on heritable traits (Pulido & Berthold 2004, Gienapp et al. 2008). Of these three scenarios there is only good empirical evidence of the two first mentioned ones. For example, birds have been show to shift their breeding and overwintering ranges (Thomas & Lennon 1999, Austin & Rehfisch 2005), as well as to change the phenological patterns of migratory arrival at their breeding areas and the initiation of breeding (e.g. Przybylo et al. 2000, Jonzén et al. 2006). Climate-driven microevolutionary responses, however, are scarcely documented.

The documented examples of phenotypic and genetic changes together with their implications for evolutionary changes yet lack the answer on whether avian populations will be able to persist under a changing climate. These examples are:

(i) Earlier egg laying in birds, despite having a large heritability in many populations, is best explained by individual adjustments to increasing temperatures (i.e. phenotypic plasticity; Przybylo et al. 2000, Both & Visser 2001). Investigations on phenotypic and genetic changes on breeding time and clutch size of collared flycatchers confirmed the role of phenotypic plasticity, as no evidence for an evolutionary change was found (Sheldon et al. 2003). The extent of phenotypic plasticity may also be heritable (as shown for great tits), and selection may favour highly plastic females that lay their eggs early on average (Nussey et al. 2005). The timing of breeding, nonetheless, seems to lag behind the timing of the food peak, such that lifetime reproductive success is declining and threatening the viability of the population (Nussey et al. 2005). This is in marked contrast to the findings of a recent study showing that a population of great tits in the United Kingdom responds to changing environmental conditions by adaptive individual plasticity alone, with population fitness parameters indicating a thriving population in synchrony with the timing of caterpillar emergence (Charmantier et al. 2008). While phenotypic plasticity provides an important mechanism to cope with changing environmental conditions its responses will, however, be limited. If, for example, environmental changes progress to a point where plastic responses are not able to mitigate fitness losses or when the existing reaction norm and fitness change over time, which, in the case of climate change, seems quite likely (Gienapp et al. 2008). Adaptations through phenotypic plasticity will thus be unable to match the adaptations achievable through microevolutionary change.

(ii) The one of the best examples for a genetic response to climate change is the evolution of a new migration pattern (Berthold et al. 1992). Blackcaps (*Sylvia atricapilla*) breeding in middle Europe have adopted a new westerly migration route over the last 30 years, with an increasing fraction of the population wintering in Britain instead on the Iberian peninsula (Berthold et al. 1992). In the blackcap, genetic correlations among migratory traits, such as the incidence, intensity and timing of migratory activity, suggest that selection on one migratory trait will strongly influence other traits. Existing genetic correlations among migratory traits may thus facilitate a rapid adaptation to changes in breeding and wintering latitude or to phenological changes (Pulido & Berthold 2004).

The fact that evidence for microevolutionary changes is largely non-existent does not imply that these changes are not taking place, but that they might be so small that they escape detection. On the other hand, we also should not be satisfied by the large amount of evidence in favour of phenotypic plasticity alone. Phenotypic trends not necessarily have to be good indicators of according genotypic changes, as phenotypic responses observable as changes in population mean trait values can occur without corresponding changes at the genetic level (Gienapp et al. 2008). Thus, the indication that phenotypic plasticity exists within populations will not guarantee the successful adaptation to climatic changes in the long run.

5 Conclusion

The current available evidence gained through long-term datasets gives ample support for the impacts of global warming on avian life histories and individual fitness. However, the observed patterns of changes in fitness correlates in relation to increasing temperatures are far from showing a uniform picture. Even between closely related species or between populations within species observed responses to increasing temperatures vary (e.g. clutch size of pied or collared flycatchers; Sanz 2003, Both et al. 2004). A key issue to the understanding of this variation may be a corresponding variation in prior adaptation to local climate and food sources. Therefore we expect the genetic architecture of traits such as breeding time, clutch size and the probability of laying multiple clutches to vary between populations and species. However, at present this between- and within-species variation in the genetic architecture of traits and their responses to increasing temperatures are not understood. Future studies on adaptive variation in relation to population histories in terms of climate and selection pressures may help to resolve this lack of understanding.

At present most results are based on a few well studied species (i.e. mainly pied flycatchers, collared flycatchers, great tits, and blue tits). All these studies have been made in broad-leaved forests (mainly oak

Quercus spp.) were individual fitness is strongly dependent on matching the nestling period with the peak abundance of winter moth larvae. As many other woodland species and species breeding in other habitats (e.g. grasslands, wetlands) rely on other food sources one may question the generality of the present results. Similarly, there is a lack of studies on both, changes in climate and the response of bird species in other ecosystems than non-temperate ones. Clearly, there is a need to broaden the perspectives to include studies of species breeding in other habitats and climatic regions.

