THE ROYAL SOCIETY

Received 12 August 2002
Accepted 23 October 2002

Variable responses to large-scale climate change in European *Parus* populations

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Spring temperatures in temperate regions have increased over the past 20 years and many organisms have responded to this increase by advancing the timing of their growth and reproduction. However, not all populations show an advancement of phenology. Understanding why some populations advance and others do not will give us insight into the possible constraints and selection pressures on the advancement of phenology. By combining two decades of data on 24 populations of tits (*Parus* sp.) from six European countries, we show that the phenological response to large-scale changes in spring temperature varies across a species' range, even between populations situated close to each other. We show that this variation cannot be fully explained by variation in the temperature change during the pre- and post-laying periods, as recently suggested. Instead, we find evidence for a link between rising temperatures and the frequency of second broods, which results in complex shifts in the laying dates of first clutches. Our results emphasize the need to consider links between different life-history parameters in order to predict the ecological consequences of large-scale climate changes.

Keywords: life history; laying date; climate change; *Parus major*; *Parus caeruleus*

1. INTRODUCTION

Many bird species have advanced their laying date in response to the increase in spring temperatures over the past two decades (Crick *et al.* 1997; McCleery & Perrins 1998; Brown *et al.* 1999; Crick & Sparks 1999; Both & Visser 2001; Houghton *et al.* 2001; Wuethrich 2001; Walther *et al.* 2002). However, most of these studies just show that spring phenology has advanced, but do not consider whether this response is strong enough, or perhaps even too strong, to match the phenological changes in the parts of the ecosystem on which the birds rely for successful reproduction. One way to gain insight into whether the observed changes in phenology are adaptive is to compare these changes within species. It is striking that within a single species some populations have, while others have not responded to the large-scale climate change. In England and Germany, for example, the great tit has shown a clear shift towards earlier breeding (Winkel & Hudde 1997; McCleery & Perrins 1998), while in the Netherlands, the same species has not altered its laying date (Visser *et al.* 1998). Understanding variation between populations in their response to climate change is crucial if we are to understand the capacity of populations to adapt to a changing environment.

As an explanation for the variation in the response of great tit populations to climate change, the temperature hypothesis has been proposed. In the Dutch Hoge Veluwe (HV) population, temperatures have only increased after laying (Visser *et al.* 1998), in contrast to the great tit population from Wytham Wood (WW) in England where there has been an advancement of the laying date (McCleery & Perrins 1998) as well as an increase in both the pre-laying and breeding period temperatures (Stevenson & Bryant 2000). As egg production at low temperatures is associated with high daily energy expenditure (Stevenson & Bryant 2000) and egg production is also costly in terms of future fitness benefits (Visser & Lessells 2001), this lack of an increase in early spring temperatures may constrain advancement of laying date in the HV population. The temperature increase in the period after laying, the breeding period, will obviously not play a part in the causal mechanism determining laying date but will affect the time of maximum food abundance, and hence the need to advance laying date to maintain synchronization between offspring needs and food abundance.

European great tits (*Parus major*) and blue tits (*P. caeruleus*) are widely studied and offer a rare opportunity to investigate geographical variation in phenological response to large-scale climate change (see also Dunn & Winkler 1999). Here, we examine changing laying dates in great and blue tits from different parts of Europe (table 1) over the 20 years from 1979 to 1998, for which we have

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DOI 10.1098/rspb.2002.2244

Table 1. Some characteristics of the 14 study sites from which data on *Parus major* (GT) and *P. caeruleus* (BT) have been used. The p-values, as well as the slopes (s.e.), are from regressing the annual mean population laying date of first clutches against year for all populations separately.
(Country abbreviations: B, Belgium; F, France; FIN, Finland; NL, The Netherlands; RU, Russia; UK, United Kingdom.)

