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Climate warming results in phenotypic and evolutionary changes in spring events: a mini-review

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Abstract

The impact of climate change, in particular increasing spring temperatures, on life-cycle events of plants and animals has gained scientific attention in recent years. Leafing of trees, appearance and abundance of insects and migration of birds, across a range of species and countries, have been cited as phenotrends that are advancing in response to warmer spring temperatures. The ability of organisms to acclimate to variations in environmental conditions is known as phenotypic plasticity. Plasticity allows organisms to time developmental stages to coincide with optimum availability of environmental resources. There may, however, come

a time when the limit of this plasticity is reached and the species needs to adapt genetically to survive. Here we discuss evidence of the impact of climate warming on plant, insect and bird phenology through examination of: (1) phenotypic plasticity in (a) bud burst in trees, (b) appearance of insects and (c) migration of birds; and (2) genetic adaptation in (a) gene expression during bud burst in trees, (b) the timing of occurrence of phenological events in insects and (c) arrival and breeding times of migratory birds. Finally, we summarise the potential consequences of future climatic changes for plant, insect and bird phenology.

8.1 Introduction

The recent resurgence of interest in phenology (the timing of recurring life-cycle events in plants and animals) has stemmed from research on the impact of climate change, in particular, global warming. As many life-cycle events are influenced by temperature, trends in the timing of phenophases, in both plants and animals, reflect the impact of warming on the environment. For example, when spring temperatures are relatively high, leaves on trees tend to emerge earlier than usual (Peñuelas and Filella, 2001; Donnelly et al., 2006; Menzel et al., 2006), insects appear earlier (Roy and Sparks, 2000; Stefanescu et al., 2003; Gordo and Sanz, 2006) and migratory birds arrive earlier (Lehikoinen et al., 2004; Sparks et al., 2005; Donnelly et al., 2009). These trends have been observed in many countries around the world (Peñuelas and Filella, 2001; Menzel et al., 2006). Long-term historic records of the timing of spring phenology provide us with indicators of climate change. The inclusion of pan-European phenological data (Menzel et al., 2006) in the 2007 Intergovernmental Panel on Climate Change Fourth Assessment Report on Impacts, Adaptation and Vulnerability (IPCC, 2007) illustrates the strength of these data in convincing policy makers that climate change is having a direct impact on the environment.

Traditionally, climate change and phenology studies have focused on examining historical trends in the timing of key phenophases and relating these to climate variables (Roy and Sparks, 2000; Menzel et al., 2006; Donnelly et al., 2009). While these trends provide some excellent environmental indicators of climate warming, phenological research is now moving towards an examination of genetic adaptation occurring through natural selection as a result of environmental pressure (Bearhop et al., 2005; Jonzén et al., 2006).

Phenotypic plasticity is a mechanism through which an organism can adjust the timing of development in response to environmental pressures (Bradshaw, 1965). It occurs over the short term and ensures the continued survival of organisms in a changing environment. It enables plants and animals to acclimate to seasonal changes in, for example, temperature. It also allows birds to adjust their behaviour

according to real-time environmental cues, which they may experience at wintering grounds or during migration (Hüppop and Hüppop, 2003; Vähätalo et al., 2004). However, when an organism is no longer able to adjust to these environmental cues by way of phenotypic plasticity, selective pressure can result in adaptation at a population level. If there is sufficient selective pressure, climate change has the potential to result in genetic adaptation and eventually the evolution of new species. For example, recent evidence suggests that rapid climate change has been implicated in the evolution of poorly adapted wild bird populations in the UK (Charmantier et al., 2008).

Here we discuss evidence of the impact of climate warming on plant, insect and bird phenology through examination of (1) phenotypic plasticity in (a) bud burst in trees, (b) appearance of insects and (c) migration of birds; and (2) genetic adaptation in (a) gene expression during bud burst in trees, (b) the timing of occurrence of phenological events in insects and (c) arrival and breeding times of migratory birds. Finally, we summarise the potential consequences of future climatic changes for plant, insect and bird phenology.

Given the diversity of research methods used to study these discrete categories of organism, it was a challenge to find some common ground upon which to evaluate the effects of global warming on spring phenology. For example, we found in the literature many more research publications related to phenological traits of plant genes than either insect or bird genes, which hindered direct comparisons. However, we have chosen to adopt an interdisciplinary approach to address the issue. We believe that this is the first review that attempts to integrate the impact of rising temperature on three distinct categories of organism.

8.2 Plant phenology

With a rapidly changing climate that brings about rising average global temperatures, increasing frequency of extreme weather events, and new pests and diseases, trees may no longer be able to adapt to their changing environment. The only solutions for the survival of trees are to adapt rapidly to the changing conditions or to migrate to ecological niches that are more suitable, or alternatively to become extinct (Aitken et al., 2008). Shifts in plant phenology and species' ranges in response to changing temperature have been widely reported (Chmielewski and Rötzer, 2001; Parmesan, 2006; Cleland et al., 2007), while evidence of rapid evolutionary change in response to climate warming has also been demonstrated (Jump et al., 2006). As with other organisms, certain questions remain unanswered. How far can phenotypic plasticity stretch? What possibilities exist for genetic adaptation of populations? How drastic are the consequences of climate change in terms of migration and extinction?

