

S08-2 Mistimed reproduction due to global climate change

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Abstract Climate change may affect the phenology of some parts of food chains more strongly than others, which leads to a disruption of synchronization within food chains. We describe three different methods to assess whether the change in laying date in bird populations has been able to maintain synchronization, illustrated with our own work on great tits (*Parus major*). These show: (1) the date of peak abundance of caterpillars has advanced, but great tits have not started to lay earlier, hence the difference in synchronization between great tits and their prey has increased; (2) selection for early laying has become stronger; and (3) great tits have reduced the incubation period (the time between laying the last egg and first hatching) to speed up their reproduction. Clearly, the change in laying date in the studied great tit population has not been able to match the shifts in underlying levels of the food chain. We offer two hypotheses in explanation, and discuss how they can be tested by manipulating laying date under field conditions and by comparing populations on a large spatial scale. We argue that the lack of advancement of laying date may be caused by a differential change of temperature in early and late spring, rather than an increase in spring temperature *per se*. We also report mistiming in two other species due to correlative disruptions from weather variables, and encourage studies on other systems to find out how general this pattern is.

Key words *Parus major*, Climate change, Phenology, Timing of reproduction

1 Introduction

There is now ample evidence that global climate change affects a wide range of biological systems (Wuehrich, 2001; Walther et al., 2002). One important biological system affected is phenology, particularly the timing of reproduction. For many organisms in the temperate zone, there is only a short period in the annual cycle when conditions are suitable for reproduction. In order to breed successfully, birds need to provide their nestlings with adequate food, which is often only abundant within a short period. The food, in turn, is itself dependent on the development of food or mother plants. Therefore, as other organisms in the food chain set the conditions for reproduction, and as different levels in the food chain may be affected differently by climate change, a multi-trophic perspective is needed to understand the changes in phenology in bird populations. Because there is no *a priori* reason to assume that climate change will affect the phenology of these different levels in the same way, and as the synchronization between these levels is crucial for successful reproduction, we then focus on how climate change affects the synchrony between the different levels in the food chain (Fig. 1).

Birds are adapted to year-to-year variation in the timing of favorable conditions, and hence in the optimal laying date. They have physiological control mechanisms that translate the cues from their environment to a laying date (Visser and Lambrechts, 1999). As the cues vary from year to year, so birds lay at different times. It is important to stress, nevertheless, that a physiological control mecha-

nism should not just cue an optimal laying date in one particular year, but should lead to laying dates which are (close to) optimal for a whole range of years. Natural selection will therefore act not so much on the laying date in a particular year but rather on the whole set of laying dates produced by a genotype, and so the underlying physiological control mechanisms.

It is also important to appreciate that natural selection on these mechanisms will have taken place under a specific set of abiotic variables (e.g., weather pattern). A serious but very often ignored aspect of global climate change is that temperatures have not just simply increased, but have changed in different ways or at different rates in different regions (e.g., wintering versus breeding area) or periods (Walther et al., 2002). Thus, global climate change also disrupts the correlated environmental variables under which physiological control mechanisms have evolved.

2 Is advancement of laying date adequate?

Over the past several decades, an advancement in laying date has been reported for many bird species (Crick et al., 1997; McCleery and Perrins, 1998; Brown et al., 1999; Both and Visser, 2001), although, we stress, not for all populations studied (Visser et al., 2002). For instance, Crick et al. (1997) analyzed data on laying date for 65 British species over the period 1971–1995, and found that the date had advanced significantly in only 20 (31%). One might wonder about the lack of advancement in the other 69%; but our

