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

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Advances in the phenology of organisms are often attributed to climate change, but alternatively, may reflect a publication bias towards advances and may be caused by environmental factors unrelated to climate change. Both factors are investigated using the breeding dates of 25 long-term studied populations of *Ficedula* flycatchers across Europe. Trends in spring temperature varied markedly between study sites, and across populations the advancement of laying date was stronger in areas where the spring temperatures increased more, giving support to the theory that climate change causally affects breeding date advancement.

Keywords: life history; laying date; clutch size; climate change; *Ficedula hypoleuca*; *Ficedula albicollis*

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

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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 in most instances, and the laying date of each nest was calculated assuming that one egg was laid every day. In cases where the laying date could not be determined in this way, but the hatching date was known (in only three study sites, and a rather small percentage of nests within these sites), we calculated the laying date by assuming 13 days of incubation (beginning on the last egg) and again, that one egg was laid per day. For each year and study site combination, we calculated the median laying date and the arithmetic mean clutch size (clutch size was not known for all populations). Only first broods were included, which excluded broods of females that were previously known to have started a brood in that year, as well as broods that were started later than 30 days after the very first brood in that year for each study site. The first year that nest-boxes were provided on a study site is excluded from the analyses, because newly established populations contain a high proportion of young birds that tend to lay later in the season (Lundberg & Alatalo 1992).

Study sites covered most of the species' breeding range, from Spain in the south to northern Finland in the north, and from Wales in the west to Moscow in the east. Study sites were not spread evenly over Europe because we used existing datasets collected for other purposes. Daily mean temperatures were obtained from meteorological stations close to the study sites. Populations at different latitudes breed at different dates, and are therefore expected to respond to temperatures at different times of year. We do not know precisely the periods over which breeding flycatchers respond to temperatures, so to obtain an objective period over which we calculated the temperatures, we used the 30 day period before the mean of the median laying date in the first 5 years of each study (Visser *et al.* 2003). This period approximately covers the arrival and start of the laying period of most birds in the population. The initial year of the study varied between study populations, and consequently the 5 year period differed. This may bias the results, and therefore we present a separate analysis of only the populations that were started in 1980 or 1981. In some cases, study sites in close proximity show different trends in temperatures because the years for which data were available differed (most notably the two areas in southern Sweden), and for each area we included only the years for which laying dates were available in the calculation of the temperature trend.

(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 $F_{1,20} = 7.01$, $p = 0.02$; populations started 1980–1981: $F_{1,12} = 4.92$, $p = 0.047$), probably as a consequence of the reported strong effect of

