

## The impact of climate change on birds

HUMPHREY Q. P. CRICK\*

British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

---

Weather is of major importance for the population dynamics of birds, but the implications of climate change have only recently begun to be addressed. There is already compelling evidence that birds have been affected by recent climate changes. This review suggests that although there is a substantial body of evidence for changes in the phenology of birds, particularly of the timing of migration and of nesting, the consequences of these responses for a species' population dynamics is still an area requiring in-depth research. The potential for phenological miscuing (responding inappropriately to climate change, including a lack of response) and for phenological disjunction (in which a bird species becomes out of synchrony with its environment) are beginning to be demonstrated, and are also important areas for further research. The study of climatically induced distributional change is currently at a predictive modelling stage, and will need to develop methods for testing these predictions. Overall, there is a range of intrinsic and extrinsic factors that could potentially inhibit adaptation to climate change and these are a high priority for research.

The impact of weather on the population biology of birds has been a major field of study by ornithologists over the past half century. It has featured prominently in reviews of the subject since Lack's seminal books *The Natural Regulation of Animal Numbers* and *Population Studies of Birds* (Lack 1954, 1966) up to present-day works, such as Newton's *Population Limitation in Birds* (Newton 1998). Weather not only affects the metabolic rate of birds (e.g. cold weather requiring increased energy expenditure for body maintenance) but also exerts other indirect and direct effects on bird behaviour. For example, it can influence foraging conditions and the ability to carry out other essential behaviours, such as courtship. Weather also impacts on breeding success through, for example, chilling or starvation of young (Newton 1998). Extreme weather events, such as prolonged frozen spells and droughts, can have catastrophic effects on bird populations, including long-term effects on whole cohorts (Stenseth *et al.* 2002). An example of regularly occurring catastrophic events that affect seabirds over a large geographical scale are those due to El Niño events, when periodic warming alters oceanic currents along the west coast of the Americas, leading to crashes in fish abundance and catastrophic breeding failure or even adult mortality

among seabirds in the Pacific (Barber & Chavez 1983, 1986, Schreiber & Schreiber 1984).

The implications for birds of climate change, i.e. long-term shifts in average weather, have only recently begun to be addressed. There is already compelling evidence that animals and plants have been affected by recent climate change (e.g. Walther *et al.* 2002, Parmesan & Yohe 2003, Root *et al.* 2003). These effects include earlier breeding; changes in timing of migration; changes in breeding performance (egg size, nesting success); changes in population sizes; changes in population distributions; and changes in selection differentials between components of a population. Birds have the capacity to be important bioindicators, a concept that is readily understandable by the general public and policy-makers because birds are both popular and often have an iconic or totemic status throughout the world (for example, storks are known as 'rain birds' in Africa and eagles have been used for centuries as heraldic symbols throughout Europe and North America).

In this paper I briefly review evidence to show that recent climate change has already affected populations of birds and consider the key areas where future research is required. The paper will not address the impact of sea-level changes as these are dealt with elsewhere in this supplement (Atkinson *et al.* 2004, Watkinson *et al.* 2004).

\*Email: humphrey.crick@bto.org

## CHANGES IN DISTRIBUTIONS AND GEOGRAPHICAL RANGE

Speculations that the northward spread of southern species is due to climate change are difficult to substantiate. There is a wide range of potentially confounding factors that might also affect bird distributions. Thus, although the expansion of the range of Dartford Warbler *Sylvia undata* in the UK since the 1960s is likely to be due to a lack of severe winters (Gibbons & Wotton 1996), this hypothesis has yet to be tested rigorously. Sparks *et al.* (2002) provide a range of suggestions of the potential 'winners and losers' among bird species in the UK with climate change, based on the biological attributes of each species. The truth about such speculations can only be tested by careful monitoring and spatial modelling exercises.

Changes in distributions can best be measured by repeated large-scale surveys of suitable habitat, but these require substantial effort, often by a large number of observers. In practice, this is mainly achieved by mass-participation surveys such as those carried out in the UK by volunteers for the British Trust for Ornithology (BTO). For example, two atlases of breeding bird distribution in the British Isles were carried out in 1968–72 (Sharrock 1976) and in 1988–91 (Gibbons *et al.* 1993). These were analysed by Thomas and Lennon (1999), who compared the mean locations in the two atlases of (a) the ten northernmost 10-km grid squares for 59 species with southern distributions and (b) the ten southernmost squares for 42 species with northern distributions. They first had to take into account any overall increases or decreases in distribution, because these would tend to change the margins irrespective of climate change. They concluded that the mean shift in the northern edge of southern species was 19 km northwards (after controlling for any change in the number of squares occupied). However, northerly species showed no significant change in the southern edge of their boundaries. They suggested that the most likely cause of the shift in the northern edge of southern species was climate warming and, although mean temperatures in the UK were warmer in the latter period than the in the former, other possible explanations for the pattern, such as land-use change, were not considered.

