The Bernard Tucker Memorial Lecture

Birds and climate change

James Pearce-Higgins

Richard Johnson

Red Grouse *Lagopus lagopus*

Introduction

The subject of climate change is much discussed, and can polarise opinion like few other scientific issues. If the predictions from climate modelling become reality, then the world will change significantly, placing additional pressure on the biodiversity with which we share this planet. Estimates of the percentage of the world's bird species threatened with extinction as a result of climate change vary from 0.5% to 21.2%, depending on the methods and approach used (e.g. Thomas *et al.* 2004, Jetz *et al.* 2007). There is wide uncertainty because predicting the future is difficult, although there is a general consensus that the proportion of species at risk will increase in line with the projected amount of global warming (Pearce-Higgins & Green 2014). These changes will affect the birds that we see around us, and their populations.

A number of assessments of the likely future impact of climate change on birds in the UK have been published (e.g. Huntley *et al.* 2007, Ausden *et al.* 2015, Pearce-Higgins *et al.* 2015b). These predict range contraction and losses of northern species, but increases in southern species and potential colonisation of new species from continental Europe. But before thinking too much about the future, it is valuable to consider what we can learn from the past, and to look at how bird populations have responded to the climatic changes that have been observed to date. Presenting this evidence, with a particular focus on the UK but with reference to the wider European and global context as appropriate, is the aim of this paper.

Red Grouse: a case study

Before we look backwards, and consider the evidence from studies of changes in bird populations over recent decades, it is worth considering conceptually the reasons why bird species should be affected by climate change. The Red Grouse *Lagopus lagopus scotica*, the British and Irish subspecies of the Willow Grouse of northern Europe, is a good place to start. The Red Grouse population in Britain must rank as one of the most heavily managed wild bird populations in the world. Where the Red Grouse occurs at high density, populations are actively managed on grouse moors for sport shooting, to yield a shootable surplus of birds in the late summer. This is achieved through a combination of Heather *Calluna vulgaris* management (heather being the primary food of adult grouse), predator control and the provision of medication to reduce the incidence of disease in high-density populations (Hudson 1992). As a result of this management, Red Grouse abundance is significantly greater on grouse moors than in other upland areas of similar character (Hudson 1992; Tharme *et al.* 2001).

Despite this very strong association with management, the distribution and abundance of grouse is ultimately related to weather conditions and climate in a number of different ways. Firstly, cold and wet weather tends to have a directly detrimental impact on grouse populations, particularly during the chick-rearing period. As a result, grouse breeding success tends to be positively correlated with spring temperature, and negatively with spring precipitation (Cattadori *et al.* 2005). Secondly, the strong association between grouse abundance and heather cover and quality (Smith *et al.* 2001; Pearce-Higgins & Grant 2006) is strongly affected by climate, which plays a major role in determining heather condition and extent (Thompson *et al.* 1995). Thirdly, the growth and survival of young grouse chicks, and therefore overall breeding success, is dependent upon the abundance of their invertebrate prey, particularly adult craneflies (Tipulidae) (Park *et al.* 2001). The number of adult craneflies that emerge in a particular spring is largely a function of the survival of their larvae. These live close to the surface of the peat soil, and during the summer are vulnerable to desiccation when hot weather


Edmund Fellowes/BTO

215. Red Grouse *Lagopus lagopus scotica* populations are strongly affected by weather conditions through a variety of mechanisms, while their current distribution and previous distributional changes can be well described by climate.

causes the peat surface to dry out (Pearce-Higgins *et al.* 2010; Carroll *et al.* 2011). As a result, rising summer temperatures may have a negative impact on grouse breeding success the following year (Fletcher *et al.* 2013).

Fourthly, predation by raptors, particularly Peregrine Falcons *Falco peregrinus* and Hen Harriers *Circus cyaneus*, can reduce high-density Red Grouse populations (Thirgood *et al.* 2000). Since the reproductive success of these raptors is sensitive to rainfall during the breeding season, which limits the foraging ability of adults and their capability to provision the chicks (Pearce-Higgins & Green 2014), then variation in spring weather has the potential to affect grouse predation rates by raptors. Finally, high-density grouse populations are also sensitive to disease, the incidence of which is linked to the weather, at least in the absence of effective medication. The incidence of strongylosis, caused by a nematode worm, is greatest in warm, wet springs (Cattadori *et al.* 2005), while the occurrence of ticks, which can cause louping ill, is related to altitude, and therefore temperature (Gilbert 2010). Thus, despite the strong influence of human management on grouse populations, fluctuations in those populations remain affected by a range of weather-related mechanisms.

As might be expected from these associations, the global distribution of the Willow Grouse can be well described by climate (Huntley & Green 2011). Using reconstructions of the climate during the last ice age (taking the glacial maxima), it is possible to predict what the global distribution of Willow Grouse would have been some 20,000 years ago, under this altered climate. These predictions suggest that the species would have occurred in Iberia, the Balkans and other parts of southern Europe. This is useful because these predictions can be matched to the distribution of palaeontological bone records, providing important validation of the Willow Grouse distribution model (Pearce-Higgins & Green 2014). In brief, not only can annual changes in the abundance of Red Grouse be strongly linked to the weather, but their current distribution and long-term changes in their past distribution are also well predicted by climate. If this is the case for one of the most heavily managed wild bird populations, it is also likely to be the case for many of the world's other 10,000 or so bird species.

Edmund Fellowes/BTO

216. Populations of Grey Herons *Ardea cinerea* in Britain have been counted since 1928, and fluctuate in response to winter severity.

Edmund Fellowes/BTO

217. Wrens *Troglodytes troglodytes* in Scotland are much better adapted to cold weather than those in southern England, probably because they are larger.

Impacts of recent climate change upon UK bird populations

Resident species

Given the plausibility of climate change affecting the abundance and distribution of even the most heavily managed wild birds, what is the evidence that recent climate change has affected bird populations in the UK? To answer that question I will focus primarily on terrestrial species of the wider countryside, and rely heavily on long-term citizen science monitoring schemes such as the Common Birds Census (CBC) and BTO/JNCC/RSPB Breeding Bird Survey (BBS), which can be combined to produce joint population trends that extend back to the 1960s (Freeman *et al.* 2007). Data from periodic national atlases (e.g. Gibbons *et al.* 1993, Balmer *et al.* 2013) provide a more comprehensive but periodic snapshot of species distributions and relative abundances, whilst the national Ringing Scheme and Nest Record Scheme can be used to identify changes in breeding success and survival through time (Baillie *et al.* 1999; Crick *et al.* 2003). Given the availability of data from these schemes, I will focus primarily on changes from the 1960s or, in many cases, the 1980s.

Since 1960, mean air temperatures in the UK have increased, with the rate of warming being particularly marked during the 1980s. Precipitation has also tended to increase, particularly in the autumn and winter, but less strongly than temperature (Thackeray *et al.* 2016). Similar warming trends are apparent across Europe and North America (Stephens *et al.* 2016), with a particularly strong trend towards warming in spring (Schwartz *et al.* 2006).

A simple analysis of some long-term data shows how bird populations can be affected by these trends. The BTO's Heronries Census is the world's longest-running monitoring scheme for birds in the breeding season; it has provided an annual estimate of apparently occupied nests of the Grey Heron *Ardea cinerea* in the UK since 1928. A simple overlay of the estimate of annual abundance with an estimate of mean winter temperature shows how Grey Heron populations are negatively affected by cold winter weather (fig. 1). Cold snaps in the 1940s, 1960s, and even around 2010 each led to detectable population declines, while milder winter weather, particularly since the 1980s, has largely stabilised the UK population at around 14,000 breeding pairs (Pearce-Higgins & Green 2014) or 8,000 pairs in England (fig. 1).

