

How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature

WILL CRESSWELL and ROBIN MCCLEERY

Edward Grey Institute, Zoology Department, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

Summary

1. Breeding birds increase their fitness by synchronizing their production of chicks with a peak of food abundance. Synchronization is primarily achieved by varying first egg date, but yearly temperature variations may delay or accelerate the food peak after the first egg has been laid. We tested the extent to which great tits (*Parus major* L.) can strategically change their synchronization of hatch date with the food peak after the first egg has been laid by changing clutch size, laying interval and the amount of incubation. We also tested whether these possible synchronization change mechanisms resulted in changes in breeding success, because if the food peak is late relative to first egg date, we would predict more of the population to have larger clutches and/or a hatch date synchronous with the food peak date.
2. Great tits modified synchronization strategically by varying clutch size and the onset of incubation after clutch completion. When first egg date was early but then followed by cold weather so that the food peak was late, clutch sizes were larger, and when first egg date was late and temperatures were low, mean incubation periods were shorter if the food peak was early.
3. Over the 39-year period of the study, the period between the first egg date and food peak increased significantly by 1.7 days more than the period between the food peak and hatch date. Great tits have maintained synchronization by significantly increasing their incubation period.
4. Overall, the proportion of nests that had synchronous hatch dates depended on the yearly temperature pattern: the decline in variance between date of clutch completion and hatch was significantly greater in years where prelaying temperatures were higher (i.e. early first egg dates) and has therefore increased in recent years because of climate change. In warm early seasons (and more often in recent years) more of the great tits that laid relatively late had sufficient time to complete their clutches before having to start incubation in order to hatch in time for the food peak.
5. The increased proportion of synchronized nests in recent years probably resulted in increased chick output: a greater proportion of recent nests successfully fledged all of the chicks that hatched and the number of young fledged per successful nest also increased in recent years. These changes may have arisen because the proportion of nests with disadvantageous asynchronous hatching and/or smaller clutches has decreased. As the proportion of great tits that start nesting too late to synchronize has declined so selection for early laying has also declined in recent years.

Key-words: climate change, great tit, timing of breeding.

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Introduction

Timing of breeding in birds is crucial because those birds that produce chicks when food is seasonally most

abundant have the greatest fitness (Lack 1968; Perrins & McCleery 1989; van Noordwijk, McCleery & Perrins 1995). Recently, seasonal peaks in food abundance have advanced owing to higher spring temperatures (Ellis, Donner & Kuchlein 1997; Myneni *et al.* 1997) and so mean first egg dates of several bird species have advanced to maintain synchronization of production

of their chicks with the peak of food availability (Crick *et al.* 1997; McCleery & Perrins 1998). Yearly temperature variations may, however, delay or accelerate the food peak after the first egg has been laid. For example, in a Dutch population of great tits (*Parus major* L.) local low early spring temperatures have apparently constrained early egg laying, but higher late spring temperatures have advanced the peak of nestling food availability, resulting in a consistent mismatch and strong selection for early laying (Visser *et al.* 1998). In a British population of great tits at Wytham Woods, however, laying date has advanced with increasing temperatures (McCleery & Perrins 1998) and a mismatch and strong selection for early laying only occurs when springs warm rapidly (van Noordwijk *et al.* 1995). Climate change may therefore affect first egg date and the peak of food abundance differently, dependent on the detailed patterning of spring temperatures (Stevenson & Bryant 2000), resulting in either an increase or decrease in the duration of the period between first egg and hatch.

Although climate change may alter the duration of the period between first egg and the food peak, the ability of birds to strategically control their date of hatch after laying the first egg may compensate for any changes. Changes in hatch date to synchronize with a food abundance peak can be achieved after the first egg has been laid by changes in clutch size (Klomp 1970), variation in the laying interval between eggs (Nilsson & Svensson 1993), the onset of full incubation (van Balen 1973; Haftorn 1981) and pauses in incubation (Haftorn 1988). The costs and benefits of synchronizing via delaying or advancing hatch date will be different however. Delaying hatch date can allow larger clutches, but increasing the effective incubation period may increase the probability of nest predation (Bosque & Bosque 1995). Advancing hatch date by starting incubation before clutch completion results in asynchronous hatching because the first laid eggs have already started development before the last eggs are laid (Haftorn 1981) and leads to reduced fledgling success (Amundsen & Slagsvold 1998).

The effects of climate change on populations therefore depend crucially on the change in the duration of the period between first egg and the food peak, and the mechanisms of synchronization (first egg date, clutch size, laying interval and the timing of incubation). In years where the food peak is late relative to first egg date then even relatively late laying birds will also be able to hatch their chicks at the optimum time by simply laying small clutches and/or starting incubation after less of a delay. We would expect therefore a decrease in the variance of hatch date in delayed food peak years. We would also expect a smaller proportion of nests to have started incubation before clutch completion. We would then expect fewer nests to have asynchronous hatching and as a result an increase in the proportion of nests that fledge all their chicks successfully. We would also expect clutch size to increase and

therefore a larger number of young to fledge per nest. Overall, we would expect the selection differential for early laying to decrease (van Noordwijk *et al.* 1995). In contrast, in years where the food peak is advanced relative to first egg date we would expect smaller clutches, a decrease in incubation period and possibly an increase in asynchronous hatching and so reduced fledging success; the selection differential for early laying would also be stronger.

In this study we test the extent to which great tits breeding at Wytham Wood, Oxford, can strategically change their synchronization of hatch with the food peak by changing clutch size, laying interval and/or the timing of incubation. We then determined whether the use of these synchronization mechanisms resulted in the predicted changes in breeding success and the selection differential for early nesting dependent on whether the food peak was early or late relative to first egg date. We investigated the mechanisms of strategic synchronization and their consequences over a 39-year period where climate change has resulted in earlier springs and much variation in the interval between first egg date and the food peak date.

Methods

Data were analysed from the long-term study of great tit populations based at Wytham Woods, Oxford, UK (see Perrins 1965; Perrins & McCleery 1989). Data from 1960 onwards were used because methods were standardized from this date. Nests were visited at least once a week, at similar times of day, during the laying season. The date of appearance of eggs in the nest was recorded, together with the clutch size. The first egg date was found by counting back from the day of observation on the assumption that one egg was laid each day. The frequency of nest visits and egg skipping are such that errors in calculating first egg date that would arise when eggs are skipped are trivial. Over 39 years (1960–99), 88% of 780 nests (20 selected randomly per year, see below) had no egg skipping in a week period, and 97% had skips of two days or less. First egg dates extend over a period of 3–4 weeks and so errors that are more than 1 day (and that are almost always less than 6 days) will have minor effect.