Altitudinal shifts are also likely to occur as a result of climate warming, and the best demonstration of this comes from the montane cloud forests of Costa Rica. Pounds *et al.* (1999) show how warming has raised the average altitude at the base of the orographic cloudbank, resulting in the colonization of

previously cloud-forest areas by bird species from lower altitudes. There are concerns that similar effects will occur in temperate zones (Watt *et al.* 1998); for example, modelling in the UK suggests that the range of species such as Snow Bunting *Plectrophenax nivalis* will contract or that it will even disappear from its current breeding areas in the montane zones of the Grampians in Scotland under different standard scenarios of climate change (Berry *et al.* 2001).

Opportunistic observations of unusual events of charismatic species can provide sufficient evidence of range changes in response to climate change. For example, Kinzelbach *et al.* (1997) collated historical records of the occurrence of European Bee-eaters *Merops apiaster* north of the Alps between 1500 and 1900 and found a close correlation with warmer winter temperatures. Bee-eaters were absent in years of longer, colder winters.

Change in distributions is the field of study in which predictive modelling is particularly strong. When species distributions are accurately mapped, it is possible to correlate the presence or absence of a species with environmental variables, including climate. For example, Root (1988a, 1998b) and Root and Schneider (1993) found strong statistical correlations between the distribution and abundance of a majority of 148 wintering landbirds and six large-scale environmental factors, mainly climatic ones. They suggested that climate change is likely to have a large effect on their future distributions. Gates *et al.* (1994) used multivariate regression to model the distributions of several species in the UK, in relation to land-use and climate factors. The latter factors were shown to have strong influences on bird distribution, with large-scale redistributions predicted with climate warming. A more recent development has been the use of neural network modelling to relate bird distributions to climate factors in Europe and the UK as a means of exploring the potential impact of scenarios of climate change (Berry *et al.* 2001). A similar method is the Genetic Algorithm for Rule-set Prediction (GARP), based on an iterative artificial intelligence-based approach, which Peterson *et al.* (2002) have used to show how the ecological niches of 1870 species of birds, mammals and butterflies in Mexico will respond to various scenarios of climate change. They showed that although extinctions and drastic range reductions are likely to be relatively infrequent, species turnover in some communities may become > 40%, suggesting severe ecological perturbation. The use of climate envelopes to describe the spatial distribution of birds is a useful heuristic approach, but the testing

of such predictions can only be made against current patterns of distribution and will need to await measurements of distributional change before they can be properly validated. Furthermore, one needs to be aware that current distributions may be due to factors other than climate, although they may correlate well with it. To take a theoretical example, Red Kites *Milvus milvus* in the UK were restricted for much of the 20th century to parts of Wales, where game preservation did not take hold, due mainly to persecution in the 19th and 20th centuries (Newton 1998). But the Welsh climate would have given a naïve modeller an entirely false indication of the species' climatic needs, and it has now been re-introduced very successfully to parts of central and eastern England and Scotland (Wotton *et al.* 2002), where the climate is very much drier.

## CHANGES IN PHENOLOGY

This is the area of study for which there is the strongest evidence of the impact of climate change on birds. In particular, there have been studies to show changes in the timing of migration and in average laying dates, many of which are based on observations made over wide geographical areas or over long time periods by networks of volunteers.

Changes in the phenology of autumn migration are reviewed elsewhere in these proceedings (Sparks & Mason 2004), but observations made over broad areas such as English counties and those made at point locations show general trends towards earlier spring arrivals for many species (e.g. Mason 1995, Forchhammer *et al.* 1998, Bradley *et al.* 1999, Sparks 1999, Loxton & Sparks 1999, Jenkins & Watson 2000, Sparks & Mason 2001, Sueur & Triplet 2001, Gilyazov & Sparks 2002, Hüppop & Hüppop 2003). In some areas, although timing in the arrival of spring migrants is earlier in warmer springs, no trends are yet apparent, because local temperatures have yet to show any trend (e.g. Barrett 2002) or there are trends towards later arrival because local temperatures have tended to become cooler (e.g. Sparks & Braslavskaya 2001). Although many of these datasets are based on records of the first arrival, such data appear to be relatively robust for the analysis of trends (Sparks 1999, Sparks *et al.* 2001). Far fewer data are available on the departure of migrants in the autumn, but such data suggest that last observations of birds have tended to become later, with a consequence that duration of stay on the breeding grounds has increased for some species (Sparks & Mason 2001, Gilyazov & Sparks 2002).

Long-term observations of the passage of migrants at a long-term ringing station ('Fringilla') on the Courish Spit of the Baltic coast of Russia have shown that warmer springs are not only associated with earlier spring arrivals but are also associated with earlier migration of juveniles in the autumn, suggesting earlier breeding (Sokolov *et al.* 1998). In the UK, a correlation between timing of spring arrival and mean laying dates has been demonstrated for a small number of species (Sparks *et al.* 2001).