8.2.1 Evidence of evolutionary responses to climate warming

Evolutionary responses to climate are apparent from biogeographic patterns. Species' distributions are generally defined by their climate envelope (Pearson and Dawson, 2003). Over time species have adapted and evolved in response to climatic pressures. Here, we focus on evidence from studies involving populations of tree species, as these often have wide distributions across multiple climatic zones. Many of these studies involve common garden experiments, where plants from different regions are grown at one site with common environmental conditions. These studies can be used to distinguish between environmental and genetic influences to determine, for example, if phenological events are genetically controlled. We report on current adaptations of populations and assess the potential for future changes in response to warming. We examine evidence of phenotypic plasticity as a strategy used by trees to respond to climate change and assess the underlying genetic mechanisms responsible for adaptation.

Variation across climatic gradients

Populations of different tree species across Eurasia can be used to demonstrate the evolutionary response of plants to climatic gradients. For example, species such as *Populus tremula* L. (aspen) are distributed from the Mediterranean to the subarctic, and across a broad longitudinal range from the European Atlantic coast to inland regions as far as continental Russia. These species are adapted to the local growing conditions as a result of an interaction between physical limitations and competition (Savolainen et al., 2007). Local adaptation to climate has been well documented in numerous tree species through provenance testing (Aitken et al., 2008). Plant species may be capable of surviving outside their normal range, but are prevented from doing so by competition with other species. This is clearly demonstrated by the fact that a species from a discrete climatic zone is able to grow, when placed in a series of botanic gardens, across a diverse range of environmental conditions in a number of continents. In the case of *P. tremula*, a common garden study of Swedish populations showed that trees from lower latitudes flushed earlier than ones from higher latitudes (Hall et al., 2007). A similar study on bud set of *Pinus* (pine) across a latitudinal gradient from Spain to Finland showed that the timing of bud set was determined by the origin of the plant rather than the conditions of growth (García-Gil et al., 2003).

Other studies confirm that these phenology-related traits such as bud set and bud burst are highly heritable rather than plastic responses to changes in conditions (Yakovlev et al., 2006). Bradshaw and Stettler (1995) calculated that up to 98% of the total phenotypic variance of bud burst in *Populus* hybrids could be explained by heritability. Gene flow is a process that helps homogenise populations, but adaptive differentiation of populations in temperate and boreal forests persists

despite substantial gene flow taking place (Savolainen et al., 2007). Although they are well adapted to their environment, forest trees can survive and grow outside their natural range (Savolainen et al., 2007), but different co-occurring tree species can also show considerable interspecific variation in their response to the environment they are adapted to (Lechowics, 1984; Ogaya and Peñuelas, 2007). Thus, while populations of trees do show phenotypic variation along climatic clines, questions remain as to the potential of an evolutionary response to rapid climate change within tree species. In particular, separating phenotypic plasticity from underlying genetic variation will be an important step in understanding phenological changes.

Phenotypic plasticity in phenological traits in plants

Recent phenotypic changes are well documented in tree phenology studies across Europe (Menzel et al., 2006). Tree species are responding to warmer spring temperatures and are adjusting bud burst to coincide with an earlier spring. Thus, trees are capitalising on earlier spring warming and benefiting from an extended growing season. However, whether these changes are due predominantly to phenotypic plasticity or to genetic variation is still unknown, although some studies are showing evidence of an inadequate capacity of trees to adapt swiftly enough to climate changes (Aitken et al., 2008).

Response to recent climate change: adaptation and genetic variation

Large-scale biogeographic patterns are the result of thousands of years of migration, adaptation and competition. However, recent climate change relates to a timescale spanning only decades. It is important to know whether or not plant species can respond to this rapid change in climatic conditions and, if so, how fast they can do this. Unlike insects and birds, plants cannot readily migrate when environmental conditions change rapidly. Potential outcomes of climate change on plant populations depend on their ability to change, which in turn, depends on phenotypic plasticity, underlying genetic variation, dispersal ability and establishment rates (Savolainen et al., 2007). The ability of plants to acclimate to a changing environment is evident from historical records of the timing of phenological events in the recent past in which tree species have shown earlier bud burst and flowering times across Europe in response to increases in spring temperatures (Menzel et al., 2006). As trees are long-living sedentary organisms they must withstand considerable variation in environmental conditions over their lifespan. In addition, as a species can be spread over a large range, each population must acclimate to local conditions to ensure survival. Therefore, there must be a balance between local adaptation (genotype) and phenotypic plasticity.