Nests were visited again at around the expected date of hatching. Where chicks were not observed on the day of hatching itself the date of hatch was established by weighing the heaviest chicks and reading the age from growth curves (Gibb 1950). Although food supply may affect growth rates, potentially leading to longer estimates of incubation in poor food years, we can discount this potential bias because incubation periods became significantly shorter later in the season in 28 out of 29 years (17 out of 29 years at $P < 0.001$; see also Figs 2 and 3) when food supply is known to be reduced.

Although most visits to nests were at weekly intervals it was possible to detect laying gaps because of the

large clutch sizes laid by great tits and the large sample sizes in the study. The frequency and pattern of laying gaps was determined for each of the 39 years by manually checking randomly selected nest record cards until 20 cards were found that contained data where the clutch size had been started on one visit and had not been completed on a second visit. The proportion of the 20 nests sampled per year that had laying gaps in a week period was then calculated, as was the mean proportion of skipped days per nest in a week period for each year.

Incubation period was calculated as (hatch date – first egg date – clutch size – 1), in other words the number of clear days between the last egg laid and the first chick hatched. In reality incubation may start before clutch completion, and may continue a day or so after the first chick due to asynchronous hatching. We are also assuming that one egg is laid each day. The effects of laying gaps in each year (as calculated above) were later incorporated into any models of incubation period in order to distinguish between changes due to incubation scheduling and/or laying gaps. All outlying values were manually checked from original notebooks. In 1991 and 1992 some nests were used in an experiment where eggs were exchanged between nests, and all these records were excluded, reducing the sample size for those years. Post hatching manipulations did not affect this analysis and those nests were not excluded. Apart from the considerations above, the selection criteria for data to be included in the analyses presented here is exactly as in van Noordwijk *et al.* (1995), in particular the criteria for selecting first clutches.

Data are missing for some years because hatching dates were not recorded accurately (this resulted in 1979, 1981 and 1982 being eliminated from all hatching date analyses): inclusion of these data does not change the general results reported here. Data on caterpillar timing and on local recruitment were not available for all years. We chose to use the maximum data set in each analysis.

The caterpillar data used were mainly from the long-term study of the winter moth (*Operophtera brumata*, L.) at Wytham supplied by Dr L. Cole. Yearly caterpillar half fall date was used; this is the date by which 50% of the seasonal total of caterpillars are collected in traps and this provides a robust index of the peak of tit food abundance (van Noordwijk *et al.* 1995). Caterpillars are sampled intensively in one place in the woods and we have assumed that the degree of spatial heterogeneity of the caterpillar phenology has not changed between years. We believe this is a reasonable assumption because any consistent spatial change in the phenology of the caterpillar peak with year would be reflected in changes in the relative timing of nests between different areas of the wood and this has not occurred. Temperature data were from the School of Geography, Radcliffe Observatory in Oxford, about 5 km east of Wytham. The raw figures used were the

mean air temperatures for each 24-h period taken at 09:00 hours. Mean temperatures were calculated for three periods from mean daily temperatures. (i) The prelaying period that encompasses 1 March to 25 April: temperatures during this period have been shown to significantly affect first egg date (McCleery & Perrins 1998); t_{prelay} . (ii) The laying period that encompasses the 9-day period from the mean first egg date for a year and that will encompass the laying period on average for that year; t_{1-9} . (iii) The incubation period that encompasses a 9-day period from 10 days from first egg date to 18 days after first egg date and that will encompass the majority of the incubation period on average for that year; t_{10-18} .

Where the variance of first egg date, clutch completion date and hatch date were compared, only nests that hatched successfully were included, so that any changes in the variance were due to changes in timing rather than selection. Changes in variance between first egg, clutch completion and hatch dates were compared between years by expressing any change in variance between two periods as a proportion of the variance of the first period; e.g. (variance first egg date – variance clutch completion date)/variance first egg date. The selection differential for laying date was calculated according to the methods in van Noordwijk *et al.* (1995). The selection differential is the mean laying date weighted for the number of subsequent breeding birds each nest has produced minus the unweighted population mean. Negative values imply that early clutches have greater fitness than late clutches.

The mechanism of clutch and timing of the onset of full incubation was studied in April–May 2000 in nest boxes in Bean Wood, part of the Wytham Wood long-term study population. Nests were visited once every 2 days to determine date of clutch completion, clutch size and date of hatch. A sample of nests had a small flexible temperature probe placed next to the eggs when 2–4 eggs had been laid. The temperature of the eggs was logged every 30 s using Tinytag Dataloggers (Gemini Dataloggers Ltd). Each temperature trace from a nest was then analysed with respect to a reference temperature trace from an empty nest box. If the nest temperature was more than 25 °C, and this was at least 5 °C above the reference temperature then the eggs were considered to be being incubated (typically nest temperatures were 30–35 °C, and reference temperatures rarely exceeded 18 °C). Defining the onset of incubation is difficult because tits incubate for at least part of the night from the first egg (see Haftorn 1981). We therefore use the proportion of the day of clutch completion spent incubating as an index of the timing of the onset of full incubation because this increases steadily to a peak around the day of clutch completion (see Fig. 1 and Haftorn 1981). The proportion of the day of clutch completion spent incubating also correlates well with the days from clutch completion to the onset of more than 75% of the day spent incubating (see below). Once a female great tit starts incubating for

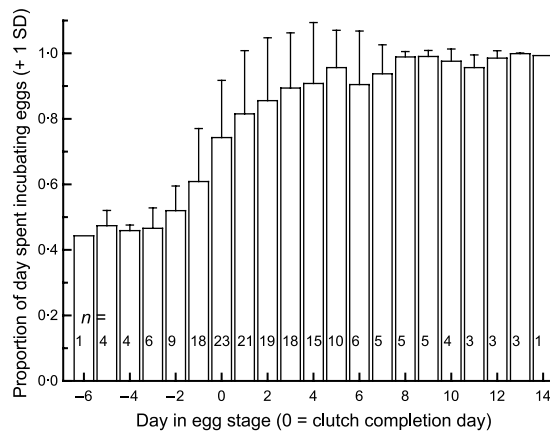


Fig. 1. Variation in the proportion of a day spent incubating eggs with respect to the number of days before, during and after clutch completion.

more than 75% of the day, this level remains uniformly high, increasing throughout the incubation period (Fig. 1 and Haftorn 1981).