The Grey Heron is one of our larger breeding birds, but populations of one of our

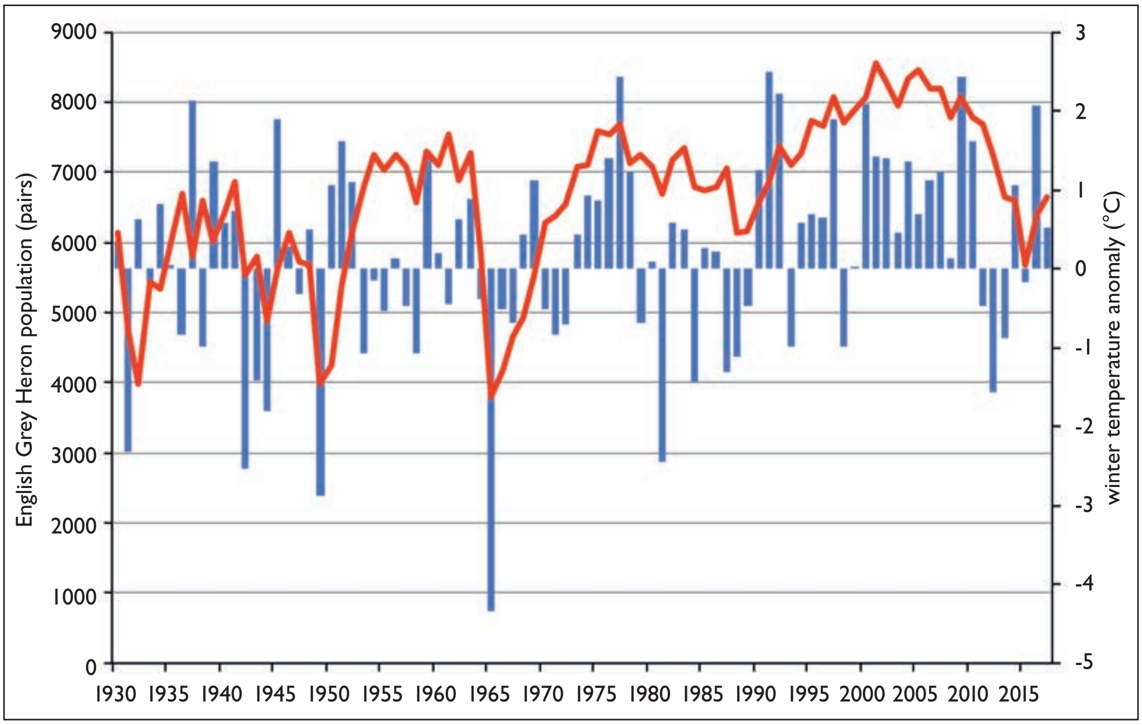


Fig. 1. Annual fluctuations in the Grey Heron *Ardea cinerea* population of England, 1930–2017 (red line), as estimated by the Heronries Census, are closely related to annual variation in mean winter temperature (blue bars), as measured by the anomaly from the 1961–1990 average in the Central England Temperature (December–February) time series.

smallest, the Wren *Troglodytes troglodytes*, are similarly affected by cold weather. Since the Wren is a small-bodied insectivore, cold weather poses a double problem by increasing thermoregulatory demands and reducing insect availability. As a result, long periods of continuous frost have a strong negative impact on Wren survival rates (Robinson *et al.* 2007). A winter with more than ten consecutive days of frost may halve Wren survival rates to 20%, having a significant impact on the population (Pearce-Higgins & Green 2014). Annual fluctuations in the Wren population can be linked to winter severity in the same way as for the Grey Heron (fig. 2). Interestingly, recent analyses have shown how the impact of cold weather upon populations varies strongly between regions of the UK. Wren populations in the south and west, where winters are relatively mild, tend to decline after only seven days of frost per month during the winter, while Scottish Wrens can cope with up to 12 days of frost. In other words, Wren populations appear to be locally adapted to their climate (Morrison *et al.* 2016a). The precise mechanism seems unclear, but is probably related to body size. We know that larger-bodied individuals tend to cope with cold temperatures better than small individuals, and analysis of ringing data shows that Wrens that occupy colder climates in Scotland are significantly larger (by about 5%, or 0.5 g) than those in the warmer south-west (Morrison *et al.* 2016a).

These findings for the Grey Heron and Wren are not unusual and perhaps not surprising. Plenty of other studies have shown how winter temperature affects the survival or abundance of a range of resident species in the UK (e.g. Robinson *et al.* 2007). Indeed, a cross-species analysis of joint population trends in England from 1966 to 2011 shows an overall positive effect of winter (December–February) temperatures on population growth rates (Pearce-Higgins *et al.* 2015a). The most plausible mechanism for this relationship is the link between winter conditions and overwinter survival rates for resident species. There is also a matching relationship between spring (April–June) temperatures and population growth rates, which is likely to reflect the positive impact of warm, dry conditions on the breeding success of the same species. Such conditions are likely to reduce the thermoregulatory demands of the chicks, increase invertebrate

