10.1 Introduction

Life-history traits reflect how individuals allocate their time and energy to competing activities, such as growth, maintenance, and reproduction (Roff, 2002). The ability to adjust these traits is likely to determine the response of populations to long-term modifications of the environment, such as global climate change and habitat loss. Some populations may be able to change quickly because individuals show high levels of phenotypic plasticity, defined as the ability of a single genotype to modify its phenotype under different environmental conditions (Houston and McNamara, 1992; Pigliucci, 2001). In terms of adjusting to climate change, phenotypic plasticity in birds may involve changes in diet, habitat selection, and migratory behaviour, but one of the most studied aspects has been phenology or the timing of breeding. Plasticity in the timing of breeding appears to be relatively high in many songbirds (Przybylo et al., 2000; Brommer et al., 2005; Nussey et al., 2005) because in different years some individuals may vary their breeding dates by almost a month in response to local weather conditions (Wesolowski and Cholewa, 2009). Nonetheless, plasticity in timing of reproduction can also be limited by developmental, hormonal (Sockman et al., 2006), genetic, and evolutionary constraints. For example, the ability of migratory species to shift their breeding date in response to climate change will be constrained if the time of arrival on the breeding grounds from wintering areas is inflexible because it is set by photoperiod, rather than temperature or food availability (Both and Visser, 2001). Thus, a change in the reliability of environmental cues can sometimes result in maladaptive behaviour (evolutionary traps; Pulido and Berthold, 2004; Miner et al., 2005). Understanding the ecological and evolutionary basis of plasticity in varying environments is necessary for predicting the effects of climate change on bird populations. However, at present, little is known about the mechanisms and consequences of plasticity for bird populations facing climate change (Nussey et al., 2007; Lyon et al., 2008).

There is mounting evidence from long-term studies that birds are advancing their date of laying associated with increasing mean temperatures (see Appendix). Indeed, this is some of the strongest evidence for the effects of climate change on wild populations (see reviews by Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003). Part of this attention may simply reflect the fact that laying (or hatching) dates are some of the most easily gathered and least biased measures of avian reproduction. However, timing of laying has profound effects on overall breeding performance as there are often strong genetic (Garant et al., 2008) and phenotypic (Winkler and Allen, 1996; Mills et al., 2008) couplings between timing of breeding and clutch size, which set a fixed upper limit on overall reproductive success. Indeed, it is becoming increasingly apparent that timing of breeding, number and size of clutches, duration of parental care, and survival are integrated and respond in a coordinated fashion to environmental factors, particularly relative food abundance (Both and Visser, 2005; McNamara et al.,
By advancing the timing of breeding, climate change may also affect other aspects of reproduction such as the number (Verboven et al., 2001) and size (Both and Visser, 2005) of clutches, incubation behaviour (Cresswell and McCleery, 2003; Cooper et al., 2005), and recruitment (Drent, 2006; Wilson et al., 2007). Our review focuses primarily on timing of breeding (laying or hatch dates) because this generally has a strong connection with clutch size and subsequent reproductive success, but we also discuss the effects of climate on other reproductive traits. We begin with a review of proximate factors influencing laying date, summarize the causes and rate of change in laying date, and then analyse how climate change is influencing laying date at the intra- and inter-specific levels.

10.2 What factors influence laying date?

Although most birds lay earlier when spring temperatures are warmer (Dunn, 2004), there are a variety of other proximate factors influencing the start of breeding, including precipitation (Skinner et al., 1998; Leitner et al., 2003; Rodriguez and Bustamante, 2003), food abundance, breeding density, and photoperiod and hormones (Dawson, 2008). For most temperate-breeding birds, these factors are thought to act in a hierarchy, starting with increasing daylength (photoperiod) as the primary cue for gonadal maturation and release of hormones in the spring. In tropical species, it was previously thought that daylength cues were too small to time breeding seasons, but there is now evidence from tropical species and experiments with temperate species showing that small changes in daylength can initiate reproduction (reviewed by Dawson, 2008). In more unpredictable climates, such as those in deserts, breeding appears to be more flexible, depending on favourable environmental conditions, particularly the onset of rainfall (Hau et al., 2004). Although some species such as zebra finches (Taeniopygia guttata) can breed at almost any time of year when food becomes abundant, other opportunistic species, such as crossbills (Loxia spp.), appear to require regular changes in photoperiod to initiate a physiological window during which breeding can occur once food conditions are adequate (Dawson, 2008). Increasing photoperiod often initiates reproductive activity in temperate birds, but species differ in terms of the threshold amount of light required to start gonadal growth, and they also differ in the rate at which growth proceeds under increasing daylength (Dawson, 2008). Photoperiod is fixed at the same latitude, but these inter-specific differences in gonadal responses could influence the rate at which various species respond to other environmental conditions. The timing of breeding varies between years, so there is clearly more than just photoperiod regulating breeding, and it is likely that photoperiod interacts simultaneously with other environmental cues such as food abundance, temperature, and social stimulation to set the physiological window during which egg-laying will occur (Dawson, 2008; Schoech and Hahn, 2008).