				number of years 1979–1998		mean number of first broods		p-value laying date versus year		slope laying date versus year (s.e.)	
study site	full name	country	coordinates (long./lat.)	GT	BT	GT	BT	GT	BT	GT	BT
PI	Pirio (Corsica)	F	42°23′ N, 08°45′ E	0	20	n.a.	43.4	n.a.	0.963	n.a.	−0.008 (0.168)
VT	Ventoux	F	44°35′ N, 05°25′ E	20	20	11.6	13.0	0.175	0.158	−0.367 (0.260)	−0.326 (0.221)
HP	Hutsepot	B	51°01′ N, 03°70′ E	20	20	37.6	22.5	0.025	0.015	−0.509 (0.209)	−0.535 (0.200)
BW	Boswachter	B	51°27′ N, 03°70′ E	20	20	43.5	30.1	0.003	0.006	−0.667 (0.195)	−0.594 (0.190)
LB	Liesbos	NL	51°35′ N, 04°40′ E	20	20	40.5	20.0	0.383	0.134	−0.177 (0.198)	−0.337 (0.215)
WW	Wytham Wood	UK	51°47′ N, 01°20′ W	20	20	251.6	295.7	0.014	0.019	−0.578 (0.213)	−0.528 (0.206)
OH	Oosterhout	NL	51°55′ N, 05°50′ E	20	19	37.3	16.6	0.626	0.112	−0.101 (0.204)	−0.409 (0.244)
WB	Warnsborn	NL	52°05′ N, 05°50′ E	20	20	49.0	11.1	0.017	0.134	−0.404 (0.153)	−0.290 (0.185)
HV	Hoge Veluwe	NL	52°05′ N, 05°50′ E	20	20	117.9	42.1	0.540	0.068	−0.105 (0.168)	−0.34 (0.176)
VL	Vlieland	NL	53°15′ N, 05°00′ E	20	20	125.2	37.9	0.227	0.493	−0.200 (0.160)	−0.086 (0.123)
TW	Treswell	UK	53°18′ N, 00°51′ W	20	20	17.4	28.7	0.021	0.093	−0.538 (0.213)	−0.417 (0.236)
ZV	Zvenigorod	RU	55°44′ N, 36°51′ E	19	0	19.4	n.a.	0.544	n.a.	−0.118 (0.190)	n.a.
OU	Oulu	FIN	65°03′ N, 25°26 E	13	0	21.0	n.a.	0.200	n.a.	−0.534 (0.392)	n.a.
HA	Haukipudas	FIN	65°05′ N, 25°34′ E	16	0	21.1	n.a.	0.395	n.a.	0.236 (0.269)	n.a.

almost complete time-series, thereby minimizing possible biases. We show that changes in laying date over this period vary significantly between populations, and we test the temperature hypothesis that this variation is due to geographical differences in the increase of early- and late-spring temperatures.

2. METHODS

(a) *Breeding data*

Basic data collection was the same for all populations. Nestboxes were checked at least weekly and laying date (the date on which the first egg was laid) was estimated assuming that one egg was laid per day (van Balen 1973). Parents were caught at the nest for individual identification. Mean laying date is the average for all first clutches (the first clutch that a female produces in that year) of that year. First clutches sometimes failed before the female had been identified so we assumed that all clutches initiated more than 30 days after the first clutch of the year are not first clutches. Second clutches are clutches produced by females that had a successful first clutch (at least one fledged young) in the same year. For one of the Belgian great and blue tit populations (Hutsepot (HP)), no checks were made for second clutches in three out of the 20 years. No checks for blue tit second clutches were made in two of the Dutch populations (Oosterhout (OH) and Liesbos (LB)) and in one of the French populations (Ventoux (VT)).