Probably the longest and largest scale dataset on the timing of breeding derives from the BTO's Nest Record Scheme (NRS; Crick *et al.* 2003). Started in 1939, it currently collects c. 30 000 individual nest histories per annum for c. 120 species of bird from throughout the UK. Initial analysis of data for 65 species over a 25-year period (1971–95) showed that 20 exhibited statistically significant trends towards earlier laying and only one had become significantly later. Overall, 51 species showed trends towards laying earlier (regardless of significance), which was a statistically significant proportion (Crick *et al.* 1997). The results showed that trends were not restricted to particular ecological or taxonomic groups, with trend-revealing representatives including waterbirds, corvids, resident and migrant insectivores and seed-eaters. Early nesting species (such as Magpie *Pica pica*) were as likely to show earlier laying as late nesting species (such as Corn Bunting *Miliaria calandra*). A subsequent analysis of those species for which the scheme held more than 1000 laying dates, and over a longer time period (spanning 57 years: 1939–95), found that laying date was related to temperature or rainfall for 31 of 36 species (86%) (Crick & Sparks 1999). Just over half of the species (53%) showed long-term trends in laying date over time, of which 37% could be statistically accounted for by changes in climate. Using national-level climate scenarios of future change, Crick and Sparks (1999) predicted that average laying dates will be earlier for 75% of species by the year 2080. Over the longer term, trends in laying date were often curvilinear, mirroring curvilinear trends in spring temperatures since 1940, suggesting the results are unlikely to be the consequence of spurious correlation. The only other major study using extensively gathered data also shows a general trend towards earlier laying. Dunn and Winkler (1999) analysed 3450 nest records from the North American nest record schemes between 1959 and 1991 and found that the mean lay date of Tree Swallow *Tachycineta bicolor* had shifted an average of 9 days earlier and that the main factor correlated with this was change

in air temperature. The results from such schemes provide some of the best evidence to date of the widespread impact of existing climate change on wildlife.

To complement such extensive studies, intensive studies undertaken at single locations have also been able to provide evidence for changes in laying date in relation to climate change (e.g. Järvinen 1989, McCleery & Perrins 1998, Slater 1999). An unusual study from outside the temperate zone is of Mexican Jays *Aphelocoma ultramarina* (Brown *et al.* 1999) in arid zone Arizona. Trends towards earlier laying in this species were related to trends of warming in the two months prior to egg-laying. Stevenson and Bryant (2000) suggested that, on the basis of energetics studies, one would predict that the impacts of climate warming should be more evident in smaller bodied species than in larger bodied ones. They showed, using data in Crick and Sparks (1999), that the degree of advancement for a species, per °C warming, was inversely correlated to body mass. Thus, there may be physiological reasons why species may differ in their response to climate change.

Meta-analyses of results from intensive studies have allowed the generality of findings from individual studies to be tested. Sanz (2002) drew together information from 92 study sites of Great Tit *Parus major* and from 75 study sites of Blue Tit *P. caeruleus* from across the Western Palaearctic. He correlated annual estimates of laying date with values of the North Atlantic Oscillation (NAO), a north-south alternation in relative atmospheric masses between the high-pressure system over the Azores and the low-pressure system centred on Iceland. The NAO affects the strength of westerly winds blowing across the North Atlantic and positive values of the NAO are associated with warmer, moister winters (see Stenseth *et al.* 2002). The slopes of the relationship between laying dates and NAO varied geographically for these species. They were more negative in the west than in the east for both species, but were more negative in the north for Blue Tit and in the south for Great Tit. These results were obtained even though potentially confounding factors, such as latitude, longitude, elevation and habitat, were included in the analyses. A similar investigation of 24 other such datasets gathered over a smaller geographical part of Europe also found variation in response to climate warming (Visser *et al.* 2003). However, differences in response, even between spatially close populations, appeared to be linked to changes in the degree of double brooding within a population. Where populations decreased

the likelihood of double brooding in response to warming, laying dates were retarded, probably because individuals were no longer attempting to 'fit two broods into the season' but were attempting to optimize the laying of a single clutch in response to likely changes in the abundance of food (cf. Crick *et al.* 1993).

## IMPACTS ON DEMOGRAPHIC FACTORS

The impacts of climate change on demographic factors, breeding performance and survival, which affect the population dynamics of species, have been less well explored than phenology. There is often a range of interacting factors that may influence any one demographic parameter, such that the influence of weather or climate may be difficult to elucidate clearly. For example, clutch size may vary with laying date (both calendar and with respect to the start of the nesting season), age and experience, population density, and a range of environmental factors such as latitude, altitude and habitat. However, several studies have shown trends in various aspects of breeding performance that correlate with trends in climate.