Food abundance is thought to be one of the most important of the secondary cues used to fine-tune time of breeding. Females appear to time the laying of their clutch such that hatching occurs near the peak of food availability, when the energetic demands of offspring are presumably the greatest (Figure 10.1a). However, food availability earlier in the season during egg-laying may also be important in some species (Perrins, 1970; Bryant, 1975), and other aspects of life history, such as the number of broods per season (Crick et al., 1993; Visser et al., 2003), may have an influence. In multi-brooded species, total reproductive success for the season depends more on the duration of the season than on single-brooded species, so the timing of the first brood relative to peak food abundance is less important, and they generally start breeding as soon as possible in the spring (Crick et al., 1993). If climate change reduces the period when food is available for second broods, then the reproductive value of second broods declines and fewer birds will produce second broods (Visser et al., 2003; Husby et al., 2009). These females, which now only have a single brood, are expected to start laying closer (relative to double-brooded females) to the peak of insect abundance (Visser et al., 2003). This appears to be occurring in great (Parus major) and blue (P. caeruleus) tits, as populations that show a larger decline in the proportion of second broods also show a relatively small change in laying date over time (Visser et al., 2003). In contrast, populations that are primarily single brooded have shown larger advancement in laying dates because of a greater...
proportion of these females are adjusting their single clutch to the time of peak food abundance, which is generally advancing. Thus, single-brooded populations appear to be more sensitive to climate change (see also Section 10.5). Note that across species, food supplementation experiments suggest that multi-brooded species advance their laying date more than single-brooded species (Svensson, 1995), which may not seem consistent with the discussion above. However, the timing of food supplements in these experiments may not be similar to changes in food abundance caused by climate change and thus the results from experiments and unmanipulated birds may not be directly comparable.

In addition to acting on lower trophic levels to influence food abundance, temperature could also have direct effects on thermoregulation of birds or their ability to maintain viable eggs (Stevenson and Bryant, 2000). Thus, temperature could be an energetic constraint on laying date and not just a cue for breeding. Experiments that heat and cool aviaries under controlled conditions (Meijer et al., 1999; Salvante et al., 2007; Visser et al., 2009) also suggest that there can be direct effects of temperature on timing of laying. Furthermore, increasing temperatures might select for smaller clutches if larger clutches are currently maintained by the benefits of reduced clutch cooling when females take breaks from incubation (Cooper et al., 2005).

It is thought that climate change is making the current cues for breeding (photoperiod, temperature, and food) poorer predictors of food supply and, hence, the optimal time for breeding. In other words, the cues become decoupled from peaks in food abundance, which will potentially lead to mismatches between the start of breeding and the availability of food for nestlings. For example, these mismatches may occur when birds base their spring migration on photoperiod and arrive ‘too late’ on the breeding grounds to take advantage of a peak in food abundance that has shifted earlier because of warmer spring temperatures. These mismatches are thought to arise in insectivorous birds because increased spring temperatures lead to much faster development of ectothermic insect prey than their own homoeothermic nestlings. For example, the development of winter moths can accelerate from 56 to 23 days (Buse et al., 1999). Thus, warmer spring temperatures can lead to earlier peaks in insect abundance and, consequently, a mismatch between the timing of peak food abundance and maximum food requirements of developing young (Visser et al., 1998).

The mismatch hypothesis is primarily applicable to species in which the main selective force on timing of laying is synchronization between the food supply and the peak energy demands of the offspring. Even though it has been over 50 years since Lack (1954) proposed that parents time their