(b) *Test of differential changes in laying date*

To analyse the relationship between annual mean laying date and year (1979–1998) for the 13 great and 11 blue tit populations across Europe, we used an ANCOVA-like model with year as a continuous covariable and both species and study site as discrete factors. However, because, on the one hand, within-species and within-site observations could be correlated in time and, on the other hand, within-site and within-year observations could be correlated between-species, these potential sources of statistical dependency had to be taken into account. This was achieved by explicitly modelling these correlations (using a first-order autoregressive correlation structure for time dependence (covariance = 0.030) and compound symmetry for between-species correlation (correlation = 0.745)) and adjusting the degrees of freedom of the tests of the fixed effects accordingly (using Satterthwaite's procedure (Verbeke & Molenberghs 2001)). In addition, to correct for average year effects that operate across the whole of Europe, year was also treated as a discrete factor and added as a random effect. Because sample sizes

Table 2. Statistical analysis on mean annual laying date for 13 *Parus major* and 11 *P. caeruleus* populations in Europe from 1979–1998. Interactions are indicated with variable names separated with a dot. The year.species interaction and the year.area.species interaction were not significant ($F_{1,112} = 0.36$, $p = 0.55$ and $F_{9,96} = 1.41$, $p = 0.20$, respectively). The significant year.study site interaction indicates that there are differences in the change of laying date over the 20-year period among the study sites.

variable	statistic	*p*-value
study site	$F_{13,109} = 2.79$	0.0018
species	$F_{1,103} = 14.89$	0.0002
species.study site	$F_{9,96} = 8.70$	<0.0001
year.study site	$F_{14,83} = 3.04$	0.0008

(number of clutches) differed considerably among samples, all data points were weighted by 1/(standard error)^2.

(c) *Temperature data*

We obtained daily minimum and maximum temperatures between 1 January and 15 June for the 20-year period on an area level (The Netherlands (NL); Belgium (B); France (F); United Kingdom (UK); Finland (FIN); and Russia (RU) as well as the island populations: Vlieland (VL), the Netherlands and Corsica (CO), France) rather than on a population level since populations within countries are situated close to each other. We used daily average temperature ((minimum + maximum)/2), but results were very similar when either daily minimum or maximum temperature were used.

(d) *Test of differential changes in temperature*

We calculated the average mean daily temperature for two periods: the pre-laying period is the six-week period before the median laying date for that population for 1980–1984 (the first 5 years for which we have data for all populations) and the breeding period is the four weeks after this median date (van Balen 1973; Visser *et al.* 1998; Stevenson & Bryant 2000). We used these fixed periods because annual mean laying date is correlated with temperature, and keeping the periods fixed over the 20-year period avoids biases. Also, these two periods are in accordance with those used when the temperature hypothesis was formulated (Stevenson & Bryant 2000). We related mean daily temperature to year for these two spring periods from 1979–1998 in eight areas (NL, B, F, UK, FIN, RU, VL and CO) for which we have data on great and/or blue tit populations. We also used a first-order autoregressive correlation and Satterthwaite's procedure to correct for possible temporal dependency and included year as a random effect to correct for average year effects. In the analysis on the change in temperature patterns over the years, we excluded 1991 as this year had an exceptionally cold breeding period (1991 is the only year in which, for NL, VL and B, the temperatures in the breeding period were lower than in the pre-laying period: all $p < 0.05$ in an outlier test (Dixon 1950)). When 1991 was included, the interaction area.period.year in table 3*a* became marginally non-significant ($F_{4,132} = 2.27$, $p = 0.065$).

3. RESULTS

We find that laying dates have become significantly earlier in only five out of the 13 great tit populations and only three out of the 11 blue tit populations (table 1). Laying date has advanced significantly, for one or both of the species, only in the English (WW and Treswell (TW)), the Belgian (Boswachter (BW) and HP) and one of the Dutch (Warnsborn (WB)) populations. Furthermore, when combined in a single analysis, we find that the differences in the patterns of changing laying date between populations are statistically significant ($F_{14,83} = 3.04$, $p = 0.0008$; table 2) and thus there are differences among study sites within Europe in the rate of change of the mean laying date (figure 1). The responses to climate change are likely to be affected by local climate and/or ecological circumstances because the variation in responses between study sites was greater than the variation between the two species within a site, as we found no evidence that responses differed between the great and blue tits breeding in the same area (table 2).