The study is based on correlation and several independent variables of interest and potential confounding variables were correlated. In particular the age structure of the population (calculated as the proportion of birds greater than 1 year old in the breeding population) and the size of the breeding population (the number of first brood nests) were correlated ($r_p = -0.43$, $P = 0.007$, $n = 39$) and both the population size (number of nests = $-49.8(\text{year}) + 0.3(\text{year}^2) + 2002$; $F_{2,36} = 22.3$, $P < 0.001$, $R^2 = 0.55$) and proportion of adults were correlated with year (proportion of adults = $-0.04(\text{year}) + 0.002(\text{year}^2) + 2.0$; $F_{2,36} = 4.5$, $P = 0.02$, $R^2 = 0.20$). Population size was also correlated with mean first egg date ($r_p = -0.44$, $P = 0.005$, $n = 39$) and mean daily temperature in the prelay period ($r_p = 0.39$, $P = 0.01$, $n = 39$). Mean daily temperature in the prelay period was correlated with year ($r_p = 0.34$, $P = 0.04$, $n = 39$), as was first egg date (see Results). Of the temperature variables used all were uncorrelated apart from temperature during the laying period (t1–9), which was correlated with mean daily temperature in the prelay period ($r_p = -0.44$, $P = 0.005$, $n = 39$). All of the variables were investigated for temporal autocorrelation and only hatch date ($P = 0.02$) and first egg date ($P = 0.02$) were significant predictors of the following year's value for these variables when the data was detrended for time (with year and year squared in the model). Spurious correlations as a result of several temporally autocorrelated predictor variables in the same model were therefore not a problem in the analyses. In any case, neither hatch nor first egg date was a significant predictor of the following year's values without the effects of year in the model.

Models to test the hypotheses were determined by stepwise deletion of all independent variables if they were significant at $P > 0.1$ until a minimum adequate model was determined with all variables significant at

the $P < 0.05$ level. In order to deal with the multicollinearity of some of the independent variables, alternative minimum models but using the correlated and potentially confounding variables are then presented. For example, where we test for an effect of year, we also then test the final model by adding population size or age structure to the model, so that we could determine the confounding effects of yearly changes in population size and/or age structure.

Analysis was carried out using SPSS (Norusis 1990); all probabilities quoted are two-tailed, all R^2 values quoted are adjusted and means are presented with one standard error (mean ± 1 SE). All dependent variables used in parametric tests were found to be normally distributed (including those measured as proportions); proportions were arcsine transformed only where necessary according to the recommendations in Sokal & Rohlf (1981).

Results

LAYING GAPS

The proportion of nests that had laying gaps was on average 0.12 ± 0.02 ($n = 20$ nests in each of 39 years, range 0–0.5). The proportion of days in which eggs were skipped in a week period was on average 0.04 ± 0.01 days (range 0–0.39). The two measures of egg skipping rate were highly correlated ($r_s = 0.93$, $P < 0.001$, $n = 39$) because most laying gaps were a single day (72%, $n = 92$ laying gaps, maximum = 5 days).

The occurrence of laying gaps was dependent on temperature, when analysing between years, in a manner consistent with temperature acting as a constraint, rather than a cue for delaying hatch. If temperature always acts as a constraint, we would always predict a negative correlation between the rate of egg skipping and temperature, but if temperature acts as a cue we would only predict an increase in egg skipping with low temperatures in springs with early first egg dates. The proportion of nests that had laying gaps in a year decreased as temperature during laying increased (arcsine transformed proportion of nests with laying gaps = $-0.02(\text{xt1 to } 9) + 0.29$; $F_{1,37} = 4.0$, $P = 0.05$, $R^2 = 0.07$). This model was not, however, improved by including first egg date ($F_{1,35} = 0.7$, $P = 0.42$) and the interaction between first egg date and temperature ($F_{1,35} = 0.6$, $P = 0.46$).

THE MECHANISM OF SYNCHRONIZATION (I): CHANGES IN CLUTCH SIZE

Clutch size depends on both the timing of the season and temperature. Data from the 2000 breeding season showed that larger clutch sizes were produced significantly earlier in the year, but for any given day, there was likely to be a significantly larger clutch produced if the mean temperature during the 4 days prior to the first egg was higher (linear regression, clutch size =

-0.33 (first egg date, $t = -3.9$, $P < 0.001$) $+ 1.2$ (mean temperature during the previous 4 days, $t = 2.5$, $P = 0.02$) $+ 2.4$; $F_{2,17} = 7.6$, $P = 0.004$, $R^2 = 0.41$). Note sample sizes ($n = 20$ nests) were smaller here because temperature data were only recorded from the start of the first nest, but analyses using mean temperature from 1, 2 or 3 previous-day periods gave similar results.

Clutch size was strongly dependent on the timing of the breeding season and temperature when analysing between years. Clutch size was larger in years with early first egg dates and years with lower temperatures during the prelaying period (linear regression, clutch size $= -0.07$ (first egg date, $t = -2.9$, $P = 0.006$) $- 0.40$ (tprelay, $t = -2.5$, $P = 0.018$) $+ 13.9$; $F_{2,36} = 4.3$, $P = 0.022$, $R^2 = 0.15$). Proportion of adults was not significant if included in the model ($F_{1,35} = 0.8$, $P = 0.37$) and clutch size was independent of population size ($F_{1,37} = 0.02$, $P = 0.88$). The final model demonstrates that clutch size is larger in early nests and that for any given first egg date, if temperatures were lower prelaying then clutch size will be larger. Note that the effect of prelaying temperature differs from the result above. If the season is early, but temperatures are then low during the month before laying so that the caterpillar peak is probably delayed, then clutches are larger (i.e. a strategic response). However, if temperatures are lower in the few days immediately before laying then smaller clutches result (i.e. possibly an energy constraint).