Breeding time displays a high degree of phenotypic plasticity in relation to temperature in most studied populations. Thus, observed phenotypic changes in breeding time may not reflect an evolutionary change in breeding time (Gienapp et al. 2008). A central question to be answered, however, is whether this degree of plasticity, that probably is a result of climatic variations of the past, is enough to keep populations at track when the climate changes further. A linked question is whether phenotypic plasticity in itself has a heritable component and whether selection for an increased degree of plasticity causes and evolutionary change in the reaction norm in relation to climate. Although these questions have been touch upon recently (e.g. Nussey et al. 2005, Charmantier et al. 2008), much remains to be done.

The future will show in which way the various bird species are able to cope with and adapt to climate change. More profound information on evolutionary responses would thereby be highly valuable to make predictions if evolution will be able to keep up with the challenges climate change imposes on the persistence of species and populations in the long run.

6 References

Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K. & Lehikoinen, E. 2004 Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology* 10, 1610-1617.

Austin, G. E. & Rehfisch, M. M. 2005 Shifting nonbreeding distribution of migratory fauna in relation to climate change. *Global Change Biology* 11, 31-38.

Bairlein, F. & Hüppop, O. 2004 Migratory fuelling and global climate change. *Advances in Ecological Research* 35, 33-47.

Berthold, P., Helbig, A. J., Mohr, G. & Querner, U. 1992 Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360, 668-670.

Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V., Järvinen, A., Metcalfe, N. B., Nyholm, N. E. I., Potti, J., Ravussin, P.-A., Sanz, J. J., Silverin, B., Slater, F. M., Sokolov, L. V., Török, J., Winkel, W., Wright, J., Zang, H. & Visser, M. E. 2004 Large-scale geographic variation confirms that climate change causes birds to lay earlier. *Proccedings of the Royal Society London B* 271, 1657-1662.

Both, C., Bijlsma, R. G. & Visser, M. E. 2005 Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. *Journal of Avian Biology* 36, 386-373.

Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. 2006b Climate change and population declines in a long-distance migratory bird. *Nature* 441, 81-83.

Both, C., Sanz, J. J., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Enemar, A., Järvinen, A., Nyholm, N. E. I., Potti, J., Ravussin, P.-A., Silverin, B., Slater, F. M., Sokolov, L. V., Visser, M. E., Winkel, W., Wright, J. & Zang, H. 2006a Pied fliycatchers *Ficedula hypoleuca* travelling from Africa to breed in Europe: differential effects of winter and migration condition on breeding date. *Ardea* 94, 511-525.

Both, C. & Visser, M. E. 2001 Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411, 296-298.

Both, C. & Visser, M. E. 2005 The effect of climate change on the correlation between avian life-history traits. *Global Change Biology* 11, 1606-1613.

Butler, C. J. 2003 The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *The Ibis* 145, 484-495.

Charmentier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B. & Sheldon, B. C. 2008 Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320, 800-803.

Cotton, P. A. 2003 Avian migration phenology and global climate change. *PNAS* 100, 12219-12222.

Cresswell, W. & McCleery, R. H. 2003 How great tits maintain synchronisation of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology* 72, 356-366.

Crick, H. Q. P. & Sparks, T. H. 1999 Climate change related to egg-laying trends. *Nature* 399, 423-424.

Davis, M. B., Shaw, R. G. & Etterson, J. R. 2005 Evolutionary responses to climate change. *Ecology* 86, 1704-1714.

Forchhammer, M. C., Post, E. & Stenseth, N. C. 1998 Breeding phenology and climate... *Nature* 391, 29-30.

Forchhammer, M. C., Post, E. & Stenseth, N. C. 2002 North Atlantic Oscillation timing of long- and short-distance migration. *Journal of Animal Ecology* 71, 1002-1014.

Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. & Merilä, J. 2008 Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology* 17, 167-178.

Gordo, O. & Sanz, J. J. 2008 The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. *Journal of Ornithology* 149, 199-210.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R. & Thomas, C. D. 2006 The distribution of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12, 450-455.

Hurrell, J. W., Kushnir, Y. & Visbeck, M. H. 2001 The North Atlantic Oscillation. *Science* 291, 603-605.

Hüppop, O. & Hüppop, K. 2003 North Atlantic Oscillation and timing of spring migration. *Proccedings of the Royal Society London B* 270, 233-240.

IPCC. 2007 Summary for Policymakers. In *Climate Change 2007: The Physical Sciences Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panal on Climate Change*. Cambridge, UK and New York, USA: Cambridge University Press.

Jenni, L. & Kéry, M. 2003 Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proccedings of the Royal Society London B* 270, 1467-1471.

Jonzén, N., Lindén, A., Torbjørn, E., Knudsen, E., Vik, J. O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R. & Stenseth, N. C. 2006 Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312, 1959-1961.