Geographical variation in the increase in spring temperature (Houghton *et al.* 2001; Walther *et al.* 2002) is a possible explanation for differences in the advancement of laying date between populations. Indeed, when we examined this, we found that long-term changes in the mean temperatures during the pre-laying and breeding periods did vary significantly between the areas ($F_{7,225} = 2.37$, $p = 0.02$). In Russia and Finland, temperatures did not increase (estimate for Russia: 0.016 °C yr^{-1}, Finland: -0.039 °C yr^{-1}, both non-significant). It is therefore no surprise that laying date did not change significantly in either of the Finnish populations (Oulu (OU) and Haukipudas (HA)) or the Russian population (Zvenigorod (ZV)). Laying date itself also differed between populations. Blue tits on Corsica (Piro (PI)) laid comparatively late (figure 1), feeding their offspring on caterpillars that do not emerge until much later in the season, as this population breeds in evergreen habitat (Blondel 1985). Being unaffected by changing temperatures earlier in the season, the date at which caterpillars were most abundant on Corsica has not changed ($F_{1,10} = 1.35$, $p = 0.27$, for 1987–1998), the laying dates of the Corsican blue tits showed no correlation with spring temperatures (Blondel *et al.* 1993) and laying dates have not become earlier (table 1). We therefore suggest that both in the northernmost and southernmost populations there has been no need to lay earlier, either because spring temperatures have not changed (in the north) or because the phenology of the entire food chain (trees–caterpillars–birds) is less temperature sensitive (in the south). This emphasizes that, over a large geographical scale, different variables may account for the variance in changes in laying date.

(a) *Test of the temperature hypothesis*

At intermediate latitudes, however, the differences in temperature changes or sensitivity cannot account for the differences seen in the response of laying date to climate change as the food chains are temperature sensitive and the temperatures have changed. To understand the variation in the response of laying date to climate change in the F, B, UK and NL populations we tested the hypothesis that the laying date in some areas has not advanced because the increase in spring temperature has occurred only for the period of spring after the birds have already started laying, and not in the pre-laying period (Visser *et al.* 1998). We calculated mean annual temperatures both

Table 3. Statistical analysis on mean daily temperature for two spring periods from 1979–1998 (excluding 1991, which is an outlier (Dixon 1950)) in four countries (NL, B, F and UK) and one island (VL) for which we have data on *Parus major* and/or *P. caeruleus* populations. The two periods are defined as the six weeks before (pre-laying period) and the four weeks after (breeding period) the median laying date for the period 1980–1984 per area. (*a*) Interactions are indicated with variable names separated with a dot. The area.year and the year.period interaction were not significant ($F_{4,123} = 1.74$, $p = 0.15$ and $F_{1,29} = 2.33$, $p = 0.14$, respectively). (*b*) Inspection of the estimates for the area.period.year interaction of table 3*a* (°C yr^{-1}) reveals that temperatures have increased equally strongly in both periods for the UK and VL, while for NL, B and F the temperatures in the breeding period have increased more strongly than in the pre-laying period.

(*a*)

variable	statistic	*p*-value
year	$F_{1,29} = 11.73$	0.0018
period	$F_{1,29} = 193.24$	<0.0001
area	$F_{4,123} = 334.87$	<0.0001
area.period	$F_{4,123} = 4.23$	0.030
area.period.year	$F_{4,123} = 3.19$	0.016

(*b*)

area	NL	VL	B	F	UK
pre-laying period	0.025	0.052	0.046	0.059	0.060
breeding period	0.183	0.060	0.168	0.152	0.072