THE MECHANISM OF SYNCHRONIZATION (II): DELAYING THE ONSET OF FULL INCUBATION

The pattern of incubation during the 2000 breeding season was similar to that described by Haftorn (1981). Partial nocturnal incubation commenced with the first egg and diurnal incubation started around clutch completion (Fig. 1). Once a female had commenced diurnal incubation the percentage of the day the eggs were incubated (at least 5°C above ambient temperature as an index of incubation; see Methods) increased to near 100% over a 1- or 2-day period. The percentage of the day spent incubating then remained near 100% until hatch (Fig. 1): of 16 nests monitored to the first day where incubation exceeded 98%, only 3 nests then showed a subsequent day's nest attendance of less than 98%, with the minimum attendance being 92% ($n = 5$ days of less than 98% attendance out of 72 monitored from the first day where incubation exceeded 98%). Therefore there was little evidence that incubation varied sufficiently after the onset of full incubation to influence hatch date.

Data from the 2000 breeding season showed that variation in the amount of the incubation (as measured by temperature probes in 23 nests) is greater on the day of clutch completion than on days either preceding or following (Fig. 1; Spearman's rank correlation, $r_s = -0.87$, $P < 0.001$, $n = 19$ days from 5 days before clutch completion to 13 days after, correlation of unbiased

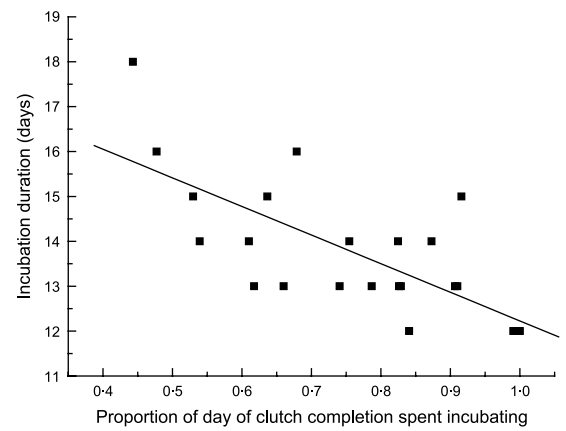


Fig. 2. Length of incubation period (days between clutch completion and first hatch) depends on the proportion of time spent incubating on the day of clutch completion ($y = -6.4x + 18.6$; $F_{1,21} = 21.8$, $P < 0.001$, $R^2 = 0.49$). Both clutch size ($F_{5,15} = 1.6$, $P = 0.23$) and mean temperature on day before, during and after clutch completion ($F_{1,15} = 2.5$, $P = 0.13$) were not significant if included in the model.

estimate of the coefficient of variation of proportion of day spent incubating with number of days before or after clutch completion). Hatch date was influenced by how much incubation was carried out on the day of clutch completion, with 49% of the variance in length of incubation being accounted for by variation in the amount of incubation on the day of clutch completion (Fig. 2). These results are robust when different time periods around clutch completion are used to measure the amount of incubation (e.g. the proportion of the day spent incubating on the day before clutch completion or after clutch completion).

There was a good correlation between the proportion of the day of clutch completion spent incubating and the number of days that elapsed from clutch completion to when the great tit started full time incubation (more than 75% of the day on the eggs): Spearman's rank correlation $r_s = -0.82$, $n = 23$, $P < 0.001$). Therefore, hatch date was also determined by the number of days from clutch completion to the day when the great tit started incubating for more than 75% of the time, with 66% of the variance in length of the period between clutch completion and hatch being accounted for by variation in the amount of incubation on the day of clutch completion (linear regression, incubation period $= 0.64$ (number of days until full incubation) $+ 13.1$; $F_{1,21} = 43.3$, $P < 0.001$). Clutch size ($F_{5,15} = 1.2$, $P = 0.34$) and mean temperature on day before, during and after clutch completion ($F_{1,15} = 1.8$, $P = 0.20$) were not significant if added to the model.

Early completed clutches were incubated much less on the day of clutch completion on average than later completed clutches (Fig. 3). Date accounted for 33% of the variance in proportion of time spent incubating on the day of clutch completion (linear regression, proportion of time spent incubating $= 0.03$ (date of clutch completion) $- 0.004$; $F_{1,21} = 11.8$, $P = 0.002$). Clutch

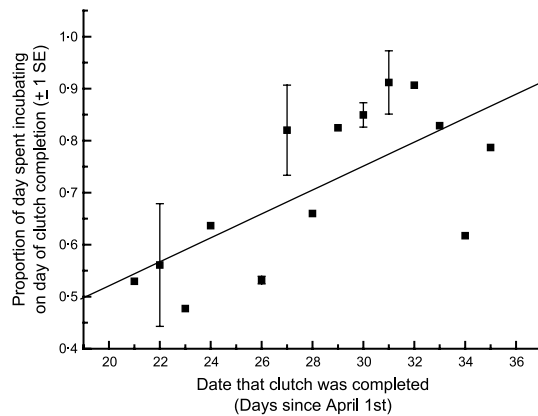


Fig. 3. Great tits at later nests incubate for a much greater proportion of the day on which the clutch was completed ($y = 0.023x + 0.07$; $F_{1,12} = 10.9$, $n = 14$ days and $n = 23$ nests, $P = 0.006$, $R^2 = 0.43$).

size ($F_{5,15} = 0.8$, $P = 0.57$) and mean temperature on day of clutch completion ($F_{1,15} = 1.9$, $P = 0.19$) were not significant if added to the model. Although both temperature and date were positively correlated with proportion of time spent incubating, temperature did not have a significant effect suggesting that great tits are not starting incubation later generally, or in early years, because of energetic constraints. Daily mean temperature (mean of 288 daily samples at 5 min intervals from the reference temperature probe) was not dependent on date (linear regression of date and mean temperature, $F_{1,14} = 0.6$, $P = 0.46$).