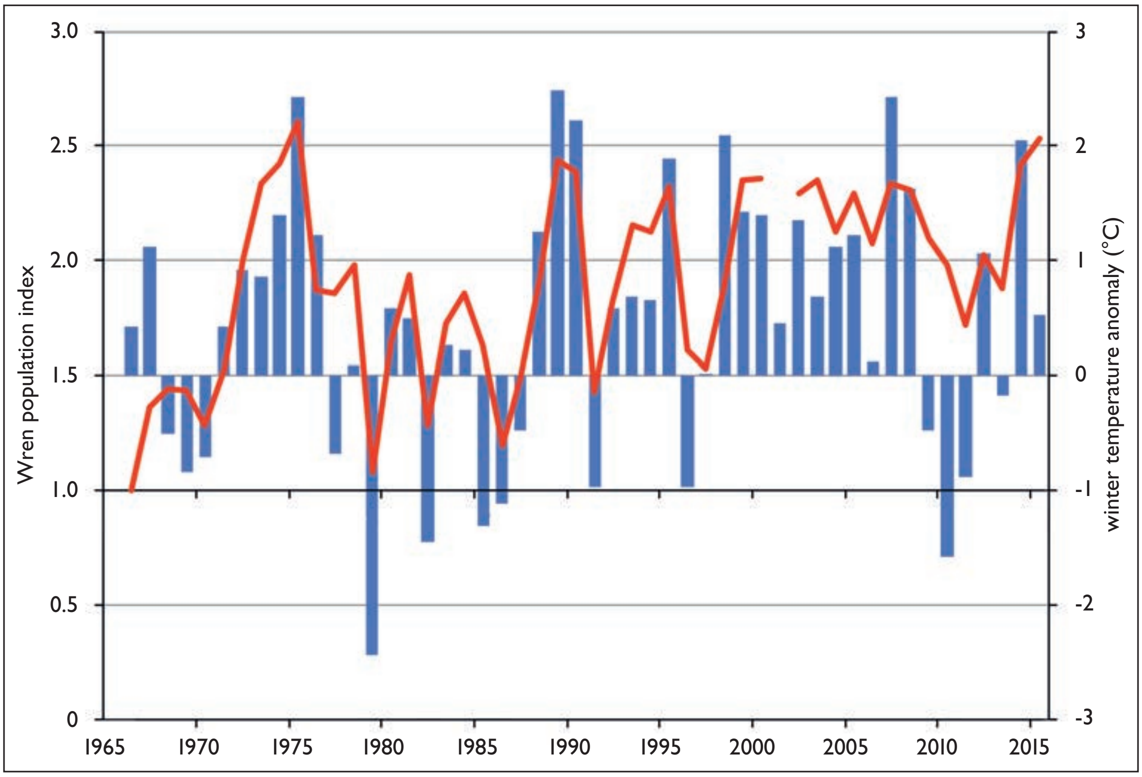


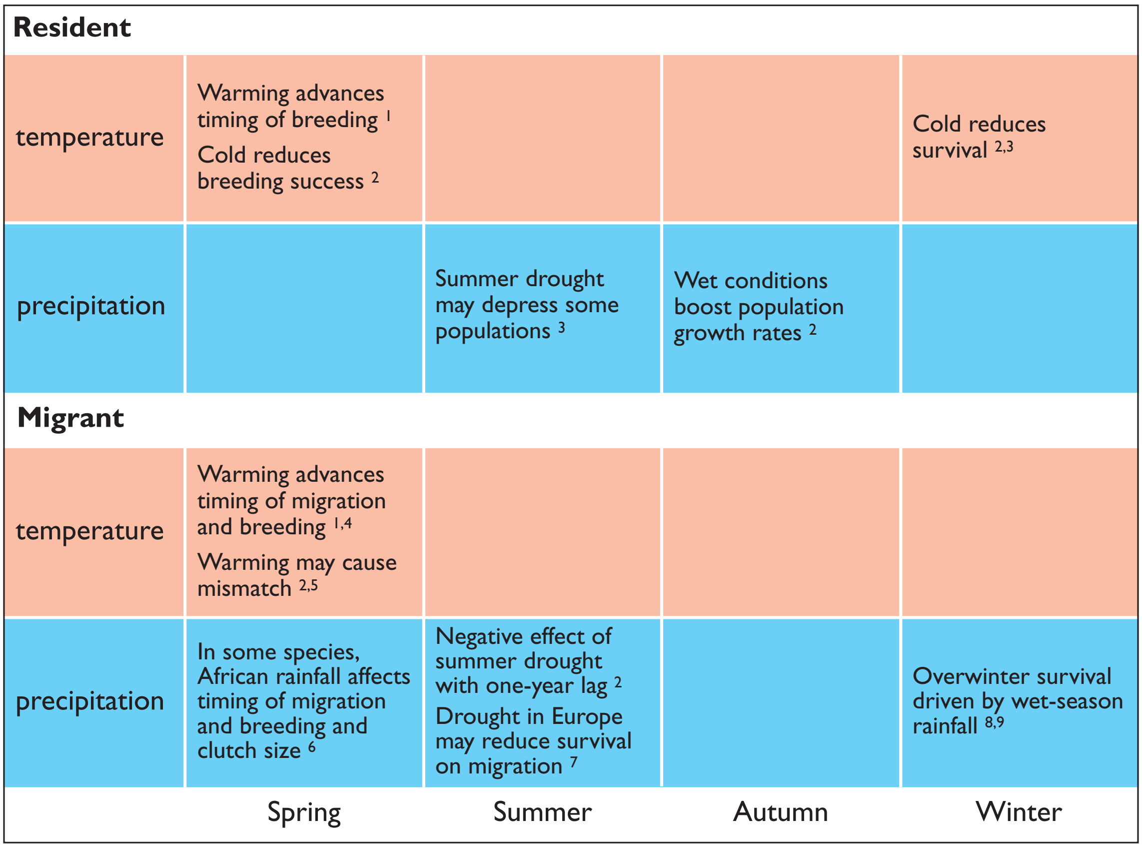
Fig. 2. Annual fluctuations in the Wren *Troglodytes troglodytes* population of England (red line), as estimated by CBC and BBS surveys, are closely related to annual variation in mean winter temperature (blue bars), as measured by the anomaly from the 1961–1990 average in the Central England Temperature (December–February) time series. The break in 2001 was due to access restrictions caused by foot-and-mouth disease.

and other food resources for them, and make provisioning and caring for the chicks much easier than in a cold, wet spring (Pearce-Higgins & Green 2014). These findings suggest that climate warming has probably had a significant positive impact on the population trajectories of many resident UK species (fig. 3), and probably accounts for the observed increases in the populations of many such species in recent years.

Migrant species

The population trends of migratory species tell a quite different story, as many long-distance migrants have declined (e.g. Sanderson *et al.* 2006, Thaxter *et al.* 2010). This is at least partially related to the fact that migrant and resident populations show different responses to variations in UK weather (Pearce-Higgins *et al.* 2015a). As might be expected, since they winter elsewhere, migrants do not show the same positive response to warmer winter temperatures in the UK as resident species. The effects of temperature during the breeding season are also more mixed for migrants. Although there are positive associations between temperatures in April and July and subsequent migrant population growth rates, a negative effect of May temperature means that overall the benefits of warmer spring weather are more equivocal for long-distance migrants than for resident species. In addition, there is evidence that hot, dry summer weather can have a negative, though time-lagged, effect on bird populations, which particularly affects long-distance migrants (Pearce-Higgins *et al.* 2015a). In combination, this means that populations of long-distance migrants have not experienced the benefits of warming that many resident species have (fig. 3).

Instead, populations of long-distance migrants are much more strongly affected by weather conditions in Africa. In particular, the level of rainfall at key stopover or wintering areas can affect overwinter survival rates and population changes. High levels of rainfall during the wet season in the Sahel can have a positive impact on the survival of migrants which overwinter there (Johnston *et al.* 2016), leading to relatively consistent positive associations between Sahel rainfall and



	Spring	Summer	Autumn	Winter
Resident				
temperature	Warming advances timing of breeding [1] Cold reduces breeding success [2]			Cold reduces survival [2,3]
precipitation		Summer drought may depress some populations [3]	Wet conditions boost population growth rates [2]	
Migrant				
temperature	Warming advances timing of migration and breeding [1,4] Warming may cause mismatch [2,5]			
precipitation	In some species, African rainfall affects timing of migration and breeding and clutch size [6]	Negative effect of summer drought with one-year lag [2] Drought in Europe may reduce survival on migration [7]		Overwinter survival driven by wet-season rainfall [8,9]

Fig. 3. Summary of impacts of temperature (pink) and precipitation (blue) during different seasons upon resident (top) and long-distance migrant (bottom) bird species in the UK. Superscripts denote references supporting each statement as follows: [1] Thackeray *et al.* 2016; [2] Pearce-Higgins *et al.* 2015a; [3] Robinson *et al.* 2007; [4] Finch *et al.* 2014; [5] Newson *et al.* 2016; [6] Ockendon *et al.* 2013; [7] Hewson *et al.* 2016; [8] Ockendon *et al.* 2014a; [9] Johnson *et al.* 2016. These references tend to use long-term data of relatively widespread species covered by BTO monitoring schemes (see Robinson *et al.* 2016).

population growth rates in migratory species (Ockendon *et al.* 2014a). The mechanism underpinning this relationship is that high rainfall during the wet season (May–October) means that the Sahel is wet and green when our migrants arrive in autumn. This provides them with sufficient resources to refuel after their desert crossing. In wet years, those resources persist throughout the winter, ensuring a continued supply of food up to the departure for the breeding grounds. In such years, there can be a significant knock-on impact on the timing of nesting in the UK – and even in some species, such as the Sand Martin *Riparia riparia*, upon the number of eggs laid – although in most species the magnitude of this effect is relatively small (Ockendon *et al.* 2013). Conversely, in dry years, food resources for migrants become scarce during the winter, overwinter survival is reduced, and this potentially leads to a delayed return and delayed breeding.

