Selection for the timing of great tit breeding in relation to caterpillar growth and temperature

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Summary

1. We investigated the relation between the timing of great tit breeding, measured as the mean date of laying the first egg in each clutch, the timing of caterpillar availability, measured as median pupation dates of winter moth, selection for laying dates, measured from the recruitment into the local breeding population in subsequent years, and temperaturé in the period after egg laying.

2. There was a significant positive correlation between the timing of the great tit's laying and the timing of the caterpillars.

3. In most years there was selection for earlier laying in this great tit population. The selection differentials were usually the same for male and female recruits.

4. The selection differential for laying date was strongly correlated ($r = 0.84$, $n = 21$, $P < 0.0001$) with the difference in timing between birds and caterpillars. This difference in timing was in turn strongly correlated with temperatures in the period after egg laying.

5. When the period after the laying date was subdivided, the selection differential was strongly correlated with the mean temperature during the period when most birds were incubating.

6. We discuss six alternative hypotheses explaining a consistent selection differential for earlier laying. One of these is new and is based on the fact that the birds can delay their breeding more succesfully than they can speed it up, once they have started laying.

Key-words: caterpillar pupation, insectivorous birds, natural selection, timing of breeding, Wytham Wood.

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Introduction

The timing of laying is very important in the great tit *Parus major*, L. Laying a few days earlier or later may lead to measurable differences in nestling weight and in local recruitment rates of the resulting offspring (e.g. Perrins 1965, 1970; van Noordwijk, van Balen & Scharloo 1981; Boyce & Perrins 1987; Tinbergen & Boerlijst 1990; Gebhardt-Henrich & van Noordwijk 1991). The main reason is the short period during which caterpillars are abundant on oaks (e.g. Gibb 1950; van Balen 1973); parents feeding late broods cannot provide as much food as those feeding early broods, with the result that their chicks leave the nest at lighter weights and do not survive so well. The time during which caterpillars are available to the tits is often characterized by the median pupation date, or half-fall date, of the winter moth. This is the date at which half the caterpillars of the winter moth have descended to the ground to pupate.

The laying period of the birds roughly coincides with the hatching of the caterpillar eggs. Once the birds have started to lay, their nesting cycle is relatively inflexible, whereas the period when caterpillars are plentiful may vary markedly because their rate of growth is strongly influenced by ambient temperature (see Perrins 1979 and refs therein). The relations between the onset of laying and temperature have recently been reinvestigated (Perrins 1991). Here we concentrate on the period immediately after the onset of laying. Using the data from the population study in Wytham near Oxford, UK, we have analysed the relationships between the timing of laying, the timing of caterpillar pupation, mean temperatures over various periods after the laying dates and selection for laying date in the great tit.

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Materials and methods

The analyses are based on data from the great tit population study in Wytham Wood, Oxford, UK (see Perrins 1965, 1979; Perrins & McCleery 1989). We tried to restrict ourselves to first broods, omitting replacement clutches. Where no indication of previous nesting in the same year by the same pair existed, we assumed that clutches that were started more than 30 days after the first clutch in that year were repeat clutches after a failed earlier attempt. Using the very first clutch to define the cut-off date carries a risk that an extremely early clutch could lead to the cutting-off of late proper first clutches. This does not seem to have happened. In only 4 years out of 40 did the mean laying date fall in the second half of the 30-day period, and in each of these years, as well as in all other years, the cut-off point was more than two standard deviation units later than the mean. In comparison with earlier analyses (notably those of Perrins 1991), mean laying dates used in this analysis are slightly later, indicating that we may have included a few replacement clutches. The effects on the analyses presented here are minor.

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. There were no indications that years with missing data were systematically different in any of the variables for which data were available.

For a detailed description of the study area and the standard methods see Perrins & McCleery (1989). The caterpillar data used were mainly from the long-term study of the winter moth *Operophtera brumata*, L. in Wytham woods by G.C. Varley and others, with data for some recent years supplied by Dr L. Cole. Temperature data were from the School of Geography/Radcliffe Observatory in Oxford, about 5 km east of Wytham. The raw figures used were the maximum and minimum air temperatures for each 24-h period taken at 09.00 h.

Results

The starting point for these analyses was the existence of a strong correlation between the mean laying dates and the timing of the caterpillars, measured by their half-fall dates, i.e. the date on which half the caterpillars of the winter moth had dropped from the trees to pupate in the ground. (Perrins 1965; van Noordwijk 1988; Perrins & McCleery 1989). Although the correlation was high (Fig. 1; $r = 0.78$, $n = 32$, $P < 0.0001$), one would expect some of the scatter to be due to weather in the period between the bird's egg laying and hatching. In the following, we concerned ourselves mainly with the deviations from an equal timing of birds and caterpillars, to be called a difference in timing.