Some studies have assessed genetic variation related to climate and have shown population differentiation based on differing climatic conditions (Jump

and Peñuelas, 2005). A small number of studies have assessed levels of variation in phenology-related genes in wild plant populations across broad geographic ranges (García-Gil et al., 2003; Ingvarsson et al., 2006; Savolainen et al., 2007; Savolainen and Pyhäjärvi, 2007). These studies aim to identify selection pressure on genes in wild populations and to provide associations of gene variants and phenotypes with climatic pressures. Association studies are a relatively new method in plant genetics, but it is expected that they will become useful in determining the mechanisms of complex traits and provide an understanding of the interaction between genotype and phenotype (Neale and Savolainen, 2004). A study carried out on *Populus tremula* showed significant variation in a gene involved in the control of light response in plants (phytochrome B2 - *phyB2*) along a latitudinal gradient (Ingvarsson et al., 2006). However, this was not the case in a homolog of *phyB2* in *Pinus sylvestris* L. populations across Europe (García-Gil et al., 2003). The difference in response between species highlights the need for further investigation in this area. These analyses are vital to understanding the genetic variation underlying phenological responses. Most studies have used a small sample size or a restricted geographical distribution, and therefore extrapolation of the results to different species or to larger areas is not feasible. Further studies will be key to identifying natural selection pressures resulting from current and future climate change, firstly to establish the potential inherent in species, and secondly to assess whether climate change results in selection of favoured variants.

8.2.2 Dormancy

In climate studies, the most commonly reported plant spring phenophase is leaf unfolding (Donnelly et al., 2006; Menzel et al., 2006). In temperate climates deciduous trees lose their leaves in autumn, remain dormant during winter months and resume growth in spring when environmental conditions become favourable. Dormancy is a complex process that allows trees to survive adverse conditions (Lang et al., 1987). Dormancy release is triggered by environmental cues and precedes leaf unfolding; thus, it is an important determinant of the timing of spring phenology in temperate trees. Bud dormancy is a mechanism induced by short day lengths and colder temperatures. It allows the vulnerable meristems to be protected and to cease growth while conditions are unfavourable (Lang et al., 1987). Bud burst has been shown to be controlled by the cumulative sum of temperatures to which buds are exposed after a requisite cold period. This relationship with temperature shows how dependent plants are on their environment and how they need to be finely tuned, or adapted, to the conditions in which they grow. Dormancy and bud burst may also be indirectly affected by climate change through, for example, changes in the availability of resources, such as carbon, soil nutrients and water (Rathcke and Lacey, 1985), susceptibility to embolism in early-versus late-leafing species, heterogeneity in leafing dates to avoid herbivory, and

natural selection on interdependent traits. These factors can act as constraints on phenological patterns (i.e. limit the ability to evolve). It is therefore important to understand the mechanisms underlying dormancy, to enable predictions of how subsequent phenophases, such as bud burst and flowering, may be influenced by future climatic changes. In the following sections, we examine the various phases of dormancy and explore current knowledge on gene expression involved in its regulation.

Regulation of dormancy: molecular aspects and gene expression

Despite the role of dormancy in determining the time course of phenophases such as bud burst, flowering and bud set, our current knowledge of the molecular mechanisms involved in dormancy are still limited. The slow progress in understanding the biology of dormancy is perhaps due to the theory, prevalent in the last century, that the transition from dormancy to growth was the result of the balance between promoting and inhibiting hormones (Arora et al., 2003). However, this view has recently been questioned by a number of different studies showing that dormant status could not be unequivocally linked to hormone concentrations (Arora et al., 2003) and suggesting a multi-tiered control of dormancy in plants (Crabbe, 1994).

Current research in the impacts of climate change on plant phenology has focused on the climatic control of dormancy (Menzel and Fabian, 1999; IPCC, 2007). The advent of functional genomics and the availability of new technologies have resulted in a series of studies that have shed new light on possible pathways involved in dormancy induction and release (Yanovsky and Kay, 2002; Böhlenius et al., 2006; Rohde and Bhalerao, 2007; Ruttink et al., 2007). Many of these studies have used *Populus* as test material, as its genome has been sequenced and it is considered the model species for tree biology (Jansson and Douglas, 2007) in the same way as *Arabidopsis* is for most other plants.

Growth cessation and dormancy induction

The signal for growth cessation is triggered by detection of short days (SDs - i.e. days below a critical photoperiod) by phytochrome (*phy*) in plant leaves. Recent findings show that in *Populus tremula* the response to SDs is mediated by orthologues to the gene *Constans* (*CO*) and the floral integrator gene *Flowering Locus T* (*FT*) in *Arabidopsis* (Böhlenius et al., 2006). Transcript profiles from *P. tremula* grown with different critical photoperiods showed different diurnal oscillation patterns in the expression of *PtCO* (the *Populus CO* homologue). The importance of this finding was supported by the fact that the diurnal phase of *CO* expression affects flowering time and the expression of *FT* in *Arabidopsis*. In addition, SD-insensitive transgenic trees did not show any repression in *PtFT* expression. The findings of Böhlenius et al. (2006) supported the view that the transition between long days (LDs) and SDs was perceived by the plant as the moment when the expression of

PtCO peaked in darkness. This, in turn, triggered a downregulation of *PtFT*, and induced growth cessation (Böhlenius et al., 2006). Regulation of growth and floral transition by *FT* has also been found in potato (Rodriguez-Falcon et al., 2006) and poplar (Hsu et al., 2006).