Changes in species' distribution

In addition to changes in abundance, warming has been associated with significant shifts in the distribution of species. Two effects have been noted. The first is a general northward shift in species' ranges. The potential for climate change to drive poleward shifts in the distribution of species was first identified through analyses of data from the second national atlas of Britain & Ireland's breeding birds (Gibbons *et al.* 1993) compared with the first atlas (Sharrock 1976). Between the two atlases, the northern range limit of a variety of southerly distributed species shifted northwards by 18.8 km on average (Thomas & Lennon 1999). Data from the third national atlas (Balmer *et al.* 2013) has shown that this trend has continued, with a further northwards shift of 13.5 km on average of southern species between 1988–91 and 2007–11. More detailed analyses of these patterns have shown that range expansions in individual species tend to be in a northwesterly or northeasterly direction rather than on a more direct south–north axis. At the same time, there is also some evidence for northward contractions along the southern range margin of some species. As a result of these changes, the geographical centre of species' ranges has also shifted. The average shift across 122 species is of 20.4 km in a northerly direction. This is roughly equivalent to a 1-km shift northwards in the distribution of breeding birds in Britain per year, or almost 3 m per day. While changes in temperature would drive northwesterly shifts in distributions if species were responding only to that factor, the greater spread of shifts observed suggests additional effects of precipitation or other climatic variables, or the influence of additional non-climatic factors, such as land-use change (Gillings *et al.* 2015).

The second effect is that, in addition to a northwards shift, species' distributions have expanded. There is an intrinsic relationship between a species' population size and its range size. As populations increase in abundance, that often drives an expansion in geographical range, while declining species tend to suffer range contraction (Fuller *et al.* 1995; Thomas & Lennon 1999). Hence the population increase of resident species in response to warmer temperatures will tend to cause range expansion too. Analyses of BBS data for a subset of 80 relatively common and widespread species has shown that the rate of northwards expansion of the northern range boundary of a species has been greater than that at the centre of the species' range, while southerly range boundaries have shifted little. Over the 15-year period 1994–2009, the latitudinal spread of those species' range extent increased by an average of 14.5 km (Massimino *et al.* 2015a).

Northward shifts and range expansions have resulted in a number of changes in the assemblage of bird communities that are found at particular locations. There is a latitudinal gradient in species richness across the country, with a greater number of bird species present in the south than the north (Eglington *et al.* 2015). As a result, northward range shifts have led to an increase in the number of species observed at any one location (Davey *et al.* 2012), particularly as a result of the population increase and range expansion of common and widespread generalist species (Davey *et al.* 2012; Sullivan *et al.* 2016). Generalist species, such as the Common Chaffinch *Fringilla coelebs* and Wood Pigeon *Columba palumbus,*


Edmund Fellowes/BTO

218. Willow Warbler *Phylloscopus trochilus* populations in southern England have declined rapidly in recent decades due to a reduction in breeding success, while populations in the north have remained stable or increased.

which occupy a wide range of habitats, have tended to increase in abundance most, probably because warming has a more positive impact upon their population trends than on those of habitat specialists (Pearce-Higgins *et al.* 2015a). Populations of habitat specialists are also more likely to be limited by non-climatic factors.

A general northward shift in species distributions also means that, at a given location, it is the more southerly distributed species, associated with warmer temperatures, which have tended to increase in abundance relative to more northerly distributed, cold-associated species. By calculating the association between each breeding species and temperature from its breeding range in Europe (the species temperature index, or STI), and averaging that value across species occurring at a particular location (the community temperature index, or CTI), breeding bird surveys across Europe have shown a consistent pattern of increasing CTI values through time, including in the UK (Devictor *et al.* 2012). Recent warming has therefore favoured species associated with warmer temperatures over those associated with cooler temperatures. Indeed, population trends of birds across both Europe and North America demonstrate a significant climate change signal since the 1980s. The trends of those species which models suggest are likely to increase in response to warming, which indeed tend to be more southerly distributed, have increased in abundance through time compared with population trends of species' predicted to decline in response to climate change (Stephens *et al.* 2016).

Mechanisms underpinning observed changes

The majority of the changes outlined above are based on observational data and simple correlation analyses. Although in many cases there are up to 50 years of bird data, and the findings are often supported by multiple studies, there remains a real challenge in attributing the observed changes specifically to climate change. Understanding the mechanisms that underpin these correlations can help to increase our confidence that observed changes are driven by the changes in temperature, precipitation and other variables that they are correlated with, and not due to other factors.

Studies that have attempted to examine the mechanisms underpinning population responses to changes in temperature and precipitation have generally found that biological mechanisms, associated with changes in species' interactions, are the most important, particularly in the context of climate change (Ockendon *et al.* 2014b). This means that the physical impacts of changes in climate – for example, rising temperatures causing heat stress, or heavy rainfall washing out all the nesting attempts of a breeding colony – appear much less important than the potential for climate change to alter factors such as the availability of prey or the abundance of predators. In relation to the UK's birds, two mechanisms in particular have been widely examined: the effect of warming on changes in the timing of biological events, leading to a potential mismatch between the availability of food resources and the timing of bird breeding; and the effect of climate change upon the abundance of key prey species.

The timing of breeding

Data from the BTO Nest Record Scheme first alerted the world to the impact of climate change on the timing of bird breeding (Crick *et al.* 1997; Crick & Sparks 1999). Since then, a range of studies have shown how the timing of a wide range of biological events has changed through time, whether it is the arrival of long-distance migrants or egg-laying (reviewed in Pearce-Higgins & Green 2014), or the timing of insect emergence or plant leafing and flowering (Thackeray *et al.* 2010). Recent analyses of BirdTrack data, compared with similar historical data from the 1960s, have shown how the spring arrival dates of 16 migratory species have advanced by an average of ten days over a 40-year period (Newson *et al.* 2016). The timing of autumn departure has become slightly delayed in some species, so that migrants now spend an average of two weeks longer in the UK than they used to. Similarly, the timing of egg-laying has also advanced, by an average of 3.7 days per decade for birds breeding in the UK. This means that species like the Barn Swallow *Hirundo rustica* are now arriving 15 days earlier in the UK than they did in the 1960s, and breeding 11 days earlier.

Changes in the timing of migrant arrivals and particularly changes in egg-laying dates are driven by increases in spring temperature (Thackeray *et al.* 2016). Where this has been studied in detail, air temperature during a 1–2 month window in advance of egg-laying provides the best predictor of laying date (Phillimore *et al.* 2016). These patterns are apparent in both long-distance migrants and resident species. For example, not only does spatial variation in the advance in Pied Flycatcher *Ficedula hypoleuca* laying dates vary with the extent that warming has occurred between countries (Pearce-Higgins & Green 2014), but annual variation in Pied Flycatcher laying dates in the UK is correlated with spring temperature in April and May (Phillimore *et al.* 2016). Although the timing of arrival of the flycatchers, which is determined by processes on the wintering grounds and on migration (Both 2010), might be expected to play an important part in laying date, current evidence suggests it is not a key driver of breeding phenology. While the laying dates of migratory species are advanced by rainfall in Africa (particularly in the Sahel) and warmer spring temperatures in the Mediterranean (Ockendon *et al.* 2013; Finch *et al.* 2014), for most species, spring warming in the UK has been the strongest driver of earlier laying (Ockendon *et al.* 2013).