The duration of incubation was strongly dependent on temperature when analysing between years but in a manner consistent with temperature acting as a cue, rather than a constraint on incubation. If temperature acts simply as a constraint we would always expect a negative correlation between temperature and incubation duration. However, if temperature acts as a cue we would predict that great tits should only show decreased incubation duration with increasing temperature after clutch completion in springs when they lay late. This was the case: linear regression, mean incubation duration = $0.97(\text{xt}10 \text{ to } 18, t = 2.3, P = 0.03) + 0.45$ (mean first egg date, $t = 2.4$, $P = 0.02$) $- 0.04(\text{xt}10 \text{ to } 18 \times \text{mean first egg date}, t = 2.8, P = 0.01) + 3.1$; overall model $R^2 = 0.34$. Population size ($F_{1,32} = 0.1$, $P = 0.75$) and the interaction between population size and temperature during incubation ($F_{1,32} = 0.3$, $P = 0.61$) were not significant if used in the model instead of first egg date and proportion of adults was not significant if added to the model ($F_{1,31} = 0.4$, $P = 0.56$). The best model for these data is where first egg date is split into two periods, early and late spring, before and after April 25th, respectively (linear regression, mean incubation duration = $1.1(\text{xt}10 \text{ to } 18, t = 3.7, P = 0.001) + 8.1$ (period, $t = 4.1, P < 0.001$) $- 0.71$ (period \times xt10 to 18, $t = -4.4, P < 0.001$) $+ 0.82$; $F_{3,32} = 10.1$, $P < 0.001$; overall model $R^2 = 0.44$). In springs where tits lay early, incubation duration therefore *increases* with higher early spring temperatures.

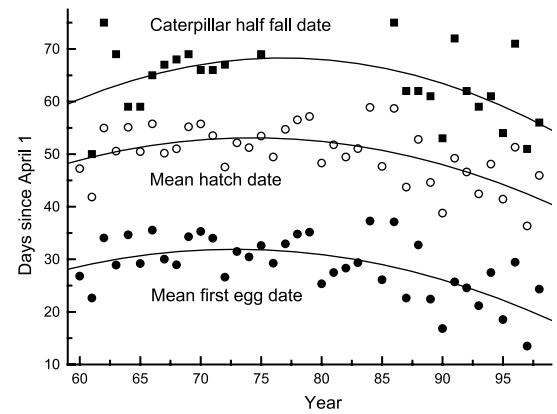


Fig. 4. Changes in mean first egg date, mean hatch date and caterpillar half fall date with year. Quadratic regression lines are plotted (R^2 values for quadratic functions are roughly double that of linear functions). First egg date = $2.9(\text{year}) - 0.02(\text{year}^2) - 73.0$; $F_{2,36} = 11.9$, $P < 0.001$, $R^2 = 0.39$; hatch date = $3.0(\text{year}) - 0.02(\text{year}^2) - 57.8$; $F_{2,33} = 9.2$, $P = 0.001$, $R^2 = 0.36$; and caterpillar half fall date = $4.3(\text{year}) - 0.03(\text{year}^2) - 95.2$; $F_{2,23} = 3.5$, $P = 0.05$, $R^2 = 0.23$).

CHANGES IN FIRST EGG DATE, HATCH DATE, PEAK OF FOOD ABUNDANCE, INCUBATION PERIOD, LAYING GAPS AND CLUTCH SIZE WITH YEAR

First egg date has changed significantly with year, becoming earlier in recent years (Fig. 4a, see also McCleery & Perrins 1998); hatch date follows a similar pattern, as does caterpillar half fall date (Fig. 4a). First egg date was also significantly correlated with population size (first egg date = $-0.06(\text{number of nests}) + 0.00005(\text{number of nests}^2) + 40.5$; $F_{2,36} = 4.6$, $P = 0.02$, $R^2 = 0.20$) but this effect was not significant when controlling for year (nest, $F_{1,34} = 0.4$, $P = 0.52$; nest², $F_{1,34} = 0.6$, $P = 0.46$; model as in Fig. 4a but including nest and nest²). Hatch date was also significantly correlated with population size (hatch date = $-0.04(\text{number of nests}) + 0.00006(\text{number of nests}^2) + 58.7$, $F_{2,33} = 3.6$, $P = 0.04$, $R^2 = 0.20$), but this effect was not significant when controlling for year (nest, $F_{1,31} = 0.03$, $P = 0.86$; nest², $F_{1,31} = 0.07$, $P = 0.80$; model as in Fig. 4a but including nest and nest²). First egg date was not correlated with proportion of adults ($F_{2,36} = 0.04$, $P = 0.97$), nor was hatch date ($F_{2,33} = 0.07$, $P = 0.93$).

Although first egg, hatch and caterpillar half fall date have all become earlier in recent years, the period between first egg date and hatch date (egg days) has increased significantly with year (egg days = $0.05(\text{year}) + 17.6$; $F_{1,34} = 16.8$, $P < 0.001$, $R^2 = 0.31$) but the period between hatch date and caterpillar half fall date has not increased significantly with year ($F_{1,25} = 1.3$, $P < 0.26$, $R^2 = 0.01$). To exclude the possibility that the lack of a significant change in the period between hatch and half fall date was due to reduced power (i.e. missing half fall data in the 1970s and 1980s, see Fig. 4) we compared the means of both the difference between hatch and first egg date, and the difference between half

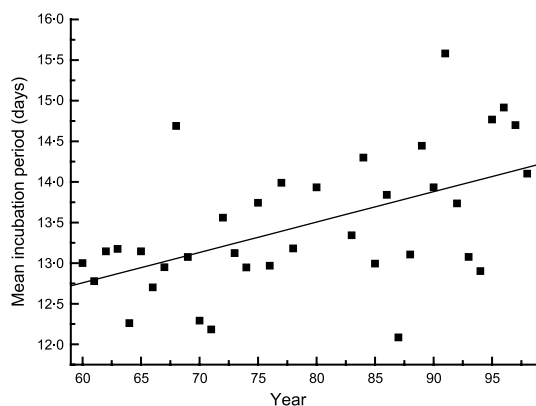


Fig. 5. Mean incubation period (days between clutch completion and first hatch) has increased since 1960 (incubation period = $0.04(\text{year}) + 10.5$; $F_{1,34} = 13.5$, $P = 0.001$, $R^2 = 0.26$). Population size was not significant if added to the model ($F_{1,33} = 1.3$, $P = 0.26$) nor proportion of adults ($F_{1,33} = 2.1$, $P = 0.16$).

fall and hatch date using only data from 1961 to 1972 and 1986–98. The number of egg days has significantly increased between the sets of years ($t_{12,13} = -3.3$, $P = 0.003$) but not between half fall date and hatch date ($t_{12,13} = -1.2$, $P = 0.25$). Therefore it is apparent incubation period that has increased in recent years (Fig. 5) without a corresponding change in the degree of synchronization.

