

*Review*

# The impacts of climate change on the annual cycles of birds

Cynthia Carey\*

*Department of Integrative Physiology, University of Colorado, Boulder, CO 80309-0354, USA*

Organisms living today are descended from ancestors that experienced considerable climate change in the past. However, they are currently presented with many new, man-made challenges, including rapid climate change. Migration and reproduction of many avian species are controlled by endogenous mechanisms that have been under intense selection over time to ensure that arrival to and departure from breeding grounds is synchronized with moderate temperatures, peak food availability and availability of nesting sites. The timing of egg laying is determined, usually by both endogenous clocks and local factors, so that food availability is near optimal for raising young. Climate change is causing mismatches in food supplies, snow cover and other factors that could severely impact successful migration and reproduction of avian populations unless they are able to adjust to new conditions. Resident (non-migratory) birds also face challenges if precipitation and/or temperature patterns vary in ways that result in mismatches of food and breeding. Predictions that many existing climates will disappear and novel climates will appear in the future suggest that communities will be dramatically restructured by extinctions and changes in range distributions. Species that persist into future climates may be able to do so in part owing to the genetic heritage passed down from ancestors who survived climate changes in the past.

**Keywords:** bird; climate change; avian reproduction; bird migration; phenology; egg laying

## 1. INTRODUCTION

Living organisms are confronted with many man-made challenges, including climate change, habitat destruction, introduction of novel chemicals and exotic species into the environment, emergence of novel pathogens from or transport of pathogens into areas into which they have not formerly occurred and synergistic effects of these and other factors. The number of relatively undisturbed ecosystems in the world is decreasing rapidly. By the year 2050, 15–37% of existing animal and plant species on Earth are predicted to become extinct (Thomas *et al.* 2004) and half of all species on Earth may experience extinction by 2100 (Myers & Knoll 2001). It is important to predict how current man-made challenges will affect key species in ecosystems, so that, if possible, steps can be taken to ameliorate these threats.

This paper will focus on the challenges that current changes in global climate are posing for annual cycles of birds, with emphasis on the timing of migration and reproduction and mismatches of food availability with energetically demanding phases of this cycle.

## 2. CLIMATE CHANGE THROUGH GEOLOGICAL HISTORY

While considerable attention is currently directed at the degree of global warming and climate change in

the past century, climate change is not a new, unique feature of the global climate. The combined results of instrument recordings and paleoclimatic proxy data (climatic data derived from growth of tree rings, and stalagmites, cores through glaciers and coral reefs, sediment samples from oceans and lakes, etc.) indicate that some degree of climate change has apparently been the rule rather than the exception throughout the evolution of life (Jones *et al.* 2001). Periods of relative climatic stability have alternated with dramatic, and sometimes quite abrupt, change (Alley *et al.* 1997; Lang *et al.* 1999; Severinghaus & Brooke 1999; Taylor 1999; Birks & Ammann 2000).

Analysis of deep-sea sediment cores indicates that the global climate has undergone almost continuous change over the last 65 million years, from periods of warmth with ice-free poles to intervals of intense cold with the extension of continental glaciers (Zachos *et al.* 2001). Estimates of surface temperatures in the Northern Hemisphere over the last millennium indicate that the eleventh and twelfth centuries were relatively warm, and, in fact, averaged approximately 0.1° below the average for the last 30 years of the twentieth century. This period was followed by a cooling trend culminating in a long period of relatively cold temperatures in the seventeenth century, termed ‘The Little Ice Age’ (Jones *et al.* 2001). Significant cooling also occurred in the early part of the nineteenth century. The twentieth century was the warmest in the last millennium, with an average of 0.2° above the mean temperature of the last 500 years. The most rapid warming in the last millennium occurred in the last

\*careyc@colorado.edu

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30 years of the twentieth century (Jones *et al.* 2001). Although relatively few proxy and instrumental records are available for the Southern Hemisphere, temperatures in this region appear to have increased significantly over the last century, in comparison to those between 1600 and 1900 (Jones *et al.* 2001).

Precipitation patterns, as judged by tree ring chronologies and lake sediments, have also varied considerably over time (Woodhouse & Overpeck 1998). Intense, short and relatively geographically restricted droughts, such as those in the 1930s and 1950s in the USA, have occurred roughly one to two times per century over the last millennium. Extremely severe and geographically widespread droughts, such as a 22 year drought in the late 1500s and a 26 year drought in the late 1200s in the American southwest, have recurred once or twice every 500 years (deMenocal *et al.* 2000).