**Figure 10.1** Mean date of laying in relation to the date of peak food abundance of (a) pied flycatchers and (b) tree swallows. Laying date was related to date of peak caterpillar abundance in a Dutch population of flycatchers (1985–2004, r = 0.82, n = 19, P < 0.001; Both and Visser, 2005), but it was not significantly related to biomass of flying insects in two populations of tree swallows in North America (1986–2005, r = 0.17, n = 17 site-years, P = 0.31; Dunn et al., in preparation). The lines are the linear regression lines. Panel (a) reprinted with the permission of Wiley-Blackwell.
breeding to coincide with seasonal peaks of food abundance, there have been relatively few studies with direct measurements of natural food abundance in relation to timing of breeding. In contrast to Lack’s hypothesis, several studies indicate that laying date is not timed to match a peak in food abundance later in the season when offspring demands are greatest. For example, reed warblers *Acrocephalus scirpaceus* feed on insects that are abundant throughout the season and there is no clear peak in abundance (Halupka *et al.*, 2008). Similarly, in tree swallows *Tachycineta bicolor*, food remains abundant long after chicks fledge (Winkler, in preparation), and temperatures and insect abundance are highly variable prior to laying and do not provide reliable cues to food abundance during the nestling period (Figure 10.1b, Dunn *et al.*, in preparation). In other species, such as waterfowl, timing of laying also appears to have little influence on the number of fledglings because success is most strongly influenced by nest predation (Drever and Clark, 2007; but see Brinkhof *et al.*, 1997).

The absolute abundance of food and its distribution throughout the breeding season may also affect reproductive success in addition to its timing. For example, Durant *et al.* (2005) showed that chick survival in Atlantic puffins *Fratercula arctica* was only related to the abundance of herring *Clupea harengus*, their main food, and not to the degree of mismatch between the average hatch date and the date of herring arrival. Thus, abundant food resources may compensate for mismatches in timing. The effect of mismatches is also thought to depend on the length of time food is available and other aspects of life history such as adult mortality. In a theoretical model for migratory species, Jonzén *et al.* (2007) predicted that advances in laying date will be weaker when food for nestlings is available for a longer period of time. In general, longer availability of food will reduce the risk of breeding failure and adult mortality and allow a wider range of breeding times. For example, in pied flycatchers, birds have not changed their arrival date on the breeding grounds (Both and Visser, 2001), which is consistent with theory, if the mortality risk to adults is moderate and there is strong competition to arrive early and gain access to limited nest sites. However, any change in adult mortality (higher or lower) is predicted to lead to shifts in the optimal arrival date. Timing of breeding can also respond to adult mortality rates during the breeding season, with earlier breeding being selected if the risk of adult mortality later in the season is not negligible (Goutis and Winkler, 1992). Thus, accurate predictions about the impact of climate change on breeding dates may require information about the size and shape of the distribution of food, as well as patterns of adult mortality throughout the season.

Understanding the ecological and physiological mechanisms behind the decision to breed will be increasingly important in the future as temperatures are predicted to increase dramatically, and at these higher temperatures we may find that there are thresholds or other non-linearities that dramatically alter the relationships between temperature, resources, and breeding decisions (Stenseth and Mysterud, 2002; Lyon *et al.*, 2008). For example, some North American tree species are predicted to advance their date of leaf unfolding for the first half of this century, but later, when temperatures are higher, they are expected to show delays and abnormal unfolding (Morin *et al.*, 2009). These delays are also predicted to be stronger in the southern USA, where warmer temperatures will produce a lack of the chilling temperatures necessary to break bud dormancy. Non-linear responses to climate could also occur if there are some cohorts of birds that respond differently because of previous experience or conditions at birth that affect their plasticity to temperature (Wilson *et al.*, 2007).

### 10.3 What are the causes of changes in laying date?

Inferences about the causes of change in timing of breeding have to be made cautiously because most studies are based on correlations between breeding date and temperature or other climate variables (North Atlantic oscillation, NAO; precipitation). Thus, analyses could be confounded by changes in human land use, pollution, or changes in breeding density. For example, if habitat changes lead to smaller populations and lower breeding density, then there might be more resources available for each individual, which could reduce competition and allow individuals to shift to an earlier breeding date.
Changes in population size are known to bias estimates of first arrival dates (Tryjanowski et al., 2005; Miller-Rushing et al., 2008), so they may also bias estimates of the earliest date of egg-laying. In a Scottish seabird colony, common guillemots Uria aalge are increasing in numbers and laying eggs later (Frederiksen et al., 2004), as might be predicted if intra-specific competition affects the timing of reproduction. However, in the same breeding colony, black-legged kittiwakes Rissa tridactyla are laying eggs later and declining in numbers, so laying dates may also be influenced by factors such as social stimulation and individual experience (Frederiksen et al., 2004, personal communication). The effects of changes in population density and habitat quality have rarely been addressed, but might be discounted if the study is conducted in a pristine area where anthropogenic effects on breeding conditions are lacking (e.g. Wesolowski and Cholewa, 2009) or if researchers test for effects of density on laying date (Dunn and Winkler, 1999; Sanz et al., 2003; Dyræc and Halupka, 2009; Wanless et al., 2009).