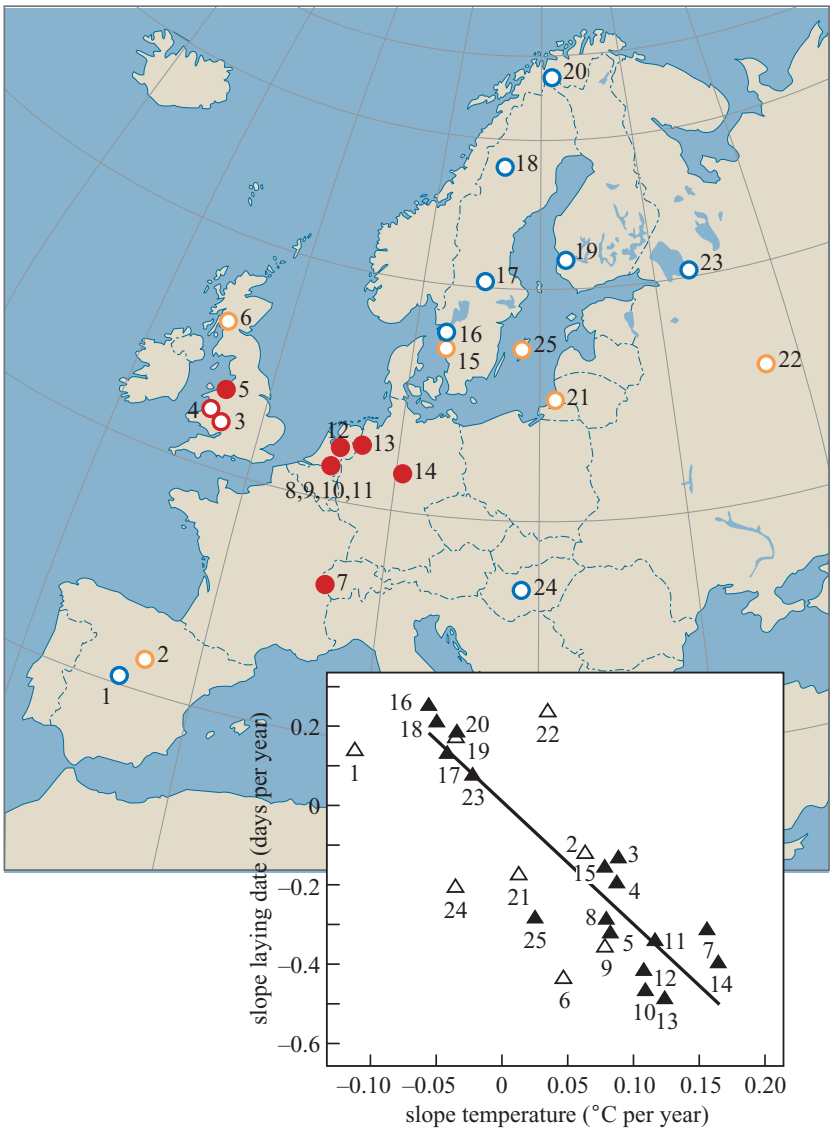

Figure 1. Location of sites of long-term studied flycatcher populations in Europe. The colours show the trend in temperature: blue, trends towards colder springs; yellow, mild warming (trend between 0 and +0.08 °C yr^{-1}); red, strong warming (greater than 0.08 °C yr^{-1}). The filled symbols are for 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

2001). Whether these birds can cope with global warming depends, to a large extent, on whether they can track the advancement of their main food supplies. In one Dutch population we found that the advancement of laying date was indeed not strong enough to track the advancement of spring (Both & Visser 2001). In the Spanish pied flycatcher populations' laying date did not advance, but the phenology of vegetation did, and probably prey abundance also advanced, leading to a decline in reproductive success (Sanz *et al.* 2003). The reproductive success of the collared flycatchers on Gotland also declined which, it was suggested, was caused by an inappropriate response to advancement of prey availability (Merila *et al.* 2001). The observed increase in clutch size as a response to rising temperatures does not automatically lead to a higher reproductive success, and the genetic correlation between laying date and clutch size (Sheldon *et al.* 2003) may no longer be adaptive under the present environmental change. The current evidence suggests that flycatchers suffer, rather than benefit from climate change, at least at existing rates of change.

Flycatchers clearly respond with their laying date to climate change, but a similar analysis for the great tit *Parus major* and blue tit *P. caerulescens* populations over Europe reveals a more varied pattern. As in the flycatchers, north European and Mediterranean populations did not advance their laying date because temperatures did not increase, but within western Europe populations differed markedly in whether they advanced their laying date despite the general increase in local temperature (Visser *et al.* 2003). Tree swallows in North America also differed geographically in their response to local climate change, but the cause is unknown (Dunn & Winkler 1999). The reason for this interspecific and intraspecific variation in response to climate change is unclear, but the similarity between tits and flycatchers is that the response to climate change is, in most cases, less than the advancement of their food availability (Visser *et al.* 1998; Both & Visser 2001; Sanz *et al.* 2003; Cresswell & McCleery 2003). The observed variation among species in their response to climate change (Crick *et al.* 1997; Crick & Sparks 1999; Dunn & Winkler 1999; Winkler *et al.* 2002; Parmesan & Yohe 2003; Visser *et al.* 2003) may thus depend on the variation in local temperature trends and the specific ecology of the species concerned. Our results indicate that publication bias may be a minor problem, and that advancements of laying date observed in several species are indeed caused by climate change.