Except for those living in protected refugia during paleoclimatic climate shifts, organisms have had to respond to such variations in temperatures and moisture as environmental conditions approached lethal levels or otherwise negatively impacted their biology. Shifts in geographical distributions of various taxonomic groups in response to climate change are common in the paleontological record (Clarke 1996). For instance, several multi-proxy studies have measured  $^{14}\text{C}$  in terrestrial plant macrofossils and used  $\delta^{18}\text{O}$  stratigraphy from glacial sediments to estimate the responses of plants, diatoms and insects to climate change during the glacial–Holocene transition (14 000–9000 years before present) (Birks & Ammann 2000). As glaciers melted and temperatures rose above critical thresholds for individual species, various species altered their distributions within about a 50 year time span, each group at its own speed but with surprisingly little lag (10–60 years) after the transition between glacial and fully interglacial conditions (Coope 1995). During such rapid climate changes, the cumulative responses of individual species can be telescoped together, with the result that major alterations in the species composition of ecosystems can occur quickly (Birks & Ammann 2000). Many species associations and biomes existing during the last deglaciation have no modern counterpart (Williams *et al.* 2007).

It is estimated that approximately 99 per cent of the species that have lived on this planet are now extinct (Raup 1991). Although extinctions have occurred throughout the evolution of life, at least five episodes have been noted in which a greater number of taxonomic groups than average seem to have gone extinct (Hubbard & Gilinski 1992). Several of these events are thought to coincide with major climate changes (Donovan 1989). For example, the fossil record documents extinction of numerous tropical molluscan species during the cooling accompanying the onset of northern glaciation during the Pliocene three million years ago. However, some groups survived even the mass extinctions of many plant and animal species during major climatological transitions, such as the Cretaceous–Tertiary boundary (approx. 65 Ma) and are some of the ancestors of currently existing flora and fauna (Erwin 2001).

### 3. CURRENT GLOBAL CLIMATE CHANGE

In the twentieth century, the Earth experienced moderate warming: surface temperatures rose an average of  $0.5^{\circ}\text{C}$ , with concurrent changes in precipitation patterns and an increase in the frequency and severity of extreme weather events (Schneider & Root 1996; Easterling *et al.* 2000). The increase in global temperatures is far from uniform: daily minimum temperatures have risen about twice as fast as daily maxima (Easterling *et al.* 2000). Although this moderate warming is cause for concern, the current cause for alarm among biologists is the warming expected by AD 2100. Global mean temperatures are expected to increase by  $1.4$ – $5.8^{\circ}\text{C}$  (Houghton *et al.* 2001). At least one scenario predicts that temperatures in some areas of the Earth may increase by up to  $10^{\circ}\text{C}$  (Intergovernmental Panel on Climate Change 2002).

These temperature alterations and associated changes in diurnal and seasonal temperature fluctuations and precipitation patterns are likely to cause major shifts in world climates. Some existing climates are likely to disappear and novel (unknown in either the paleontological record or at present) climates are likely to appear (Williams *et al.* 2007). Using two (high and low) emission scenarios provided by the fourth assessment report of the Intergovernmental Panel on Climate Change, Williams *et al.* (2007) predict that between 4 and 39 per cent of the Earth's land masses may experience novel climates by AD 2100, while existing climates on 4–48% of Earth's land surface are predicted to disappear. If sea level rises as predicted, many coastal areas will be inundated.

### 4. BIOLOGICAL EFFECTS OF CURRENT GLOBAL CLIMATIC CHANGES

The information in previous sections suggests that many organisms living today are probably descended from ancestors that survived considerable, and sometimes rapid, climate change. Therefore, they should have inherited from their ancestors some degree of effective physiological and behavioural mechanisms for coping with certain ranges of climate variation. Over the last 15 years, a large number of studies showing a correlation between global climate change and changes in biological phenomena have been published (Harrington *et al.* 1999; Shaver *et al.* 2000; McLaughlin *et al.* 2002; Stenseth *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003 and many others). McCarty (2001) noted that most such studies are based on anecdotal observations or correlations, rather than on definitive proof of causality. Indeed, it is difficult to determine a causal relationship between an event like a local temperature change and, for instance, a species extinction, because multiple environmental variables are likely to interact. Additionally, long-term records of geographical ranges, life-history phenology, etc. of most organisms do not exist with which to identify any biological impacts that may be correlated historical climate shifts. Because of the difficulty in establishing cause and effect, it is likely that some published studies claiming an association between global climate change and biological phenomena may ultimately prove invalid.