Phytochrome A (*phyA*), a photoreceptor that is sensitive to red light, also plays a role in growth cessation, through the regulation of *FT* and *CO* transcription (Yanovsky and Kay, 2002). Transgenic *P. tremula* overexpressing the oat *phyA* gene initiated growth cessation only in response to very short photoperiods of six hours, compared to the usual 14–16 hours (Olsen et al., 1997). The amount of *phyA* expressed by the plant might thus affect photoperiodic responses in trees (Olsen et al., 1997). Ruttink et al. (2007) applied metabolite and transcript profiling to bud samples taken at weekly intervals during the time course of the study from SD-induced dormancy induction to endodormancy in *P. tremulus* × *P. alba*. Their results showed that light, ethylene and abscissic acid transduction pathways consecutively controlled the transition from bud formation to acclimation and to dormancy. However, while considerable molecular and biochemical changes occurred in the first few weeks of SDs, changes in gene expression were not significant during the time of transition to endodormancy, suggesting that other factors may be involved (Ruttink et al., 2007).

Little is known about the changes occurring during the establishment of endodormancy. This particular phase is the final step in a series of transformations that are difficult to separate. Ruttink et al. (2007) showed that photoperiod was responsible for a signalling cascade, which probably triggered subsequent molecular events and activated different pathways. In an extensive survey, Rohde and Bhalerao (2007) examined gene expression during the induction, maintenance and release from dormancy in *P. tremula* × *P. alba*, and found a global change in expression patterns after 24 SDs, in accordance with previous findings (Ruttink et al., 2007). This termination of dormancy occurred concurrently with bud set and was thus related to changes in apical bud morphology (Rohde and Bhalerao, 2007). The transition to endodormancy was not marked by dramatic changes in gene expression, but a cluster of novel candidate genes was proposed for functions during chilling requirement. One of these is a DNA binding protein with linker-histone domains that has a potential regulatory role in dormancy release (Rohde and Bhalerao, 2007).

Once endodormancy is established, chilling temperatures are required to release it and restore growing ability. However, the control of this process is still a matter of speculation. The similarities between chilling fulfilment and vernalization might suggest a role of genes that are orthologous to *Flowering Locus C (FLC)*, whose repression in *Arabidopsis* occurs after exposure to cold temperatures (Sung and Amasino, 2005). Indeed, *FLC*-like genes have been found to be differentially expressed during dormancy release in poplar (Coleman and Chen, 2008).

Similar to endodormancy fixation, dormancy release is also characterised by the expression of DNA binding proteins (Yakovlev et al., 2006). This, and additional evidence for DNA methylation observed in potato buds (Law and Suttle, 2003), suggests that epigenetic changes (changes that can alter gene expression that do not depend on the DNA sequence but involve other types of chemical modifications) might play an important role in dormancy (Horvath et al., 2003).

8.2.3 Plant phenology conclusions

There is no doubt that plants have the ability to respond to climate warming through a plastic response in the timing of bud burst. However, there is no clear understanding of the limits of this phenotypic plasticity or of the underlying potential variation in the genes controlling it. Many studies have shown genetic variation associated with climate and phenology, but evidence for an evolutionary response to climate change remains scarce (Jump and Peñuelas, 2005; Jump et al., 2006, 2008). Tree species are known to be highly variable, but the extent of their ability to adapt genetically to rapid change is currently unknown. Although the importance of evolutionary adaptation in response to short-term climate change has been downplayed (Huntley, 2007), it is likely to be a key element in the long term. Short-term changes are likely to be dominated by plasticity, migration and selection of competitive species over others. In the longer term, evolution of tree species could be affected through climate change pressures selecting favoured variants.

The impact of future increases in temperature on dormancy is complex, as it has the potential to impact on both dormancy induction and release. Our understanding of the mechanisms underlying dormancy is improving rapidly, despite the fact that many of its components are still unclear. The information that molecular biology is offering for model plant systems like poplar is of critical value in unravelling the different processes and signals involved in dormancy induction and release. The integration of this knowledge into a coherent framework and the testing of functional hypotheses will be crucial to the development of a holistic model of dormancy that will help us to understand and mitigate the impacts of climate change on plants.