The highest energy demand for the birds starts about 30 days after the laying of the first egg, when
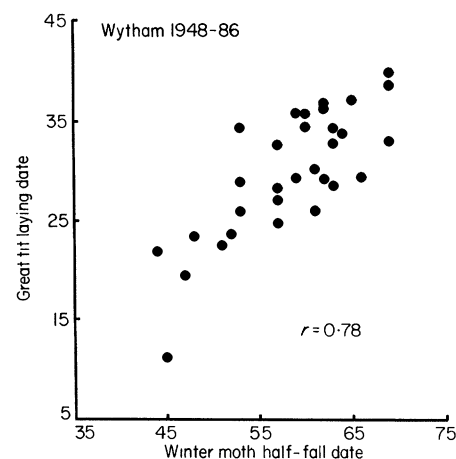
Fig. 1. The correlation between the mean laying dates of great tits and the winter moth half-fall date, which is the date on which half the caterpillars of the winter moth (*Operophtera brumata*) have dropped from the trees to pupate in the ground ($r = 0.78$, $n = 32$, $P < 0.0001$). Data from Wytham 1948–72, 1975, 1980, 1982–86. No caterpillar data were available for the intervening years. Dates are given in 'April dates' (1 = 1st April).

nestlings are about 1 week old (9 days of egg laying + 14 days of incubation + 7 days of nestling growth; van Balen 1973; Betts 1955; R.G. Nager & A.J. van Noordwijk, unpublished data). If the birds time their laying in such a way that having 1-week-old nestlings coincides with the peak in caterpillar availability in average years, one would expect that the birds are too late in warm years—because the caterpillars develop relatively fast—and that they are too early in cold years—because the caterpillars develop relatively slowly (van Balen 1973).
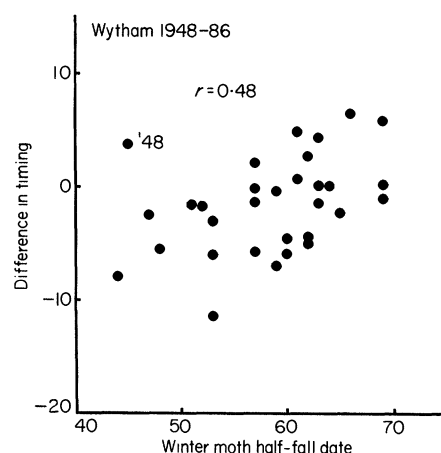
There was indeed a strong correlation between the difference in timing (between birds and caterpillars) and temperature in the 30-day period after the mean laying date, which was roughly equivalent to the period between egg laying (of the birds) and caterpillar pupation (Fig. 2). The difference in timing was also
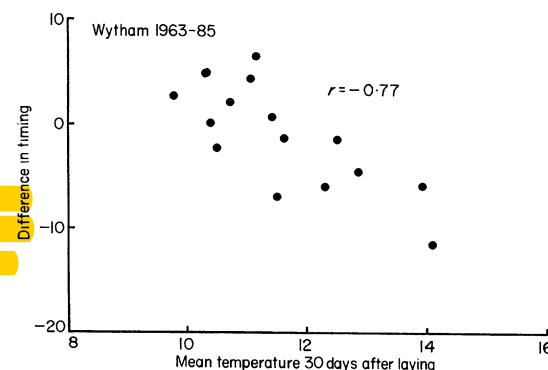
Fig. 2. The correlation between the mean temperature during the 30 day period after the mean laying date and the difference in timing between great tits and winter moth, taken as the half-fall date—the mean laying date of the great tit − 30. Thus positive values indicate that the caterpillars are relatively late, which is the same as the birds being relatively early ($r = -0.77$, $n = 16$, $P < 0.001$). Data from Wytham 1963–72, 1975, 1980, 1982–85. No caterpillar data were available for the intervening years.

correlated with the caterpillar pupation dates (Fig. 3). Negative differences in timing—implying that the birds were late relative to the caterpillars—were found in years with a high mean temperature in the period after egg laying (Fig. 2) and in years when caterpillar half-fall was early (Fig. 3). Thus, the correlation between difference in timing and temperature cannot be explained simply from the normal seasonal increase in temperature. It is compatible, however, with birds being less variable in their timing than the caterpillars and the caterpillars being early in warm years. The next question is, of course, whether it really matters. This can best be judged from the selection differentials, i.e. the difference between the mean laying date of the total population and the mean laying date weighted for the number of local recruits produced (but see Discussion hypothesis 4). Figure 4 gives the correlation between the difference in timing versus the selection differential for laying date. The very high correlation of $r = 0.84$ ($n = 21$, $P < 0.001$) implies that 70% of the variation in selection differentials can be explained/could be predicted from the difference in timing. We are not aware of any comparable case where moderate selection differentials can be explained to such a high degree from a single aspect of the environment, although it is in some cases with strong selection under extreme conditions, e.g in the study of medium ground finches (*Geospiza fortis*, Darwin) in the Galapagos during a drought (Grant 1986).