On average period between first egg date and hatch date has increased by 1.7 days over the study, this represents a clutch size change of 2 eggs (with one egg being laid per day) or an increase in incubation period of 13% (with an incubation period of 13 days) over the 39-year period. Clutch size has not, however, changed significantly with year (linear regression, mean clutch size = $0.010(\text{year}) + 7.9$; $F_{1,37} = 1.3$, $R^2 = 0.01$, $P = 0.26$; a quadratic term does not improve this model as in Fig. 4; population size was not significant if added to the model ($F_{1,33} = 0.3$, $P = 0.59$) nor was proportion of adults ($F_{1,33} = 0.2$, $P = 0.63$). The increase in mean incubation period was also not due to the effect of egg laying gaps (as a consequence of our calculation of incubation period as days from first egg date to hatch – clutch size) because egg laying gaps to have not changed with year (proportion of nests with egg laying gaps = $-0.002(\text{year}) + 0.26$; $F_{1,34} = 2.6$, $P = 0.11$, $R^2 = 0.05$; note the trend is actually a decrease with year). Although incubation period depended on both year and egg laying gaps (incubation period = $0.04(\text{year}) + 3.3(\text{proportion of nests with laying gaps}) + 9.7$, $F_{2,33} = 9.9$, $P < 0.001$, $R^2 = 0.34$), there was a change in incubation period over the 39-year period of 1.5 days after controlling for the effect of laying gaps (the residuals of incubation period after correcting for the proportion of nests with laying gaps = $0.04(\text{year}) - 3.2$, $F_{1,34} = 17.1$, $P < 0.001$, $R^2 = 0.32$). Neither population size ($F_{1,32} = 0.5$, $P = 0.50$) nor proportion of adults ($F_{1,32} = 2.7$, $P = 0.11$) was significant if added to the model. The results are

practically identical if incubation period is controlled for the proportion of days in which eggs were skipped in a week period. Overall the proportion of nests skipping eggs during laying was not dependent on the period between first egg date and caterpillar half fall date ($F_{1,24} = 0.7$, $P = 0.40$); neither population size ($F_{1,23} = 2.4$, $P = 0.13$) nor proportion of adults ($F_{1,24} = 0.6$, $P = 0.44$) was significant if included in the model. Also the proportion of days in which eggs were skipped in a week period was not dependent on the period between first egg date and caterpillar half fall date ($F_{1,24} = 0.02$, $P = 0.89$); neither population size ($F_{1,23} = 0.6$, $P = 0.43$) nor proportion of adults ($F_{1,24} = 0.5$, $P = 0.51$) was significant if included in the model.

THE FITNESS CONSEQUENCES OF SYNCHRONIZATION VIA CLUTCH SIZE AND DELAYING THE ONSET OF FULL INCUBATION

The synchronization of nests increases from laying to hatch: although first eggs may be laid over several days, the same nests will hatch over a shorter period of days. The variance of first egg date is greater, on average, than the variance of clutch completion date [note that this is a surrogate for clutch size] (a decline of $5.0 \pm 0.8\%$ in the variance, matched pairs t -test, $t_{35} = 6.3$, $P < 0.001$), and the variance of clutch completion date is greater, on average, than the variance in hatch date (a decline of $4.9 \pm 1.5\%$ in the variance, matched pairs t -test, $t_{35} = 3.3$, $P = 0.002$). The variance in first egg date was not significantly correlated with year ($F_{1,34} = 2.5$, $P = 0.12$) or population size ($F_{1,34} = 3.1$, $P = 0.09$) but was significantly correlated with proportion of adults (linear regression, variance in first egg date = $4.4(\text{proportion of adults}) + 3.3$; $F_{1,34} = 7.4$, $P = 0.01$, $R^2 = 0.12$). The variance in the date of clutch completion was not significantly correlated with year ($F_{1,34} = 1.9$, $P = 0.17$), or population size ($F_{1,34} = 3.2$, $P = 0.08$) but was significantly correlated with proportion of adults (linear regression, variance in clutch completion date = $4.3(\text{proportion of adults}) + 3.1$; $F_{1,34} = 9.5$, $P = 0.004$, $R^2 = 0.17$). The variance in the date of hatch, however, was significantly correlated with year (Fig. 6). The variance of hatch date was also significantly correlated with population size (linear regression, variance in hatch date = $-0.003(\text{number of nests}) + 5.8$; $F_{1,34} = 5.5$, $P = 0.025$, $R^2 = 0.11$) and proportion of adults (linear regression, variance in hatch date = $3.2(\text{year}) + 3.3$; $F_{1,34} = 7.0$, $P = 0.012$, $R^2 = 0.15$). Both year and proportion of adults were significant in a model containing both variables (linear regression, variance in hatch date = $-0.02(\text{year}) + 2.5(\text{proportion of adults}) + 5.4$; $F_{2,33} = 6.0$, $P = 0.006$, $R^2 = 0.22$); population size was not significant if included in the model ($F_{1,32} = 0.2$, $P = 0.63$). Therefore variance in hatch date increased as the proportion of adults increased but decreased overall with year.

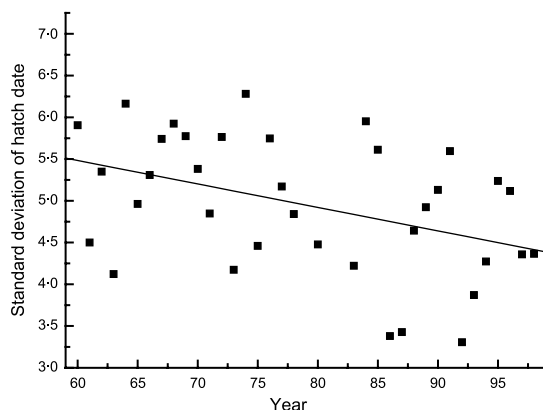


Fig. 6. The standard deviation in hatch date has decreased since 1960 ($F_{1,34} = 7.1$, $P = 0.012$, $R^2 = 0.15$).

