Managing time in a changing world
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Chapter 2

Climate change impacts: birds

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The text is presented here with minor formatting alterations and lacking the following sections:
References and Further Reading.
Abstract

Climate change can affect populations and species in various ways. Rising temperatures can shift geographical distributions and lead to (phenotypic or genetic) changes in traits, mostly phenology, which may affect demography. Most of these effects are well documented in birds. For example, the distribution of species has shifted polewards, and birds are nowadays breeding or migrating earlier. An important aspect of the observed phenological changes is whether species are thereby able to maintain synchrony with phenological changes in their environment, for example the phenology of their prey species. Disrupted synchrony, for example between predator and prey, can lead to reduced reproductive success or survival, which can negatively affect demography. Evidence for this happening in birds is – so far – limited but theoretical models predict that extinction risks could arise through insufficient adaptation to such phenological mismatches.

Introduction

Over the past 100 years, the global climate has warmed considerably, mainly from the 1980s onwards. This increase in temperature is not globally uniform but differs between regions and within seasons. For example, winter temperatures have increased more than summer temperatures, and temperatures in the northern hemisphere have increased more than in the southern hemisphere (Walther et al., 2002). This spatial and temporal heterogeneity can have important consequences for species and populations. Numerous studies covering a wide range of taxa have shown biological responses to global warming and a “coherent fingerprint of climate change” is visible (Root et al. 2003; Parmesan & Yohe, 2003; Parmesan 2006). For example, insects, birds and even fish have extended their geographical distribution polewards because the geographic distribution of their “bioclimatic envelopes” shifted.

Climate can affect any species in two fundamentally different ways. First, ambient temperature can directly affect the organism itself. The rates of cellular processes are temperature dependent: a temperature increase of 10 ºC doubles it. Therefore, all physiological processes in ectotherm organisms, as, for example, insects, fish or reptiles, are strongly dependent on ambient temperature. Endotherm organisms, that is mammals and birds, keep their body temperature constant and consequently, their physiological processes are independent of the ambient temperature. However, to achieve this they have to spend energy on thermoregulation, which can be substantial under extreme conditions.

Second, ambient temperatures affect the organism’s biotic environment by effects on interacting species, that is predators, prey or competitors. Rising temperatures can
disrupt the phenological synchrony between species, for example between the time when
great tits, an insectivorous passerine, breed and need abundant prey to raise their large
broods and the time when this prey is most abundant (Visser et al. 1998, 2006). Such
indirect climatic effects can also be more complex and have a more dramatic impact:
the regularly occurring El Niño atmospheric phenomenon causes a shift in the cold
Humboldt current in the Pacific ocean. This current brings nutrients to surface waters
where they sustain rich algae growth, which in turn sustains abundant fish populations.
During an El Niño, the fish populations crash, which leads to complete breeding failure
and even increased adult mortality among seabirds along the West Coast of North
America and South America (Barbraud & Weimerskirch 2003).

Birds are generally well studied and many bird populations have been monitored for a long
time, sometimes even for more than half a century. This presents a unique opportunity
to study the impact of climate change as it is possible to combine extensive data sets with
comparably good knowledge about relevant biological effects and mechanisms.

**Observed impacts of climate change on birds**

*Geographical distributions*
The current distribution of bird species can be mapped as a function of their environment
using the so-called bioclimate envelopes (Howard et al. 2015). Under global warming
these “envelopes” are expected to shift, leading to latitudinal or elevational shifts in
species’ distributional ranges (Huntley et al. 2008). Various bird species in Great Britain
and North America, for example, have shifted their northern range margins towards
higher latitudes, with southern birds moving at a rate of 0.95 and 2.35 km year−1,
respectively (Thomas & Lennon 1999; Hitch & Leberg 2007). Not every species, however,
is expected to shift its distribution at the necessary rate expected from changing abiotic
conditions. For example, migratory birds are likely to suffer increased competition for
resources with resident birds under increased winter temperatures, as these more benign
winter conditions increase the survival probability of residents and may enhance their
dispersal and colonisation of new sites (Schaefer et al. 2008). Conversely, if temperatures
and resource availability increase in spring, migrants may benefit because they can
colonise new breeding sites previously too cold or resource limited. As another example,
montane birds, confined to mountains, may be inhibited in their dispersal abilities and
therefore be susceptible to extinction due to global warming (Sekercioglu et al. 2008).
Species may further be limited in their dispersal ability if this will result in decoupling of
crucial trophic interactions, for example, if birds’ dispersal abilities exceed that of their
resources (van der Putten et al. 2010). Ultimately, a species’ propensity to change its
distributional range over decadal scales will depend, amongst others, on the life-history
of the species, average climate conditions, geographical context and human land-use
practices (Bradshaw et al. 2014; Lehikoinen & Virkkala, 2016).