8.3 Insect phenology

Recent global warming has been cited as the driving force behind the advancement (i.e. earlier occurrence) of phenological events in insects, including the first appearance of cabbage root fly (Collier et al., 1991), butterflies (Roy and Sparks, 2000; Stefanescu et al., 2003) and bees (Gordo and Sanz, 2006). As is the case with plants and birds, there is a strong association in insects between development and

temperature. When environmental change is so great that the limits of phenotypic plasticity are reached, genotypic change within a population becomes necessary to ensure survival (Tauber and Tauber, 1976; Bale et al., 2002; van Asch and Visser, 2007).

The following sections discuss how increasing spring temperature associated with climate change has been shown to influence phenological events in insects, thereby acting as the driving force behind evolution through natural selection. In addition, further impacts of climate change on insects are presented by examining evolutionary adaptation with reference to research that considers several of the intratrophic interactions exhibited by insects.

8.3.1 Evidence of evolutionary responses to climate warming

Much of the empirical evidence for the effects of climate change on natural selection in insects comes from pomace or vinegar flies (*Drosophila* spp.). Indeed, several studies on *Drosophila* have demonstrated genetic change in response to warming. In Australia (Umina et al., 2008) and the USA (Levitan and Etges, 2005), latitudinal variation in the chromosomal arrangements and allele frequencies, respectively, have been reported in *Drosophila* populations. In both of these studies, microevolution has occurred, as demonstrated by an increased selection for, and resultant increase in, the relative abundance of types that display greater ability to survive in warmer climates. Similar selection within warm-preferring populations has also been noted in Spain (Rodriguez-Trelles and Rodriguez, 1998). For such genetic change to occur, van Asch et al. (2007) suggested two prerequisites: (1) that significant genetic variation existed, and (2) that severe fitness consequences existed. However, none of the studies described above made specific reference to pressures on phenological events. Indeed, van Asch et al. (2007) reported that, with respect to phenology, there existed only a few examples of genetic change in response to climate change. It has also been suggested that the extent of genetic variation required for adaptation is largely unknown (Davis and Shaw, 2001). In their study of the pitcher plant mosquito (*Wyeomyia smithii* Coquillett, 1901), Bradshaw and Holzapfel (2001) reported genetic change as a response to an increase in the length of the growing season, suggesting that the change was evidence of a genetic response to climate warming.

Although the populations studied to date exhibited an ability to respond to increased temperatures, it is worthwhile considering the implications of further increases in temperature. It has been suggested that the large-scale viability of populations will be affected where natural selection cannot keep up with climate change (van Asch and Visser, 2007). Consideration of fitness consequences becomes particularly important when considering insects' interactions with other trophic levels on which their fitness is reliant. The potential for mismatch in interdependent phenophases exists when responses to climate change are

asynchronous, meaning that the potential for negative fitness consequences is increased.

8.3.2 Insect–plant interactions

Insects often rely on mutualisms with a host plant (e.g. plant–pollinator), which in some cases are very specific, having coevolved over long periods of time (Herre et al., 1999; Pellmyr and Leebens-Mack, 1999). It is important to consider evolutionary processes in insects within the context of their interactions with plants. As a result of different responses to climate change between trophic levels, the synchrony of phenological events can be disrupted, resulting in mismatches either spatially (e.g. range shifts) or temporally (timing of phenological events) (Harrington et al., 1999; Stenseth et al., 2002; Edwards and Richardson, 2004; Both et al., 2006). Here we focus on temporal mismatches due to climate change.

Mismatches have been investigated for both plant–herbivore (insect) interactions (van Asch et al., 2007; Forkner et al., 2008) and plant–pollinator interactions (Memmott et al., 2007; Hegland et al., 2008). Van Asch and Visser (2007) considered the fitness consequences of hatching time in forest caterpillars, for which an optimum time exists, to ensure maximum feeding potential for the population. Asynchrony can disrupt this optimum, and negative fitness consequences may result. Hegland et al. (2008) suggested that such asynchrony can be projected by considering the ‘potential for adaptation’. Where asynchronous changes are found, selection will occur for those individuals best able to match the changing environmental conditions at the same rate as the host plant (van Asch et al., 2007). The extent of mismatch, resulting through asynchrony and fitness consequences, is likely to be amplified by the degree of specificity of the relationship (specialist or generalist – Gilchrist, 1995; van Asch and Visser, 2007). Hegland et al. (2008) further described future synchrony through the use of models of interactions, suggesting that responses are not only driven by the organism’s ability to respond to climate change itself, but are also compounded by the insect’s ability to adapt to the changing nature of the interaction with its host plant.

8.3.3 Insect phenology conclusions

Hegland et al. (2008) warned that most models produced to project potential future plant–pollinator mismatches are only approximations, given the limited amount of research used to produce the models. This suggests the need for further research on the insects themselves, as well as the species with which they interact, in order to produce models that will be able to predict future interactions under future climate change conditions. Our understanding of insects’ potential to evolve as a result of climate change is important in predicting future population trends both of insects and of interdependent species. It is therefore critical that future research should consider both genotypic and phenotypic flexibility, and be

carried out over the long term to ensure that models are both accurate and reliable (Bale et al., 2002; van Asch et al., 2007).