What difference do these trends make? The majority of bird species time their reproduction to coincide with peak availability of food resources, particularly of key invertebrate groups. The timing of peak availability of these resources has also shifted through time, and by more than the changes already described for birds. Thus, on average, plants are now flowering and leafing some 17 days earlier than they did in the 1970s, while insects are emerging some 15 days earlier (put another way, the advance in plant and insect phenology averages about four days per 1°C, while for birds, the rate of change is about two days per 1°C warming). This has the potential to cause a mismatch in the timing of peak food demands of breeding birds and peak food availability, leading to a potential reduction in breeding success (Durant *et al.* 2007). Studies of populations of a number of insectivorous bird species, notably Great Tits *Parus major* and Pied Flycatchers, have shown that this is the case,

Mike Lane

219. Annual variation in Pied Flycatcher *Ficedula hypoleuca* laying dates in the UK is correlated with spring temperatures in April and May.

although these responses are by no means ubiquitous, and vary between habitats (Pearce-Higgins & Green 2014).

Migratory species which have shifted their arrival times most, and therefore might have the greatest capacity to adapt to changes in the timing of peak food availability during the breeding season, are those which have more stable or increasing populations, whether across Europe (Møller *et al.* 2008) or in the UK (Newson *et al.* 2016). This provides large-scale support for the mismatch hypothesis. Additional evidence consistent with this hypothesis comes from the negative correlation that exists between May temperature and long-distance migrant population growth (Pearce-Higgins *et al.* 2015a).

Yet there are only a limited number of studies that provide evidence that climate change has led to a sufficient divergence in the phenology of bird breeding and peak food abundance to cause a long-term reduction in breeding success – and it could be argued that none have strongly linked these changes to a declining population trend. There is some evidence from woodlands in the Netherlands that spring warming has reduced both Pied Flycatcher and Great Tit breeding success as a consequence of an increasing mismatch between peak caterpillar availability and the timing of peak food demands by a brood of hungry chicks (Both & Visser 2005; Visser *et al.* 2006). A decline in the Dutch Pied Flycatcher population during the 1990s has been at least partly linked to that mismatch, although other factors may have been important and the population has subsequently recovered (Pearce-Higgins & Green 2014). Similarly, the impact of mismatch on Great Tit breeding success had little impact on long-term population trends owing to the importance of overwinter survival (Reed *et al.* 2013). There is even less evidence from detailed species-specific studies that these processes have caused problems for woodland breeding birds in the UK including Great Tits (Cresswell & McCleery 2003) and Pied Flycatchers (Goodenough *et al.* 2009).

Given this uncertainty and limited evidence for mismatch having a strong link to population declines in well-studied populations, a panel of experts concluded there was only limited support for the statement that ‘migratory birds suffer from increased trophic mismatch on the breeding grounds’ (Knudsen *et al.* 2011). It is therefore difficult to discount the possibility that a common environmental driver might be causing long-term changes in bird populations and affecting their ability to alter their timing of breeding, and therefore that correlations between changes in timing and long-term trend are not causative (Pearce-Higgins & Green 2014).

Prey populations

An alternative biological mechanism is the potential impact of climate change on prey populations themselves, rather than on the timing of their availability. If climate change reduces the abundance of a key prey organism, that is likely to significantly reduce the breeding success, survival and abundance of species that depend on it, irrespective of timing. The potential for this to be important has been shown in a population of European Golden Plovers *Pluvialis apricaria* in the Peak District. The growth and survival of Golden Plover chicks is positively related to the abundance of craneflies when the chicks are young (<10 days), leading to a relationship between cranefly abundance and overall breeding success (Pearce-Higgins & Yalden 2004; Pearce-Higgins *et al.* 2010). The main cranefly species involved have an annual life-cycle. The adults emerge in May and June and live for a few days during which time they mate and lay their eggs. Those eggs hatch in July and the larvae live in the surface layer of the peat, passing through a number of instars over the course of the summer and autumn; they pupate the following spring and then emerge as adults. As described earlier, the young larvae are sensitive to desiccation, so that hot dry summer weather, particularly in August, has a negative impact on the size of the cranefly population the following spring (Pearce-Higgins *et al.* 2010). As a result, Golden Plover population change is negatively correlated with August temperature with a two-year time lag (Pearce-Higgins *et al.* 2010): a hot August will lead to few craneflies emerging the following spring, reducing Golden Plover breeding success, and a lack of surviving chicks to recruit into the breeding population. This impact of summer warming is also likely to affect other upland birds that rely on drought-sensitive invertebrates (Pearce-Higgins 2010; Fletcher *et al.* 2013), and has been specifically related to spatial variation in population trends of Dunlin *Calidris alpina,* Red Grouse and Golden Plover in the Peak District (Carroll *et al.* 2015). Although there are limited data on the long-term impact of changes in invertebrate prey upon breeding bird populations in the UK, correlations between soil moisture or rainfall and the breeding success (Miller *et al.* 2017), survival (Robinson *et al.* 2004, 2007) and population trend (Beale *et al.* 2006) of a number of thrush species, all of which prey upon drought-sensitive invertebrates, suggest that this phenomenon may be widespread, at least in species that rely on soil invertebrates for food.

Populations of moths, another key invertebrate group for birds, have declined in the UK (Conrad *et al.* 2003), with potential impacts on their avian predators. Although this decline is at least partially attributable to agricultural intensification (Fox *et al.* 2014), recent analyses suggest that there is also a significant climatic component, which may account for about half of the total reduction (Martay *et al.* in press). Although the link between the impacts of climate change upon caterpillar populations, and declines in the abundance or breeding success of birds that eat caterpillars has not been formalised, this may be an important component in the decline in some woodland specialists and is worthy of further investigation.

Geographical variation

Population trends of many bird species, including a range of our long-distance migrants, tend to be more negative in southern parts of the UK than in the north (Ockendon *et al.* 2012; Morrison *et al.* 2013; Massimino *et al.* 2015b). These patterns are consistent with what we might expect for trends being driven by climate change, with conditions in general deteriorating in the south, and improving in the north (where later and less synchronised food resource peaks benefit breeding birds; Smith *et al.* 2011). However, many other pressures may also be greater in the south – for example the intensification of land use and habitat fragmentation – and more work is required to disentangle and understand the causes of these trends.

One long-distance migrant that exhibits this pattern of strong decline in the south but increase in the north is the Willow Warbler *Phylloscopus trochilus*. Recent analyses of BTO long-term data have aided our understanding of this decline, combining Nest

Edmund Fellowes/BTO

220. Breeding European Golden Plovers *Pluvialis apricaria* are sensitive to the negative impacts of summer warming upon their cranefly prey.

Chris Hewson/BTO

221. Divergent Common Cuckoo *Cuculus canorus* population trends in Britain may be at least partly caused by variation in adult survival rates during the southwards migration route taken by birds through Europe.

Record Scheme data to estimate productivity, ringing data to estimate survival rates, and abundance data. This shows that in Scotland, where the population has remained stable or increased, there are plenty of years where both survival and breeding success are sufficiently high to permit population growth. In southern England, where the species is declining, reproductive success is significantly lower than in Scotland, and in very few of the last 20 years has the Willow Warbler population produced enough chicks and had a sufficiently high survival rate to prevent the population declining (Morrison *et al.* 2016b). This strongly suggests that the problem for Willow Warblers is a reduction in breeding success in the south, which may be partly related to changes in phenology, since researchers have observed a greater decline in productivity through the season (Morrison *et al.* 2016b). Other factors may also be important, such as declining invertebrate populations in the south compared with the north (e.g. Conrad *et al.* 2006).