**Phenology**

**a) Breeding time**

One of the first reported impacts of climate change on avian biology was the advancement in breeding time (Crick et al. 1997; Dunn & Winkler 1999). Avian breeding time is strongly plastic in response to ambient temperatures with birds breeding early under warmer temperatures. As climate change has increased spring temperatures in recent decades, avian breeding time has advanced along with it, with the magnitude of the response differing between species or populations within a species (Both et al. 2004; Torti & Dunn 2005).

One exceptionally well-studied example of changes in avian phenology and arising mismatches between trophic levels comes from a Dutch long-term study on great tits (Visser et al. 1998, 2006). The great tit is the secondary consumer in the great tit–winter moth–oak food chain. The phenology of great tits needs to be well timed with that of lower trophic levels as the birds rely heavily on caterpillars as the main food source for their nestlings. Caterpillars of the winter moth (*Operophtera brumata*) hatch in April and have to feed on the fresh leaves of oaks, as they grow less rapidly and attain lower fecundity if they feed on older leaves (van Asch & Visser 2007). They develop through all instar stages in May to pupate in late May or June. These caterpillars thus show a clear biomass peak generally around mid-May but depending on spring temperature this can vary by about 2 weeks. Great tits use this biomass peak to provision their nestlings, whose energy demands are highest when they are 9–12 days old (Visser et al. 2006; Both 2010b) and brood success is highest when this energy demand coincides with biomass peak date (Visser et al. 2006; Reed et al. 2013a, b; see left-hand side of Fig. 2.1). Owing to warming springs, however, the caterpillar biomass peak has advanced by about 2 weeks, whereas the time of peak nestling energy demand has advanced by about 5 days (Visser et al. 1998, 2006; see right-hand side of Fig. 2.1). Consequently, there is now asynchrony between nestling food demand and food availability.

Why is there a mismatch between the caterpillar and great tit phenology? The lack of an adequate response to warming springs has been related to two, mutually nonexclusive theories (Visser et al. 2012). First, birds may be constrained in the advancement of their reproduction in early spring simply because they cannot obtain enough resources to meet the physiological demands associated with egg production (the constraint hypothesis). This means that birds either cannot lay eggs in early spring or, if they can, will incur high survival costs. This hypothesis is unfortunately very difficult to test as experimentally advancing breeding time without providing the birds with additional
resources (which would lift the very constraint one aims to test; Verhulst & Nilsson 2008; but see Gienapp & Visser 2006).

A second hypothesis states that the cues that birds use to time their reproduction are no longer adaptive (the cue hypothesis). Great tits have to plan their reproduction about a month in advance of the caterpillar biomass peak. By the time this peak occurs, the birds should have built the nest, laid and incubated the entire clutch of eggs and raised the chicks up until the moment when their energy requirements are highest. Thus, the birds make their reproductive decision (i.e., when to lay eggs) in a different environment to where selection (i.e., nestling survival) takes place (Visser et al. 2004). The phenology of both caterpillars and great tits depends on temperature. However, owing to imperfect cue reliability, consumer (e.g., great tit) phenology tends to be always less plastic than the resource (e.g., caterpillar) phenology; this means that even under homogeneous

Figure 2.1. Schematic representation of the great tit–caterpillar phenology in the Hoge Veluwe. Three important life-history events in the great tit reproduction cycle are denoted with the red line and nestling peak food need with a green line in the top half of the schematic; the caterpillar phenology is indicated with the green line in the lower half. Before the effects of climate change were apparent, peak food demands and availability coincided (left-hand side of the schematic); owing to increasingly warmer springs, the caterpillar biomass peak has advanced by ~2 weeks, whereas the timing of nestling peak food need has advanced at a slower rate, leading to “phenological mismatch” (right-hand side).
environmental change phenotypic plasticity of the consumer phenology will be insufficient and this will inevitably lead to selection on consumer phenology (Gienapp et al. 2014). Ultimately, therefore, birds will only be able to keep their phenology in synchrony with that of their prey through a genetic shift (advance) in their average breeding time (see the section titled “Plastic versus Genetic Changes”). Not all species or populations have become maladapted to these novel environmental conditions. Great tits in UK forest systems, for example now breed too early but maintain their synchrony with the food peak by increasing the incubation period (Charmantier et al. 2008).

