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Climatic effects on arrival and laying dates in a long-distance migrant, the Collared Flycatcher *Ficedula albicollis*

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Long-distance migrants may respond to climate change in breeding, wintering or staging area by changing their phenology. The geographical variation in such responses (e.g. coastal vs. continental Europe) and the relative importance of climate at different spatial scales remain unclear. Here we analysed variation in first arrival dates (FADs) and laying dates of the Collared Flycatcher *Ficedula albicollis* in a central European population, from 1973 to 2002. The North Atlantic Oscillation (NAO) index correlated weakly with local temperature during the laying period. Decreasing spring temperatures until 1980 were associated with a trend towards later laying. The rate of warming (0.2 °C per year) and laying advancement (0.4 days per year) since 1980 are amongst the highest values reported elsewhere. This long-term trend in laying date was largely explained by the change in climatic factors. The negative effect of local spring temperature on laying was relatively stronger than that of NAO. The number of clutches initiated on a particular day was marginally affected by the temperature 3 days prior to laying and the response of females to daily variation in temperature did not change over years. Correspondence between the average population-level and the individual-level responses of laying date to climate variation suggests that the advancement of laying was due to phenotypic plasticity. Despite warmer springs and advanced laying, FADs did not change over years and were not correlated with local spring temperature. Marginal evidence suggests later departure from wintering grounds and faster migration across staging areas in warmer conditions. Advancement of arrival was probably constrained by low local temperatures in early spring just before arrival that have not changed over years. The interval between first arrival and laying has declined since 1980 (0.5 days per year), but the increasing temperature during that period may have kept the food supply approximately unchanged.

Good evidence exists for global warming, especially during the past two decades (Watkinson *et al.* 2004). Many bird species have responded to rising temperature by changing their phenology (Crick 2004), although such adjustments are not always sufficient to cope with change in phenology of food supply (Visser & Both 2005). The best documented responses include earlier spring migration and arrival times (Tryjanowski *et al.* 2002, Hüppop & Hüppop 2003, Hubálek 2004, Sparks *et al.* 2005) and laying dates (Crick & Sparks 1999), but effects on breeding success (Both & Visser 2001, Saino *et al.* 2004a, Weatherhead 2005), morphology (Kanuščák *et al.* 2004), covariation of multiple life-history traits (Both & Visser 2005), demography (Sæther *et al.* 2003, Both *et al.* 2006) and interspecific competition (Sætre *et al.* 1999) also have been reported. The degree of such responses varies not only among species (Crick & Sparks 1999, Torti & Dunn 2005), but also within species (Sanz 2003, Visser *et al.* 2003, Both *et al.* 2004), the latter being partly attributable to spatial variation in rates of warming. Birds respond to climate variation at different spatial scales and during different parts of their life cycle. Increasing evidence suggests that conditions at wintering grounds (Saino *et al.* 2004a, 2004b, Gordo *et al.* 2005) and along the migratory flyways (Ahola *et al.* 2004, Both *et al.*

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2005, Hüppop & Winkel 2006, Zalakevicius *et al.* 2006) also influence phenology and breeding in long-distance migrants.

Although the overall patterns of climate variation and the associated changes in avian phenology are now reasonably well documented for many species, several aspects deserve more attention. Because the rate of climatic change is not uniform (Hurrell 1995, Watkinson *et al.* 2004), we expect that phenology data may not be adequately described by single linear trends over the long term, but quantitative tests of this are rare (e.g. McCleery & Perrins 1998, Crick & Sparks 1999). Little is known about the relative importance of climate variation at different spatial scales because most previous studies have related phenology or breeding performance to either local weather or large-scale climate phenomena, such as the North Atlantic Oscillation (NAO). The NAO-index is a good predictor of local climate in coastal areas over northwest Europe (Stenseth *et al.* 2003), where the majority of studies have been performed and where the influence of NAO may differ from that in more continental locations (Sanz 2003, Menzel *et al.* 2005). Another problem associated with some previous analyses is the use of simple correlations to assess effects of multiple weather variables, while not accounting for their possible interactions. Little explored is whether the response of birds to within-season variation in temperature (Saino *et al.* 2004c) has changed over the years (Nussey *et al.* 2005). Finally, only a few studies have tried to discriminate between the two potential mechanisms of adjustment to climate – phenotypic plasticity (Przybylo *et al.* 2000, Saino *et al.* 2004a, Both & Visser 2005) and microevolutionary change (Berthold *et al.* 1992).

Here we analyse variation in arrival and laying dates recorded over a 30-year period in a central European population of Collared Flycatcher *Ficedula albicollis*. Compared with its congener, the Pied Flycatcher *F. hypoleuca*, the demography of the Collared Flycatcher is more strongly influenced by climate variation (Sætre *et al.* 1999). Yet, its phenology has received less attention, possibly because its geographical range is confined to central and eastern Europe, where long-term datasets are scarce (Bauer 2006). These two flycatcher species represent a suitable model offering new insights into climatic effects on phenology of long-distance migrants. Our goal was to extend the previous studies by asking whether the phenology patterns reported from populations of Pied Flycatchers across northwest (coastal) Europe apply to Collared Flycatchers in a more continental location. Specifically, we examined: (1) simultaneous effects of a large-scale climatic factor (NAO) and local temperature at breeding, wintering and staging areas on arrival and laying date; (2) correspondence between the average population-level and the individual-level responses of laying date to climatic factors; and (3) responses of laying females to day-to-day variation in ambient temperature and long-term changes in these responses.

