

S08-1 Changes in the phenology of breeding and migration in relation to global climate change

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Abstract The timing of life history events is often critical for the fitness of organisms. Among birds, the timing of events at the start of the breeding season can, for example, determine an individual's chance of obtaining breeding territory and of achieving a level of reproductive success. The timing of migration and egg-laying can be affected by weather conditions, and it has been predicted that climate change could thus have a major impact. Data from a variety of sources strongly suggests that the timing of migration and nesting have already been affected by climate change, and provide some of the strongest early signals of likely impacts from the relatively moderate climate change that has occurred to date. We review information from intensive study sites and extensively gathered data to draw out general patterns, and then briefly consider the potential consequences of such changes for birds.

Key words Phenology, Nesting, Migration, Climate change

1 Introduction

The timing of life history events is often critical for the fitness of organisms. Natural selection tends to act to optimize the timing of these events such that individuals achieve the best chance of passing their genes on to the next generation. Among birds, the timing of events at the start of the breeding season can, for example, determine an individual's chance of obtaining breeding territories (Kokko, 1999) and of achieving a certain level of reproductive success (Perrins, 1970). The timing of migration to breeding grounds and, of egg-laying, is determined by an interaction of endogenous and environmental factors; and key among the latter is the influence of weather conditions (Berthold, 1993). Thus the effect of climate change on these factors could have major impacts on bird populations.

The study of the timing of natural events, phenology, is an area which has attracted much interest not just from scientists but also from amateur natural historians over the last two or three centuries. As a result, many long-term datasets exist which have now begun to be explored, revealing insights into historical phenological changes in relation to climate change (e.g., Sparks and Carey, 1995; Sparks et al., 2001).

Here we review evidence which strongly suggests that the timing of bird migration and nesting has already been affected by climate change. This has occurred despite the relatively modest degree of climate change to date. Such changes currently provide some of the strongest signals of potential impacts of climate change on the natural world. If

components of ecological communities respond at different rates to climate change, these differential responses could lead to "phenological disjunction" between trophic levels, with major consequences for each level and ultimately for the functioning of their ecosystems (Harrington et al., 1999).

2 Timing of breeding

Two main types of investigation have been used to study long-term trends in the timing of breeding in birds: (a) intensive studies, usually of a single species and at a single location by professional scientists; and (b) studies of extensively gathered data, collected by volunteers as part of a monitoring network. The latter can provide the most conclusive evidence of effects from widespread climatic change because the data are often gathered at a national scale. The Nest Record Scheme of the British Trust for Ornithology (BTO) is probably the most studied dataset in this respect. It holds more than a million detailed records of individual nesting attempts collected by volunteer ornithologists from the 1930s onwards (Crick and Baillie, 1996).

Using this dataset, Crick et al. (1997) demonstrated that 51 of 65 species showed a trend towards earlier nesting between 1971 and 1995. The average advancement in the 20 species in which the trend was most marked was 8 d, ranging from 4 to 18 d. These species belonged to no one taxonomic or ecological group; they included shorebirds (*Numenius arquata*), resident insectivores (*Cinclus cinclus*), migrant insectivores (*Anthus trivialis*), corvids (*Pica pica*) and seedeaters (*Fringilla coelebs*). This suggested that a wider environmental factor, such as climate

change, was the likely driver. Forchhammer et al. (1998) re-analyzed examples of data from Crick et al. (1997) to show that laying date trends in *Miliaria calandra* and *Phylloscopus collybita* were related to the North Atlantic Oscillation (NAO), a large-scale atmospheric phenomenon that determines the extent to which western Europe is affected by damp Atlantic or dry continental weather.

Subsequent examination of the BTO's nest record data for 1939–1995 showed that 19 of 36 species (53%) exhibited significant long-term shifts in laying, most of which tended to be curvilinear, becoming later during the period of spring cooling from 1950–1970 and then earlier during the period of warming from 1970 to 1995 (Crick and Sparks, 1999). In 31 (86%), there were significant correlations between laying dates and weather (temperature and precipitation); and of the 17 that showed long-term trends as well, seven (41%) showed no residual trends after weather factors had been included in the regression models. These were among the most common and widespread species in the dataset, and for which the weather variables used were probably most appropriate: *Troglodytes troglodytes*, *Prunella modularis*, *Sylvia atricapilla*, *Phylloscopus trochilus*, *Muscicapa striata*, *Aegithalos caudatus* and *Carduelis chloris*. For the other 10 species, the causes of residual trends could have been inappropriate choice of weather variables (e.g., soil rather than air temperature) or factors unrelated to climate (e.g., land-use change).