Although McCarty (2001) suggests that multiple anecdotes and correlations compiled together contribute importantly to the weight of evidence concerning the existence of a causal relation between environmental change and a biological event, it is important that researchers make a concerted attempt to go beyond correlation to establish a linkage. As an example, Root *et al.* (2005) used a statistical approach to evaluate causality with a two-step process. First, they found a significant effect of anthropogenic activities on global temperatures. Then, those same temperature data were shown to have significantly detrimental effects on a number of plant and animal species. Other suggestions for evaluating possible causal relations between environmental changes and biological phenomena are provided by Carey *et al.* (2003).

Major shifts in climates seem certain to cause a considerable number of species extinctions, although a causal link between recent global warming and species extinctions has been difficult to prove. The relationship between climate change and species extinction is not simple and undoubtedly reflects more than a physiological lack of tolerance of temperature and moisture variation. Other factors, such as population dynamics, predator/prey relationships, availability of food supplies, dispersal capabilities and genetic composition, must be undoubtedly involved (Clarke 1996). It is estimated that human activities have so altered the world's environments that extinction rates of species are now about 1000-fold the rate in the fossil record (Millennium Ecosystem Assessment 2005). For example, recent extinctions of two populations of a butterfly species (*Euphydryas editha bayensis*) have been attributed to variability in precipitation and habitat loss (McLaughlin *et al.* 2002). However, not all species are equally as important in ecosystems as others, and ecosystems may be able to function adequately until one or more keystone species become extinct (Schindler 2007). For example, a recent analysis of several extinction scenarios within tropical fish communities suggests that an extinction of one key species in a freshwater community could be compensated for by a second species, but that loss of both species would severely disrupt nutrient cycling and have profound detrimental effects on the ecosystem (McIntyre *et al.* 2007).

Changes in geographical distribution have occurred frequently for reasons other than climate change, such as emergence of new habitats or release of captive animals into new environments (Aldrich & Weske 1978). The degree of climate change occurring to date has already been implicated in significant range changes in some birds (Böhning-Gaese & Lemoine 2004). Future changes in climates seem certain to alter distributions of many species. Changes in distribution are potentially problematic for many species. Individual species migrate, not entire communities, and therefore shifts in distributions and variation in the rate of migration among species are likely to lead to changes in interactions among species that might prove equally or even more disruptive for the survival of a species than variations in temperature or precipitation (Clarke 1996). Attempts by species to alter their distribution in response to current climate changes may

prove more difficult now than in the past because man-made habitat fragmentation might impede migration and/or gene flow (Keller *et al.* 1994; Davis & Shaw 2001). In the future, as species extinctions and changes in various species' distributions occur, disruptions among species associations, such as those between predators and prey, pollinators and their floral hosts, etc. are likely to occur.

## 5. PHENOLOGY OF BREEDING IN BIRDS

Because the annual cycle of birds varies considerably from species to species, it is impossible to generalize about all species. Therefore, a few specific examples will be presented, with the understanding that any potential effects of climate change on birds' annual cycles will be species-specific.

Several breeding patterns are observed in birds living in tropical areas or on tropical oceanic islands. In areas in which daily temperatures and precipitation vary relatively little throughout the year, many species of birds exhibit continuous breeding. However, observations on such species indicate that few, if any, individuals of such species breed continuously. Instead, each individual may become sexually inactive for several months, while others in the population, on their own schedule, are breeding (Immelmann 1971). Other species living in tropical areas coordinate their breeding with seasonal patterns of rainfall and dry periods. For instance, reproduction of a community of 22 species of hummingbirds in lowland Costa Rica occurred in the dry season, coinciding with a peak in flowering of many plant species (Stiles 1980).

A typical annual life cycle of many species breeding in north temperate and arctic areas includes a post-nuptial molt after breeding, preparation for migration (fat deposition), migration to wintering grounds, pre-nuptial molt and pre-migratory fattening, partial development of the gonads, migration, followed by breeding activities (completion of recrudescence of the gonads, courtship, nest building, egg laying, raising and fledging young) (Berthold 2001). The annual cycle of non-migratory species usually includes post-nuptial molt, possibly some degree of winter fattening, pre-nuptial molt, gonadal recrudescence and breeding activities.

Most birds that breed in temperate zones have definite breeding seasons correlated with warm temperatures and increased food supplies in late spring and early summer. At high latitudes and in temperate mountains, optimal times for breeding are restricted to the few snow-free months, which results in synchrony of breeding for almost all species. Because the number of snow-free days decreases with latitude, compression of some aspects of breeding activities occurs at higher latitudes. White-crowned sparrows (*Zonotrichia leucophrys*) breed over a wide latitudinal gradient from at least 40° N to above 65° N (Morton 1976, 2002). The pre-nesting interval is shortened considerably at high latitudes. Nest building takes 8 days in southerly populations and 3 days in the far north. The pre-laying interval (the time between nest building and laying the first egg) is 3.6 days at 48.5° N and 1.2 days at 62° N. The nestling period

is compressed from an average of 10.1 days at 3° N to 9.6 days at 48.5° N, and 9 days at 62° N (Morton 1976).