MATERIALS AND METHODS

Study species and area

The Collared Flycatcher is a small (13-g), hole-nesting, insectivorous passerine breeding in deciduous forests of central and eastern Europe. The species is a long-distance migrant wintering in Africa south of the equator (Cramp & Perrins 1993). All data were collected in 1973–2002 during a long-term nestbox study running in central Moravia (49°50′N, 17°15′E), Czech Republic. The study plots are situated on SE–NW slopes at an altitude of 300–480 m. The area is mainly a managed deciduous forest (conifers < 1%) with trees 45–120 years old, dominated by Oak *Quercus petraea* (40%) and Beech *Fagus sylvatica* (40%). Plots were established in 1973 and the number of nestboxes increased steadily throughout the study period from 43 to 192 (annual mean 156). Nestboxes were provided at a density of about 6 boxes/ha, well above the breeding density of Flycatcher pairs (mean occupation rate 23%). Density varied from 0.9 to 2.0 pairs/ha (mean = 1.4) and did not show a directional trend over the years ($r = -0.12$, $n = 30$, $P = 0.52$). Breeding in natural holes was not recorded after providing nestboxes, but occurred regularly outside the study plots at a density of about 0.1 pairs/ha. For details of the breeding biology of the local population see Král (1982).

Field methods

Arrival dates were recorded each year by standardized daily visits to study plots from 10 April onward. The whole study area was checked less frequently before that date. For subsequent analyses we used only the first arrival date (FAD = the date when the first male was recorded, regardless of its activity), because we do not have quantitative data on the progress of arrival and territory occupation. Casual repeated captures of marked individuals revealed that many moved around the study area, including in non-forest habitats, during the first days after arrival. Contents of nestboxes were checked at least once every 5 days and the date of clutch initiation was then back-calculated from the number of eggs on the assumption that one egg was laid every day. In the analyses we included only first clutches; we excluded repeated clutches of the same female and repeated clutches in the same nestbox. We used the first laying date (FLD = the date when the first clutch in that year was initiated), the median laying date (MLD = median initiation date of the first clutches) and the length of FAD–FLD interval for each year. All nestlings and a variable proportion (limited by researchers' capacity) of breeding adults were marked each year with an individually numbered aluminium ring. The fieldwork was done by the same person (M.K.) and all field procedures were kept unchanged so we do not anticipate any systematic bias in accuracy of data over the study period.

Weather data

Local temperature was obtained from the weather station at Paseka (3 km from the centre of the study area, altitude 370 m). To evaluate landscape-scale representativeness of these local data we compared them with records from another weather station (Smržice, 37 km south of the study area, altitude 250 m) representing the same geographical unit of the upper part of the Morava river basin. In the analyses we used either daily means or their averages over a defined period. We determined the breeding temperature (T_{BREED}) as the average daily temperature for the 30 days before the mean of the median laying date in the first 5 years of the study (Both *et al.* 2004). This period (16 April–15 May) included the FAD and MLD in 26 and 27 years, respectively, during the 30-year study. The interval temperature ($T_{\text{mean FAD–FLD}}$) was defined as mean daily temperature averaged over the FAD–FLD interval each year. We used the sum of mean daily temperatures above 5 °C over the FAD–FLD interval (day-degrees; $T_{\text{sum FAD–FLD}}$) as a rough measure of potential development of vegetation and Flycatchers' invertebrate prey (Laaksonen *et al.* 2006). Temperature at FAD, FLD and MLD ($T_{\text{FAD,FLD,MLD}}$) was defined as mean daily temperature averaged over 5 days (days –4 to 0) before the focal date (day = 0) each year. Temperature data for the wintering area (T_{WIN}) and migration route (T_{MIG}) for the period 1973–2000 were obtained as mean country values (http://www.cru.uea.ac.uk/~timm/cty/obs/TYN_CY_1_1.html). We averaged February temperature for Malawi, Tanzania, Zambia and Zimbabwe, to represent the conditions in the wintering area (east-central Africa, south of the equator to about 20°S; Cramp & Perrins 1993) just prior to departure. We averaged March temperature for Egypt and Libya to represent the conditions encountered during the spring migration through the eastern Mediterranean. We cannot use more site-specific weather data because the exact wintering area and the migratory route of our population is unknown. The eastern route and the wintering areas in eastern Africa are generally less explored than those for the Pied Flycatcher because of the low recovery rates of ringed birds. Finally, we used the standardized NAO index (ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/tele_index.nh) averaged over the months December–March to represent large-scale climatic patterns for the region. The NAO is a natural, large-scale atmospheric fluctuation between the subtropical and the subpolar North Atlantic region. Positive values of the winter NAO-index are associated with relatively warm, moist winters in western and northern Europe, whereas negative values are associated with cold, dry winters in that region (Stenseth *et al.* 2003). We used winter NAO-index (1) because NAO is most pronounced during winter with long-lasting effects on subsequent spring conditions, and (2) to ensure comparability with previous studies (e.g. Przybylo *et al.* 2000).

Analyses

We performed simple linear regressions to evaluate trends in phenology and climatic variables over the years of the study. To assess whether the data were adequately described by a single linear trend, we first estimated potential breakpoints by fitting piecewise linear regression models (Neter *et al.* 1985) with four parameters (common intercept, two separate slopes, breakpoint). Next we refitted the piecewise model with a fixed value of the estimated breakpoint (i.e. with three estimable parameters) and tested improvement of its fit against the simple linear regression (two estimable parameters). Apart from this, we present separate linear regression analyses for both the entire study period (1973–2002) and the period after 1980, for the following reasons. First, climate change has become more pronounced since about 1980 (Hurrell 1995); secondly, trend estimates are sensitive to the starting point of data series (Sparks & Tryjanowski 2005) and our analyses suggested a change in the linear trend around 1980 for some variables; thirdly, previous analyses of other major datasets considered only the period after 1980 (Both *et al.* 2004); fourthly, by restricting analysis to the latter period we eliminated possible bias because the phenology of a newly established nestbox population may have differed from the phenology of an established population.