For 33 species, data were sufficient for investigating how the distribution of laying dates had changed over time. This we did by screening trends through the interval between the median and the 5th percentile or 95th percentile of the laying date distribution, as measures of the relative lengths of the first and second halves of the nesting season respectively. Significant lengthening of the first half occurred in only eight species, and significant shortening in just one. Similarly, significant lengthening of the second half occurred in only four species, and significant shortening in two. The general lack of significant change suggests that, for most species, changes in the timing of nesting involved a whole shift in the frequency distribution. A few species had increased the length of the nesting season, suggesting that a proportion of individuals could potentially fit in an extra breeding attempt. Unfortunately, individual pairs are not followed within the Nest Record Scheme protocols, a gap that can only be explored further from records of individually marked birds.

The only other major study using such extensive data also shows a general trend towards earlier laying. Dunn and Winkler (1999) analyzed 3 450 nest records from the North American nest record schemes between 1959 and 1991 and found that the laying date of *Tachycineta bicolor* had advanced by an average of 9 days and that the main correlative factor was change in air temperature.

A number of intensive studies at single locations have also demonstrated shifts towards earlier laying in response to warmer spring temperatures in recent years. In Britain,

McCleery and Perrins (1998) showed changes in the average laying date of a population of *Parus major* between 1947 and 1997 to be linked to shifts in spring temperatures. Over the course of their study, temperatures had cooled and then warmed, with associated trends towards later then earlier laying, corresponding with the results of Crick and Sparks (1999). They showed that the relationship between laying date and temperature was the same in cooling and warming phases.

Winkel and Hudde (1997) also found that hatching dates for *Parus major* and *P. caeruleus* had advanced between 1975 and 1995 in northern Germany, in response to warmer springs, and obtained a similar result for *Ficedula hypoleuca*, as have several other studies (e.g., Jarvinen, 1989; Slater, 1999; Both and Visser, 2001) and Przybylo et al. (2000) for the closely related *F. albicollis*. The latter study showed, as well, that the response to warmer temperatures could be explained entirely by individual phenotypic plasticity rather than microevolutionary process. A rare example of a study involving an open-nesting species comes from a very different climatic zone: arid Arizona. There Brown et al. (1999) showed that, in a population of *Aphelocoma ultramarina*, the mean first clutch date had advanced by 10 d between 1971 and 1998, associated with warmer minimum temperatures in the month prior to laying.

Two meta-analyses of data gathered across a large number of studies throughout Europe have explored the generality of the results from these intensive projects. Sanz (2002) found that within and across breeding sites, the laying date of *Parus major* and *P. caeruleus* was related to the winter NAO index, showing that both species tend to lay earlier after warmer, moister winters. Moreover, the rate of change in laying date with respect to the NAO differed geographically but not between species. Visser et al. (2003) analyzed a different set of data for these two species from 14 study sites and found that differences in the degree of advancement may be related to changes in the degree of broodedness (single vs double brooding) in response to climate change.

3 Timing of migration

Studies of the timing of arrival and departure of migrants have derived more from the observations of amateur natural historians than from professional biologists. Some species, particularly *Hirundo rustica*, *Cuculus canorus* and *Ciconia ciconia*, have long been popular subjects of phenological recording in Europe because of their association with spring (e.g., Sparks and Carey, 1995). For the most part, such records are based on the first observation of a species at a particular location in each year. Although such records are subject to error and prone to biases, they have also been shown to be remarkably robust when used within long-term time series with respect to investigations of climate change (e.g., Sparks, 1999; Sparks et al., 2001).