Some birds breeding in temperate zones, however, do not lay eggs in the spring or early summer. For instance, American goldfinches (*Carduelis tristis*), a small cardueline finch that ranges throughout most of the USA and southern Canada, breed in late summer when the thistle seeds ripen (Stokes 1950).

Some birds live in environments in which food supplies adequate to foster breeding vary unpredictably. Zebra finches (*Taeniopygia guttata*) breed over approximately 45 per cent of the Australian continent, including in some very arid and semiarid deserts in which rainfall is highly unpredictable. These finches feed almost exclusively on grass seeds throughout the year, but breed only following rainfall of sufficient quantity to cause seed set (Zaan 1996). Zebra finches can lay eggs within two weeks following rain because the gonads do not regress fully following the previous breeding episode. Instead, they remain in a semideveloped state from which rapid follicular growth can occur more quickly than if the ovaries were fully regressed (Vleck & Friedkalns 1985).

Egg laying in red crossbills, *Loxia curvirostra*, has been documented in every month of the year throughout their range in North America. This species has a very long period of reproductive competence compared with most species breeding in temperate North America. This ability allows crossbills to adjust to both seasonally predictable and unpredictable food supplies (Hahn 1995).

## 6. ENERGETICS OF THE ANNUAL CYCLE OF BIRDS

The annual cycles of birds appear to be programmed so that breeding takes place at the most propitious time of the year, which is, in most cases, the time of both moderate air temperatures and optimal food supplies (Lack 1950). The other phases of the annual cycle are arranged around the breeding schedule so that the birds are physiologically and behaviourally ready to breed at the right place and at the right time (Berthold 2001).

Lack (1950) proposed that seasonal variations in food supply would select for genotypes that would produce nestlings near the time of peak food availability. Further study on many species has not only confirmed this trend, but also revealed additional information that some species produce young at the peak of food supply, whereas others do so on the upward slope or downward slope of food availability (Perrins 1970; Daan *et al.* 1988; Baines *et al.* 1996; Verboven & Visser 1998; Visser & Verboven 1999). Availability of micronutrients, in addition to calories and macronutrients, can also play a role in shaping the relationship between breeding and food availability (Carey 1996).

Energetic costs of each phase of the life cycle of birds are sufficiently higher than daily energetic expenditures that they must be timed so that the overlap among energetic and nutritional demands of migration, reproduction, molt and pre-migratory fattening is minimal. Although molting and breeding of some species that breed in tropical rainforests may overlap

(Foster 1974), the ability to partition energetically demanding activities is essential for most species breeding in mid- to high latitudes, especially migrants. The amount of energy expended in each phase of the annual cycle varies between the sexes and among species (Walsberg 1983; Williams & Vézina 2001). The cost of producing a single egg, calculated using the average caloric content of an egg of a given species, has been estimated to range between 13 and 41 per cent of daily basal metabolic rate (BMR) for passerines to over 200 per cent of BMR in waterfowl (Carey 1996). Costs of foraging vary significantly throughout the year, as food and nutrient supplies necessary to support molt, migration, egg synthesis, feeding of nestlings and possibly winter fattening require extra foraging above levels in other phases of the annual cycle (Walsberg 1983).

For many species, the period in which young are being fed is the most expensive period of the annual cycle. However, some migratory species, in particular, expend far more calories during migration than during any other time of the annual cycle. For instance, Arctic terns (*Sterna paradisaea*) migrate over 20 000 km between their breeding grounds in Greenland and their wintering areas in Antarctica. Feeding young and molting in this species cost around 9000 and 3000 kJ, respectively, whereas their round-trip migratory costs total at least 20 000 kJ (Biebach 1996). Not only must sufficient food be available for pre-migratory fattening on breeding or wintering grounds prior to departure of any migratory species, but also at stop-over points during their journey. The availability of adequate food at stop-over points could be threatened by future range expansions, alterations in the phenology of migration and/or habitat destruction.

Both timing of arrival and the nutrient reserves of the adults upon arrival are important determinants of reproductive success and ultimate fitness (Both & Visser 2001). Not all fat and other nutrient supplies are necessarily exhausted during migration. Ducks and geese arriving on breeding grounds in the Arctic use unused fat and other reserves left over from migration for fostering survival upon arrival on the breeding grounds, where food supplies may be lacking for periods of time (Biebach 1996).