Pied Flycatchers *Ficedula hypoleuca* have been studied in both Germany and Finland, showing increases in egg size with warmer springs (Järvinen 1994), and clutch sizes have tended to increase with earlier laying dates and warmer springs (Järvinen 1996, Winkel & Hudde 1997). However, nest success in Finland has not increased because it is related most to June temperatures, which had not shown any trend in that region (Järvinen 1989), whereas it had improved in Germany, at a lower latitude (Winkel & Hudde 1997). Interestingly, Sanz's (2002) meta-analysis of tit studies showed no trend of increasing clutch sizes across the Western Palaearctic, despite trends towards earlier laying. This suggests that distribution of the seasonal trend in clutch sizes for these species has shifted earlier rather than 'extrapolating earlier' from the 'normal' trend to produce larger clutches with an earlier calendar date. Winkler *et al.* (2002) has found a similar pattern for Tree Swallows in North America, which they describe as adopting the 'relative' rather than 'absolute' model of seasonal variation in clutch size.

Several long-term studies of seabirds have demonstrated a climatic influence on breeding performance. Aebischer *et al.* (1990) showed that the laying date, clutch size and brood size of Kittiwakes *Rissa tridactyla* at a colony by the North Sea were related to a measure of 'westerly weather', which is analogous

to the impact of the NAO (see above). They were also able to demonstrate parallel impacts at lower levels in the food chain, through phytoplankton and zooplankton and herring stocks, which suggests the mechanism for such changes. A more recent study of Fulmars *Fulmarus glacialis*, based on data gathered at a colony in Orkney (off the north coast of Scotland) between 1950 and 2000, showed that hatching and fledging success were related to the NAO, due potentially to the climate effects on the abundance of their crustacean and fish food supplies or due to the impact of severe winter weather on parental body condition (Thompson & Ollason 2001). Furthermore, the cohort recruitment rate of Fulmars was related to growing season temperatures in the year of their birth, despite recruitment occurring some 5 years later due to delayed maturity (Thompson & Ollason 2001). The response of marine seabirds to climate change may depend on the response of their main prey to changes in warmth. In a site in Siberia, the planktivorous auklets (Crested *Aethia cristatella* and Parakeet *Cyclorhynchus psittacula*) increase their reproductive success when sea-surface temperatures (SSTs) are lower, because they feed on macro-zooplankton that are favoured under such conditions; by contrast, the piscivorous puffins (Horned *Fratercula corniculata* and Tufted *Lunda cirrhata*) have better reproductive success when SSTs are higher, because this favours the mesoplankton that are eaten by the fish that are eaten by the puffins (Kitaysky & Golubova 2000). In this case, long-term changes in SSTs are likely to affect the viability of the populations of each group of species in different ways and may alter the seabird community in the area.

The only demographic study that also investigated the impact of climate change on survival rates is of a large colony of Emperor Penguins *Aptenodytes forsteri* in Terre Adelie, Antarctica, since the 1960s (Barbraud & Weimerskirch 2001). This colony declined in the mid-1970s due to decreased adult survival during a relatively warm period. High SSTs are associated with poorer Antarctic Krill *Euphausia superba* production and reduced populations of the fish and squid that feed upon them, all prey of the penguins. Although higher SSTs reduce the distance that parent penguins must travel to reach the sea (because of reduced pack ice), the benefit of this, in terms of improved hatching success, was relatively insignificant for maintaining colony size. Thus climate change can affect different aspects of a species' demography in both positive and negative ways at the same time.

## POPULATION CHANGE

The detection of population change in response to climate change is likely to be affected by the masking effects of density-dependent population regulation. Populations will often tend to regulate themselves to a certain level after transient or longer-term changes in a particular component of a species' demography (Newton 1998). Green (1999) also showed how density-dependent processes will tend to mask short-term demographic changes that lead to population change. Thus, long-term census datasets, such as that of Grey Heron *Ardea cinerea* measured annually in the UK since 1928, show significant weather-driven population crashes (after severe winters) due to poor survival, followed by recovery over the following years (Marchant *et al.* 2004). Other census studies show annual fluctuations in relation to fluctuations in weather (e.g. Crick 1999; Forchhammer *et al.* 1998) but these are not likely to show any trend of population increase. They might show changes in the degree of fluctuation as winter temperatures become less variable (and higher).

The study of Emperor Penguins partly illustrates these effects: a transient decline in survival rates led to a decline in population size, which stabilized at a new lower level once survival recovered (Barbraud & Weimerskirch 2001). However, density-dependent processes have not facilitated a return to former population levels, possibly in this case because the environment has become more variable, thereby inhibiting density-dependent recovery.

A similar major decline in a penguin population is reported for Rockhopper Penguins *Eudyptes chrysolome* on Campbell Island (Cunningham & Moors 1994). These have declined by 94% since the early 1940s, associated with rises in SSTs and declines in their fish prey (although it should be noted that overfishing was not considered as a factor in this study). Veit *et al.* (1996, 1997) also report declines in the numbers of Sooty Shearwaters *Puffinus griseus* off the west coast of North America in the non-breeding season. The population declined by 90% since 1987, associated with increased SSTs and declines in their zooplankton prey (Roemmich & McGowan 1995). Although there is some suggestion that this population may have re-distributed itself towards the northwest Pacific (Spear & Ainley 1999), it provides evidence of significant change in the marine ecosystem as a result of apparently minor climate warming (a 0.7 °C increase in SSTs).

