Large-scale geographical variation confirms that climate change causes birds to lay earlier.

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Large-scale geographical variation confirms that climate change causes birds to lay earlier


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1-INTRODUCTION

There is now compelling correlational evidence that many organisms have responded to climate change by advancing their phenology during the past few decades (Stenseth et al. 2002; Walther et al. 2002; Parmesan & Yohe 2003). However, one potential problem with these correlational studies is that there may be a publication bias towards reporting advances because of the general expectation that climate change should cause advancements, rather than no trends, or even delays. The other problem is that, for most species, it is difficult to assess whether it is really climate change that causes the observed advancement, rather than other environmental changes. Although the general pattern in published responses is consistent with the direction predicted by climate change, there are many organisms for which no response has been found. For instance, in birds 78 out of 168 studied species have...
advanced their breeding date over recent decades, whereas 14 species delayed their breeding date (Parmesan & Yohe 2003). Moreover, within species some populations show strong advancements, whereas other populations lack such a response (Visser et al. 2003). Such discrepancies could be a result of spatial variation in the direction of temperature trends in recent years, but this has not previously been demonstrated. The mechanisms causing the generally observed advancement of laying date can be examined by focusing on this intraspecific variation in response to climate change, and may reveal under which ecological circumstances populations are most vulnerable to the effects of climate change. We address the question of why populations of the same bird species differ in their advancement of breeding date over the past two decades by using all of the available population data, thereby circumventing the problem of publication bias. Geographical variation in both the extent of the advancements, and the trends in ambient temperature, are used to assess whether climate change really does cause any advancement in breeding date. Our within-species comparison is especially informative, because it shows why different populations respond differently to climate change and how spatial variation in climate change hampers adaptation over a large geographical scale.

Data were used from 23 long-term studies of pied flycatcher, Ficedula hypoleuca, populations and two populations of the closely related collared flycatcher, F. albicollis. In total, we monitored approximately 40,000 nests. Both species are small (12–13 g), insectivorous passerines, which breed in the forests of Europe and western Asia and winter in tropical Africa. They both readily breed in nest-boxes, and this fact has made it easy to obtain comprehensive information on their reproduction and long-term population data over almost their entire breeding range. Significant advances in laying date have been reported in three long-term studied populations (Winkel & Hudde 1997; Slater 1999; Both & Visser 2001) whereas data from two further populations showed no significant trend towards earlier laying (Sanz et al. 2003).

2. MATERIAL AND METHODS

To avoid any reporting bias in the response of flycatcher populations to climate change, we used all populations for which accurate laying dates had been collected for at least 10 years during the period 1990–2002. Longer time-series are used from only 1980 onwards, since most warming occurred after this year (IPCC 2001). In the study sites nest-boxes were checked weekly from 2000 onwards, since most warming occurred after this year (IPCC 2001). In the study sites nest-boxes were checked weekly from 2000 onwards, since most warming occurred after this year (IPCC 2001). To avoid any reporting bias in the response of flycatcher populations to climate change, we used all populations for which accurate laying dates had been collected for at least 10 years during the period 1990–2002. Longer time-series are used from only 1980 onwards, since most warming occurred after this year (IPCC 2001). In the study sites nest-boxes were checked weekly from 2000 onwards, since most warming occurred after this year (IPCC 2001). In the study sites nest-boxes were checked weekly from 2000 onwards, since most warming occurred after this year (IPCC 2001).

(a) Analyses

For each study site we performed a linear regression to assess trends in laying date, clutch size and temperature over the years of study. The slopes from the regression analyses were used to assess whether the trends in laying date and clutch size over time were determined by the degree of warming on a local scale. We used linear regression to investigate whether trends in bird breeding parameters over time were affected by trends in temperature. In some cases, study sites were close to each other, but we regarded them as independent populations because, from other species, we know that on such a small spatial scale populations can also differ in whether laying date advanced over the years (Visser et al. 2003). Furthermore, if we constrain the analysis to a single data point per species per country, this does not alter our conclusion (n = 11; areas with the longest time-series and largest sample size were chosen, linear regression: $F_{1,9} = 8.40, p = 0.018, r^2 = 0.48$, analysis as in figure 1).