8.4 Bird phenology

Migratory birds are particularly vulnerable to global climatic change, as their complex annual life cycle involves breeding, moult and two migration events (Pulido et al., 2001), all of which are influenced by temperature. In general, migratory birds respond to increasing spring temperature by arriving earlier at their breeding grounds (Hüppop and Hüppop, 2003; Lehikoinen et al., 2004; Sparks et al., 2005; Donnelly et al., 2009) and by laying their eggs earlier (Both and Visser, 2001; Both et al., 2006), thus increasing their potential for breeding success. However, some long-distance migrants, such as the willow warbler (*Phylloscopus trochilus* (Linnaeus, 1758)), have been shown to arrive later in response to increasing temperature at their breeding ground (Barrett, 2002).

In the following sections we consider evidence of climate-driven impacts on phenotypic plasticity in bird migration and on mismatches between interdependent phenophases. In addition, we present examples of evolutionary responses to warming through assortative mating and genetic selection for earlier breeding. Finally, we examine the consequences of earlier arrival for populations.

8.4.1 Phenotypic plasticity in phenological traits in birds

As is the case for plants and insects, phenotypic plasticity enables birds (both resident and migratory) to adjust the timing of their development in response to changing environmental conditions. Short-distance migrants are able to respond relatively quickly to environmental changes at the breeding grounds, but long-distance migrants may be constrained in their plastic responses by endogenous rhythms that control migration, as migration onset is unlikely to be directly linked to climate at the breeding ground (Visser et al., 1998; Cotton, 2003; Lehikoinen et al., 2004; Jonzén et al., 2006; Pulido, 2007). However, recent research proposed that trans-Saharan migrant birds may be able to gauge climatic conditions in the breeding grounds if meteorological conditions in Europe (during the breeding season) co-vary with those in Africa (during late winter) and phenotypically adjust their migration to optimise arrival time (Saino and Ambrosini, 2008). At present, it is unclear whether the observed changes in migratory behaviour that have been attributed to climatic variability are due to phenotypic plasticity, or whether they are a consequence of adaptive evolution (Pulido et al., 2001; Jonzén et al., 2006).

Recently, Both and te Marvelde (2007) compared geographical variation in egg-laying dates of a short-distance migrant (European starling – *Sturnus vulgaris* Linnaeus, 1758) and a long-distance migrant (pied flycatcher – *Ficedula hypoleuca*

(Pallas, 1764)) over a 25-year period in Europe. The authors reported that spatial and temporal heterogeneity in annual median egg-laying dates across Europe resulted from climate warming being stronger in some regions than in others. Møller et al. (2008) also reported that the impact of climate change on the timing of spring migration may have increased in recent years. Therefore, conditions along the migration routes appear to vary over space and time, and egg-laying date varies accordingly. It is thus evident that egg-laying date is strongly linked to temperature, which varies over space and time. As a result, within a species, phenological change may differ at different locations.

8.4.2 Mismatch between interdependent phenophases

As stated earlier, mismatches between interdependent phenophases can result in negative consequences for population survival. A study in the UK by Charmantier et al. (2008) has shown that, over a 47-year period, the egg-laying dates of a resident great tit (*Parus major* Linnaeus, 1758) population have been brought forward by two weeks. In addition, an advance in peak larval biomass of the winter moth (*Operopthera brumata* Linnaeus, 1758), a key food source for great tit offspring, has also been observed over the same time period. The authors have reported a strong correlation between these events and increasing spring temperature. Therefore, synchronisation between the egg-laying date and the maximal food source was found to be maintained over the study period. They concluded that changing environmental conditions resulted in phenotypic change alone, with no evidence of adaptive evolution being reported.

However, this was not found to be the case for other populations of passerine birds, where a mismatch in phenophases has been reported. For example, Visser et al. (1998) reported no advance in the egg-laying date of resident great tits in the Netherlands over a 23-year period, even though spring temperature increased, and both leaf and caterpillar emergence occurred earlier. The authors concluded that this mismatch caused increased natural selection for early-egg-laying birds, thus indicating a potential evolutionary change due to climate change. In addition, Both et al. (2005) reported a mismatch between arrival time in the Netherlands of the long-distance pied flycatcher and its main food source. These results suggest that warming temperatures are causing a mismatch between both resident and migratory birds and their main food sources.

Lyon et al. (2008) suggested a possible reason for the different responses in the timing of egg laying between the Dutch and UK tit populations. They proposed that the birds may be using different environmental cues to trigger egg laying. For example, birds that showed little plasticity in response to temperature (many of the Dutch population) may be using photoperiod as their sole cue. Accordingly, it is important to ensure that the cue under examination is the cue that is driving the phenological response.