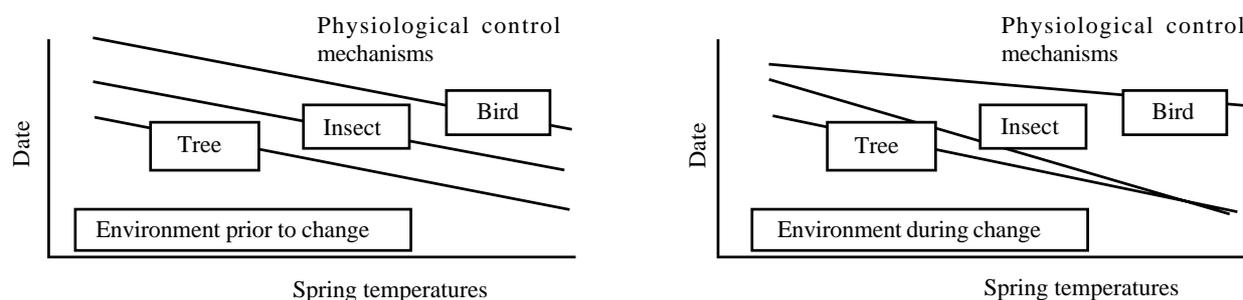


Fig. 1 Schematic responses of different levels of the food chain to climate

The phenology of the different levels is affected differently by climate change. Prior to climate change, the physiological control mechanisms of bud burst in trees, of egg hatching date in insects and of laying date in birds responded equivalently to annual environmental conditions such that the phenology of the different levels in the food chain were synchronized. Climate change alters the relationships between the weather variables that affect different parts of the food chain, destabilizing the pre-adapted physiological control mechanisms, leading to mistimed reproduction in warmer springs.

concern here is whether the advance in the 31% that did shift was sufficient to match the shift in the period of favorable conditions for reproduction. This all important question has rarely been considered so far.

How can it be determined whether a shift in laying date has been sufficient? Three practical procedures may be employed, each illustrated by our own work on the great tit population of the Hoge Veluwe National Park, The Netherlands.

2.1 Comparison of changes in phenology at different levels in the food chain

The synchronization of avian phenology with the phenology of underlying levels in a food chain is an important selection pressure on the timing of avian reproduction (Perrins, 1970). To assess whether shifts in laying date are sufficient, they have to be compared with phenological change in the underlying levels. For example, a primary mediator of the timing of reproduction in many bird species is synchronization of offspring needs with an abundance of food. For great tits in the Hoge Veluwe, the key prey are caterpillars on oak (*Quercus robur*) trees. We have measured caterpillar biomass there from 1985 onwards, and can thus compare changes in the date of maximum food abundance for great tits with changes in laying date. There has been a significant advance in the date of maximum biomass, but great tits have not advanced their laying date (Visser et al., 1998). Hence, the degree of asynchronization (the difference between the food peak and mean date at which the nestlings are 10 days old) has increased: the birds now lay too late to profit fully from the short period in which caterpillars are abundant (Fig. 2).

2.2 Calculating the strength of the selection on phenology

A second method for estimating the adequacy of catchup in the timing of reproduction is to determine whether the strength of directional selection for early laying has changed over time. If advancement of laying date is inadequate, early-nesting birds would be expected to produce increasingly more and better quality offspring than

late-laying birds. This can be quantified by calculating selection differentials. The selection differential for laying date is the difference between (a) the mean date of laying of first clutches weighted for the number of recruits produced per female over the entire season, and (b) the unweighted mean laying date of first clutches. If this value shifts to the negative over time, there is increased selection for earlier laying; early laying great tits will produce more recruits in the following year than late laying birds. For the Hoge Veluwe great tits, there is a clear decrease in selection differentials for laying date (Fig. 2; Visser et al., 1998). In the early years of the study, there was no directional selection (selection differentials around 0) whereas it is now negative, again indicating that the birds, on average, have been laying too late in recent years.

2.3 Monitoring changes in reproductive behavior

The third method investigates changes in bird behavior. Birds may shorten the duration of their reproductive attempt to compensate for laying late. In great tits, selection acts strongly on hatching date, and thus birds may attempt to shorten the time interval between laying and hatching. Laying smaller clutches achieves this, and so does advancing incubation into the laying period, shortening the time to hatching the first-laid egg). The Hoge Veluwe great tits have not changed their mean clutch size (Visser et al., 1998) but they have shortened their incubation period (between laying the last egg and hatching the first) by about 1.5 days (Fig. 2). Although shortening of incubation is an indication that the tits have not advanced their laying date sufficiently, it is not necessarily an indication of mistiming. The birds may reduce their incubation period as part of an adaptive response to reduce mistiming between hatching date and food peak, such as when the fitness costs of laying a few days earlier are higher than the fitness costs of a shorter incubation period.