**b) Migration**

The annual cycle of a temperate-zone migrant, which comprises the most studied species, can be divided into four main phases: (1) ‘wintering’, when no breeding activity occurs, (2) spring (or vernal) migration, the movement from the wintering to the breeding grounds, (3) breeding and (4) autumn migration, the movement from the breeding to the wintering grounds. A number of studies focus on the spring migration and, more specifically, on the arrival time of migratory birds, particularly passerines (Both & Visser 2001; Ahola et al. 2004; Kristensen et al. 2015). Similarly to the breeding stage, there is an optimal time to migrate and arrive at the breeding sites (Jonzén et al. 2007; Alerstam 2011). On one hand, arriving too early can be costly when environmental conditions are still harsh or unpredictable. On the other hand, late arriving individuals can face stronger competition for mates or territories and may also experience reduced reproductive success owing to the rapid decline of resources in summer. For example, in 1996, 5 days of exceptionally cold and rainy weather during the main arrival time caused mortality of about 50–70% in North American Cliff Swallows (Brown & Brown 2000). Such cold spells happen regularly during the arrival time of this species imposing a high cost of early arrival. However, selection for early arrival seems to be the general case in migratory birds (Bêty et al. 2004; Smith & Moore 2005; Rubolini et al. 2010; Gienapp & Bregnballe 2012; Arnaud et al. 2013).

As the optimal arrival time varies among years depending on the progress of spring, avian migration time also shows phenotypic plasticity similar to avian breeding time. It has been shown that birds adjust the timing of their migration to climate and arrive earlier in warmer springs and after milder winters. Therefore, an expected effect of climate change on bird migration would be the earlier arrival of migrants to their breeding grounds (Walther et al. 2002).

However, the observed pattern is not uniform and while advancements were reported for some species (Marra et al. 2005), in others there was very little change (Both & Visser 2001). For example, long- and short-distance migrants could differ in the degree of phenotypic plasticity expressed in arrival time. Short-distance migrants are likely to
show more flexible responses as climatic conditions at their wintering areas are more closely related to the ultimately important conditions at the breeding areas. Thus, more reliable cues may be available for them than for long-distance migrants. For long-distance migrants (e.g., those wintering south of the Sahara) climatic conditions at the wintering areas correlate less closely with climatic conditions at the breeding areas. They are therefore supposed to rely mainly on internal rhythms and photoperiod to time their departure from the wintering areas (Gwinner 1996). This would mean that their departure time is more or less constant among years, which in turn means that these species may be too inflexible to adjust to climate change. Alternatively, by adjusting their migration speed to environmental conditions en route would be a way for long-distance migrants to express some degree of phenotypic plasticity and be able to adjust their arrival time accordingly (Both 2010a). Another way of compensating would be the shortening of migration distances observed in some species. This not only reduces the distance needed to be covered by the migrant but also potentially allows cues to be more correlated and predictable (Visser et al. 2009).

A meta-analysis combining data on 249 species from 18 studies found that arrival time of migratory birds has advanced, with birds arriving earlier after milder winters and in warmer springs (Gienapp et al. 2007). However, in this case, no clear differences between European long- and short-distance migrants were found, which indicates that also long-distance migrants have been able to respond to climate change. The remaining question is whether the observed advancements in migration time match the supposed shifts in the optimal arrival time. Unfortunately, almost no study has reported data on reproductive success or survival in relation to arrival date, mainly due to the difficulties in getting such information for most species.

The majority of studies on climate change effects on birds have been conducted on passerines. However, similar patterns are observed in other avian orders, with variable responses according to species characteristics. For example, earlier arrival time at the breeding grounds in Iceland has been reported for several nonpasserine taxa (gulls, waders and geese; Gunnarsson & Tomasson 2011). Arctic-breeding geese are an interesting example as they present marked differences from passerines: their northward migration is related to the timing of vegetation growth, their main food source, and if a bird is able to fatten enough during migration, it will also be able to breed earlier upon arrival (van der Graaf et al. 2006; van der Jeugd et al. 2009). Similarly to passerines, geese such as the brent goose seem to also suffer from mismatches: climate-related changes in timing of vegetation growth mean the birds are now late in relation to their food, which means less fattening opportunities for themselves or their offspring (Clausen & Clausen 2013). Analysis of long-term datasets also shows that some populations of the barnacle goose shortened their migration distance and/or became resident in the temperate wintering location. This change in breeding location, however, may also make the birds more
mismatched, as their chicks are born too late in relation to the onset of vegetation growth in the new location (van der Jeugd et al. 2009).