Common Cuckoos *Cuculus canorus* show a similar geographical pattern, with strongly declining populations in the south, but stable or increasing populations in the north. In this case, spatial variation has been linked to the survival of adult Cuckoos during their southward migration after breeding. Satellite tracking has shown that males from declining populations in the southeast show a greater tendency to migrate southwest through Iberia before crossing the Sahara, with an associated survival rate of 54%, while birds from the north tend to head southeast and migrate through central Europe and Italy, with a comparable survival rate to the completion of the Sahara crossing of 96% (Hewson *et al.* 2016). The mortality of birds from declining southern populations was therefore much greater than that of northern birds. This may reflect deteriorating environmental conditions in Iberia relative to elsewhere in Europe; Hewson *et al.* (2016) suggested that drought in Spain provides one plausible explanation. Alternatively, such mortality could occur through carry-over effects of environmental conditions in the UK, such as the decline in large-moth populations in the south (Conrad *et al.* 2006), whose caterpillars form an important food source for adult Cuckoos.

Conclusions

In spite of the difficulties of identifying the impacts of climate change on species' populations in the context of multifarious environmental changes and pressures, it is increasingly clear that climate change is affecting the behaviour, survival, breeding success, abundance and distribution of many UK bird species. Warmer temperatures have directly increased the overwinter survival and breeding success of many resident bird species, leading to population increases and range expansions, particularly among generalists. Climate change has had a more equivocal or negative impact on long-distance migrants, northern species and some habitat specialists, with the majority of impacts likely to have occurred through changes in the abundance or availability of food resources. The effect of changing spring temperatures on the relative timing of peak food availability and bird breeding seasons may have widespread impacts, particularly on late-nesting, long-distance migrants, although this has not been clearly identified as a driver of long-term population declines. The impact of climate change on the abundance of key invertebrate groups, such as moths and soil invertebrates, may be equally or more important. Although not the focus of this article, seabirds may have been one of the groups most affected by climate change in the UK, through an increasing mismatch between the timing of their breeding and prey availability, and the declining availability of fish and plankton prey as sea surface temperatures rise (reviewed in Pearce-Higgins & Green 2014).

What of the future? A range of northern, upland and woodland species are widely regarded as threatened by climate change in the UK, while southern freshwater wetland and coastal species are likely to colonise from the Continent (Ausden *et al.* 2015), matching the evidence of recently observed trends. The ability of species threatened with climate change to persist in the UK will probably depend upon our ability to maximise the quality of their habitat and reduce other pressures that they face, in order to increase their resilience to climate change. Given that many of the negative impacts of climate change may operate through changes in food resources, this in particular will require management to boost the abundance of prey (i.e. Carroll *et al.* 2011).

The colonisation of species in response to climate change may be limited by inappropriate human activity. Indeed, many potential colonists of the UK in a warmer climate are likely to be constrained by unfavourable population trends in Europe (Ausden *et al.* 2015). One of the strongest predictors of colonisation, both of range-expanding species in the UK (Thomas *et al.* 2012) and of colonists from continental Europe (Hiley *et al.* 2013), is the availability of protected areas. Our network of nature reserves maintains important areas of semi-natural habitat for range-expanding species to occupy (Pearce-Higgins & Green 2014), and nature reserves are likely to become even more important in a changing climate (Johnston *et al.* 2013). They can also reduce rates of extinction in northerly distributed species (Gillingham *et al.* 2015). In the same way, the provision of semi-natural areas of habitat in the wider countryside also helps populations to adapt to climate change (Newson *et al.* 2014; Oliver *et al.* 2017). The message is clear: birds will be better able to cope with climate changes if we are able to maintain and expand a network of protected areas, provide areas of appropriate habitat within the wider countryside, and manage those sites effectively.

Acknowledgments

Many of the studies that provide evidence about the impact of climate change on British birds are long-term and rely on data collected by volunteers. I particularly want to acknowledge their contribution to the information in this article. If you want to help us track the impacts of future climate change, and other drivers, upon British birds, please do consider taking part in one of our monitoring schemes and submitting your bird records to BirdTrack (www.bto.org/volunteer-surveys). Thank you.

References

Ausden, M., Bradbury, R., Brown, A., Eaton, M., Lock, L., & Pearce-Higgins, J. 2015. Climate change and Britain's birdlife: what might we expect? *British Wildlife* Feb 2015: 161–175.

Baillie, S. R., Furness, R. W., Clark, J. A., Green, R. E., Gosler, A. G., Ormerod, S. J., Peach, W. J., Stroud, D. A., Sutherland, W. J., & Wilson, J. D. 1999. The scientific strategy of the BTO Ringing Scheme. *Ringing & Migration* 19 (Suppl.): 129–143.

Balmer, D. E., Gillings, S., Caffrey, B. J., Swann, R. L., Downie, I. S., & Fuller, R. J. 2013. *Bird Atlas 2007–11: the Breeding and Wintering Birds of Britain and Ireland*. BTO, Thetford.

Beale, C. M., Burfield, I. J., Sim, I. M. W., Rebecca, G. W., Pearce-Higgins, J. W., & Grant, M. C. 2006. Climate change may account for the decline in British Ring Ouzels *Turdus torquatus*. *J. Anim. Ecol.* 75: 826–835.

Both, C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Current Biology* 20: 243–248.

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

Carroll, M. J., Dennis, P., Pearce-Higgins, J. W., & Thomas, C. D. 2011. Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. *Global Change Biology* 17: 2991–3001.

—, Heinemeyer, A., Pearce-Higgins, J. W., Dennis, P., West, C., Holden, J., Wallage, Z. E., & Thomas, C. D. 2015. Ecosystem processes and the survival of species under climate change. *Nature Communications* 6: 7851.

Cattadori, I. M., Haydon, D. T., & Hudson, P. J. 2005. Parasites and climate synchronize Red Grouse populations. *Nature* 433: 737–741.

Conrad, K. F., Woiwod, I. P., & Perry, J. N. 2003. East Atlantic teleconnection pattern and the decline of a common arctiid moth. *Global Change Biology* 9: 125–130.

—, Warren, S. W., Fox, R., Parsons, M. S., & Woiwod, I. P. 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation* 132: 279–291.

Cresswell, W., & McCleery, R. 2003. How Great Tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *J. Anim. Ecol.* 72: 356–366.

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

—, Baillie, S. R., & Leech, D. I. 2003. The UK Nest Record Scheme: its value for science and conservation. *Bird Study* 50: 254–270.

—, Dudley, C., Glue, D. E., & Thomson, D. L. 1997. UK birds are laying eggs earlier. *Nature* 338: 526.

Davey, C. M., Chamberlain, D. E., Newson, S. E., Noble, D. G., & Johnston, A. 2012. Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography* 21: 568–578.

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Linström, Å., Reif, J., Roy, D. B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., De Vries, M. W., Wynhoff, I., & Jiguet, F. 2012. Differences in the climate debts of birds and butterflies at a continental scale. *Nature Climate Change* 2: 121–124.

Durant, J. M., Hjermann, D. Ø., Ottersen, G., & Stenseth, N. C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33: 271–283.

Eglington, S. M., Brereton, T. M., Tayleur, C. M., Noble, D., Risely, K., Roy, D. B., & Pearce-Higgins, J. W. 2015. Patterns and causes of covariation in bird and butterfly community structure. *Landscape Ecology* 30: 1461–1472.

Finch, T., Pearce-Higgins, J. W., Leech, D. I., & Evans, K. L. 2014. Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. *Biodiversity and Conservation* 23: 2427–2444.

Fletcher, K., Howarth, D., Kirby, A., Dunn, R., & Smith, A. 2013. Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. *Ibis* 155: 456–463.