One such dataset that has been analyzed in Britain comes from records collated each year by the network of

County Bird Recorders, who publish annual bird reports for each county. These often include a section of the first and last reported dates for each species of migrant. Mason (1995) analyzed the data for 23 such species in the mid-England county of Leicestershire over a 50-year period from 1942–1991. For eight species he found significant negative correlations between arrival date and spring temperatures. Sparks (1999) investigated the same dataset and compared it with data from the county of Sussex, on the south coast of England, over the period from 1966 onwards. He found that 54 of the 56 species/site series showed a negative coefficient, 22 being significant ($P < 0.05$). The synchrony between records from the two counties was often strong, despite a 250 km spatial separation. Comparisons with spring temperatures in Britain produced 49 negative regression coefficients, of which 19 were significant; only 1 positive relationship was significant.

A network of coastal Bird Observatories around the British Isles collects data that are more systematic. These are manned throughout the migration period and are staffed by skilled volunteers and professional staff who not only catch and ring migrants, but also make daily counts around each observatory. Analyses of data from four such observatories (Sparks, 1999) showed that, of 90 species/site combinations, 68 showed trends towards earlier arrival, of which 29 were statistically significant. Only four of the trends towards later arrival were significant. Similarly, 69 showed negative responses to spring temperatures (13 significant); and no positive relationships were significant. The relationships were stronger if French or Iberian temperatures were used, presumably because these are the conditions experienced by the migrants en route.

Across Europe, similar observations have also been made at fixed ringing (banding) sites. Preeminent among these are the records from the banding station on the Courish Spit on the Baltic Sea. Sokolov et al. (1998) have shown long-term trends in the dates of first capture and mean dates of spring migration for 33 passerine species there between 1959 and 1996. Higher spring temperatures tended to be associated with earlier arrival. In addition, arrival date tended to be more variable for earlier arriving species than later, as has also been found by Sueur and Triplet (2001).

Series of long-term observations from a single locality by independent natural historians, either singly or in groups, are also an important source of information on migration phenology. In Britain, Jenkins and Watson (2000) report on a series of such observations made in Scotland between 1974 and 1999. They found an interesting difference between resident, short-distance migrant species and those that winter in Africa. The latter showed generally weak trends over time (8 out of 14 being negative), whereas almost all (9 out of 10 species) of the short-distance migrants showed trends towards earlier arrival.

Berthold (1990), in a speculative review, suggested that long-distance migrants would suffer detrimental effects

more than short-distance migrants because the initiating conditions on their wintering grounds might not track the changes on their breeding grounds. Indeed, Both and Visser (2001) provide evidence for this from their studies of the trans-Saharan migrant, *Ficedula hypoleuca*. On their study site in the Netherlands, this species has shown no shift towards early arrival; and a trend towards earlier laying with warmer springs has not been sufficient to eliminate an increasing selection differential towards earlier nesting. Interestingly, a long time series gathered in northern Spain showed that 5 of the 6 long-distance migrants there showed significant trends towards later arrival over the period between 1952 and 2000 (Penuelas et al., 2002). These trends could reflect different climatic processes acting on wintering and breeding grounds, though later arrival may be a function of declines in population size, as in *Cuculus canorus* and *Luscinia megarhynchos* (Tryjanowski and Sparks, 2001).

4 Conclusions

There is good evidence from both intensive and extensive datasets that birds are showing trends towards earlier migration and nesting. Overall, the response to per degree C warming is an advance in arrival and nesting of 1–3 days. However, plants and invertebrates tend to respond to equivalent rises in temperature at *c.* 6 day rates, leaving considerable scope for mismatching between birds and their food supplies (e.g., Visser et al., 1998). There is some evidence that earlier springs can result in larger numbers of juveniles in autumn (Sokolov et al., 2000); and Winkel and Hudde (1997) found that fledgling production had increased for *Ficedula hypoleuca* as a result of earlier laying. However, the results of Both and Visser (2001) and the evidence that long-distance migrants respond differently to climate change than short-distance migrants suggests that climate change may pose more threats to long-distance migrants than others.

Acknowledgements Humphrey Crick gratefully acknowledges the support of The Royal Society, The British Chamber of Commerce, China, and Virgin Airways towards his attendance at the 23rd International Ornithological Congress in Beijing. The Nest Record Scheme of the British Trust for Ornithology is funded by a BTO/JNCC partnership.

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