We used multiple linear regression to assess relationships between each phenology variable and year together with the four climate variables (T_{WIN}, T_{MIG}, T_{BREED}, NAO). The relative effect of year and each climate variable, controlled for effects of the remaining variables, was expressed by the partial correlation coefficient. We did not include breeding density as an additional predictor, but we present simple correlations between phenology variables and density. All the above analyses are cross-sectional using composite data from the population of Collared Flycatchers present in each year. To evaluate whether similar patterns were observed within individuals as those found at the population level, we conducted a longitudinal analysis of laying dates of individually marked birds by fitting a general linear mixed model (Proc Mixed; SAS Institute Inc. 2005). Details and advantages of this method over cross-sectional analysis are discussed by Przybylo *et al.* (2000). The response variable in our model was individual laying date, and the fixed effect predictors were the climate variables (T_{BREED} and NAO-index) and individual age (to control for possible age dependence of laying date). We modelled the random intercept for each female (to account for individual properties) and year of study (to account for the non-independence of observations from the same years) by entering individual identity and year as random effects, assuming variance-component covariance structure. In order to keep the model simple, we did not include the climate variables (T_{WIN}, T_{MIG}) that showed weak relationships with MLD in cross-sectional analysis. Of the original dataset (1051 laying dates) we included only those females that bred at least twice during 1980–2002 (119 females, 298 laying dates).

To visualize the link between phenology and within-season variation in mean daily temperature we calculated for each day a 'backward' 5-day running average (average for that day and the four preceding days). Before examining average trend across years, we centred days within each year at the focal day analysed (FAD/FLD/MLD = 0). To assess the effect of temperature on the number of first clutches initiated on each particular day during the laying period, we fitted generalized linear mixed models with a Poisson error distribution and log link function (Proc Glimmix; SAS Institute Inc. 2005). The fixed effect predictors were the mean temperature for the laying period (period between the first and the last initiation date of the first clutches in a given year), daily temperature (centred at the above annual mean) and interaction of these effects (removed from the final model because of non-significance; see Results). Included as fixed effects were the linear and squared terms of date, to account for seasonal unimodal distribution of clutch initiation dates, resulting from factors other than temperature. We modelled random intercepts and temperature slopes for each year of study by entering year and year × daily temperature interaction as the random effects, assuming an unstructured covariance matrix. Because we had no *a priori* predictions on the days before clutch initiation at which temperature has an effect, we fitted separate models for the temperature on individual days from day –1 (0 = clutch initiation) to day –5 and a model for temperature averaged over these 5 days. To assess the possibility that females respond to trend in temperature variation over the past days rather than its mean, we fitted a model where the predictor variable was the slope of linear regression of daily temperature on days –5 to –1.

Given the large number of examined relationships and a few *a priori* hypotheses, our analysis was largely exploratory and entirely correlational. We report unadjusted *P*-values for consistency with other studies, but we focus more on the values of correlation and regression coefficients as descriptive statistics. We do not adopt a step-wise approach to model building. Instead we present results for the models containing all predictors selected *a priori* on the basis of their potential biological significance.

RESULTS

Variation in climate

Correlations between climate variables measured at different spatial scales were generally weak (n = 28–30, all $P > 0.25$): NAO vs. T_{WIN} ($r = -0.07$), NAO vs. T_{MIG} ($r = -0.18$), NAO vs. T_{BREED} ($r = 0.20$), T_{WIN} vs. T_{MIG} ($r = -0.22$), T_{WIN} vs. T_{BREED} ($r = 0.02$), T_{MIG} vs. T_{BREED} ($r = -0.21$). Locally, a strong correlation existed between spring temperatures at the two weather stations close to our study area, both between years (1980–2000, April: $r = 0.89$, May:

Table 1. Piecewise linear regression of phenology and temperature variables against year. Dependent variables were: first arrival date (FAD), first laying date (FLD), median laying date (MLD), interval between the dates (FAD–FLD), mean temperature (T) at wintering/migration/breeding area, mean temperatures during the interval, sum of daily temperatures above 5 °C during the interval, mean temperature on days –4 to 0 relative to FAD, FLD and MLD (day = 0). $n = 30$ (1973–2002) except for T_{WIN} and T_{MIG}, where $n = 28$ (1973–2000). An overall fit of the model was tested against the simple linear regression. P-values < 0.05 are shown in bold type.

Variable	Breakpoint year	Regression slope before	Regression slope after	*P*	*r*
FAD	1976	–2.351	–0.036	0.102	0.38
FLD	1979	0.861	–0.488	**0.033**	0.65
MLD	1979	1.379	–0.408	**0.001**	0.67
FAD–FLD	1980	1.475	–0.514	**0.002**	0.61
T_{WIN}	1982	0.082	–0.007	0.074	0.45
T_{MIG}	1985	0.032	–0.043	0.431	0.18
T_{BREED}	1980	–0.177	0.210	0.123	0.62
$T_{\mathrm{mean\ FAD–FLD}}$	1980	–0.338	0.236	0.086	0.54
$T_{\mathrm{sum\ FAD–FLD}}$	1985	1.797	0.195	0.449	0.32
T_{FAD}	1989	0.128	–0.152	0.215	0.24
T_{FLD}	1985	0.127	0.033	0.721	0.22
T_{MLD}	1999	0.062	2.047	**0.043**	0.51

$r = 0.81$; $n = 21$, both $P < 0.001$) and within years (April and May: $r > 0.9$, $n = 61$, $P < 0.001$ for all years). Temperature in the wintering area and along the migration route did not show directional trends. Temperature in the breeding area showed an increasing trend over the study, which was more pronounced after 1980 (Tables 1 & 2). We examined the long-term trends in local temperature and correlation with NAO index for all overlapping 5-day periods from March to May. We found that the period (16 April–15 May) defined *a priori* to represent temperature at the breeding area (T_{BREED}; see Methods) coincided with a period of marked warming over the years (Fig. 1b). Temperature before and after this period did not show any clear directional trend. NAO-index was a weak correlate of the local temperatures during the period of egg-laying (Fig. 1c).