Fox, R., Oliver, T. H., Harrower, C., Parsons, M. S., Thomas, C. D., & Roy, D. B. 2014. Long term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land use changes. *J. Applied Ecol.* 514: 949–957.

Freeman, S. N., Noble, D. G., Newson, S. E., & Baillie, S. R. 2007. Modelling population changes using data from different surveys: the Common Birds Census and the Breeding Bird Survey. *Bird Study* 54: 61–72.

Fuller, R. J., Gregory, R. D., Gibbons, D. W., Marchant, J. H., Wilson, J. D., Baillie, S. R., & Carter, N. 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology* 9: 1425–1441.

Gibbons, D. W., Reid, J. B., & Chapman, R. A. 1993. *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*. Poyser, London.

Gilbert, L. 2010. Altitudinal patterns of tick and host abundance: a potential role for climate change in regulating tick-borne diseases? *Oecologia* 162: 217–225.

Gillingham, P. K., Bradbury, R. B., Roy, D. B., Anderson, B. J., Baxter, J. M., Bourn, N. A. D., Crick, H. Q. P., Findon, R. A., Fox, R., Franco, A., Hodgson, J. A., Holt, A. R., Morecroft, M. D., O'Hanlon, N. J., Oliver, T. H., Pearce-Higgins, J. W., Hill, J. K., Procter, D. A., Thomas, J. A., Walker, K. J., Walmsley, C. A., Wilson, R. J., & Thomas, C. D. 2015. The effectiveness of protected areas to conserve species undertaking geographic range shifts. *Biol. J. Linn. Soc. Lond.* 115: 707–717.

Gillings, S., Balmer, D. E., & Fuller, R. J. 2015. Directionality of recent bird distribution shifts and climate change in Britain. *Global Change Biology* 21: 2155–2168.

Goodenough, A. E., Elliot, S. L., & Hart, A. G. 2009. The challenges of conservation for declining migrants: are reserve-based initiatives during the breeding season appropriate for the Pied Flycatcher *Ficedula hypoleuca*. *Ibis* 151: 429–439.

Hewson, C. M., Thorup, K., Pearce-Higgins, J. W., & Atkinson, P. W. 2016. Population decline is linked to migration route in the Common Cuckoo. *Nature Communications* 7: 12296.

Hiley, J. R., Bradbury, R. B., Holling, M., & Thomas, C. D. 2013. Protected areas act as establishment centres for species colonising the United Kingdom. *Proc. Royal Soc.* B 280: 20122310.

Hudson, P. J. 1992. *Grouse in Space and Time*. Game Conservancy Trust, Fordingbridge.

Huntley, B., & Green, R. E. 2011. Bioclimate models of the distributions of Gyrfalcons and Ptarmigan. In: Watson, R. T., Cade, T. J., Fuller, M., Hunt, G., & Potapov, E. *Gyrfalcons and Ptarmigan in a Changing*

World. The Peregrine Fund, Boise, Idaho.

—, —, Collingham, Y. C., & Willis, S. G. 2007. *A Climatic Atlas of European Breeding Birds*. Durham University, RSPB and Lynx Edicions, Barcelona.

Jetz, W., Wilcove, D. S., & Dobson, A. P. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol*. 5(6): e157. https://doi.org/10.1371/journal.pbio.0050157

Johnston, A., Robinson, R. A., Gargallo, G., Julliard, R., van der Jeugd, H., Baillie, S. R. 2016. Survival of Afro-Palearctic passerine migrants in western Europe and the impacts of seasonal weather variables. *Ibis* 158: 465–480.

—, Ausden, M., Dodd, A. M., Bradbury, R. B., Chamberlain, D. E., Jiguet, F., Thomas, C. D., Cook, A. S. C. P., Newson, S. E., Ockendon, N., Rehfisch, M. M., Roos, S., Thaxter, C. B., Brown, A., Crick, H. Q. P., Douse, A., McCall, R. A., Pontier, H., Stroud, D. A., Cadiou, B., Crowe, O., Deceuninck, B., Hornman, M., & Pearce-Higgins, J. W. 2013. Observed and predicted effects of climate change on species abundance in protected areas. *Nature Climate Change* 3: 1055–1061.

Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A., Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P. P., Møller, A. P., Nilsson, A. L. K., Péron, G., Ranta, E., Rubolini, D., Sparks, T. H., Spina, F., Studds, C. E., Sæther, S. A., Tryjanowski, P., & Stenseth, N. C. 2011. Challenging claims in the study of migratory birds and climate change. *Biological Reviews* 86: 928–946.

Martay, B., Brewer, M. J., Elston, D. A., Bell, J. R., Harrington, R., Brereton, T. M., Barlow, K. E., Botham, M. S., & Pearce-Higgins, J. W. In press. Impacts of climate change on national biodiversity population trends. *Ecography*.

Massimino, D., Johnston, A., & Pearce-Higgins, J. W. 2015a. The geographical range of British birds expands during 15 years of warming. *Bird Study* 62: 523–534.

—, —, Noble, D. G., & Pearce-Higgins, J. W. 2015b. Multi-species spatially-explicit indicators reveal spatially structured trends in bird communities. *Ecological Indicators* 58: 277–285.

Miller, M. W., Leech, D. I., Pearce-Higgins, J. W., & Robinson, R. A. 2017. Multi-state, multi-stage modelling of nest-success suggests interaction between weather and land-use. *Ecology* 98: 175–186.

Møller, A. P., Rubolini, D., & Lehikoinen, E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc. Nat. Acad. Sci. USA* 105: 16195–16200.

Morrison, C. A., Robinson, R. A., Clark, J. A., Risely, K., & Gill, J. A. 2013. Recent population declines in Afro-Palaearctic migratory birds: the influence of breeding and non-breeding seasons. *Diversity & Distributions* 19: 1051–1058.

—, —, & Pearce-Higgins, J. W. 2016a. Winter Wren populations show adaptation to local climate. *Open Science* 3: 160250.

—, —, Butler, S. J., Clark, J. A., & Gill, J. A. 2016b. Demographic drivers of decline and recovery in an Afro-Palaearctic migratory bird population. *Proc. Royal Soc.* B 283: 20161387.

Newson, S. E., Oliver, T. H., Gillings, S., Crick, H. Q. P., Morecroft, M. D., Duffield, S. J., Macgregor, N. A., & Pearce-Higgins, J. W. 2014. Can site and landscape-scale environmental attributes buffer bird populations against weather events? *Ecography* 37: 872–882.

—, Moran, N. J., Musgrove, A. J., Pearce-Higgins, J. W., Gillings, S., Atkinson, P. W., Miller, R., Grantham, M. J., & Baillie, S. R. 2016. Long-term change in spring and autumn migration phenology of common migrant breeding birds in Britain: results from large-scale citizen science bird recording schemes. *Ibis* 158: 465–695.

Ockendon, N., Hewson, C. H., Johnston, A., & Atkinson, P. W. 2012. Declines in British-breeding populations of Afro-Palaearctic migrant birds are linked to bioclimatic wintering zone in Africa, possibly via constraints on arrival time advancement. *Bird Study* 59: 111–125.

—, Leech, D., & Pearce-Higgins, J. W. 2013. Climate effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. *Biology Letters* 9: 20130669.

—, Johnston, A., & Baillie, S. R. 2014a. Rainfall on wintering grounds affects population change in many species of Afro-Palaearctic migrants. *J. Ornithol*. 155: 905–917.

—, Baker, D. J., Carr, J. A., Almond, R. E. A., Amano, T., Bertram, E., Bradbury, R. B., Bradley, C., Butchart, S. H. M., Doswald, N., Foden, W., Gill, D. J. C., Green, R. E., Sutherland, W. J., Tanner, E. V. J., & Pearce-Higgins, J. W. 2014b. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biology* 20: 2221–2229.