## 7. TIMING OF THE ANNUAL CYCLE

Because mistakes in timing of breeding would have severe consequences for reproductive success and fitness, selection has favoured the use of the most reliable cues to indicate what time of year it is and when, in advance of an event, to start physiological preparations (such as molt and fattening). Initial predictive cues (such as photoperiod) provide a rough timing mechanism with which other factors on the breeding grounds (i.e. food supply, temperature, availability of nest sites, snow cover, etc.) can accelerate or delay actual breeding. The long-term predictability of the environment in which a species breeds determines the degree to which secondary cues are used and the strength of their influence (Wingfield 1983). The annual cycles of birds living all or part of the

year in middle to high latitudes are principally timed by the annual change in daylength, coupled with an endogenous rhythm of photosensitivity in some species (Hamner 1963). Even though daily changes in photoperiod do not appear to be the major environmental factor (*Zeitgeber*) timing the annual cycle of some tropical species, gonads of at least a few species respond to photoperiodic cues in laboratory experiments (Epple *et al.* 1972). Red Crossbills are sensitive to photoperiod and may use it to time their annual cycle, but plentiful food supplies can stimulate actual breeding at any time of the year (Hahn 1995). The annual cycles of many avian species that live in tropical regions in which photoperiod varies little throughout the year are timed by circannual rhythms (Gwinner 1977). Predictable rainfall patterns in some tropical regions serve as a timing mechanism for the coordination of annual cycles of some species with optimal food supplies (Immelmann 1971).

Sensitivity to a particular *Zeitgeber* varies significantly among species. Species that begin migration early in the spring use a shorter daylength on their wintering grounds as the cue to begin molt and fattening compared with the longer daylengths used by species that begin migration later (Gwinner 1977; Berthold 2001). Coordination of annual cycles with a very predictable *Zeitgeber* can also vary within species distributed over broad geographical ranges and even within populations. For instance, variation of several weeks in the first date of egg laying has been noted between upland and marsh populations of song sparrows (*Melospiza melodia*) (Immelmann 1971).

Seasonal phenology of the annual cycle and its variation associated with latitude has been intensively studied in four subspecies of white-crowned sparrows (*Z. leucophrys*) in the western USA. One subspecies (*Zonotrichia leucophrys nuttalli*) is sedentary, one (*Zonotrichia leucophrys pugenensis*) is either migratory or sedentary and two subspecies (*Zonotrichia leucophrys gambelli* and *Zonotrichia leucophrys oriantha*) are migratory (Morton 1976, 2002). When the first date of egg laying among the four species is examined as a function of the latitude of breeding grounds, egg laying begins in mid-March at 37.8° N, the last week in April at 40.8° N and the last week in May at 67–69° N (Morton 1976). Gonadal recrudescence is strongly controlled by photoperiod in this species (Wingfield 1983). Sensitivity to changing daylength as a *Zeitgeber* has not been studied in all of the subspecies. However, the differences in breeding schedules as a function of latitude suggest strongly that different daylengths on the wintering grounds, coupled with variations in circadian rhythms of photosensitivity, are used by each population as the cue with which to begin migratory and breeding preparations.

## 8. IMPACTS OF CURRENT AND FUTURE CLIMATE CHANGES ON ANNUAL CYCLE OF BIRDS

Climate changes are expected to affect not only reproduction but also the entire annual cycle of birds (Coppack & Both 2002; Møller *et al.* 2004). Life-history traits may be genetically linked in a way that selection for one trait will also affect one or more

other aspects of the annual cycle (Both & Visser 2005). Perhaps the bird species that principally coordinate their annual cycle and breeding with temperature, rainfall and/or food supply will be less challenged in coming years than those species that coordinate their annual cycle by a rigid *Zeitgeber*, like photoperiod. Because photoperiod will not be affected by climate change, but food supplies and other factors are likely to be altered, these species will have significant challenges adjusting their cycle so that sufficient food supplies are available for breeding and other energy-requiring activities.

### (a) Migration

The timing of arrival on the summering grounds for most species breeding at mid- to high latitudes has been selected over time so that the birds miss most, if not all, adverse spring weather and arrive when food supplies are beginning to increase. Climate change can affect the cues given by local weather on the wintering grounds that affect departure, the food supply and weather en route at stop-over points and/or the weather on the summering ground. It is likely that the greater the distance over which a species has to migrate, the more likely one or more aspects of the annual cycle may become mistimed with local weather and food supplies on the summering ground.