It is evident that migratory birds depend on a plentiful food supply being available when they arrive at their breeding grounds. However, not all organisms respond to increasing spring temperature to the same degree, as response has been shown to be species-specific (Sparks and Tryjanowski, 2007). Therefore, as in the case of insects, any asynchrony between interdependent phenophases of different species (i.e. between arrival time of migratory birds and peak in abundance of their caterpillar food source), could have negative consequences on the reproductive success of birds and, thus, their population size.

Given the fact that insects are appearing earlier in warmer springs, it may also be the case that resident birds competing for the same food resource as their migrant counterparts have a competitive advantage, as they are already in situ when the insect food supply emerges (Ahola et al., 2007). This could, again, have negative implications for migratory birds, given that their food resource may be even further depleted by the time they arrive at their breeding grounds.

8.4.3 Evidence of evolutionary responses to climate warming

Assortative mating

Assortative mating is the non-random selection of mating partners with respect to one or more traits; it is positive when like phenotypes mate more frequently than would be expected by chance and is negative when the reverse occurs (Hartl and Jones, 2009). A recent study found evidence of assortative mating in populations of blackcaps (*Sylvia atricapilla* (Linnaeus, 1758)) in Europe (Bearhop et al., 2005). In the 1960s, blackcaps that spent their summers in Germany/Austria wintered in Iberia and northern Africa. However, since then, more and more of these birds have begun to overwinter in Britain and Ireland. Thus a change in migration pattern emerged. This resulted in the birds that spent the winter in Britain and Ireland arriving at their breeding grounds earlier, because critical photoperiods that trigger migration were found to be 10 days earlier than in more southern latitudes. In addition, because of the shorter migratory distance, these birds were possibly in better condition on arrival. The birds that arrived early tended to mate together and choose the best breeding territories, all of which resulted in greater reproductive success. The arriving birds that arrived later also mated together, and therefore these two populations paired assortatively. According to Bearhop et al. (2005), this temporal separation can promote speciation. Consequently, it may be that changes in environmental conditions that result in new migration routes may lead to the evolution of new species. It is therefore likely that, for some birds, future climate warming that results in earlier arrival times at breeding grounds has the potential to lead to speciation, especially if coupled with other factors such as geographical allopatry.

Jonzén et al. (2006) suggest that climate-driven evolutionary change in migration is evident in long-distance migrant birds from Africa as their arrival time at

breeding grounds in Europe has advanced. They argue that, because these birds reproduce from the age of one year and migration timing is heritable, there is potential for a rapid evolutionary response to climate change to occur. However, this claim is disputed by Both (2007). He agrees that evolutionary change is expected but, given the absence of evidence that early arrival and breeding are selected for (Jonzén et al., 2006), he considers phenotypic responses more likely than an evolutionary response in driving these processes.

It has been suggested by Bradshaw and Holzapfel (2006) that rapid climate change results in genetic change related to altered seasonal events rather than to higher temperature alone. The authors reported that genetic changes in a range of animals, including birds, are an adaptation to changes in seasonal events resulting in earlier reproduction. In addition, Sparks and Tryjanowski (2007) suggested that the earlier arrival time of the sand martin (*Riparia riparia* (Linnaeus, 1758)) in Britain may be an adaptive response to changes in food supply. Therefore, indirect effects of climate change should be borne in mind when considering observed phenological changes in bird migration.

Genetic selection for earlier breeding in migrant birds

The extent to which birds can, and are, tracking changing climatic conditions by altering the timing of reproduction has been explained largely by phenotypic plasticity (Wingfield et al., 1992). However, changing climatic conditions may also be selecting for changes in the frequency of genes that regulate the timing of reproduction in populations. This may allow species to adapt and move past the limits imposed by phenotypic plasticity (Nussey et al., 2005). However, in order for natural selection to occur and allow species to adapt to climatic warming over time, there must be a genetic foundation with sufficient genetic variability between individuals for directional selection of particular traits to take place (Kellermann et al., 2006). Therefore, phenotypic plasticity does not appear adequate to allow birds to match changes at lower trophic levels.

The degree of plasticity in the timing of reproduction has been shown to be a heritable trait (Nussey et al., 2005; Reed et al., 2008). Selection of this heritable component could allow some individuals to track climatic changes better than others. Selection of these individuals may enable the population to track food resources and reduce phenological mismatches beyond points imposed by current plastic limits (Stenseth and Mysterud, 2002). However, not all species may be able to select for these more plastic individuals. In some species, very little variation in plasticity occurs between individuals in a population (Nussey et al., 2005; Charmantier et al., 2008). This might not be indicative of a lack of plasticity, since populations may be highly plastic in response to a large-scale environmental cue (Reed et al., 2006). For instance, although the timing of breeding in the common guillemot (*Uria aalge* (Pontoppidan, 1763)) is highly plastic at the population level

in response to the North Atlantic oscillation, there is very little variation between individuals (Reed et al., 2006). Instead, this lack of an individual response may be because social cues dominate the regulation of the timing of reproduction (Reed et al., 2006). In these species the dominance of sociality may limit an individual's potential response and the possibility for directional selection of a trait (Reed et al., 2006). This will affect the ability of these species to genetically adapt to changing climatic conditions, and they will only be able to rely on the degree of phenotypic plasticity already within the population.