Variation in phenology

The FAD (13–30 April, median/mean = 23/22 April) did not show a directional trend over the years (Tables 1 & 2, Fig. 2), but was negatively correlated with annual population density (1973–2002: $r = –0.52$, $n = 30$, $P = 0.003$; 1980–2002: $r = –0.67$, $n = 23$, $P < 0.001$). FLD (27 April–16 May, median/mean = 5/6 May) and MLD (3–20 May, median/mean = 11 May) showed a trend over the years that changed from delaying to advancing in 1980 (Tables 1 & 2, Fig. 2) and were not correlated with population density ($r = 0.19$, $n = 23$ or 30, all $P > 0.37$). Because no trend existed in FAD, the length of the FAD–FLD interval (6–28 days, median/mean = 12/13) showed a trend over the years similar to that for FLD (Tables 1 & 2, Fig. 2). FAD correlated weakly with FLD ($r = 0.34$, $n = 30$, $P = 0.068$) but not with MLD ($r = 0.14$, $n = 30$, $P = 0.48$); FLD correlated strongly with MLD ($r = 0.80$, $n = 30$, $P < 0.001$).

Table 2. Simple linear regression of phenology and temperature variables against year for the entire study period and the period after 1980. Dependent variables as in Table 1. $n = 28$ (1973–2000) and 21 (1980–2000) for T_{WIN} and T_{MIG}. P-values < 0.05 are shown in bold type.

Variable	1973–2002 ($n = 30$) *r*	*P*	Slope	se	1980–2002 ($n = 23$) *r*	*P*	Slope	se
FAD	–0.24	0.202	–0.121	0.093	0.03	0.885	0.022	0.148
FLD	–0.57	**0.001**	–0.326	0.090	–0.65	**0.001**	–0.488	0.124
MLD	–0.41	**0.024**	–0.193	0.081	–0.66	**0.001**	–0.412	0.101
FAD–FLD	–0.33	0.078	–0.205	0.112	–0.60	**0.002**	–0.510	0.148
T_{WIN}	0.30	0.118	0.017	0.011	–0.07	0.777	–0.005	0.017
T_{MIG}	–0.10	0.619	–0.012	0.023	–0.14	0.553	–0.022	0.036
T_{BREED}	0.57	**0.001**	0.150	0.041	0.58	**0.003**	0.213	0.064
$T_{\mathrm{mean\ FAD–FLD}}$	0.45	**0.012**	0.146	0.054	0.51	**0.012**	0.234	0.085
$T_{\mathrm{sum\ FAD–FLD}}$	0.29	0.120	0.797	0.498	0.15	0.485	0.587	0.826
T_{FAD}	0.03	0.870	0.009	0.055	0.02	0.931	0.008	0.091
T_{FLD}	0.21	0.273	0.068	0.061	0.20	0.370	0.093	0.101
T_{MLD}	0.37	**0.047**	0.136	0.065	0.33	0.128	0.148	0.094

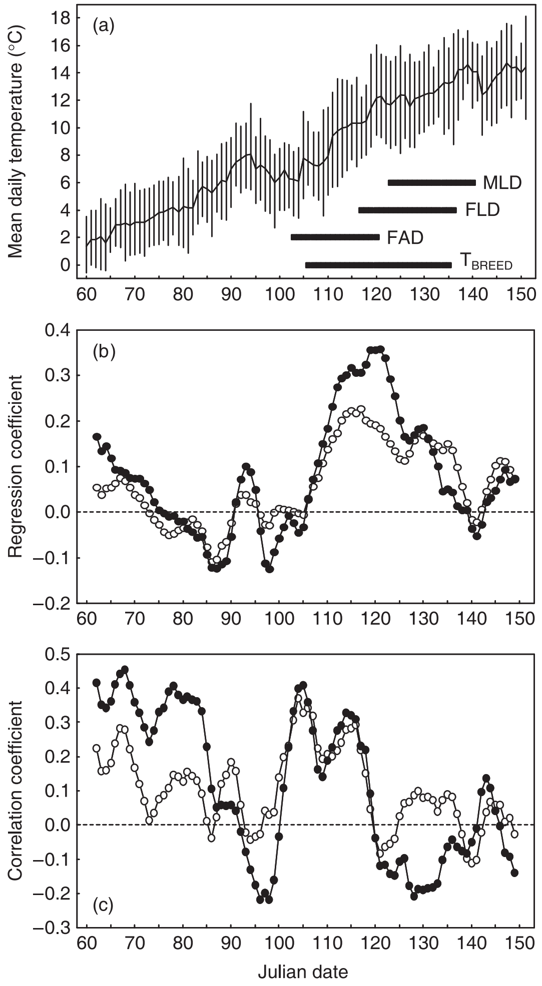

Figure 1. Seasonal variation in (a) mean daily temperature at the study area, (b) rate of its change over the years and (c) strength of its correlation with the annual winter NAO-index. Shown in (a) is the mean and interquartile range calculated across years; horizontal bars delimit the annual variation in timing of first arrival date (FAD), first laying date (FLD) and median laying date (MLD), and the fixed 30-day period (16 April–15 May) defining the temperature at the breeding area (T_{BREED}). Coefficients shown in (b) and (c) were calculated from 5-day running average of daily temperature and were plotted against the middle day of the overlapping periods; analysis was performed separately for the years 1973–2002 ($n = 30$, open circles) and 1980–2002 ($n = 23$, filled circles). Julian date 60 = 1 March.