The date of first observation of a particular species arriving at a breeding location has been measured by many investigators over the years, although the accuracy of such observations may be dependent on population size and sampling frequency (Miller-Rushing *et al.* 2008). However, the variability in arrival date within the population is as important to measure as the date of first arrival, when judging whether a population is arriving earlier, at the normal time or later than normal. Additionally, more information than most studies provide is needed on the length of the arrival period, such as is available for mountain white-crowned sparrows (Morton 2002). For example, an advance of 6 days in the first arrival or the average arrival date of a population would be highly meaningful if the length of arrival period for the entire population was 12 days. If, instead, the length of the arrival time was 30 days, a 6 day advance would not be as meaningful. Much more information than is currently available is also needed for an examination of the consequences for reproductive success and population viability of early arrivals on or late departures from the summering ground.

Changes in migratory behaviour of some species have recently been observed, but not all are necessarily caused by climate change. Human activities, like feeding birds in winter, have altered the need for migration in blackcaps (*Sylvia atricapilla*). Before about 1940, cold winters and lack of food supplies in England necessitated migration to the Mediterranean region for the winter. Currently, supplemental feeding, possibly coupled with slightly warmer winters, fosters successful wintering in England (Berthold *et al.* 1992).

In general, an analysis of spring migration to northern Europe shows that many species have advanced their date of arrival (Leihonen *et al.* 2004).

Additionally, delayed departures from breeding grounds in the fall and early returns from wintering grounds in the spring of at least 30 species in Central Europe have recently been linked to climate change (Berthold 2001). Formerly sedentary populations have become partially migratory, or fully migratory species or populations have become partially migratory or sedentary. Berthold (2001) suggests that these rapid changes in behaviour stem from population-specific traits that are quickly passed on to future generations in response to environmental change.

The average arrival dates of 17 of 20 migrant species breeding in England have advanced about 8 days over the last 30 years. The earlier arrival in spring is correlated with rising temperatures on their wintering ground in sub-Saharan Africa. Interestingly, the duration of their stay in England is the same as 30 years ago because they have also shifted their departure time earlier in the fall by an average of 8 days (Cotton 2003).

A comparison of arrival dates of short- and long-distance migrants illustrates the problems that long-distance migrants face in timing their arrival on the breeding grounds. Analysis of the first arrival dates of 103 species on their summering grounds in the northern USA indicated that short-distance migrants that wintered in the southern USA arrived an average of 13 days earlier than during the interval between 1903 and 1950. The timing of migration of those species migrating from wintering grounds in Central and South America, which have no way to judge the weather conditions of their summering grounds, is more likely timed by endogenous clocks that are not affected by climate change. In this study, those species arriving from Central and South America arrived an average of only 4 days earlier than in the first part of the twentieth century (Butler 2003).

Many species of birds that migrate to high altitudes or high latitudes fly for some distance to reach their breeding grounds. Their departures for summering grounds are probably controlled principally by photoperiod and/or endogenous clocks. Although it might be argued that this characteristic could put them at risk of mismatches with the situation on their breeding grounds, it might also be proposed that they have experienced considerable variation over time in the degree of snow cover and food availability upon arrival at their breeding grounds. Consequently, they may be more adept than other species at dealing with weather and climate variations. Mountain white-crowned sparrows (*Z. leucophrys oriantha*) arrive in mid- to late May at 3000 m in the Sierra Nevada of California. In years in which there is heavy snowpack or late season snowstorms, they return to lower altitudes until food becomes available on their nesting area (Morton 2002). Inouye *et al.* (2000) have shown that the date on which the first arrival of American robins (*Turdus migratorius*) migrating from low-altitude wintering grounds to around 3000 m in the Colorado Rocky Mountains averages 14 days earlier than in 1980. However, the dates of snowpack melting and the appearance of bare ground have not varied substantially with time, so the relatively early arrival of robins challenges them with longer periods than

previously in which snow covers their food resources. Inouye *et al.* (2000) hypothesized that the earlier arrival of robins now than in 1980 signifies a response to warming temperatures on their wintering grounds, which induce them to depart earlier for their montane breeding grounds, only to find that spring is not advanced on their breeding grounds. Survival during this period is probably not an issue because robins can also fly to lower altitudes until conditions improve. However, much more information is needed to determine whether breeding population size or reproductive success is impaired by their early arrival on snow-covered breeding grounds.

### (b) *Breeding*

As noted earlier in this review, the energetic costs of egg laying and feeding young comprise the largest energy expenditure of many species relative to costs of other parts of the annual cycle. Even so, regardless of its relative costs, reproduction must be successful over time for a species to persist. Therefore, the potential effects of future climate changes on reproduction may have disastrous consequences, including species extinctions.