There appears to be little direct genetic evidence of evolution in the timing of reproduction in birds. However, in wild bird populations the genetic components of variance in reproduction dates have been calculated using crossbreeding experiments and models that estimate genetic parameters (Kruuk, 2004; Nussey et al., 2005). Using this method, Nussey et al. (2005) concluded that significant genetic variation for laying-date plasticity existed in the Dutch Hoge Veluwe great tit population, and that laying-date plasticity was significantly heritable. The models used for quantitative genetics enabled an analysis of genetic (co)variances in populations in the wild (Kruuk, 2004). This technique relies on parents resembling offspring more closely than randomly sampled individuals from the population. However, closely related individuals are also more likely to experience similar environmental conditions. Therefore variation in the timing of reproduction may appear to be genetically based but may instead be due to environmental conditions. Despite these studies being very convincing, evidence at the DNA level would be useful to confirm that the observed trends in the timing of bird breeding do indeed have a genetic basis and that observed trends are not due to parental effects (Kruuk, 2004).

Even if some populations or species are tracking climatic changes at the genetic level, this is not feasible for all populations. For instance, no heritable variation has been shown in the plastic responses of reproduction in collared flycatchers (*Ficedula albicollis* (Temminck, 1815)) (Brommer et al., 2005). If traits for earlier reproduction are not heritable, or if only a small proportion of individuals carry the genetic traits required for natural selection, selective processes may not be possible or may be too slow to allow species to track climatic changes (Nussey et al., 2005). Species that rely on cues that do not reliably indicate changing seasons or physiological requirements are particularly at risk, as evolutionary processes may have little or nothing to select upon. For example, migratory bird species which rely on large-scale climatic patterns may be relying on cues at the wintering ground that no longer match seasonal conditions at the breeding grounds. The capacity for evolutionary change in phenological events may enable some species or populations to reduce mismatches and ultimately increase chances of population viability (Stenseth and Mysterud, 2002; Walther et al., 2002). However, it remains to be seen if evolutionary change can occur fast enough to keep up with the rate of change observed in environmental conditions.

8.4.4 Consequences of early arrival for populations

The timing of arrival at breeding grounds has implications for population success. The earlier arrivals have a better chance of finding a mate and securing the best territory, which, as we have seen, can lead to assortative mating. In addition, if annual and in particular overwinter survival is higher because of warmer temperatures, resident birds can begin to breed earlier, which may result in a depletion of resources by the time migrants arrive. Mismatches in the timing of interdependent phenophases can result in reduced reproductive output, leading to a decline in population size and an ultimate risk of extinction. It has been shown that, of 100 European migratory bird species examined, those that did not demonstrate a phenological response to climate change over the period 1990–2000 showed a declining population trend (Møller et al., 2008). Population sizes that had either stable or increasing trends showed a phenological response in the form of an advance in mean arrival date. However, Møller et al. (2008) also reported that mean arrival date was not a good predictor of population trend for an earlier period (1970–90) and concluded that the impact of climate change on spring migration may have increased in recent years.

8.4.5 Bird phenology conclusions

It appears that, in different migrant bird species, there is strong evidence indicating that phenotypic responses have occurred as a consequence of climate warming. However, the rate and magnitude of this change is both species- and population-specific. Pulido (2007) suggested that selection for early breeding and arrival was likely to increase if the trend of increasing temperature persisted. The most likely evolutionary processes leading to a change in migration timing are adaptive changes in migration distance and changes in phenotypic plasticity of departure date in response to day length at the wintering grounds. In addition, over recent decades, climate change has led to a number of heritable genetic changes in bird populations as a result of both direct and indirect impacts.

8.5 Consequences of future climate change for plant and animal phenology

It is evident from this review that climate change is having a detectable impact on spring phenophases of both plants and animals. The effects reported result from either direct effects of increasing temperature causing an advance in the timing of spring events, or indirect effects on interdependent organisms causing a mismatch between dependent phenophases, thus having negative consequences on population size of insects and birds. As temperature is predicted to rise over the coming decades, it is assumed that these changes in phenology will continue.

The degree to which organisms can respond will be dependent on how far their phenotypic plasticity can stretch. This characteristic is, of course, species-specific. In addition, we expect to see climate change exerting selective pressure on organisms that adapt to the changing environmental conditions through heritable genetic changes. This may, in turn, under some circumstances lead to speciation. If organisms cannot keep pace with the changes in their environmental conditions, by means of either phenotypic plasticity or genetic adaptation, the consequences will be severe and extinction is a clear possibility.

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