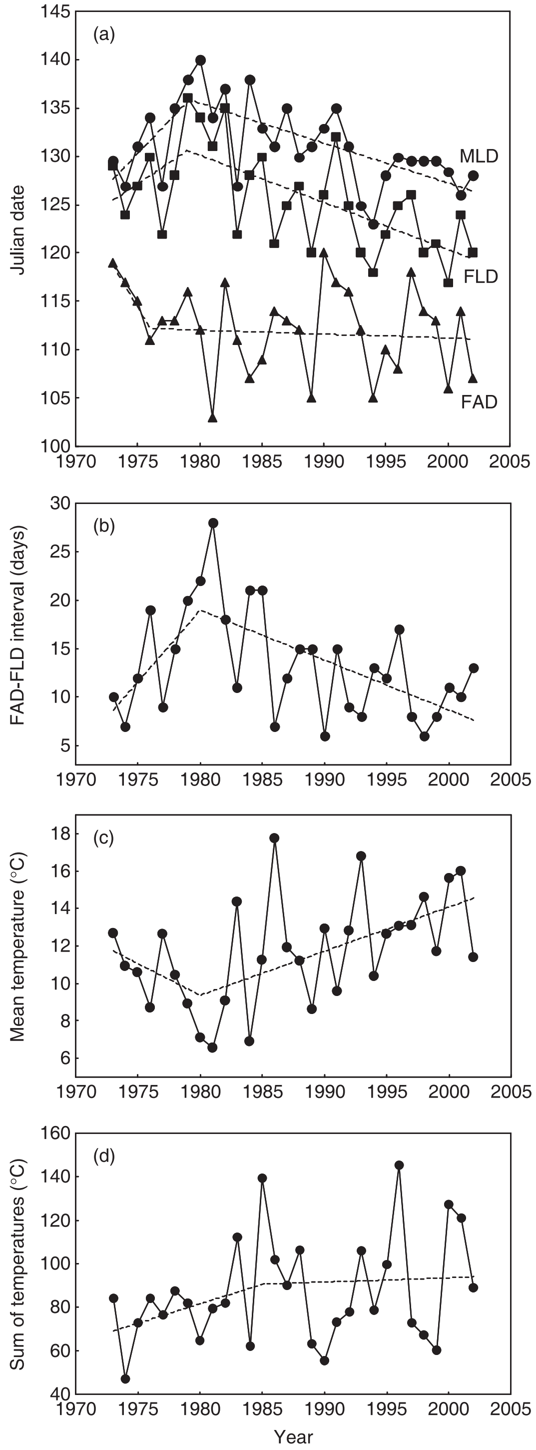

Figure 2. Annual variation in (a) timing of the first arrival date (FAD), first laying date (FLD) and median laying date (MLD), (b) length of the FAD–FLD interval, (c) mean daily temperature during the FAD–FLD interval and (d) sum of daily temperatures above 5 °C during the FAD–FLD interval. Shown is the piecewise linear regression line (dashed); parameters of the fitted models are summarized in Table 1.

Population-level response to climate

FAD was not significantly correlated with any of the climate variables, when these were analysed simultaneously by controlling for each other (Table 3). The strongest effect on FAD was that of T_{WIN}, which was also shown by a conventional simple correlation

Table 3. Multiple linear regression of phenology variables on climatic predictors and year for the period 1980–2000 ($n = 21$). Dependent variables were: first arrival date (FAD), first laying date (FLD), median laying date (MLD), interval between the dates (FAD–FLD). Predictors were: year, winter NAO-index, mean temperature (T) at wintering, migration and breeding area. P-values < 0.05 are shown in bold type.

	Climatic predictors				Climatic predictors + Year			
Variable	Partial *r*	*P*	Slope	se	Partial *r*	*P*	Slope	se
FAD								
Year					0.16	0.535	0.126	0.198
NAO	–0.15	0.551	–1.209	1.983	–0.17	0.502	–1.406	2.045
T_{WIN}	0.37	0.127	3.903	2.427	0.38	0.138	3.881	2.474
T_{MIG}	–0.23	0.355	–1.061	1.115	–0.23	0.379	–1.031	1.137
T_{BREED}	–0.02	0.938	–0.033	0.418	–0.10	0.702	–0.193	0.495
FLD								
Year					–0.49	**0.048**	–0.267	0.124
NAO	–0.57	**0.014**	–3.886	1.403	–0.57	**0.016**	–3.466	1.281
T_{WIN}	0.13	0.609	0.897	1.718	0.16	0.551	0.944	1.550
T_{MIG}	0.18	0.481	0.569	0.789	0.18	0.488	0.506	0.713
T_{BREED}	–0.74	**0.001**	–1.315	0.296	–0.63	**0.007**	–0.975	0.310
MLD								
Year					–0.40	0.108	–0.203	0.119
NAO	–0.45	0.064	–2.551	1.283	–0.43	0.089	–2.233	1.227
T_{WIN}	0.14	0.582	0.883	1.571	0.16	0.545	0.919	1.484
T_{MIG}	0.16	0.522	0.472	0.721	0.16	0.543	0.424	0.682
T_{BREED}	–0.69	**0.002**	–1.034	0.271	–0.56	**0.020**	–0.776	0.297
FAD–FLD								
Year					–0.50	**0.039**	–0.393	0.174
NAO	–0.32	0.197	–2.677	1.990	–0.28	0.269	–2.060	1.796
T_{WIN}	–0.29	0.235	–3.006	2.436	–0.33	0.197	–2.936	2.173
T_{MIG}	0.34	0.164	1.630	1.119	0.37	0.144	1.538	0.999
T_{BREED}	–0.61	**0.008**	–1.282	0.420	–0.42	0.092	–0.781	0.435