Another indicator of insufficient advancement in laying date is the within-individual change in laying date from year to year. Birds that have experienced a mismatch between offspring needs and food abundance in one year should shift their laying date in the following year (Grieco

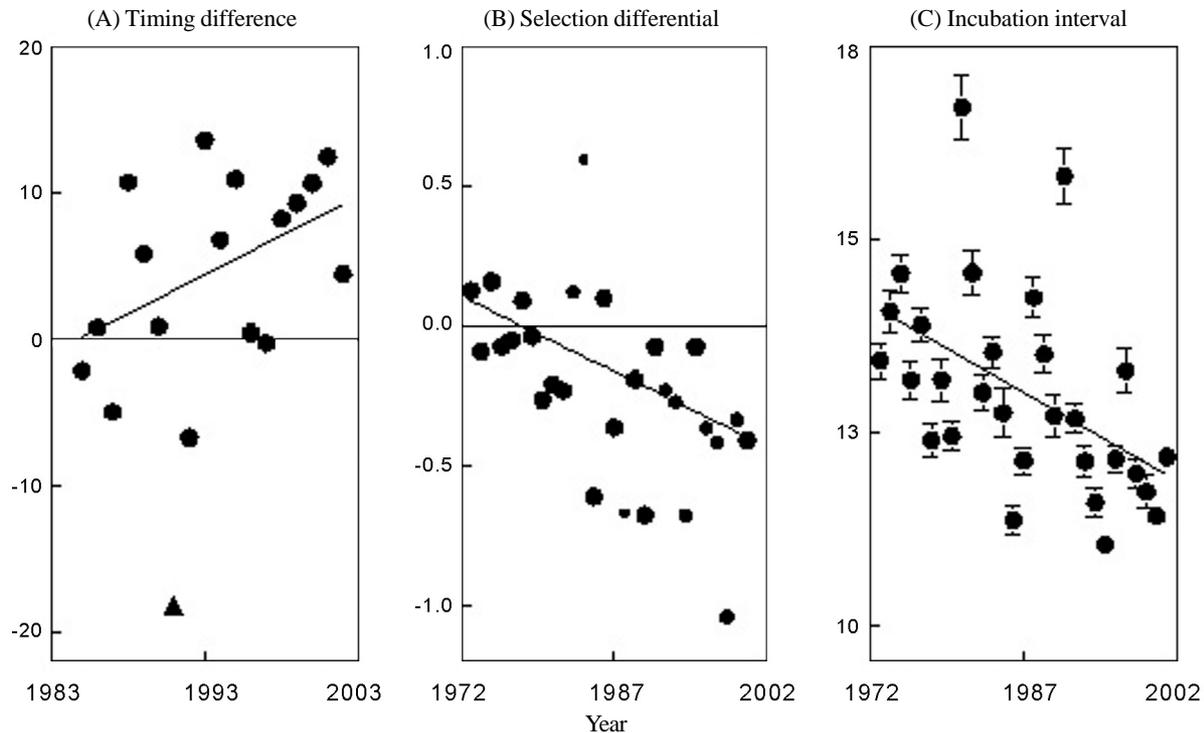


Fig. 2 Mistiming of breeding cycle due to global climate change in a great tit population (Hoge Veluwe, The Netherlands)

(A) The date of maximum food abundance (as measured by frass production of caterpillars) has advanced while the laying date of the great tits has not over 1985–2002, excluding 1991, ($F_{1,15} = 4.15$, $P = 0.06$) (Visser et al., 1998); as a consequence the difference in timing between the date of maximum food abundance and the mean date at which the great tit nestlings are 10 days old has become positive — great tits are too late (▲: a late frost, with damaged the oak leaves). (B) The selection differential for laying date (see text) has become more negative over 1973–2000 ($F_{1,25} = 11.9$, $P = 0.002$); here early-laying great tits tend to produce more recruits than late-laying birds (symbol size indicates the relative sample size for each point). (C) The duration of the incubation period [defined as hatching date of the first egg minus (laying date of the first egg + clutch size), s.e. indicated] has decreased over 1973–2001 ($F_{1,27} = 8.61$, $P = 0.007$); great tits “speed up” reproduction.

et al., 2002). Thus, if the majority of the birds in a population lay earlier than in the previous year, this can also be taken as an indication that their laying in the previous year was, on average, too late.