At the population level, timing of breeding can change because of phenotypic plasticity, demographic shifts, or natural selection (micro-evolutionary change). Phenotypic plasticity should produce changes most readily, and if for any reason the range of change allowed by plasticity is exceeded, then evolutionary changes should occur (Bradshaw and Holzapfel, 2006; Visser, 2008). Indeed, the great majority of studies reviewed in Table 10.1 are consistent with a phenotypically plastic response, and approximately half of the studies have found evidence for selection on laying date (i.e. significantly greater reproductive success for earlier nesting individuals), including great tits (Visser et al., 1998), pied flycatchers (Both and Visser, 2001), barnacle geese Branta leucopsis van der Jeugd et al., 2009), thick-billed murres Uria lomvia Gaston et al., 2009), and common guillemots (Reed et al., 2009). Several other studies explicitly searched without success for significant selection coefficients or correlations between breeding success and laying date, including great tits in the UK (Cresswell and McEwens, 2003), ducks in Saskatchewan (Drever and Clark, 2007), kittiwakes and guillemots in Scotland (Frederiksen et al., 2004), and collared flycatchers in Sweden Ficedula albicollis Sheldon et al., 2003). Ultimately, we might expect climate-related selection to produce a micro-evolutionary change in phenology, but only a few studies have actually shown this to date, which may be partly due to the difficulty in collecting long-term pedigree-based data on wild populations (see Visser, 2008 for a review). Much of this lack of evidence for micro-evolutionary change may be due to the fact that the range of phenotypic plasticity has not been exceeded (e.g. Charmantier et al., 2008).

Recent work on non-migratory great tits in England (Charmantier et al., 2008) and The Netherlands (Nussey et al., 2005) has highlighted differences between these populations in their responses to temperature: the British tits seem to be keeping up with changes in temperature and their prey and their population size is increasing, whereas many of the Dutch birds are lagging behind and average fitness is declining. One promising hypothesis to explain these differences is that the birds are responding to different cues in determining when to begin laying (Lyon et al., 2008). Have the correlations between cues and environments for some reason been less reliable in The Netherlands in the past, selecting for a greater reliance on photoperiodic cues? Or is there something different in the way that they respond to temperature and photoperiod that may arise from other selective pressures (cf. Silverin et al., 2008)? One contributing factor to these differences may be greater isolation of the tit population in Great Britain compared with the mainland population in The Netherlands. Greater gene flow on the mainland may have reduced the rate of local adaptation in the Dutch population, leading to non-optimal timing of breeding, similar to the non-optimal clutch sizes reported in Belgian tits (Dhondt et al., 1990). In migratory species, such as barn swallows Hirundo rustica and pied flycatchers, there is evidence that some of these geographic differences in arrival or breeding times may arise, at least partially, from the different environmental conditions that they experience in different parts of the winter range in Africa or along migration routes (Both et al., 2006; Balbontín et al., 2009).

There is also reason for caution in interpreting potential mismatches between the phenologies of breeding birds and their prey. Although there is good evidence from a few detailed studies that
populations are not responding to temperature changes at the same rate as their food supply (Both et al., 2009), it is not always clear what the consequences are for the populations. Most mismatch interpretations have at least implicitly assumed a sharp peak in the summer food availability for growing chicks, a peak that, if missed, has serious repercussions for offspring production. Very few studies, however, have measured the food supply directly, and at least some species have food available for a long period in the summer (Halupka et al., 2008; Winkler, in preparation), thus reducing the impacts of differential phenological shifts in birds and their prey. Extended periods of food availability probably represent successive availability of several different insect species, and Winkler et al. (2002) suggested that birds with greater diet diversity will be less impacted by phenological shifts in prey. Even in such species with a broad summer plateau of food availability, however, there is the potential for a mismatch, as the entire summer insect fauna might shift earlier, leaving a gap in late summer and autumn that may hit fledglings hard during the difficult post-fledging transition to independence and may hit all age classes preparing for migration.

Even when there are mismatches, it is not always clear that they are detrimental to population growth. In Sweden, barnacle geese young hatch several weeks after the peak in forage quality (nitrogen content), and this has produced stronger selection for earlier breeding, but, despite the mismatch, this population produces more surviving young than an arctic Russian population whose young hatch near the peak in forage quality (van der Jeugd et al., 2009). This example shows that we also need to consider other possible adjustments of the breeding cycle to climate change, such as changes in the number of broods, the amount of parental care, or post-fledging survival which could compensate. Thus, it is important to differentiate between what Winkler et al. (2002) called the adaptive and demographic effects of phenological shifts. We may sometimes think that birds would be better adapted doing things differently (adaptive effects), but if that different behaviour is not reflected in different population sizes or dynamics (demographic effects), then the distinction may not be important for conservation.