($r = 0.47$, $n = 21$, $P = 0.032$). FLD and MLD were negatively correlated with T_{BREED} and less strongly with NAO. The length of the FAD–FLD interval was negatively correlated with T_{BREED} (Table 3). The above climatic effects on FLD and MLD remained significant even after accounting for the trend over the years (Table 3), while the effect of year remained, at most, marginally significant after accounting for climatic variables (compare Tables 2 & 3). The above patterns were also found for the entire study period 1973–2000 (data not shown) but were less clear than those for the period after 1980 (Table 3). As the mean daily temperature during the FAD–FLD interval increased, the length of the interval declined ($r = –0.77$, $n = 30$, $P < 0.001$), while the sum of daily temperatures did not change with interval length ($r = 0.13$, $n = 30$, $P = 0.50$). Similarly, the mean daily temperature during the FAD–FLD interval increased over the years, but the sum of daily temperatures over this interval did not show a clear trend (Tables 1 & 2, Fig. 2).

Individual-level response to climate

Laying dates were repeatable within individual females that bred at least twice during the 1980–2002 period (intraclass correlation: 0.42 for an unconditional model with random effect of individual; 0.25 for the model shown in Table 4) and the mixed model revealed a strong negative effect of T_{BREED} and a marginal effect of NAO on laying date within individuals. The parameter estimates for this individual response (Table 4) were similar to those obtained for a population-level response (Table 3), with a difference between estimates of ±0.1 and 0.8 se units for the NAO and T_{BREED} effects, respectively.

Response to within-season variation in temperature

We examined variation in temperature on individual days relative to the focal day (FAD, FLD, MLD; Fig. 3). Timing of FAD coincided with a period of

Table 4. Mixed model analysis of laying date within individual females. Dependent variable was individual laying date (*n* = 298 clutches). Fixed effect predictors were winter NAO-index, mean temperature at breeding area and individual age. Random effects were year (1980–2002) and individual identity (119 females). Included were those females that bred at least twice during the study period. Estimates shown are slopes for fixed effects and variance components for random effects. *P*-values < 0.05 are shown in bold type.

Variable	Estimate	se	*P*
Fixed effects			
NAO	–2.104	1.127	0.076
T_{BREED}	–1.009	0.257	**0.001**
Age	0.100	0.190	0.599
Random effects			
Year	6.624	2.505	
Individual	6.093	1.643	

increasing temperature after a temporary drop in the first half of April (compare Fig. 3a with Fig. 1a). This within-season pattern become more steep over the years, as indicated by the switch of regression slopes from marginally negative to positive values before/after FAD (Fig. 3b). Hence, the temperature around FAD (T_{FAD}: mean = 9.2 °C ± 2.6 sd) did not change over the years (Tables 1 & 2), while temperature after FAD increased (Fig. 3b). Timing of FLD coincided with the end of continuous temperature increase (Fig. 3a), and this within-season pattern changed little over the years (Fig. 3c). The temperature around the onset of laying (T_{FLD}: mean = 13.3 °C ± 2.9 sd) did not show a significant trend over the years (Tables 1 & 2, Fig. 3c). No distinct pattern of within-season temperature variation was associated with the timing of MLD (Fig. 3a) but the temperature around MLD (T_{MLD}: mean = 12.6 °C ± 3.3 sd) marginally increased over the years (Tables 1 & 2, Fig. 3d).

We detected only a weak relationship between the number of clutches initiated on individual days within a season and the temperature on the preceding days. Nevertheless, the pattern emerging from the estimated slopes showed that the effect of daily temperature tended to be positive up to 4 days and its size increased up to 3 days before clutch initiation, when it reached significance (Table 5). The effect of temperature on a particular day did not depend on the annual mean temperature during the laying period (interaction: $F_{1,20}$ = 3.5, all $P > 0.07$). Yet, important variation existed in the effect of daily temperature because of random effects of year (Table 5), but these year-specific effects did not show