## CLIMATE CHANGE AND NATURAL SELECTION

The ready response of many species to recent climate change indicates that most species have the phenotypic plasticity to cope with such change. Przybylo *et al.* (2000) have demonstrated this in the responses of Collared Flycatchers *Ficedula albicollis*, with respect to variation in various aspects of their breeding performance (including laying date and clutch size) and morphological traits (tarsus and wing length).

However, there is growing evidence that some species may find it difficult to adapt to climate change because, for example, of the use of inappropriate environmental cues as phenological triggers, or because different parts of a food chain may respond differentially to climate change (Harrington *et al.* 1999).

Montane habitats in the Colorado mountains provide examples of phenological miscuing: higher spring temperatures have led to the earlier arrival of American Robins *Turdus migratorius* and the earlier emergence of Yellow-bellied Marmots *Marmota flaviventris* from hibernation (Inouye *et al.* 2000). However, despite higher temperatures, the date of snowmelt has not changed because of the greater volumes of snow present due to increases in winter precipitation with the higher temperatures. Thus the interval between arrival or emergence and the first date of bare ground has actually grown and may cause problems for migratory and hibernating species.

In Europe, there is evidence that long-distance migrants may suffer from the effects of phenological miscuing. Berthold (1990) suggested that long-distance migrants might be vulnerable to the impacts of climate change, if the cues they use to time their departure from their wintering grounds do not change sufficiently to allow them to take advantage of the earlier arrival of spring on their breeding grounds. This is the case particularly if they respond to endogenous rhythms or to environmental stimuli unrelated to temperature (Gwinner 1996). Certainly, there is some evidence that long-distance migrants have not responded as rapidly to climate change as short-distance migrants (Jenkins & Watson 2000, Penuelas *et al.* 2002).

Both and Visser (2001) report that Pied Flycatchers in The Netherlands have not advanced their arrival date, probably because of phenological miscuing on their wintering grounds, which has constrained their ability to advance the start of breeding. The latter has the potential to lead to phenological disjunction with the resources that they require for successful breeding. Although Great Tits can shift

their laying dates earlier in response to earlier warm spring weather, often in parallel with the emergence of their caterpillar prey (Perrins 1991), they cannot significantly decrease their incubation period. Their caterpillar prey, however, can halve their development time in sufficiently warm weather and pupate earlier, leading to an early shortage of the prey that Great Tits feed to their young (Buse *et al.* 1999). This phenological disjunction between predator and prey has led to a trend in selection differentials, such that an increasingly greater proportion of recruits in the following year come from early nesting individuals (Visser *et al.* 1998).

## CONCLUSIONS AND FUTURE DIRECTIONS

Ornithology has provided some of the best examples of the impacts of recent climate change on wildlife from around the world, but we have only begun to scratch the surface. The best studied area, primarily because of the existence of long-term datasets, is that of phenological change (Sparks & Crick 1999). The consequences of such change are barely explored, but the potential for phenological miscuing and phenological disjunction to the detriment of the species concerned has already been observed.

One research area where immediate attention is urgently needed is the intrinsic and extrinsic factors that could potentially inhibit adaptation to climatic change. Such factors include:

- 1 Lack of phenotypic/genotypic adaptability: species that are unable to respond to climate change may be most vulnerable to climate change.
- 2 Dispersal ability: species with poor dispersal ability may be unable to move with changes in their climate space, especially when compounded by habitat fragmentation.
- 3 Ecological specialization: rapid changes in the environment are likely to favour generalist/adaptable species and be detrimental to highly specialized species adapted to a fine ecological niche.
- 4 Small population size: will make species more vulnerable to rapid stochastic changes, if the climate becomes more variable, as predicted.
- 5 Increases in the frequency of extreme events: populations can be severely reduced by extreme climatic events, and an increase in their frequency may affect the viability of populations in the long term.
- 6 Loss of habitat or decline in habitat quality: climate change may affect the viability of the habitats that birds use, changing the timing and abundance of

their food supplies and other resources. Large-scale changes in agriculture, including crop types and pesticide usage (in response to changing pest populations), will be a particularly important factor for many bird species that live in human-modified habitats.

7 Changes in the range of other species: where species range expansion or contraction occurs in response to climate change, changes in the level of competition and predation may occur (Davis *et al.* 1998a, 1998b, Harrington *et al.* 1999). The potential for invasive and alien species to have detrimental impacts is another important factor that needs to be considered: some species that are currently benign or inhibited from colonizing certain areas may change their attributes under changed environmental conditions.

Although the complexities of multi-trophic interactions are important areas for research, there is still much work needed in the area of understanding the impact of climate change on the population dynamics of individual species. Stenseth *et al.* (2002) point out that climate variability can affect populations in a density-independent manner, but may also affect the strength of density dependence regulating a population. Population modelling, similar in scope to pioneering work undertaken by Rodenhouse (1992), is urgently needed so that we can go beyond single parameter studies and begin to understand the complexities of the interactions between different components of a species' demography.