10.4 Laying date is advancing in most species

Evidence for long-term changes in the phenology of birds is accumulating rapidly from around the world. Long-term studies of the date of laying (or hatching) have been conducted in at least 68 species (mean = 42 years of data; Table 10.1). One of the oldest continuous records of laying started in 1897 in The Netherlands, where eggs of northern lapwings Vanellus vanellus are harvested for human consumption, and newspapers record the first egg each spring, which is given to the Queen (Both et al., 2005). Some of the largest of these studies have used nest records contributed by volunteers over many years in the UK (Crick and Sparks, 1999) and North America (Dunn and Winkler, 1999; Torti and Dunn, 2005), but there are still just a handful of these large-scale studies. Most reported studies (84%, 31/37) have been long-term projects at a single site on a single species (Table 10.1).

Over the years, there has been a significant advance in laying date of 59% (40/68) of species, and 79% (53/67) of species lay earlier during warmer years, in at least one study (Table 10.1). Based on current estimates, birds are advancing their laying dates by an average of 0.13 days per year (±0.03 SE, n = 52 species, range: −0.80 to 0.51), and they are laying 2.40 (±0.27 SE) days earlier for every degree centigrade warmer (n = 52 species, range: −10.3 to −0.01; Table 10.1). Given projections for future global warming of up to 4 °C (Intergovernmental Panel on Climate Change, 2007), we might expect birds to be laying approximately 15 days earlier by the end of this century. Thus, it seems likely that even those species that have not yet responded to climate change will eventually show advancement in timing of breeding. However, the magnitude of these changes and their impacts are still unclear.

10.5 Inter-specific variation in laying date

Although birds are generally breeding earlier, there is a great deal of variation between and within species that is not well understood. Some topics that are particularly important are (1) the ability of different species to adjust their phenology to that of
the resources they need for breeding (e.g. the degree of mismatch between bird populations and their food supply) and (2) the causes of geographic variation within species, because this will indicate how much particular species can change and the causes (phenotypic or evolutionary) of intra-specific variation.

Comparative evidence indicates that, overall, bird species are keeping pace with changes in the phenology of lower trophic levels, which suggests that mismatches are uncommon. The rate of change (mean ± SE days per decade) in avian laying dates (−3.77 ± 0.70, n = 41 species) does not appear to be different from that of changes in phenology of trees (−3.3 ± 0.87), shrubs (−1.1 ± 0.68), or butterflies (−3.7 ± 0.78; Parmesan, 2007). On a per-year basis, this rate of advancement in birds (0.37 day/year) is greater than our estimate (0.13 day/year) in Table 10.1, but it was based on older data (Root et al., 2003; Parmesan and Yohe, 2003) from a variety of different estimates of timing of arrival and breeding, not just laying dates. Studies of trophic interactions at the same location are less likely to be biased by sampling differences and here there is more evidence for mismatches. Indeed, several studies have found mismatches or differences between the responses of trophic levels to climate (plankton: Edwards and Richardson (2004); plant and insects in a grassland: Voigt et al. (2003); reviewed by Visser and Both (2005)).

Species may vary in their response to climate change for a variety of ecological, life history, geographic, and phylogenetic reasons. In particular, migratory species may have a different hierarchy of cues for breeding (e.g. photoperiod and food) than resident species. There could also be differences in geography (temperate vs. tropical) that affect the magnitude of response, as there have been much larger increases in temperature in certain regions, particularly above 50°N (Myneni et al., 1997). Indeed, across a variety of taxa, there has been a small but significantly greater response at higher latitudes (Parmesan, 2007). Thus, we might predict greater phenological responses by birds at higher latitudes.

Analysis of the 52 species with long-term data on changes in laying date (Table 10.1) revealed that species that typically have a single brood advanced their laying date about three times faster than species with two or more broods per season (−0.19 vs. −0.06 days per year; t50 = 2.0, P = 0.046), as predicted in Section 10.2. Thus, it appears that single-brooded species are responding more rapidly to climate change, as Visser et al. (2003) found in blue and great tits (see also Husby et al., 2009). The response of birds to climate change may also vary across species if there are differences in how various types of food respond to changes in air temperature. For example, we might expect insects and plants to respond more rapidly than vertebrates and thus increase the response of birds that feed on these groups. However, herbivorous (−0.45 ± 0.15 day/year, n = 2) and insectivorous (−0.11 ± 0.03, n = 43) species advanced their laying dates at rates not significantly different from species that feed on vertebrates, primarily fish (−0.14 ± 0.15 day/year, n = 7, F2,49 = 2.2, P = 0.12). Note that very few studies have been published on herbivorous and vertebrate-eating species. Future analyses should also consider the spatial scale at which species forage and disperse. For example, even within the same region, different species of seabirds that rely on similar types of prey can respond differently depending on where they acquire their food (i.e. offshore or inshore; Frederiksen et al., 2004).