3. RESULTS AND DISCUSSION

Annual population laying date ($\alpha = 0.05$) advanced significantly over the years in nine out of our 25 populations, and 20 out of 25 populations showed a significant effect of local spring temperature on laying date (see Appendix A). Overall, there was a strong correlation between the change in local spring temperature on a study site and the extent of advancement in laying date: in areas that became colder, laying date delayed over the years, whereas the more that the temperature at a site increased, the stronger laying date advanced (figure 1). This pattern strongly supports the idea that the observed trends in laying date over time are indeed caused by climate change, as the more the local climate warms the more the laying date advances. In areas with a larger increase in temperature, clutch size also increased more over the years (linear regression, all populations $F_{1,10} = 7.01, p = 0.02$; populations started 1980–1981: $F_{1,12} = 4.92, p = 0.047$), probably as a consequence of the reported strong effect of...
Climate change and avian laying date

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Figure 1. Location of sites of long-term studied flycatcher populations in Europe. The colours show the trend in temperature: blue, trends towards colder springs; yellow, mild warming (trend between 0 and +0.08 °C yr⁻¹); red, strong warming (greater than 0.08 °C yr⁻¹). The filled symbols are for flycatcher populations with a significant advancement of laying date over the years, the populations at the open symbols showed no significant laying date trends over the years. Numbers correspond with numbers in the inset and Appendix A. Inset: the population response of laying date over the years in relation to the local temperature trend over time. Each symbol represents one population. Filled symbols are from populations for which data were available between 1980/81 and 1999 or later, open symbols are for populations that had a later start of the study. Linear regression shows that populations in areas with a stronger increase in temperature advance their laying date more over the years (all populations: \( F_{1,23} = 40.59, p < 0.0001, r^2 = 0.64; \) populations begun in 1980/81: \( F_{1,15} = 72.31, p < 0.0001, r^2 = 0.83 \)).

Laying date on clutch size (trends in clutch size and laying date over time were correlated: \( r = -0.46, n = 22, p = 0.03 \)) (Both 2000; Przybylo et al. 2000; Sheldon et al. 2003). Although based on correlations, these data strongly support the contention that climatic warming causes these flycatchers to lay earlier and lay more eggs.

Flycatchers lay earlier when the spring is warmer, but how do they manage? These birds spend the winter in Africa, and return shortly before the breeding season in their breeding area, which may constrain a response to local climate. In The Netherlands, the time between arrival and laying became shorter, and the advancement of the population laying date could be mostly attributed to the phenotypic responses of individuals in response to local temperature (Both & Visser 2001), rather than to a genetic response on changed selection for laying date. Despite the advancement in laying date, selection for early laying increased, and the observed response to climate change is apparently not enough to track the advancement in the environment. Because birds currently lay shortly after arrival, arrival is probably the constraint in further adaptation to climate change. Adaptation to climate change in these long-distance migrants requires changes in the annual programme for the timing of migration (Coppack & Both 2002).

The relationship between advancement of laying date and the increase in temperatures suggests that flycatchers can cope with the observed global warming, and perhaps even profit from it, because they are able to produce more offspring as clutch size also increases (Bairlein & Winkel...
APPENDIX A

Basic information on study areas and time-series of flycatcher population studies. ID refers to the numbers in figure 1. Slopes of the regression of laying date (ld), clutch size (cs) and temperature (temp) upon year are given together with the effect of temperature on laying date. Linear regression statistics are given for the effects of year on laying date and temperature, and on the effect of temperature on laying date; ld–year stats are for the five first study years. (Country codes: E, Spain; CH, Switzerland; NL, The Netherlands; D, Germany; S, Sweden; SF, Finland.)

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<th>Last year</th>
<th>Total number of years</th>
<th>Total number of broods</th>
<th>Mean clutch size</th>
<th>Mean temperature °C</th>
<th>Mean laying date</th>
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## Appendix A. (Continued.)

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<th>slope ld-year</th>
<th>slope cs-year</th>
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<td>−0.284</td>
<td>0.0114</td>
<td>0.026</td>
<td>2.700</td>
<td>2.700</td>
<td>3.06</td>
<td>0.013</td>
<td>3.06</td>
</tr>
</tbody>
</table>

**Climate change and avian laying date**

C. Both and others 1661
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