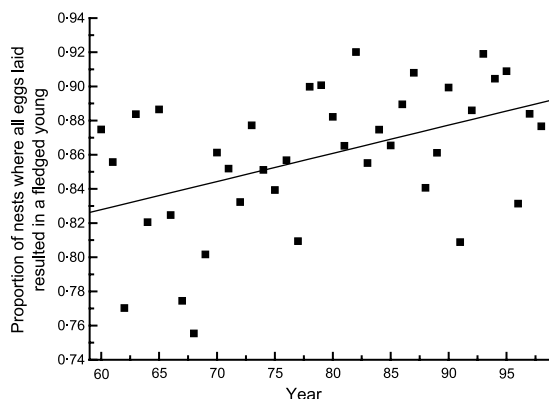


Fig. 7. The proportion of nests where all eggs laid result in a fledged young has increased since 1960 ($F_{1,38} = 9.8$, $P = 0.003$, $R^2 = 0.19$). Note that total nest failures (where number fledged = 0) are omitted because these almost certainly all represent predation events rather than insufficient chick feeding. Population size was not significant if added to the model ($F_{1,36} = 0.04$, $P = 0.84$) nor proportion of adults ($F_{1,36} = 0.6$, $P = 0.46$).

The proportionate decline in variance between first egg date and clutch completion has not changed significantly with year ($F_{1,34} = 1.1$, $P = 0.31$), population size ($F_{1,34} = 0.04$, $P = 0.83$), proportion of adults ($F_{1,34} = 0.08$, $P = 0.78$) or with temperature during the prelaying period ($F_{1,34} = 0.2$, $P = 0.69$). There was however, a trend for the proportionate variance decline between clutch completion and hatch date to increase with time (linear regression, change in variance = $0.002(\text{year}) - 0.10$; $F_{1,34} = 2.8$, $P = 0.09$, $R^2 = 0.05$) and there was a significant increase in the variance decline in years where the temperature in the prelaying period was high (linear regression, change in variance = $0.03(\text{tprelay}) - 0.17$; $F_{1,34} = 4.3$, $P = 0.046$, $R^2 = 0.09$), but there was no significant change in variance decline with population size ($F_{1,34} = 0.4$, $P = 0.52$) or proportion of adults ($F_{1,34} = 0.2$, $P = 0.67$).

Overall the variance in hatch date has decreased in recent years (see Fig. 6) therefore the proportion of the great tit population that hatches at the optimum time has correspondingly increased. Also the proportion of

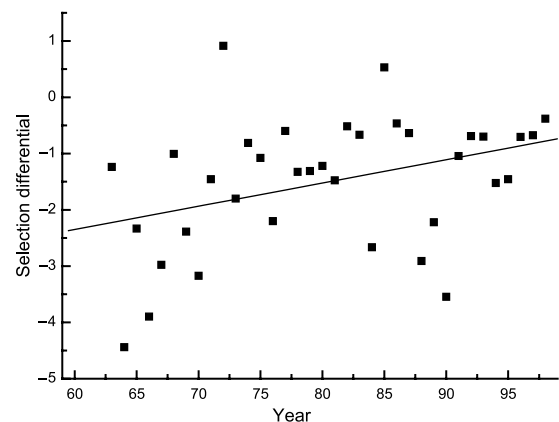


Fig. 8. The selection differential for early nesting has declined with time (a more negative selection differential represents a greater fitness for early nesting): $F_{1,34} = 5.3$, $P = 0.027$, $R^2 = 0.11$). Population size was not significant if added to the model ($F_{1,33} = 2.7$, $P = 0.11$) nor proportion of adults ($F_{1,33} = 0.02$, $P = 0.85$).

nests that fledged all chicks successfully has increased significantly in recent years suggesting that asynchronous hatching has declined (Fig. 7). As the proportion of late nesting great tits has declined so also has the selection differential for early laying in recent years (Fig. 8): there are now probably fewer nests that lay late enough to pay asynchrony costs. There was also a trend for the mean number of chicks produced per nest (excluding total nest failures) to increase in recent years (linear regression, number of chicks fledged = $0.022(\text{year}) + 5.8$; $F_{1,37} = 4.0$, $P = 0.053$, $R^2 = 0.07$). The mean number of chicks produced per nest has not changed significantly with either population size ($F_{1,36} = 0.3$, $P = 0.58$) or proportion of adults ($F_{1,36} = 0.2$, $P = 0.69$), when these terms were added to the model.

Discussion

Strategic synchronization of hatch date in great tits after the first egg has been laid was probably carried out by a combination of variable clutch size and changes to the timing of the onset of full incubation. The result with respect to synchronization via clutch size is partly confirmed by a study where Marsh Tits (*Parus palustris* L.) given supplemental food still showed a seasonal decline in clutch size (Nilsson 1991). The result with respect to synchronization by delaying the onset of full incubation is partly confirmed by a study where blue tits (*Parus caeruleus* L.) manipulated to lay early in a season then had greater delays in the onset of incubation compared to unmanipulated, later breeding blue tits (Nilsson 1994). Seasonal clutch size (reviewed in Daan *et al.* 1988) and length of incubation (Smith 1993; Wesolowski 2000) declines have been reported previously but their importance in strategic hatch date synchronization has not been examined in detail.

There was no evidence for laying or incubation gaps being used as strategic mechanisms for modifying

hatch date. Variation in laying interval is unlikely to be strategic as it would substantially increase hatching asynchrony and it arises probably as a response to food shortage (Bryant 1975): when supplemental food is supplied egg laying gaps disappear (Nilsson & Svensson 1993). Similarly, major pauses in incubation are also probably responses to food shortage or low temperatures (Morton & Pereyra 1985; Haftorn 1988). Also egg skipping may not be easily available as a physiological option (e.g. see Pulliainen, Jussila & Tunkkari 1994) and major pauses in incubation after its full onset are likely to have costs in terms of chick development (Webb 1987).

In contrast to egg skipping and incubation pauses we have good evidence that both clutch size and incubation onset were the result of strategic decisions rather than simply because the great tits were constrained by energetic costs. Firstly, larger clutches on average occur in cold prelaying periods: if great tits were constrained we would predict smaller clutches. Secondly, colder springs overall result in a shorter incubation period because more birds start laying later: if great tits are constrained we would predict longer incubation periods under these conditions.