Oliver, T. H., Gillings, S., Pearce-Higgins, J. W., Brereton, T., Crick, H. Q. P., Duffield, S., Morecroft, M. D., & Roy, D. B. 2017. Large extents of intensive land use limit community reorganisation during climate warming. *Global Change Biology* 23: 2272–2283.

Park, K. J., Robertson, P. A., Campbell, S. T., Foster, R., Russell, Z. M., Newborn, D., & Hudson, P. J. 2001. The role of invertebrates in the diet, growth and survival of Red Grouse (*Lagopus lagopus scoticus*) chicks. *J. Zool*. 254: 137–145.

Pearce-Higgins, J. W. 2010. Using diet to assess the sensitivity of northern and upland birds to climate change. *Climate Research* 45: 119–130.

— & Grant, M. C. 2006. Relationships between bird abundance and the composition and structure of moorland vegetation. *Bird Study* 53: 112–125.

— & Green, R. E. 2014. *Birds and Climate Change: impacts and conservation responses*. Cambridge University Press, Cambridge.

— & Yalden, D. W. 2004. Habitat selection, diet, arthropod availability and growth of a moorland wader: the ecology of European Golden Plover *Pluvialis apricaria* chicks. *Ibis* 146: 335–346.

—, Dennis, P., Whittingham, M. J., & Yalden, D. W. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Global Change Biology* 16: 12–23.

—, Eglington, S. M., Martay, B., & Chamberlain, D. E. 2015a. Drivers of climate change impacts on bird communities. *J. Anim. Ecol*. 84: 943–954.

—, Ausden, M. A., Beale, C. M., Oliver, T. H., & Crick, H. Q. P. 2015b. *Research on the Assessment of Risks and Opportunities for Species in England as a Result of Climate Change*. Natural England Commissioned Reports, Number 175.

Phillimore, A. B., Leech, D., Pearce-Higgins, J. W., & Hadfield, J. D. 2016. Passerines may be sufficiently plastic to track temperature-mediated shifts in optimum lay date. *Global Change Biology* 22: 3259–3272.

Reed, T. E., Grøtan, V., Jenouvrier, S., Sæther, B-E., & Visser, M. E. 2013. Population growth in a wild bird is buffered against phenological mismatch. *Nature* 340: 488–491.

Robinson, R. A., Baillie, S. R., & Crick, H. Q. P. 2007. Weather-dependent survival: implications of climate change for passerine population processes. *Ibis* 149: 357–364.

—, Green, R. E., Baillie, S. E., Peach, W. J., & Thomson, D. L. 2004. Demographic mechanisms of the population decline of the Song Thrush *Turdus philomelos* in Britain. *J. Anim. Ecol.* 73: 670–682.

—, Leech, D. I., Massimino, D., Woodward, I., Eglington, S. M., Marchant, J. H., Sullivan, M. J. P., Barimore, C., Dadam, D., Hammond, M. J., Harris, S. J., Noble, D. G., Walker, R. H., & Baillie, S. R. 2016. *BirdTrends 2016: trends in numbers, breeding success and survival for UK breeding birds*. Research Report 691. BTO, Thetford. www.bto.org/birdtrends

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.

Schwartz, M. D., Ahas, R., & Aasa, A. 2006. Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology* 12: 343–351.

Sharrock, J. T. R. 1976. *The Atlas of Breeding Birds in Britain and Ireland*. Poyser, Berkhamsted.

Smith, A. A., Redpath, S. M., Campbell, S. T., & Thirgood, S. J. 2001. Meadow Pipits, Red Grouse and the habitat characteristics of managed grouse moors. *J. Applied Ecol.* 38: 390–400.

Smith, K. W., Smith, L., Charman, E., Briggs, K., Burgess, M., Dennis, C., Harding, M., Isherwood, C., Isherwood, I., & Mallord, J. 2011. Large-scale variation in the temporal patterns of the frass fall of defoliating caterpillars in oak woodlands in Britain: implications for nesting woodland birds. *Bird Study* 58: 506–511.

Stephens, P. A., Mason, L. R., Green, R. E., Gregory, R. D., Sauer, J., Alison, J., Aunins, A., Brutons, L., Butchart, S. H. M., Campedelli, T., Chodkiewicz, T., Chylarecki, P., Crowe, O., Elts, J., Escandell, V., Foppen, R. P. B., Heldbjerg, H., Herrando, S., Husby, M., Jiguet, F., Lehikoinen, A., Lindström, A., Noble, D. G., Paquet, J-Y., Reif, J., Sattler, T., Szep, T., Teufelbauer, N., Trautmann, S., van Strien, A. J., van Turnhout, C. A. M., Vorisek, P., & Willis, S. G. 2016. Consistent responses of bird populations to climate change on two continents. *Science* 352: 85–87.

Sullivan, M. J. P., Newson, S. E., & Pearce-Higgins, J. W. 2016. Changing densities of generalist species underlie apparent homogenization of UK bird communities. *Ibis* 158: 645–655.

Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalho, L. C., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., Roy, D. B., Scott, W. A., Smith, M., Smithers, R. J., Winfield, I. J., & Wanless, S. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* 16: 3304–3313.

—, Henrys, P. A, Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Halaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., Elliott, J. M., Hall, S. J. G., Harrington, R., Pearce-Higgins, J. W., Hoye, T. T., Kruuk, L. E. B., Pemberton, J. M., Sparks, T. H., Thompson, P. M., White, I., Winfield, I. J., & Wanless, S. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535: 241–245.

Tharme, A. P., Green, R. E., Baines, D., Bainbridge, I. P., & O'Brien, M. 2001. The effect of management for Red Grouse shooting on the population density of breeding birds on heather-dominated moorland. *J. Applied Ecol*. 38: 439–457.

Thaxter, C. B., Joys, A. C., Gregory, R. D., Baillie, S. R., & Noble, D. G. 2010. Hypotheses to explain patterns of population change among breeding bird species in England. *Biological Conservation* 143: 2006–2019.

Thirgood, S. J., Redpath, S., Rothery, P., Newton, I., & Hudson, P. 2000. Habitat loss and raptor predation: disentangling long- and short-term causes of Red Grouse declines. *Proc. Royal Soc.* B 267: 651–656.

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

—, Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siquieira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., & Williams, S. E. 2004. Extinction risk from climate change. *Nature* 427: 145–148.

—, Gillingham, P. K., Bradbury, R. B., Roy, D. B., Anderson, B. J., Baxter, J. M., Bourn, N. A. D., Crick, H. Q. P., Findon, R. A., Fox, R., Hodgson, J. A., Holt, A. R., Morecroft, M. D., O'Hanlon, N., Oliver, T. H., Pearce-Higgins, J. W., Procter, D. A., Thomas, J. A., Walker, K. J., Walmsley, C. A., Wilson, R. J., & Hill, J. K. 2012. Protected areas facilitate species' range expansions. *Proc. Nat. Acad. Sci. USA* 109: 14063–14068.

Thompson, D. B. A., MacDonald, A. J., Marsden, H., & Galbraith, C. A. 1995. Upland heather moorland in Great Britain. *Biological Conservation* 71: 163–178.

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. *Oecologia* 147: 164–172.

James W. Pearce-Higgins, British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU; e-mail james.pearce-higgins@bto.org

James Pearce-Higgins is Director of Science at the British Trust for Ornithology, where he also leads the climate change work. In addition, he is an Honorary Research Fellow in the Department of Zoology, University of Cambridge.