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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 5–years is the mean of the median laying during the first five study years. (Country codes: E, Spain; CH, Switzerland; NL, The Netherlands; D, Germany; S, Sweden; SF, Finland.)

species	ID	country	area	latitude	longitude	first year	last year	n	total broods	ld 5–years	slope ld–year	slope cs–year	slope temp–year	slope ld–temp	stats ld–year	stats temp–year	stats ld–temp
PF	1	E	La Hiruela	41°04′ N	03°27′ W	1985	2001	17	1160	23 May	−0.124	0.0044	0.064	−1.286	$F_{1,15} = 0.51$, $p = 0.48$	$F_{1,15} = 0.55$, $p = 0.47$	$F_{1,15} = 10.39$, $p = 0.006$
PF	2	E	Valsain	40°48′ N	04°01′ W	1992	2002	12	1260	30 May	0.136	0.0006	−0.112	−0.779	$F_{1,10} = 0.14$, $p = 0.72$	$F_{1,10} = 0.56$, $p = 0.47$	$F_{1,10} = 0.1.06$, $p = 0.33$
PF	3	Wales	Abergwyngregyn	53°13′ N	04°00′ W	1981	2002	22	982	13 May	−0.319	−0.0058	0.083	−2.336	$F_{1,20} = 4.90$, $p = 0.039$	$F_{1,20} = 5.61$, $p = 0.029$	$F_{1,20} = 9.46$, $p = 0.006$
PF	4	Wales	Maentwrog	52°57′ N	03°59′ W	1980	2001	22	240	8 May	−0.034	0.0197	0.095	−0.767	$F_{1,20} = 0.07$, $p = 0.79$	$F_{1,20} = 8.49$, $p = 0.009$	$F_{1,20} = 1.24$, $p = 0.28$
PF	5	Wales	Llanwrthwl, Powys	52°13′ N	03°27′ W	1980	2002	21	820	13 May	−0.132	−0.0169	0.089	−1.417	$F_{1,19} = 1.82$, $p = 0.19$	$F_{1,19} = 7.86$, $p = 0.011$	$F_{1,19} = 7.21$, $p = 0.015$
PF	6	Scotland	Loch Lomond	56°15′ N	04°36′ W	1992	2002	11	183	17 May	−0.436	−0.0027	0.047	−1.135	$F_{1,9} = 3.69$, $p = 0.087$	$F_{1,9} = 0.32$, $p = 0.58$	$F_{1,9} = 1.32$, $p = 0.28$

Appendix A. (*Continued.*)