Laaksonen, T., Ahola, M., Eeva, T., Väisänen, R. A. & Lehikoinen, E. 2006 Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. *Oikos* 114, 277-290.

Lehikoinen, E., Sparks, T. H. & Zalakevicius, M. 2004 Arrival and departure dates. *Advances in Ecological Research* 35, 1-31.

MacMynowski, D. P. & Root, T. L. 2007 Climate and the complexity of migratory phenology: sexes, migratory distance, and arrival distribution. *International Journal of Biometeorology* 51, 361-373.

Marra, P. P., Hobson, K. A. & Holmes, R. T. 1998 Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282, 1884-1886.

McCarthy, J. P. 2001 Ecological consequences of recent climate change. *Conservation Biology* 15, 320-331.

Møller, A. P. 1994 Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavoral Ecology and Sociobiology* 35, 115-122.

Nussey, D. H., Postma, E., Gienapp, P. & Visser, M. E. 2005 Selection on heritable phenotypic plasticity in a wild bird population. *Science* 310, 304-.

Oba, G., Post, E. & Stenseth, N. C. 2001 Sub-saharan desertification and productivity are linked to hemispheric climate variability. *Global Change Biology* 7, 241-246.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C. & Stenseth, N. C. 2001 Ecological effects of the North Atlantic Oscillation. *Oecologica* 128, 1-14.

Parmesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annual Review in Ecology, Evolution and Systematics* 37, 637-669.

Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37-42.

Perrins, C. M. 1970 The timing of birds' breeding season. *The Ibis* 112, 242-255.

Post, E., Forchhammer, M. C., Stenseth, N. C. & Callaghan, T. V. 2001 The timing of life-history events in a changing climate. *Proccedings of the Royal Society London B* 268, 15-23.

Przybylo, R., Sheldon, B. C. & Merilä, J. 2000 Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *Journal of Animal Ecology* 69, 395-403.

Pulido, F. & Berthold, P. 2004 Microevolutionary response to climate change. *Advances in Ecological Research* 35, 151-183.

Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J. & van Bommel, F. P. J. 2006 Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation* 131, 93-105.

Sanz, J. J. 2003 Large-scale effect of climate on breeding parameters of pied flycatchers in Western Europe. *Ecography* 26, 45-50.

Sheldon, B. C., Kruuk, L. E. B. & Merilä, J. 2003 Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution* 57, 406-420.

Siikamäki, P. 1998 Limitation of reproductive success by food availability and breeding time in pied flycatchers. *Ecology* 79, 1789-1796.

Sparks, T. H., Bairlein, F., Bojarinova, J. G., Hüppop, O., Lehikoinen, E., Rainio, K., Sokolov, L. V. & Walker, D. 2005 Examining the total arrival distribution of migratory birds. *Global Change Biology* 11, 22-30.

Stevenson, I. R. & Bryant, D. M. 2000 Climate change and constraints on breeding. *Nature* 406, 366-367.

Thomas, C. D. & Lennon, J. J. 1999 Birds extend their ranges northwards. *Nature* 399, 213.

Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M. & Speakman, J. R. 2001 Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* 291, 2598-2600.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* 416, 389-395.

van Noordwijk, A. J., McCleery, R. H. & Perrins, C. M. 1995 Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *Journal of Animal Ecology* 64, 451-458.

Verhulst, S. & Tinbergen, J. M. 1991 Experimental evidence for a casual relationship between timing and success of reproduction in the great tit *Parus major*. *Journal of Animal Ecology* 60, 269-282.

Verhulst, S., van Balen, J. H. & Tinbergen, J. M. 1995 Seasonal decline in reproductive success of the great tit: variation in time or quality? *Ecology* 76, 2392-2403.

Wiggins, D. A., Pärt, T. & Gustafsson, L. 1994 Seasonal decline in collared flycatcher *Ficedula albicollis* reproductive success: an experimental approach. *Oikos* 79, 359-364.

Visbeck, M. H., Hurrell, J. W., Polvani, L. & Cullen, H. M. 2001 The North Atlantic Oscillation: past, present, and future. *PNAS* 98, 12876-12877.

Visser, M. E., Adriaensen, F., van Balen, J. H., Blondel, J., Dhondt, A. A., van Dongen, S., du Feu, C., Ivankina, E. V., Kerimov, A. B., de Laet, J., Matthysen, E., McCleery, R. H., Orell, M. & Thomson, D. L. 2003 Variable responses to large-scale climate change in European *Parus* populations. *Proccedings of the Royal Society London B* 270, 367-372.

Visser, M. E. & Holleman, L. J. M. 2001 Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proccedings of the Royal Society London B* 268, 289-294.

Visser, M. E., Holleman, L. J. M. & Gienapp, P. 2006 Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologica* 147, 164-172.

Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. 1998 Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proccedings of the Royal Society London B* 265, 1867-1870.