Local weather has been, and undoubtedly always will be, an important factor in determining when eggs are laid. Most north temperate birds start to lay eggs earlier in a warm spring than in a cold spring, independent of any global climate change (Dunn 2004; Torti & Dunn 2005; Weatherhead 2005). Storms and snowpack strongly influence reproductive schedule of birds breeding at high latitudes or altitudes. In 1997, a year in which the snowpack was light and no late spring storms occurred on their breeding ground near 3000 m, mountain white-crowned sparrows began laying on 1 June. In years of heavy snowpack and/or late spring snowstorms, egg laying is delayed. In 1969, a year in which the snowpack was the greatest in 30 years, the first egg was laid on 9 June. Over a 10-year period, the disappearance of snow cover varied by 48 days, but clutch starts varied only by 17 days. The date of first eggs varied less than the disappearance of snowpack because the birds laid eggs in nests in trees and willows in heavy snow years rather than on the ground (Morton 1978). Late spring/early summer snowstorms cause nest failures and decreases in insect and seed abundance (Ehrlich *et al.* 1972; Morton *et al.* 1972; Morton 2002) but birds re-nested quickly after the snow melted (Morton 2002).

The results of investigations to date on the effect of climate change on breeding phenology can be summarized as follows: different investigators working on different populations at different places have found different results (see review by Visser *et al.* 2004). It is likely that this variation is largely due to the inherent variability among species, local influences on breeding phenology and the magnitude of climate change in each area. These studies all contribute valuable information about how birds have responded or not to moderate climate changes over the past few decades. Hopefully, future studies will incorporate not only temperature data and information on the timing of

egg laying, but also the amount of population variability in date of the first egg, food availability, clutch sizes, hatching rates, the number of young fledged and population size over time.

In the UK, over 60 per cent of the species studied have advanced the date on which the first egg was laid or on which hatching of young occurred (Crick & Sparks 1999). In North America, the date of egg laying of tree swallows (*Tachycineta bicolor*), measured between 1959 and 1991, advanced up to 9 days (Dunn & Winkler 2009). This change was correlated with increased surface air temperatures. Between 1971 and 1998, the mean date of the first nest and first clutch of Mexican jays (*Aphelocoma ultramarina*) in southeastern Arizona occurred earlier in the spring by 10.8 and 10.1 days, respectively (Brown *et al.* 1999). These changes were correlated with increased monthly minimum temperatures. A comparison of reproduction of red-winged blackbirds (*Agelaius phoeniceus*) in southern Ontario with variation of the North Atlantic Oscillation Index (NAOI) indicated that laying dates had not changed significantly over a 25-year period, but the breeding season lasted longer than previously (Weatherhead 2005). An analysis of 50 years of data on laying dates and clutch sizes of six species of birds that are broadly distributed throughout North America indicated that laying dates of two species (red-winged blackbirds and eastern bluebirds (*Sialis sialis*)) have advanced with increasing temperature. In contrast, in areas in which temperatures have not varied markedly over the time period of the study, laying dates and clutch sizes of three other species (American robins, killdeer (*Charadrius vociferous*) and American coots (*Fulica americana*)) have not changed significantly over the last 50 years (Torti & Dunn 2005).

As noted previously, information on the population variation in laying dates would be helpful in assessing the meaning of the advancement of laying dates. In an intensive examination of laying dates of 962 clutches of mountain white-crowned sparrows breeding at 2900 m in the Sierra Nevada of California, the date of clutch starts (including first clutches, replacement clutches and second broods) ranged over 76 days. The mean onset of the first 10 clutches of the summer varied over 41 days (Morton 2002). These data indicate that, even in a highly seasonal environment dominated by snow cover for eight to nine months of the year, populational variation is very high and should be measured in future studies on possible effect of climate change on the breeding schedule of birds.

Very little information is available about how climate change is affecting annual cycles of birds south of the Equator. Records collected over a 55 year span of time indicate that a number of species of seabirds in east Antarctica are delaying arrival and egg laying, a result that is the reverse of the patterns seen in many birds in the Northern Hemisphere (Barbraud & Weimerskirch 2006). Birds are arriving, on average, 9.1 days later and laying eggs an average of 2.1 days later than in the 1950s. Only one species, the south polar skua (*Catharacta maccormicki*), laid eggs earlier than in the 1950s. Because air temperatures in this

area have not varied markedly over the time interval in the study and the extent of sea ice explained only 24 per cent of the variation in egg laying among species, more information is needed to understand these patterns (Barbraud & Weimerskirch 2006).