The complex annual cycle of migrants that makes the animals experience climatic conditions from several portions of the world brings the challenging task of assessing the impact of climate change with respect to their entire annual cycle (Visser & Both 2005; Marra et al. 2015a). For example, some studies argue that conditions experienced in the wintering grounds or during migration can be even more important than those experienced at the breeding environment to explain fitness differences or population declines (Small-Lorenz et al. 2013).

Most studies focus on the (spring) migration from the wintering to the breeding grounds, mostly based on arrival dates at the breeding ground or passage dates at a given point close to the breeding grounds. Departure dates from the breeding (Europe) to the wintering grounds (Africa) are also changing. The pattern, however, differs between short- and long-distance migrants: while advancements have been observed for long-distance migrants, delays have been observed in short-distance migrants (Jenni & Kery 2003).

The recent development and miniaturisation of better tracking devices now also allows following individuals of small species, such as most passerine long-distance migrants, throughout the annual cycle (Stutchbury et al. 2009; Bridge et al. 2011; McKinnon et al. 2013). This will enable much more detailed studies on timing, movements and site selection of migratory birds and thereby, hopefully, shed new light on our understanding of the impacts of climate change on migratory birds.

**Morphology**

Temperature is known to correlate with body size of different groups, with paleontological (Smith et al. 2009) and recent (Sheridan & Bickford 2011) evidence that warmer temperatures correlate with smaller body sizes. For homeotherms, Bergmann’s rule predicts that body size is adjusted to climate and animals would be larger in higher latitudes (i.e., colder climates) as an energetic adaptation to the colder temperatures. Although originally proposed for different species inhabiting distinct latitudes, it was later also applied to differences among populations of the same species (Salewski et al. 2010). If higher temperatures predict smaller body size, then climate change should lead to smaller body size in birds and mammals (Sheridan & Bickford 2011).

Although a number of studies have reported changes in avian body size correlated to temperature changes, the relation to temperature may, however, be indirect and a true adaptive response to changing climate is still lacking (Teplitsky & Millien 2014). This was investigated in depth in at least two species: red-billed gulls (Teplitsky et al. 2008) and great tits (Husby et al. 2011). In both the cases, a plastic rather than microevolutionary
body size adjustment was detected (see the section titled “Plastic versus Genetic Changes”). The correlation between body size and temperature is particularly difficult, as body size is also affected by other factors than heat-dissipation capability that also covary with temperature as, for example, food availability, which may determine the growth at young age and also resistance to starvation (Teplitsky et al. 2008; Sheridan & Bickford 2011; Teplitsky & Millien 2014).

Demography
Climate change can affect reproductive success and survival directly or indirectly. Extreme weather events can have strong direct effects; for example, unexpected cold spells can induce mass mortality in migrants as pointed out above. Most effects, however, will work indirectly by changing abundances or synchrony of interacting species. For example, winter climate in Antarctica affects krill (Euphausia superba) abundance, which in turn affects reproductive success and thereby population numbers in Adélie and chinstrap penguins (Trivelpiece et al. 2011).

Climate change has also disrupted the synchrony between interacting species, which could, for example, mean that a predator now does not encounter the maximum prey abundance anymore because the phenology of the predator has advanced less (or more) than that of its prey. Such disruptions have often been reported and are also predicted to be common (Gienapp et al. 2014). The demographic consequences of disrupted synchrony between predator and prey have been well studied in great tits and caterpillars. The disrupted synchrony has led – as expected – to selection on the birds’ breeding time (Visser et al. 1998). The corresponding reduced reproductive success (the “demographic load of selection”) can drive populations to extinction if selection becomes too strong or the rate of evolutionary change of the population is too small (Bürger & Lynch 1994; Lynch & Lande 1998).