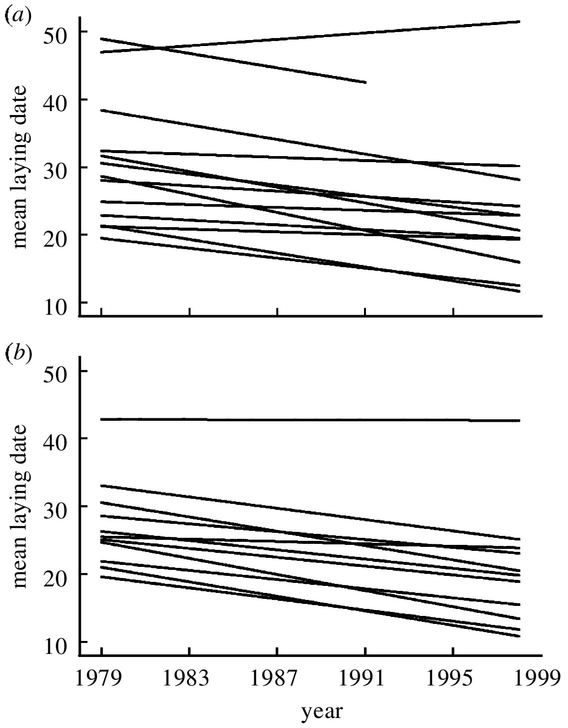

Figure 1. Changes in laying date in great tit and blue tit populations. Laying dates (expressed in April date, i.e. 31 = 1 May) of (*a*) 13 great tit, *Parus major* and (*b*) 11 blue tit, *P. caeruleus* populations (see table 1) against year (1979–1998). Only the fitted lines from a linear regression for each of the populations separately are presented. The populations are (from top to bottom for 1998) for the great tit: HA, OU (study ends in 1991), ZV, TW, VL, WB, HV, WW, LB, OH, BW, VT and HP; and for the blue tit: PI, TW, VL, WB, WW, HV, VT, LB, BW, OH and HP. There is significant variation in the slopes (see table 2).

for the pre-laying period and the breeding period for all populations included in our study and found a significant interaction between area, year and period (table 3*a*), indicating that there are differences among areas in the change of mean daily temperature for the pre-laying and breeding periods over the 20 years. Pre-laying and breeding spring temperatures have shown similar increases in UK and VL, while breeding temperatures have increased more than pre-laying temperatures in NL, B and F (table 3*b*). However, while this could account for the differences observed between the British WW and the Dutch HV populations (Stevenson & Bryant 2000), it cannot account for the different patterns of changing laying dates in general. We found no correlation between the difference in change in temperature between the pre-laying and breeding periods and the degree of change in the laying date (great tit: $r = 0.39$, $n = 10$, $p = 0.26$; blue tit: $r = 0.17$, $n = 8$, $p = 0.69$). The patterns of temperature change are very similar across Belgium and the Netherlands, but while four Dutch populations have not changed their laying dates, one has done so and so have both Belgian populations. Different patterns of change in laying date can be seen even in populations that lie very close to each other (HV–WB: 3 km, LB–BW: 50 km).

(b) *Alternative hypotheses*

What then can explain the differences in changed laying dates between these populations? There may be large differences in microclimate or vegetation between study areas that affect the shift in caterpillar peak dates, leading to different selection pressures on laying date. Areas may also differ in the amount of resources available in early spring, at the time of egg production (Visser *et al.* 1998), and hence in the costs of producing eggs early. Unfortunately, the necessary long-term data on changes in the seasonal patterns of food availability are not currently available to test these hypotheses.

We have, however, data to test an alternative hypothesis for which we find correlative evidence. This hypothesis rests on the fact that great and blue tits are facultatively double-brooded, and the percentage of pairs that produce a second clutch (a clutch started in the same season after

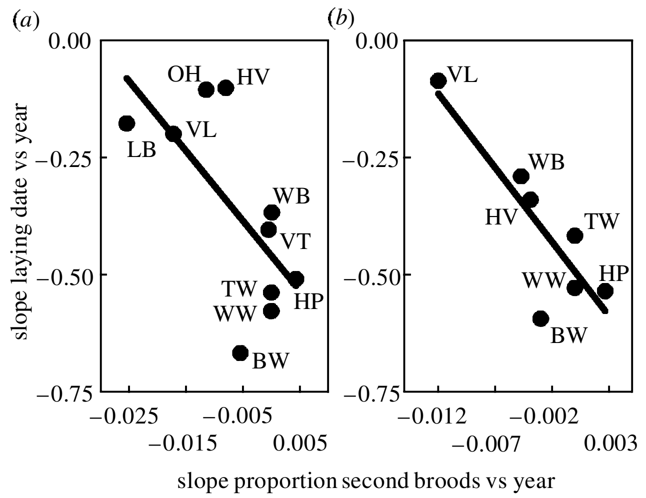

Figure 2. Changes in laying date are correlated with changes in the degree of double-brooding in great tit and blue tit populations. The correlation between the change in laying date over the 20 year period (1979–1998; see table 1 and figure 1) and the change in the proportion of pairs that start a second clutch (the slope from a linear regression of the proportion second clutches against year) for (*a*) 10 great tit, *Parus major* and (*b*) seven blue tit, *P. caeruleus* populations from NL, B, F and UK. The study sites are indicated (see table 1).