If temperature has a direct effect on thermoregulation and energy balance, then we might also expect the body size of birds to influence their response to climate change. Using the data of Crick and Sparks (1999), Stevenson and Bryant (2000) found that the long-term change in laying date was smallest in large species and greatest in small species. However, we found no effect of body mass in our analysis with our estimate (0.13 day/year) in Table 10.1, but it was based on older data (Root et al., 2003; Parmesan and Yohe, 2003) from a variety of different estimates of timing of arrival and breeding, not just laying dates. Studies of trophic interactions at the same location are less likely to be biased by sampling differences and here there is more evidence for mismatches. Indeed, several studies have found mismatches or differences between the responses of trophic levels to climate (plankton: Edwards and Richardson (2004); plant and insects in a grassland: Voigt et al. (2003); reviewed by Visser and Both (2005)).

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### 10.6 Intra-specific differences in the timing of breeding

Within species, there is substantial geographic variation in the response of species to climate change. Although global temperatures have increased an
average of 0.6°C, there have been much larger increases in certain regions, particularly above 50°N (Myneni et al., 1997). Given that 94% of species breed earlier in warmer springs, the most likely explanation for the geographic differences in the timing of breeding is local variation in temperature change. In some well-studied species, such as pied flycatchers (Both et al., 2004), great and blue tits (e.g., Visser et al., 2003; see also Sæther et al., 2003), and barn swallows (Møller, 2008), there is considerable variation among study sites that is related to local temperature differences. Similar geographic variation in the response of species has also been reported in several North American species, including tree swallows (Dunn and Winkler, 1999; Russell, 2003), killdeer Charadrius vociferus, American robins Turdus migratorius, and eastern bluebirds Sialia sialis (Torti and Dunn, 2005). In particular, killdeer, American robins, and eastern bluebirds showed a steeper negative relationship between laying date and temperature at more northerly locations (Torti and Dunn, 2005), while climate change had a stronger effect on laying date at more western locations within the range of tree swallows. Even large-scale climate indices such as the NAO can have effects that differ geographically. In an analysis of 13 species of seabirds, the NAO had a positive effect on breeding success in the south, but a negative effect in the north (Sandvik et al., 2008). The strength of climate change may vary, depending on the location and time period studied, and its effects on avian phenology should be tested whenever possible by including local-scale meteorological variables in the analysis.

Local differences in plant phenology may also produce some ‘early’ sites at a micro-geographic scale, and over time individuals could shift to these earlier sites, resulting in advances in the mean laying date for the entire population (Møller, 2008). Gienapp and Visser (2006) also found that female great tits in two nearby populations responded differently to artificial peaks in food abundance. Even within the same breeding location, the responses of species may differ depending on the particular time periods that they are sensitive to temperatures. For example, based on a large-scale model (Both and te Marvelde, 2007), starlings Sturnus vulgaris are predicted to be advancing their laying date across Europe, but pied flycatchers are expected to advance their laying dates in western and central Europe and delay laying in northern Europe. These differences between and within species are expected because starlings lay eggs 25 days earlier than pied flycatchers and temperatures are changing differently during these two time periods. Furthermore, breeding time temperatures for pied flycatchers are increasing in most of Europe (<60°N) and decreasing at more northerly breeding locations (Both and te Marvelde, 2007). Thus, intra-specific differences in the response to climate change are common and are mostly likely caused by geographic differences in the extent and timing of warming.

10.7 How does timing of breeding relate to breeding performance?

In most species, especially those that rear only one brood per season, individuals that start to lay earlier also have larger clutch sizes, and this often translates into more young fledged. Given that many species show a long-term advancement in laying date, we might also expect an increase in clutch size in these species, and possibly greater reproductive success. However, the results are much more complicated. Long-term advancement of laying and larger clutches have been reported in some populations of pied flycatchers (Järvinen, 1989, Winkel and Hudde, 1997) and first broods of barn swallows (Møller, 2002), but not in collared flycatchers (Sheldon et al., 2003), great or blue tits (Winkel and Hudde, 1997), tree swallows (Winkler et al., 2002), eastern bluebirds (Torti and Dunn, 2005), or red-winged blackbirds Agelaius phoeniceus (Torti and Dunn, 2005).