3 Insufficient advancement of laying date in Hoge Veluwe great tits

3.1 Hypothesis

It is clear that laying date advancement in the Hoge Veluwe great tit population is not keeping up with the advancement of peak caterpillar biomass. Why then has egg-laying not advanced over the years? Involved here are two conditions — one during early spring (time of decision-making) and the other in late spring (selection for synchrony between offspring needs and prey abundance) — which may have changed at different rates. Two hypotheses have been put forward in explanation: (1) Netherlands great tits currently possess a non-adaptive physiological control mechanism for laying; and (2) there are now more severe resource constraints at the time of egg formation (Visser et al., 1998; Stevenson and Bryant, 2000).

The underlying problem for these hypotheses in the Netherlands is that increase in temperature has not been

uniform over the entire spring period. Early spring has not become warmer, while late spring has (Visser et al., 1998). Therefore, the existing correlations between climate variables have changed and hence the physiological control mechanism may no longer be adaptive (cue hypothesis 1). Selection may operate on the control mechanism, given that there is sufficient additive genetic variation, and an advancement of laying date still may occur. Alternatively, due to the lack of increase in early spring temperatures, the food availability for the females during egg production has not advanced and hence there may not be enough resources to lay any earlier without severe fitness consequences (constraint hypothesis 2). Under this scenario, the birds will not be able to advance their laying and hence mistiming will continue.

There are various ways to test these hypotheses. If experimental birds can be manipulated to lay earlier than controls, they would be predicted to do better than under the cues hypothesis and worse under the constraint hypothesis, because then there would be a price to pay for having chicks in the nest at peak caterpillar abundance. It might be reflected in lower post-breeding survival, or even before and during egg laying, when conditions are harsh. The challenge here will be to manipulate birds such that

they have to pay the full costs of egg production (i.e., without supplying them with extra food, etc.). Such experiments are underway at the Hoge Veluwe.

3.2 Generality of the phenomenon

How widespread is the holdup in egg laying in great tits? To assess this we compared populations of great tits across Europe. Climate has not changed uniformly there. In the north and east there has been little or no increase in warming through the spring period, while food chains in the south are much less temperature dependent. Furthermore, only late spring temperatures have risen on mainland western Europe, whereas in Britain there has been a rise in early spring as well. When we compared advancement in laying dates across in 14 regional *Parus* populations, we found significant variation among study sites (Visser et al., 2003). No change was recorded in the north and east, nor on Corsica in the south. Nor could the variation in changes of laying dated in Belgium, The Netherlands and Britain be attributed to differences in spring temperatures across the board. Populations spatially close to each other even differed in the degree of advancement.

A clear correlation with climate change was nevertheless found in a shift in another life-history trait: in populations in which the production of second clutches has declined, there has been no advancement of laying date (Visser et al., 2002). This is evidence that the lack of advancement of laying date on the Hoge Veluwe is related to area or population specific characteristics, and fits in with a general pattern of shift in laying dates across Europe.

4 Discussion

Climate change can lead to a disruption of synchrony through the different levels of the food chain. For the Hoge Veluwe great tits this may be caused by a differential change of temperature in early and late spring, rather than an increase in spring temperatures *per se*. Such disruptions have also led to mistiming in another bird, the pied flycatcher (*Ficedula hypoleuca*) and an important prey species, the winter moth (*Operophtera brumata*). The flycatcher has suffered a change in climate across its breeding grounds but not in its wintering area (Both and Visser, 2001); and for the moth, there has been an increase in spring temperature but no change in the number of days with temperatures below zero during the winter, two parameters which determine winter moth phenology (Visser and Holleman, 2001).

As we found mistiming in all three species that we studied (great tit, pied flycatcher, winter moth), we suspect that this is a very general phenomenon. We wish to encour-

age researchers to look at their own biological systems with this in mind, and to try to use the three different procedures described here to assess responses in changes of laying dates. Only by gathering further more examples will it be possible to determine how general are the patterns described here. Comparing different biological systems is also an important tool towards understanding the shifts in phenology which are becoming so widely observed, a prerequisite to predict how climate change will affect food chains, and thereby biodiversity and ecosystem function.

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