a successful first brood) varies markedly between populations (Verboven *et al.* 2001). Pairs that produce only a single clutch per season should lay at the time which is optimal for that one clutch, while pairs producing two clutches per year should lay their first clutch earlier so that they optimize the reproductive success over both clutches, and hence produce first clutches earlier than single-brooded individuals (Crick *et al.* 1993). With an increase in spring temperature, caterpillars (the main food for nestlings) develop faster (Topp & Kirsten 1991) and hence the period of high levels of food abundance will be shortened, leading to a reduction of the reproductive value of second clutches over the years, and hence a decrease in the frequency of these second clutches. Because the first clutch laying date is no longer a compromise between the laying date of the first and the second clutch, the average laying date of first clutches will shift to later laying dates, counteracting the advancement of laying date due to the advancement of the peak date of food abundance. In populations that historically lack second clutches (or have a stable proportion of second clutches), we therefore predict a clear advancement of laying date, as the timing of first clutches follows the advancement of the peak in food abundance. By contrast, we predict that laying date will have advanced to a lesser degree or not at all in populations in which the proportion of second clutches decreased. We have data on the incidence of second clutches for all 10 NL, B, UK and F great tit populations, and for seven blue tit populations. As predicted, we find a clear correlation between the decline in the proportion of second clutches and the degree of advancement of laying date (great tits: $r = -0.67$, $n = 10$, $p = 0.035$; blue tits: $r = -0.85$, $n = 7$, $p = 0.015$; figure 2). These correlations are further strengthened by data from great and blue tit populations in Brunswick (Germany), where hatching dates also indicate earlier breeding (Winkel & Hudde 1997) and where there is a very low incidence of second clutches (W. Winkel, personal communication).

4. DISCUSSION

We conclude that the different responses to large-scale climate change in laying dates of European great and blue tit populations can be attributed to spatial variation in climate change only on a large spatial scale. However, within a more restricted geographical area, the responses are correlated with responses in other life-history traits. The outstanding challenge is now to test this second brood hypothesis for which we find only correlative support (figure 2). We expect that if spring temperatures continue to increase, all populations will eventually start to lay earlier but this change will come at a price. Once no second clutches are being produced, the number of fledged offspring will decline, with possible effects on the dynamics of these populations. Our results also show the value of replicating population studies across parts of a species' range, as the effects of climate change may differ, even within a single species, on a small geographical scale.

We thank Kate Lessells, Chris Perrins and Christiaan Both for discussion and comments on the manuscript. M.E.V. thanks Jan Visser, the late Huybert van Eck and many others for their effort to monitor the Dutch great and blue tit populations, and the board of the National Park 'de Hoge Veluwe', the State Forestry Service in Vlieland and Breda (Liesbos) and Barones van Boetzelaer van Oosterhout for permission to work in their woodlands for all these years. J.B. thanks Philippe Perret, Marcel M. Lambrechts, Jacques Haurez, Paula Dias and many others for their efforts in long term monitoring of Mediterranean tit populations. M.O. acknowledges Mikko Ojanen, Kari Koivula, Seppo Rytkönen and Nanette Verboven for their help in the field, and the Research Council for Biosciences and Environment of the Academy of Finland, and the Thule Institute, University of Oulu for funding. C.d.F. acknowledges John McMeeking and all members of the Treswell IPM group. E.M. and F.A. acknowledge support from the EU 5th framework (METABIRD project). S.v.D. is research associate with the Flemish Fund for Scientific Research.

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