## REFERENCES

- Aebischer, N.J., Coulson, J.C. & Colebrook, J.M.** 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* **347**: 753–755.
- Atkinson, P.W., Crooks, S., Drewitt, A., Grant, A., Rehfish, M.M., Sharpe, J. & Tyas, C.** 2004. Managed realignment in the UK – the first five years of colonization by birds. *Ibis* **146** (Suppl.1): S101–S110.
- Barber, R.T. & Chavez, F.P.** 1983. Biological consequences of El Nino. *Science* **222**: 1203–1210.
- Barber, R.T. & Chavez, F.P.** 1986. Ocean variability in relation to living resources during the 1982–83 El Nino. *Nature* **319**: 279–285.
- Barbraud, C. & Weimerskirch, H.** 2001. Emperor penguins and climate change. *Nature* **411**: 183–186.
- Barrett, R.T.** 2002. The phenology of spring migration to north Norway. *Bird Study* **49**: 270–277.
- Berry, P.M., Vanhinsberg, D., Viles, H.A., Harrison, P.A., Pearson, R.G., Fuller, R.J., Butt, N. & Miller, F.** 2001. Impacts on terrestrial environments. In Harrison, P.A., Berry, P.M. & Dawson, T.P. (eds) *Climate Change and Nature Conservation in Britain and Ireland: Modelling Natural Resource Responses to Climate Change (the MONARCH Project)*: 43–150. Oxford: UKCIP Technical report.
- Berthold, P.** 1990. Patterns of avian migration in light of current global 'greenhouse' effects: a central European perspective. *Acta Congr. Int. Ornithol.* **20**: 780–786.
- Both, C. & Visser, M.E.** 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**: 296–298.
- Bradley, N.L., Leopold, A.C., Ross, J. & Huffaker, W.** 1999. Phenological changes reflect climate changes in Wisconsin. *Proc. Natl Acad. Sci. USA* **96**: 9701–9704.
- Brown, J.L., Li, S.H. & Bhagabati, N.** 1999. Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proc. Natl Acad. Sci. USA* **96**: 5565–5569.
- Buse, A., Dury, S.J., Woodburn, R.J.W., Perrins, C.M. & Good, J.E.G.** 1999. Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Func. Ecol.* **13** (Suppl. 1): 74–82.
- Crick, H.Q.P.** 1999. Small bird population changes. In Cannell, M.G.R., Palutikof, J.P. & Sparks, T.H. (eds) *Indicators of Climate Change in the UK*: 66–67. London: DETR & NERC.
- Crick, H.Q.P., Baillie, S.R. & Leech, D.I.** 2003. The UK Nest Record Scheme: its value for science and conservation. *Bird Study* **50**: 254–270.
- Crick, H.Q.P., Dudley, C., Glue, D.E. & Thomson, D.L.** 1997. UK birds are laying eggs earlier. *Nature* **388**: 526.
- Crick, H.Q.P., Gibbons, D.W. & Magrath, R.D.** 1993. Seasonal variation in clutch size in British Birds. *J. Anim. Ecol.* **62**: 263–273.
- Crick, H.Q.P. & Sparks, T.H.** 1999. Climate change related to egg-laying trends. *Nature* **399**: 423–424.
- Cunningham, D.M. & Moors, P.J.** 1994. The decline of Rockhopper Penguins *Eudyptes chrysocome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. *Emu* **94**: 27–36.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S.** 1998b. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**: 783–786.
- Davis, A.J., Lawton, J.H., Shorrocks, B. & Jenkinson, L.S.** 1998a. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *J. Anim. Ecol.* **67**: 600–612.
- Dunn, P.O. & Winkler, D.W.** 1999. Climate change has affected the breeding date of Tree Swallows throughout North America. *Proc. R. Soc. Lond. B* **266**: 2487–2490.
- Forchhammer, M.C., Post, E. & Stenseth, N.C.** 1998. Breeding phenology and climate. *Nature* **391**: 29–30.
- Gates, S., Gibbons, D.W., Lack, P.C. & Fuller, R.J.** 1994. Declining farmland bird species: modelling geographical patterns of abundance in Britain. In Edwards, P.J., May, R.M. & Webb, N.R. (eds) *Large Scale Ecology and Conservation Biology*: 153–177. Oxford: Blackwell.
- Gibbons, D.W., Reid, J.B. & Chapman, R.A.** 1993. *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*. London: Poyser.
- Gibbons, D.W. & Wotton, S.** 1996. The Dartford Warbler in the United Kingdom in 1994. *Br. Birds* **89**: 203–212.
- Gilyazov, A. & Sparks, T.H.** 2002. Change in the timing of migration of common birds at the Lapland nature reserve (Kola Peninsula, Russia) during 1931–1999. *Avian Ecol. Behav.* **8**: 35–47.
- Green, R.E.** 1999. Applications of large-scale studies of demographic rates to bird conservation. *Bird Study* **46**: S279–S288.