Although many previous studies have demonstrated that first egg date (e.g. Kluijver 1951; Forchhammer, Post & Stenseth 1998), clutch size (Klomp 1970; Daan *et al.* 1988; Perrins & McCleery 1989), incubation scheduling (e.g. van Balen 1973) and hatch date (e.g. Winkel & Hudde 1997) depend on temperature, this study has demonstrated for the first time how great tit response to temperature change results in the optimal synchronization of hatch date with the peak of food abundance. Great tits optimally must aim to lay early enough so that they can produce a large clutch before they have to start incubation in order to catch up with the caterpillar peak. Many great tits are, however, probably constrained by temperature from producing eggs early enough. If this constraint is not present, because a great tit is a particularly good individual and/or it has a good territory and/or because of climate change increasing spring temperatures, then great tits will probably lay as soon as feeding conditions become sufficiently good to allow the production of eggs. This gives the opportunity for clutch size to increase without asynchronous hatching arising. Synchronization can then be achieved by the timing of the onset of full incubation after clutch completion.

Although the data presented here suggest that the number of nests with asynchronous hatching has declined with time, this has not been explicitly tested. However, unpublished data (Gibb 1953) confirms the related prediction that arises from our results that early nests will show more synchronous hatching: in all 5 years (1947–51) the proportion of great tit nests that hatched over more than 2 days was higher for late nests ($P = 0.03$, binomial test). Suggestively, the proportion of nests that hatched over more than 2 days in 2001 was only 9% ($n = 23$ nests unpublished data), compared to

an average for Gibb's data of $65 \pm 6.0\%$ ($n = 5$ years, $n = 197$ nests) 50 years previously.

Our results overall suggest strongly that more of the tits at Wytham can now match their chick production date with the peak of food production because the period between the mean first egg date and the food peak has increased. In years when spring is late, or historically in winters before 1960 (see McCleery & Perrins 1998) late-laying great tits are forced to incubate immediately on or before clutch completion otherwise they miss the food peak (e.g. see Gibb 1950). In years when spring is early (i.e. most springs currently perhaps because of climate change) more of the population can complete their clutches early and so will be able to optimize their hatch date in relation to their food supply by retarding the onset of full incubation. Historically, more great tits at Wytham laid eggs later than optimal, probably because they were constrained by food availability at the end of the winter (Perrins 1970), as currently probably occurs in Netherlands (Visser *et al.* 1998). The degree to which temperature acts as a constraint (Lack 1966; Perrins 1970) or as a cue (Lack 1954; Lack 1955) on early egg laying so a bird is able to synchronize with an early food abundance peak would appear to be crucial in determining fitness.

Directional selection for early laying now occurs less intensely at Wytham because springs are now warmer. Our results confirm the hypothesis proposed by van Noordwijk *et al.* (1995) that great tits have asymmetric response opportunities, where they have more scope to retard hatch than to speed it up, so that there is selection on average for early laying. With the current increase in spring temperatures, however, the need to retard hatch date has become more usual, with the net result that selection for early laying has decreased. Nevertheless in years where the spring warms up quickly, advancing the caterpillar peak, only those tits that have laid early will be able to synchronize by initiating incubation early enough. Early laying by tits, however, will still have a selective advantage (e.g. the selection differentials in Fig. 8 are almost all negative) because early nests can afford to have larger clutches that will be completed on time even if the spring warms up rapidly. There may also be a cost to early laying because adult survival is reduced (Nilsson 1994) and increased laying and incubation periods decrease the probability of nest survival (Bosque & Bosque 1995). In hole nesting species such as great tits daily nest predation rates are low, so selection against long incubation periods may be weak. For example, within the fairly predator proof nest boxes of the Wytham study population, nests that fail have a similar first egg date to those that fledge chicks (matched pairs t -test, $t_{38} = 0.5$, $P = 0.62$). In more natural tit populations where nest predation rates are higher then it seems likely that there will also be directional selection against early laying. There may also be selection against long periods of no incubation because low temperatures affecting embryo viability (Webb 1987) but this potential effect does not

appear to be affecting the Wytham great tits as breeding success has apparently increased as 'egg neglect' has increased.

Changes in the clutch size and the onset of full incubation in great tits may have arisen in the Wytham population by three processes. Firstly, microevolutionary processes, where there may have been selection on early laying birds to increase clutch size and delay incubation after clutch completion (e.g. van Noordwijk, van Balen & Scharloo 1981). Secondly, phenotypic plasticity, where great tits may use behavioural flexibility in response to temperature cues (e.g. Przybylo, Sheldon & Merila 2000). Thirdly, changes in gene frequency by migration, where birds from more southerly populations may have gradually replaced the population of great tits at Wytham. It is impossible to distinguish between the processes with a cross sectional study as presented in this paper, but phenotypic plasticity is perhaps the most likely to account for the observed changes. Although clutch size has shown a trend to increase with time, in 63% of pairs of consecutive years, the change in clutch size exceeded the average change in clutch size over the 39 years study period. Also, in 26% of pairs of consecutive years, the change in incubation period between years exceeded the average change in incubation duration over the 39 years study period. With a longitudinal study it is possible to demonstrate that the same individuals can vary in clutch size by 1.4 eggs and laying date by 17 days between years (Perrins & McCleery 1989). Clearly, it is only the proportion of years that require larger clutches or long incubation periods for synchronization that has increased, rather than the capacity for long incubation periods *per se*.

Any change in great tit breeding phenology depends crucially on the mismatch between the effects of climate change on first egg date and on the food peak: if temperature in any spring accelerated or retarded first egg dates and the food peak to exactly the same extent then the results we have described could not occur. This is shown well by the study by Visser *et al.* (1998), where incubation period has increased with time, synchronization has declined and the selection differential for early nests has increased because the rate of change in temperature over the season has increased: the reverse of the situation at Wytham. These two studies provide a clear example of the importance of variation in spring temperature *within* a breeding season on tit breeding success that may arise as a consequence of climate change. Complex changes in temperature patterns may change breeding phenologies (Stevenson & Bryant 2000) but they do not necessarily mean that they will be deleterious. Great tits have a clear ability to compensate for changes in the peak of food abundance as long as they are not constrained by first egg date.

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