Using a theoretical modelling approach, Gienapp et al. (2013) could show that climate change would increase the mismatch between the great tits and their caterpillar prey too strongly for the birds to adapt by microevolution and that this would lead to a non-negligible extinction risk. However, the expected negative relationship between the strength of selection and population growth rate has not been observed in this population owing to density-dependent juvenile winter survival (Reed et al. 2013a, b). Incorporating this effect of density dependence into the theoretical model by Gienapp et al. (2013) showed that density dependence can buffer populations against reduced reproductive success due to disrupted synchrony and thereby reduce extinction risk (Reed et al. 2015).
Plastic versus genetic changes

As described above, changes in the phenology of birds have frequently been observed. Such consistent trends over time could be the results of phenotypic plasticity or an evolutionary response to selection. Phenological traits show large year-to-year fluctuations mostly driven by ambient temperature and the observed advancements could hence be a phenotypically plastic response to increasing temperatures. As also pointed out above, climate change is likely to lead to selection on phenology (Gienapp et al. 2014) and these observed changes could therefore also be an evolutionary response to this selection. Disentangling phenotypic from genetic changes is difficult when a genetic change cannot be directly tested because no suitable molecular genetic markers are available. One possibility is to predict “breeding values” of individuals using quantitative genetic approaches (Wilson et al. 2010) but these require a known pedigree. These fairly high demands on data quality are likely the explanation why, so far, no study reported a genetic change in phenology in response to climate change (Charmantier & Gienapp 2014). This lacking evidence does, however, not mean that populations will not be able to adapt to climate change by phenotypic plasticity but only that we have no suitable data or methods to show this.

Possible impacts in the future

Global temperatures are predicted to rise at least by 1.5 °C until 2100, with the most extreme scenario predicting increases by 3.5 to 6 °C (Field et al. 2014). Consequently, the whole biosphere will be confronted with on-going climate change and observed changes are very likely to continue or increase. There are three ways for populations to survive: (1) they can evade by dispersing to suitable habitats elsewhere, where climatic conditions are still favourable; (2) they can stay put and adjust to the changed conditions by means of phenotypic plasticity without altering their genetic constitution; (3) they can adapt to the changed conditions by means of genetic changes through the process of evolution. Of course, it is also possible – and even likely – that all three processes happen simultaneously and the relative importance of these three different ways to cope with climate change depends on the time scale considered, the species’ life-history, the rate and the extent of (predicted) climate change, the availability of alternative habitats and the dispersal ability of the species.

Moving along with the shifting “bioclimatic envelope” is obviously only possible for a species if suitable habitat is available and the dispersal ability of the species is sufficient. In this respect, habitat degradation and loss become doubly relevant as they not only directly threaten population persistence but may also cut off populations from suitable habitat elsewhere. Thomas et al. (2004) used the observed “bioclimatic envelopes” and
climate change projections to predict the future distributions of a number of species. Then they used these predicted distributions to assess the likelihood of extinction and found that many species in mountain habitats in the tropics are prone to extinction. The rising temperatures will simply shift the suitable habitat as defined by the “bioclimatic envelopes” to the mountain tops until no suitable habitat will be left. As the tropics are biodiversity “hot spots”, this process is predicted to lead to a loss of about 25% of global biodiversity. One important assumption behind these models is, however, that whole species communities will be able to shift at the same rate and that climate zones simply will move northwards without further changes. Unfortunately, both assumptions are unlikely to be true. First, the dispersal ability of species can differ substantially. For example, distances of natal dispersal, that is dispersal to the place of (first) breeding after independence, typically range from hundreds of metres to a few kilometres in small passerines as great tits, but large predatory birds as goshawks easily cover tens of kilometres. Second, climate change-induced warming trends differ between seasons (Easterling et al. 1997) and regions (Høgda et al. 2001; Giorgi & Lionello 2008). Consequently, even species with a good dispersal ability that could track their “bioclimatic envelope” will (very) likely face a change in their biotic and abiotic environment even after shifting along with their bioclimatic envelope.

Phenotypic plasticity generally enables populations or species to cope with novel or changed environments. As pointed out above, the current phenotypic plasticity will, however, unlikely allow perfect tracking of shift in the species’ biotic environment (Gienapp et al. 2014). Consequently, neither “evasion” nor phenotypic plasticity alone seems to be sufficient mechanisms: adaptation by microevolutionary change(s) is necessary to cope with climate change. Unfortunately, while the evidence for climate change-induced changes in wild populations is indisputable, it is mostly unclear whether these changes are phenotypic plastic responses or microevolution (see the section titled “Plastic versus Genetic Changes”). Our general understanding of microevolutionary adaptation to climate change has hence not advanced very much from the statement by Holt (1990) that “There is almost no species for which we know enough relevant ecology, physiology and genetics to predict its evolutionary response to climate change”.