- Gwinner, E.** 1996. Circannual clocks in avian reproduction and migration. *Ibis* **138**: 47–63.
- Harrington, R., Woiwod, I.P. & Sparks, T.H.** 1999. Climate change and trophic interactions. *Trends Ecol. Evol.* **14**: 146–150.
- Hüppop, O. & Hüppop, K.** 2003. North Atlantic Oscillation and timing of spring migration in birds. *Proc. R. Soc. Lond. B.* **270**: 233–240.
- Inouye, D.W., Barr, B., Armitage, K.B. & Inouye, B.D.** 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proc. Natl Acad. Sci. USA* **97**: 1630–1633.
- Järvinen, A.** 1989. Patterns and causes of long-term variation in reproductive traits of the Pied Flycatcher *Ficedula hypoleuca* in Finnish Lapland. *Ornis Fenn.* **66**: 24–31.
- Järvinen, A.** 1994. Global warming and egg size of birds. *Ecography* **17**: 108–110.
- Järvinen, A.** 1996. Correlation between egg size and clutch size in the Pied Flycatcher *Ficedula hypoleuca* in cold and warm summers. *Ibis* **138**: 620–623.
- Jenkins, D. & Watson, A.** 2000. Dates of first arrival and song of birds during 1974–99 in mid-Deeside, Scotland. *Bird Study* **47**: 249–251.
- Kinzelbach, R., Nicolai, B. & Schlenker, R.** 1997. Der Bienenfresser *Merops apiaster* als Klimazeiger: Zum Einflug in Bayern, der Schweiz und Baden im Jahr 1644. *J. Ornithol.* **138**: 297–308.
- Kitaysky, A.S. & Golubova, E.G.** 2000. Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. *J. Anim. Ecol.* **69**: 248–262.
- Lack, D.** 1954. *The Natural Regulation of Animal Numbers*. Oxford: Oxford University Press.
- Lack, D.** 1966. *Population Studies of Birds*. Oxford: Oxford University Press.
- Loxton, R.G. & Sparks, T.H.** 1999. Arrival of spring migrants at Portland, Skokholm, Bardsey and Calf of Man. *Bardsey Observatory Report* **42**: 105–143.
- Marchant, J.H., Freeman, S.N., Crick, H.Q.P. & Beaven, L.P.** 2004. The BTO Heronries Census of England and Wales 1928–1998: new indices and a comparison of analytical methods. *Ibis* **146**: 323–334.
- Mason, C.F.** 1995. Long-term trends in the arrival dates of spring migrants. *Bird Study* **42**: 182–189.
- McCleery, R.H. & Perrins, C.M.** 1998. Temperature and egg-laying trends. *Nature* **391**: 30–31.
- Newton, I.** 1998. *Population Limitation in Birds*. London: Academic Press.
- Parmesan, C. & Yohe, G.** 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
- Penuelas, J., Filella, I. & Comas, P.** 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biol.* **8**: 531–544.
- Perrins, C.M.** 1991. Tits and their caterpillar food supply. *Ibis* **133**: S49–S54.
- Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sanchez-Cordero, V., Soberon, J., Buddemeier, R.H. & Stockwell, D.R.B.** 2002. Future projections for Mexican faunas under global climate change scenarios. *Nature* **416**: 626–629.
- Pounds, J.A., Fogden, M.P.L. & Campbell, J.H.** 1999. Biological response to climate change on a tropical mountain. *Nature* **398**: 611–615.
- Przybylo, R., Sheldon, B.C. & Merila, J.** 2000. Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *J. Anim. Ecol.* **69**: 395–403.
- Rodenhouse, N.L.** 1992. Potential effects of climatic change on a Neotropical migrant landbird. *Conserv. Biol.* **6**: 263–272.
- Roemmich, D. & McGowan, J.A.** 1995. Climatic warming and the decline of zooplankton in the California Current. *Science* **267**: 1324–1326.
- Root, T.L.** 1988a. Environmental factors associated with avian distributional boundaries. *J. Biogeogr.* **15**: 489–505.
- Root, T.L.** 1988b. Energy constraints on avian distributions and abundances. *Ecology* **69**: 330–339.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, A.J.** 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.
- Root, T.L. & Schneider, S.H.** 1993. Can large-scale climatic models be linked with multiscale ecological studies? *Conserv. Biol.* **7**: 256–270.
- Sanz, J.J.** 2002. Climate change and breeding parameters of great and blue tits throughout the western Palearctic. *Global Change Biol.* **8**: 409–422.
- Schreiber, R.W. & Schreiber, E.A.** 1984. Central pacific seabirds and the El Niño–Southern Oscillation: 1982–1983 perspectives. *Science* **225**: 713–716.
- Sharrock, J.T.R.** 1976. *The Atlas of Breeding Birds in Britain and Ireland*. Calton: Poyser.
- Slater, F.M.** 1999. First-egg date fluctuations for the Pied Flycatcher *Ficedula hypoleuca* in the woodlands of mid-Wales in the twentieth century. *Ibis* **141**: 497–499.
- Sokolov, L.V., Markovets, M.Yu, Shapoval, A.P. & Morozov, YuG.** 1998. Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. *Avian Ecol. Behav.* **1**: 1–21.
- Sparks, T.H.** 1999. Phenology and the changing pattern of bird migration in Britain. *Int. J. Biometeorol.* **42**: 134–138.
- Sparks, T.H. & Braslavská, O.** 2001. The effects of temperature, altitude and latitude on the arrival and departure dates of the swallow *Hirundo rustica* in the Slovak Republic. *Int. J. Biometeorol.* **45**: 212–216.
- Sparks, T.H. & Crick, H.Q.P.** 1999. The times they are a-changing? *Bird Conserv. Int.* **9**: 1–7.
- Sparks, T.H., Crick, H.Q.P., Elkins, N., Moss, R., Moss, S. & Mylne, K.** 2002. Birds, weather and climate. *Weather* **57**: 399–410.
- Sparks, T.H. & Mason, C.F.** 2001. Dates of arrivals and departures of spring migrants taken from the *Essex Bird Reports* 1950–1998. *Essex Bird Report* **1999**: 154–164.
- Sparks, T.H. & Mason, C.F.** 2004. Can we detect change in the phenology of winter migrant birds in the UK. *Ibis* **146** (Suppl.1): 58–61.
- Sparks, T.H., Roberts, D.R. & Crick, H.Q.P.** 2001. What is the value of first arrival dates of spring migrants in phenology? *Avian Ecol. Behav.* **7**: 75–85.
- Spear, L.B. & Ainley, D.G.** 1999. Migration routes of Sooty Shearwaters in the Pacific Ocean. *Condor* **101**: 205–218.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S. & Lima, M.** 2002. Ecological effects of climate fluctuations. *Science* **297**: 1292–1296.
- Stevenson, I.R. & Bryant, D.M.** 2000. Climate change and constraints on breeding. *Nature* **406**: 366–367.
- Sueur, F. & Triplet, P.** 2001. Rechauffement climatique: les