It is not clear why clutch size has not increased in populations with a shift towards earlier laying, but there are a number of possible ecological explanations. First, it may be that because of potential mismatches with the peak of food abundance for nestlings (or a general decline in fledgling survival) the date of laying has a greater effect on reproductive success than laying a few additional eggs, which will delay hatching. In pied flycatchers, for example, the probability of recruitment declined more strongly with hatch date in warmer years when birds generally laid earlier (Both and Visser, 2005). Thus, there was stronger selection against relatively larger (and later) clutches; part of this
selection might come in the form of countervailing survival selection on adults (i.e. larger clutches reduce adult survival). In collared flycatchers, Sheldon et al. (2003) suggested that there was strong directional selection on the phenotype for earlier laying, but an evolutionary response was prevented by a countervailing trade-off with adult survival. A similar type of trade-off with adult survival might occur in populations that advance laying date but show no change in clutch size. One problem with this interpretation is that there is little evidence for adult survival costs that are dependent on fecundity (e.g. in tree swallows; Shutler et al., 2006).

Second, there could be shifts in laying dates, but no change in mean clutch size, if there are demographic changes that lead to earlier breeding by a greater proportion of lower-quality individuals (e.g. younger females) that lay smaller clutches (Winkler et al., 2002). A third possibility is that in warmer years it is easier for all individuals to start laying earlier, but this does not lead to any change in how many eggs they lay because there is a shift in the relationship between clutch size and laying date without any change in slope. In this ‘relative’ model of clutch size determination (Winkler et al., 2002), the intercept of the regression line between clutch size and laying date decreases in a warmer year, but the slope stays the same (Figure 10.2). In other words, the line shifts to the left (earlier), so an earlier laying date results in a similar clutch size. This is a type of non-continuous response to climate change, as there is a new relationship between clutch size and laying date. In contrast, bird populations that follow the ‘absolute’ model move up (and down) the same regression line each year, so when spring is warmer and laying is earlier, the average clutch size increases (Figure 10.2). This would be a continuous response, as the relationship between clutch size and laying date is fundamentally the same. In at least some species, there appears to be strong selection to breed as early as possible because it leads to acquiring a higher quality mate (e.g. Kirkpatrick and Arnold, 1990) or because the risk of mortality favours breeding as soon as conditions allow (Goutis and Winkler, 1992). Such selective forces raise the possibility that birds may sometimes be laying eggs at a time when their chicks hatch before the seasonal peak in food abundance, and they suggest the possibility that the timing of laying is adapted to other factors besides the timing of food supply for the chicks. These selective forces also provide a rationale for the often-observed correlation between laying date and other aspects of individual quality (e.g. Bowlin and Winkler, 2004). To date, most studies have found that birds are laying earlier but not changing clutch size; however, it is possible that further increases in temperature will eventually lead to a change in clutch size and breeding performance.