species	ID	country	area	latitude	longitude	first year	last year	*n*	total broods	ld 5–years	slope ld–year	slope cs–year	slope temp–year	slope ld–temp	stats ld–year	stats temp–year	stats ld–temp
PF	7	CH	Baulmes	46°47′ N	06°31′ E	1980	2002	23	352	18 May	−0.312	0.0056	0.157	−1.517	$F_{1,21}=8.28$, $p=0.009$	$F_{1,21}=10.77$, $p=0.004$	$F_{1,21}=19.71$, $p<0.001$
PF	8	NL	Buunderkamp	52°01′ N	05°45′ E	1984	2002	17	870	12 May	−0.358	0.0146	0.079	−1.518	$F_{1,15}=10.42$, $p=0.006$	$F_{1,15}=1.62$, $p=0.22$	$F_{1,15}=13.11$, $p=0.003$
PF	9	NL	Deelerwoud	52°05′ N	05°55′ E	1980	2002	22	662	11 May	−0.342	—	0.118	−2.105	$F_{1,20}=10.36$, $p=0.004$	$F_{1,20}=7.33$, $p=0.014$	$F_{1,20}=41.10$, $p<0.001$
PF	10	NL	Hoge Veluwe	52°02′ N	05°51′ E	1980	2002	23	2299	14 May	−0.466	0.0329	0.110	−1.887	$F_{1,21}=28.30$, $p<0.001$	$F_{1,21}=5.20$, $p=0.033$	$F_{1,21}=28.11$, $p<0.001$
PF	11	NL	Staphorst	52°37′ N	06°17′ E	1980	2002	23	5462	12 May	−0.417	0.0340	0.108	−1.764	$F_{1,21}=24.12$, $p<0.001$	$F_{1,21}=4.97$, $p=0.037$	$F_{1,21}=28.89$, $p<0.001$
PF	12	NL	Warnsborn	52°00′ N	05°51′ E	1980	2002	23	367	11 May	−0.287	0.0123	0.080	−1.229	$F_{1,21}=9.12$, $p=0.007$	$F_{1,21}=5.31$, $p=0.032$	$F_{1,21}=7.54$, $p=0.012$
PF	13	D	Lingen	52°27′ N	07°15′ E	1980	2002	21	1922	16 May	−0.489	0.0289	0.124	−1.267	$F_{1,21}=43.52$, $p<0.001$	$F_{1,21}=5.21$, $p=0.033$	$F_{1,21}=11.43$, $p=0.003$
PF	14	D	Harz	51°53′ N	10°37′ E	1980	2002	23	910	17 May	−0.397	0.0428	0.166	−1.230	$F_{1,21}=19.59$, $p<0.001$	$F_{1,21}=7.26$, $p=0.014$	$F_{1,21}=20.63$, $p<0.001$
PF	15	S	Goteborg	57°43′ N	11°58′ E	1980	2000	17	681	25 May	−0.157	0.0160	0.079	−0.790	$F_{1,15}=4.01$, $p=0.064$	$F_{1,15}=2.08$, $p=0.17$	$F_{1,15}=5.76$, $p=0.030$
PF	16	S	Gunnebo	57°40′ N	12°05′ E	1980	1998	19	529	22 May	0.249	—	−0.056	−1.501	$F_{1,17}=2.27$, $p=0.15$	$F_{1,17}=0.62$, $p=0.44$	$F_{1,17}=10.23$, $p=0.005$
PF	17	S	Borlange	60°23′ N	15°30′ E	1981	1999	19	503	26 May	0.128	—	−0.042	−1.415	$F_{1,17}=0.73$, $p=0.41$	$F_{1,17}=0.37$, $p=0.55$	$F_{1,17}=11.84$, $p=0.003$
PF	18	S	Amernas	65°58′ N	16°13′ E	1980	2002	23	2475	2 Jun	0.207	—	−0.050	−2.290	$F_{1,21}=2.49$, $p=0.13$	$F_{1,21}=1.01$, $p=0.33$	$F_{1,21}=55.02$, $p<0.001$
PF	19	SF	Harjavalta	61°20′ N	22°10′ E	1992	2002	11	1509	28 May	−0.365	0.0233	0.067	−1.636	$F_{1,9}=0.70$, $p=0.42$	$F_{1,9}=0.13$, $p=0.73$	$F_{1,9}=7.71$, $p=0.022$
PF	20	SF	Kilpisjärvi	69°03′ N	20°50′ E	1980	2002	23	795	8 Jun	0.181	−0.0094	−0.034	−2.841	$F_{1,21}=1.05$, $p=0.32$	$F_{1,21}=0.58$, $p=0.45$	$F_{1,21}=22.27$, $p<0.001$
PF	21	Russia	Rybachy	55°05′ N	20°44′ E	1982	2002	21	954	24 May	−0.176	−0.0079	0.013	−1.813	$F_{1,19}=1.36$, $p=0.26$	$F_{1,19}=0.06$, $p=0.81$	$F_{1,19}=12.12$, $p=0.003$
PF	22	Russia	Zvenigorod	55°44′ N	36°51′ E	1988	2002	15	1293	18 May	0.232	0.0047	0.035	−0.800	$F_{1,13}=1.96$, $p=0.18$	$F_{1,13}=0.10$, $p=0.76$	$F_{1,13}=4.45$, $p=0.055$
PF	23	Russia	Karelia	60°58′ N	32°59′ E	1980	2002	23	2200	28 May	0.073	0.0004	−0.022	−1.376	$F_{1,21}=0.32$, $p=0.57$	$F_{1,21}=0.22$, $p=0.64$	$F_{1,21}=7.02$, $p=0.015$
CF	24	Hungary	Pilis mountains	47°10′ N	19°09′ E	1983	2002	16	1555	6 May	−0.207	0.0045	−0.035	−0.229	$F_{1,14}=2.58$, $p=0.13$	$F_{1,14}=0.26$, $p=0.62$	$F_{1,14}=0.19$, $p=0.67$
CF	25	S	Gotland	57°10′ N	18°20′ E	1981	2002	22	10487	26 May	−0.284	0.0114	0.026	−2.700	$F_{1,20}=3.06$, $p=0.096$	$F_{1,20}=0.24$, $p=0.63$	$F_{1,20}=38.23$, $p<0.001$

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