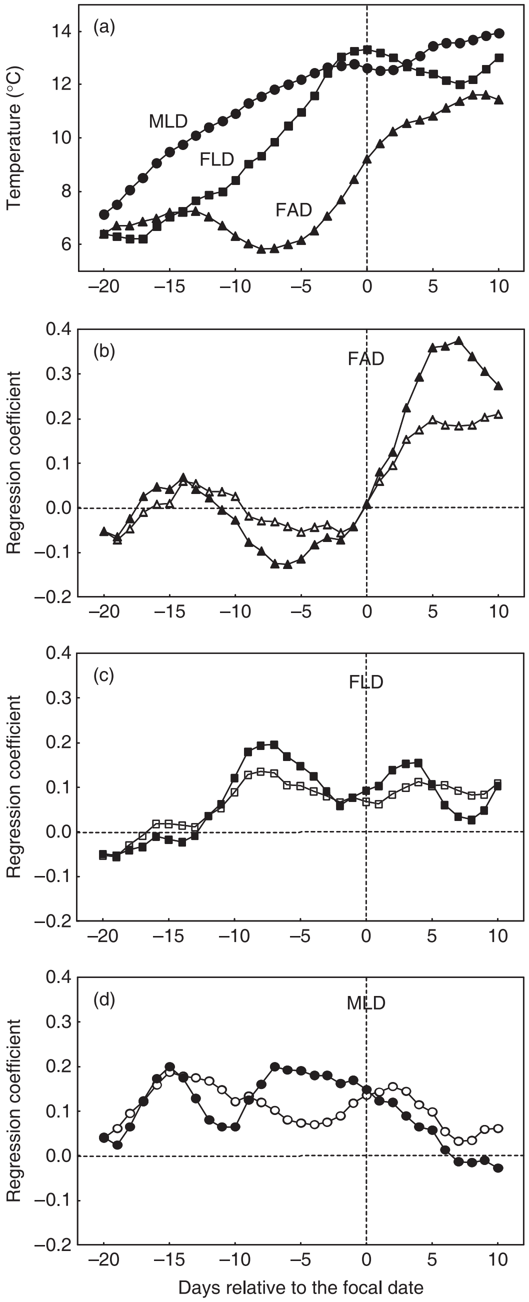

Figure 3. Seasonal variation relative to the timing of first arrival date (FAD), first laying date (FLD) and median laying date (MLD), in (a) mean daily temperature and (b–d) rate of its change over the years. Shown in (a) is the mean of the annual 5-day running averages of daily temperature plotted against the last day of the overlapping periods. Coefficients shown in (b–d) were calculated from the running averages; analysis was performed separately for the years 1973–2002 (*n* = 30, open symbols) and 1980–2002 (*n* = 23, filled symbols).

Table 5. Mixed model analysis of the number of clutches initiated on individual days within a season. Each line of the table represents a separate generalized linear mixed model (Poisson error distribution, log link) including temperature (centred within year) on days –5 to –1 (0 = clutch initiation) as a fixed effect predictor. Also evaluated were models for two composite predictors: temperature averaged over days –5 to –1 (Avg), and the slope of linear regression of daily temperature on days –5 to –1 (Slope). Fixed effect predictors common to all models were the mean annual temperature for the laying period and the linear and squared terms of Julian date. Random effects were year (1980–2002) and year × daily temperature interaction. Estimates shown are slopes for fixed effect and variance components for random effect. *P*-values < 0.05 are shown in bold type.

	Daily temperature (fixed)			Daily temperature × Year (random)	
Day	Estimate	se	*P*	Estimate	se
–1	0.009	0.021	0.689	0.007	0.003
–2	0.030	0.030	0.321	0.016	0.007
–3	0.072	0.031	**0.032**	0.018	0.007
–4	0.030	0.033	0.363	0.020	0.008
–5	–0.012	0.027	0.673	0.013	0.005
Avg	0.093	0.063	0.157	0.078	0.030
Slope	0.035	0.059	0.562	0.057	0.024

a trend over the years ($r = 0.16$, $n = 23$, all $P > 0.46$). We reached qualitatively similar conclusions by performing separate fixed-effect analyses for each year, instead of fitting mixed models with a random effect of year.

DISCUSSION

We found close coincidence between the long-term trends in laying date, local temperature and large-scale climate variation. Data before 1980 suggest delayed laying, decreasing local temperatures and mostly negative values of NAO. Since 1980, laying date has consistently advanced (about 0.4 days per year), the local temperature has increased (0.2 °C per year) and NAO has changed to mostly positive values (Hurrell 1995). At least one other dataset (Slater 1999) suggests a similar pattern in laying dates, although the switch from delaying to advancing trend occurred earlier than in the present study (see also McCleery & Perrins 1998, Crick & Sparks 1999). An analysis of 25 *Ficedula* flycatcher populations over Europe revealed strong correlation between the change in local spring temperature and the extent of advancement in laying date (Both *et al.* 2004). Our results fit nicely in this overall pattern (Both *et al.* 2004; Fig. 1), though the rates of warming and laying advancement are comparable with the highest values reported elsewhere. On the other hand, results from central Europe (this study; Bauer 2006) do not match the overall geographical pattern revealed in flycatchers (Both *et al.* 2004) and *Parus* tits (Visser *et al.* 2003), where such a strong advancement of laying dates was confined to populations in western Europe.

Annual variation in laying dates correlated with climate on both local and continental scales. The negative effect of local spring temperature on laying dates was in the same direction but relatively stronger than that of NAO. These climatic effects explain much of the long-term trend in laying dates. Results from our site in central Europe are in concert with other studies, where a tight relationship between laying date and local spring temperatures was found in almost all flycatcher populations (Both *et al.* 2004, 2005), while the relationship with NAO was found mainly in northern and western populations (Sanz 2003). Two aspects of climate at our study site deserve mention. The relatively weak correlation between local temperatures and NAO could partly be attributed to geographical location – the NAO-index represents large-scale climate fluctuations mainly over northwest Europe, while its effect on season progress (Menzel *et al.* 2005) and avian phenology (Zalakevicius *et al.* 2005) in central Europe is less clear. The rate of local spring warming was relatively steep, but could not be attributed to local anomaly – we found similar patterns in data from other regional weather stations.

Rescaling of data from the calendar (Julian dates, Fig. 1) to relative dates (days relative to the event within each year, Fig. 3) permitted us to explore the consistency of within-season patterns across years. The mean onset of laying coincided with the period of spring that underwent the most marked warming over the years. Yet, the laying dates advanced at a rate that kept the temperature at the onset of laying approximately stable (FLD) or only marginally increasing (MLD) over the years.