### (c) Mismatches between food availability and avian annual cycles

Temperature is one of the most important environmental factors for living organisms, because unless body temperature is controlled by endogenous regulation as it is in birds and mammals, biochemical, cellular and physiological rate processes of organisms generally increase by about two- to threefold for every 10°C increase in temperature. Therefore, all other factors held equal, an increase in air and water temperatures will cause rate processes like seed germination, leaf production on trees, growth and development of insects, etc. to increase. Aspects of the annual cycle of those species whose cycles are regulated by a rigid endogenous clock and/or are timed by photoperiod, which will not be affected by climate change, will probably become mismatched with their food availability as temperature rises (Visser 1998; Both & Visser 2001, 2005).

Some species demonstrating some degree of mismatching are migratory birds that have not yet advanced their arrival dates but for which the phenology of their food supplies (lepidoperan larvae and leaf production in host trees) has changed (Dunn 2004). North American wood warblers winter in the tropics. Their spring departure for breeding grounds is controlled by photoperiod, which may help time their stop-overs with food peaks en route to and their arrival on breeding grounds. Two long-term datasets indicate that these warblers have not advanced their arrival dates but that leaf production and caterpillar development are occurring earlier in the spring than previously. Therefore, as food resources advance with local warming, breeding of these warblers is becoming increasingly out of synchrony with their food supply (Strode 2003).

A similar situation has been described in a long-distance migrant, pied flycatchers (*Ficedula hypoleuca*). Spring temperatures have significantly increased over the last 20 years on their breeding ground in the Netherlands, advancing the growth and development of caterpillars, the principal food for their young. Their arrival date on the breeding grounds, however, has not changed over time, resulting in high food abundance during nest preparation and egg laying, but reduced availability during feeding of nestlings. With high food abundance during egg laying, females are able to increase clutch size, but overall recruitment to the population is reduced (Both & Visser 2001, 2005). Similar mismatches between caterpillar production and reproduction have been observed in great and blue tits (Visser *et al.* 1998). In a study on blue tits by Thomas *et al.* (2001) in Corsica and southern France, the mismatch between food supply and breeding resulted in intense foraging costs for the adults. Nestling condition and adult survival decreased as the degree of mismatching increased.

Mismatching breeding and food supplies has also been noted in thick-billed murres (*Uria lomvia*) breeding near Hudson Bay, Canada. The breakup of sea ice has advanced by 17 days between 1988 and 2007, as has the peak of food availability, judged as the date at which the number of murres reaches a yearly maximum. However, egg laying has advanced by only 5 days, with the result that the number of days between date of hatching and date of peak food availability has increased. Nestling growth is reduced in years when the number of adults peaked early relative to the date of hatching (Gaston *et al.* 2009).

Another study, which is focused on the effect of climate change on plant phenology, suggests that climate change will have a potentially damaging impact on food supply for birds throughout the summer. Warmer spring temperatures and earlier snow melt at 3000 m in the Colorado Rockies are causing some perennial plant species to produce buds earlier now than at the beginning of record-keeping in the late 1970s (Inouye 2008). The timing, however, of the last frost has not changed over the study period, with the result that buds have been damaged or killed by frost in recent years, resulting in reduced numbers of flowers, seed set and recruitment of new plants to the population. Because many montane birds eat both seeds of plants and insects that require plants as hosts for larvae, these effects of climate change can have potentially disruptive effects on avian food supplies during the summer following breeding.

## 9. PROSPECTS FOR THE FUTURE

The data available to date indicate that global climates are changing and that, to some degree, the annual cycles of some avian species are shifting in appropriate ways. It may be too early to predict which species will succeed, struggle to survive or even become extinct in the coming years, but certain species may have an advantage: Birds that breed following unpredictable availability of food, like red crossbills or zebra finches, and non-migratory birds and short-distance migrants may prove to be the most resilient as future climates develop and communities become reorganized. Migratory birds depending on endogenous clocks and rigid *Zeitgebers*, such as photoperiod, may have the most difficulty meeting the challenges of global climate change if they cannot adjust their timing mechanisms to match new conditions. In every case, however, food supplies are key: those species that specialize on a narrow range of food types, especially during breeding, may be unable to maintain population viability unless they can adopt new food resources.

If climate change were the only new challenge facing birds, one might imagine that many species could become adapted to new conditions and survive with existing population variability and the genetic information that their ancestors used to survive past climate changes. However, other man-made challenges, such as habitat disruption, release of toxic chemicals into the environment, and other factors exist that can interfere singly or synergistically with the lives of birds. Additionally, catastrophic weather

events are predicted to become more common in this century. Birds living in the most extreme environments on Earth (deserts, high altitudes and high latitudes) are already near the limits of their tolerance of stress (Carey 2002) and may fail to cope with additional complications. Many species that are already in decline for a variety of reasons may simply not be able to cope with the wealth of challenges with which they will be presented in the future (Julliard *et al.* 2004).

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