- passereaux arrivent-ils plus tôt au printemps? *Avifaune Picarde* 1: 111–120.
- Thomas, C.D. & Lennon, J.L.** 1999. Birds extend their ranges northwards. *Nature* 399: 213.
- Thompson, P.M. & Ollason, J.C.** 2001. Lagged effects of ocean climate change on fulmar population dynamics. *Nature* 413: 417–420.
- Veit, R.R., McGowan, J.A., Ainley, D.G., Wahl, T.R. & Pyle, P.** 1997. Apex marine predator declines 90% in association with changing oceanic climate. *Global Change Biol.* 3: 23–28.
- Veit, R.R., Pyle, P. & McGowan, J.A.** 1996. Ocean warming and long-term change in pelagic bird abundance within the California Current System. *Mar. Ecol. Prog. Series* 139: 11–18.
- Visser, M.E., Adriaensen, F., van Balen, J.H., Blondel, J., Dhondt, A.A., van Dongen, S., du Feu, C., Ivankina, E.V., Kerimov, A.B., de Laet, J., Matthysen, E., McCleery, R., Orell, M. & Thomson, D.L.** 2003. Variable responses to large-scale climate change in European *Parus* populations. *Proc. R. Soc. Lond. B* 270: 367–372.
- Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M. & Lessells, C.M.** 1998. Warmer springs lead to mistimed reproduction in Great Tits (*Parus major*). *Proc. R. Soc. Lond. B* 265: 1867–1870.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fremont, J.-M., Hoegh-Guldberg, O. & Bairlein, F.** 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.
- Watkinson, A.R., Gill, J.A. & Hulme, M.** 2004. Flying in the face of climate change: a review of climate change, past, present and future. In Rehfish, M.M., Feare, C.J., Jones, N.V. & Spray, C. (eds) *Climate Change and Coastal Birds. Ibis* 146 (Suppl.1): S4–S10.
- Watt, A.D., Carey, P.D. & Versham, B.C.** 1998. Implications of climate change for biodiversity. In Fleming, L.V., Newton, A.C., Vickery, J.A. & Usher, M.B. (eds) *Biodiversity in Scotland: Status, Trends and Initiatives*: 147–159. Edinburgh: Stationary Office.
- Winkel, W. & Hudde, H.** 1997. Long-term trends in reproductive traits of tits (*Parus major*, *P. caeruleus*) and Pied Flycatchers *Ficedula hypoleuca*. *J. Avian Biol.* 28: 187–190.
- Winkler, D.W., Dunn, P.O. & McCulloch, C.E.** 2002. Predicting the effects of climate change on avian life-history traits. *Proc. Natl Acad. Sci. USA* 99: 13595–13599.
- Wotton, S.R., Carter, I., Cross, A.V., Etheridge, B., Snell, N., Duffy, K., Thorpe, R. & Gregory, R.D.** 2002. Red kites *Milvus milvus* in Britain in 2000. *Bird Study* 49: 278–286.

Received 19 February 2003; revision accepted 12 December 2003.