Once laying began, the number of clutches initiated in a particular day of the breeding season was, on average (across years), marginally influenced by the temperature on the preceding days. The overall pattern of estimated effects was similar to that found in Barn Swallow *Hirundo rustica* (Saino *et al.* 2004c). A 3-day delay in response to temperature most likely represents the time a female takes to produce the first egg, a process that once started is inevitable. Our long-term study permitted us to include year as a random factor in the analysis, which revealed significant variation among years in the effect of daily temperature. This means that the effect was detectable (significant) in some years but not in others, a fact that may have serious implications for the conclusions of short-term studies (Sparks & Tryjanowski 2005). The mean temperature during the laying period entered in the model as a year-level covariate did not explain the variation among years. Most importantly, no temporal trend existed in the year-specific temperature effects, suggesting that the responses of females to day-to-day variation in ambient temperature during the egg-laying season did not change systematically over the years. We suspect, however, that analyses of this kind are confounded by variation in laying dates that is not related to ambient temperature, and which is not sufficiently controlled for by including an overall seasonal trend (linear and quadratic effect of date) in the analysis as a covariate.

We found close correspondence between the average population-level and the individual-level responses of laying date to climate variation at both local and continental scales. Although results of our cross-sectional analysis (and majority of other published studies) may have been partly influenced by uncontrolled variation (unknown age of many females) and pseudoreplication (multiple nesting attempts by the same female in different years), we believe that this does not invalidate our conclusions. First, we found only weak age-dependence of laying dates in the sample of aged females. Secondly, parameter estimates are not affected by pseudoreplication as much as their variances. Hence, we conclude from the similarity of estimated effect sizes that the population-level advancement of laying dates may be attributable to phenotypic plasticity – adjustment of laying dates by individual females to variable climatic conditions encountered during their life. Additional support for phenotypic plasticity comes from the fact that the long-term trend in laying dates was largely attributable to climatic variation among years. The evidence in favour of phenotypic plasticity, as opposed to microevolutionary change, is in line with other studies of laying dates in long-distance migrants (Przybylo *et al.* 2000, Sheldon *et al.* 2003, Saino *et al.* 2004a, Both & Visser 2005).

Despite the trend towards warmer springs at the breeding area, we found no long-term trend in arrival dates and no correlation between FADs and local spring temperature, which is in agreement with findings in several central European Pied Flycatcher populations (Hüppop & Winkel 2006). Temperatures at wintering and migration grounds did not change over the years (this study) or may even have decreased (Gordo *et al.* 2005), and their annual variation only weakly correlated with FADs. Although not significant, the direction of these correlations supports the idea of relatively later departure from equatorial Africa in warmer years (Kanuščák *et al.* 2004, Saino *et al.* 2004b, Gordo *et al.* 2005) and faster spring migration across warmer staging areas (Ahola *et al.* 2004, Both *et al.* 2005, Hüppop & Winkel 2006). The progression of spring migration in Pied Flycatchers was shown to correlate with temperature encountered along the different migration routes within Europe (Hüppop & Winkel 2006). As the rate of climatic change varies both in space (among migration routes) and in time (among different periods of spring), it has been hypothesized that migrants along the eastern route may not benefit from increasing average spring temperatures as much as their western counterparts (Hüppop & Winkel 2006). Although the exact migration route of Collared Flycatchers from central Europe is as yet unknown (see Methods), our data support the idea of environmental constraints upon arrival time through local climatic barriers. By rescaling arrival times from calendar to relative dates we found that FADs coincided with the period showing a within-season warming but no long-term trend. Because flycatchers arrive just at a period of warming, and temperature in the preceding period did not change or even decreased, they may pay a considerable cost if they had advanced their arrival date.

We acknowledge that FADs are prone to methodological bias (Tryjanowski *et al.* 2005) and may not represent the whole population (Hüppop & Hüppop 2003). Recently, FADs were shown to correlate with the shape of arrival distribution (Ahola *et al.* 2004, Sparks *et al.* 2005), which prevents us from extrapolating trends from FADs to the whole population. However, because FADs generally change more rapidly than population quantiles (Töttrup *et al.* 2006) and because FADs in our study did not change over the years, it is unlikely that the whole population arrival time had undergone a marked directional change. FADs in our study were negatively correlated with annual breeding density (note that breeding density may not represent density during the arrival period). We argue, however, that this fact alone cannot prove methodological artefacts (increased probability of early observation with higher density;

Tryjanowski & Sparks 2001). Moreover, because breeding density in our study area remained stable, our basic argument that FADs did not change over the years remains valid.

Advancement of laying dates despite a lack of a parallel trend in arrival dates means that the arrival–laying interval declined over the years (about 0.5 days per year). If we assume that FADs reasonably reflect arrival of the entire population (but see above), then the time between arrival and laying has decreased. Flycatchers are income breeders; their ability to breed depends on food obtained after arrival at the breeding area. We have no data on food availability during the pre-laying period and its variation over years, but indirect evidence (see also Bauer 2006) suggests that a similar amount of food may be available during a shorter period. The development of vegetation and invertebrate prey depends on the warmth sum above some physiological threshold rather than on the mean temperature (Visser & Holleman 2001). We found that the decline of the arrival–laying interval was partly compensated for by the increasing mean temperature, which kept the sum of daily temperatures approximately stable over the years.

Although the birds were able to lay, on average, shortly after arrival, it is not clear whether the resulting advancement of laying date was sufficient to maintain synchronization between offspring needs and a possibly advanced peak in food supply. Evidence from other flycatcher populations (Both & Visser 2001, Both *et al.* 2004, 2006) and organisms in general (Both & Visser 2005) suggests that this may not be the case. Whether the stable arrival time in our Flycatcher population is a constraint upon further adjustment of laying date to climate change and whether birds can potentially adjust their arrival dates (Both *et al.* 2005) are open to further study.

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