10.8 Conclusions and future avenues of research

There has been a tremendous increase in the number of long-term studies of avian phenology in the last 5 years, more than doubling since an earlier review (Dunn, 2004). Despite this increased interest and
information, there are still many of the same needs for additional data. Most importantly, we need a better understanding of avian responses at a broader geographic scale. Most of our research has been limited to single study sites, and we need to work collaboratively to broaden the scope (and relevance) of our results. Groups of researchers are already organized in Europe around some model species (e.g. Visser et al., 2003; Both et al., 2004), but these large-scale networks are just starting in North America, for example, among researchers studying Tachycineta swallows (www.golondrinas.cornell.edu/). A large-scale national phenology network has started in the USA (www.usanpn.org/), but, to date, it has focused on plant phenology and it will only start collecting information on animals in 2010. Networks of researchers are needed to increase the scope and sample sizes required for studying responses to large-scale phenomena such as climate change. Our review shows that there is large variation in the response to climate change within and among species. Understanding this variation is critical if we aim to predict how bird populations will respond to further temperature increases. To date, the main contributions of phenological observations of birds have been monitoring (i.e. how much bird populations are changing) and detailed studies of changes in selection on laying date (e.g. mismatches). In the future, we need to be able to link these observations at broad geographic scales to population trends of birds, as well as interactions with other trophic levels. We still have a rudimentary understanding of how temperature affects the food supply and breeding performance of birds, primarily because most researchers do not measure food abundance. Much of our understanding of avian responses to climate change comes from a handful of well-studied passerines that live in forests and feed on caterpillars. Although these studies have been fundamental in developing a mechanistic and theoretical understanding of how reproductive decisions of birds are influenced by their food supply, their applicability to other systems with different types and distributions of food, such as waterfowl (Drever and Clark, 2007), aerial and aquatic insectivores (Winkler et al., 2002; Halupka et al., 2008; Pearce-Higgins et al., 2009), raptors (Nielsen and Møller, 2006; Both et al., 2009), and seabirds (Wanless et al., 2009), may be limited. In the future, the food supplies of many species are likely to show non-linear responses to climate change, as a consequence of disruptions at lower trophic levels. For example, the phenology of some common tree species (e.g. Populus spp.) is expected to advance and then delay over the next century (Morin et al., 2009), and differences in the tolerance of various trophic levels to temperature may disrupt entire insect communities (Voigt et al., 2003), so we cannot assume a simple linear relationship based on current patterns. There are also likely to be major changes in Antarctic sea ice availability that will have profound changes on the entire marine community, reaching up to top predators such as penguins, but even here some species are declining and others increasing (McClimontock et al., 2008). Understanding the mechanistic relationships between temperature, food supply, and avian breeding performance, as well as the physiological basis for these relationships, should be top priorities because they are necessary for linking the responses of birds to general circulation models of climate and predicting long-term changes in populations. Ultimately, however, we need to examine the entire life cycle of species, as climate and other factors can sometimes have larger effects on avian populations outside the breeding season (e.g. Rolland et al., 2008; Pearce-Higgins et al., 2009).

10.9 Acknowledgements

We thank M. Frederiksen, A.P. Møller, L.A. Whittingham, and a reviewer for comments that improved the manuscript.

10.10 References


### Table 10.1
Change in laying dates of 68 species of birds from long-term studies.

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<th>Species</th>
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<th>years</th>
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<th>Laydate change°C</th>
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<td>Tachycineta bicolor</td>
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<td>−0.28</td>
<td>*</td>
<td>−1.86</td>
<td>* 1 Dunn and Winkler (1999, unpublished data)</td>
<td></td>
</tr>
<tr>
<td>Winter wren</td>
<td>Troglodytes troglodytes</td>
<td>57</td>
<td>−0.28</td>
<td>*</td>
<td>−3.88</td>
<td>* 2 Crick and Sparks (1999)</td>
<td></td>
</tr>
<tr>
<td>Blackbird</td>
<td>Turdus merula</td>
<td>20</td>
<td>−0.31</td>
<td></td>
<td></td>
<td>2 Nielsen and Møller (2006)</td>
<td></td>
</tr>
<tr>
<td>American robin</td>
<td>Turdus migratorius</td>
<td>50</td>
<td>0.14</td>
<td>−2.21</td>
<td></td>
<td>2 Torti and Dunn (2005), P. Dunn (unpublished data)</td>
<td></td>
</tr>
<tr>
<td>Song thrush</td>
<td>Turdus philomelos</td>
<td>34</td>
<td></td>
<td>−1.23</td>
<td>* 2 Crick and Sparks (1999)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mistle thrush</td>
<td>Turdus viscivorus</td>
<td>57</td>
<td></td>
<td>−5.21</td>
<td>* 2 Crick and Sparks (1999)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common guillemot</td>
<td>Uria aalge</td>
<td>20.5</td>
<td>0.03</td>
<td></td>
<td></td>
<td>1 Frederiksen et al. (2004), Reed et al. (2009)</td>
<td></td>
</tr>
<tr>
<td>Thick-billed murre</td>
<td>Uria lomvia</td>
<td>20</td>
<td>−0.27</td>
<td></td>
<td></td>
<td>1 Gaston et al. (2009)</td>
<td></td>
</tr>
<tr>
<td>Masked lapwing</td>
<td>Vanellus miles</td>
<td>46</td>
<td>0.00</td>
<td></td>
<td>−0.01</td>
<td>1 Chambers et al. (2008)</td>
<td></td>
</tr>
<tr>
<td>Northern lapwing</td>
<td>Vanellus vanellus</td>
<td>103</td>
<td>−0.03</td>
<td></td>
<td></td>
<td>1 Crick and Sparks (1999), Both et al. (2005)</td>
<td></td>
</tr>
</tbody>
</table>

Asterisks indicate significant change in laying dates over time or with temperature. N years is the number of years analysed in each study (means for multiple studies). Laydate change/year and °C are the slopes of regression lines. N broods is coded as 1 = typically one brood, 2 = typically two or more broods. Blanks indicate no data available.