There is a potential problem in that the proportion of male breeding birds identified, and hence the apparent male recruitment rate, was much lower than the comparable female figures during the early 1960s. However, the selection differentials, based on either male or female recruits only, were highly correlated,

Fig. 4. The correlation between the difference in timing and the selection differential for lay date in the great tit. 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 contribute more to the next generation than late clutches. The strong positive correlation ($r = 0.84, n = 21, P < 0.0001$) indicates that in years in which caterpillar pupation is early relative to the mean laying date there is a strong selection for earlier laying in the tits. In a few years in which the caterpillar pupation is late there is a weak selection for laying later in the great tit, as indicated by the small positive selection differentials. Data from Wytham 1959–72, 1975, 1980, 1982–86.

there was no systematic difference between them, and the magnitude of the difference depended on sample size only (Fig. 5). Thus, although female and male dispersal patterns are different (Kluijver 1951; Greenwood, Harvey & Perrins 1979; van Tienderen & van Noordwijk 1988), and although dispersal is correlated to the timing of the brood (Dhondt & Hublé 1968; van Balen & Hage 1989) there was no noticeable difference in the selection differentials for laying date.
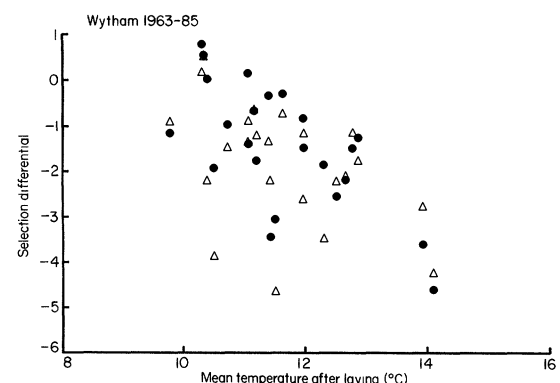

Fig. 3. The correlation between the half-fall date and the difference in timing between great tits and winter moth, taken as the half-fall date—the mean laying date of the great tit -30 ($r = 0.48$, $n = 32$, $P < 0.01$). If great tit laying is independent of caterpillar timing a correlation of $+1.0$ is expected. If great tit laying is at the same moment relative to caterpillar development, a zero correlation is expected. Data from Wytham 1948–1972, 1975, 1980, 1982–86. No caterpillar data were available for the intervening years.

Fig. 5. The correlation between the selection differential for laying date and the mean temperature in the period 30 days after the mean laying date based on female recruits (●) ($r = -0.67$, $n = 23$, $P < 0.001$) and on male recruits (△) only ($r = -0.46$, $n = 23$, $0.01 < P < 0.05$). The correlation between the selection differential based on female recruits only and that based on male recruits only is $r = 0.72$ ($n = 25$, $P < 0.0001$). If years with less than 25 recruits for either sex are omitted, the correlation is stronger ($r = 0.81$, $n = 20$, $P < 0.0001$). Data from Wytham 1962–86.

SELECTION FOR LAYING DATES IN RELATION TO TEMPERATURES

Data on recruitment were available for the period from about 1960 till present while data on caterpillar phenology were not available for 7 years during the period 1973–84. It was interesting to see whether there was a correlation between selection differentials for laying date and temperature in the period of 30 days following the laying dates, which is the growing period for the caterpillars. There was such a correlation and it was negative (Fig. 6). In years when it was warm in the month following laying, there was selection for laying earlier, whereas in years when it was cold in this period there was a weaker selection or even a small selection differential in the opposite direction. In this particular analysis there was a difference in results based on male recruits only or on female recruits only. The correlation between temperature and selection differential was higher in females and lower in males compared with the total recruits (Fig. 5). It can be seen from Fig. 5, however, that this difference was largely due to two outliers in the data on male recruits.

DECISION MAKING IN INDIVIDUALS

The basic idea in our analyses was that the discrepancy in timing between birds and caterpillars arises mainly in the period after egg laying, when the birds have limited scope for altering their timing. There are two ways in which the birds can alter their timing, though not by large amounts. First, they could stop laying earlier when it is warm during the laying period, leading to a trade-off between a smaller clutch size and presumably better timing. Secondly, they could alter the time at which incubation is started relative to clutch completion, starting before the last egg is laid or postponing incubation if it is cold. However, once
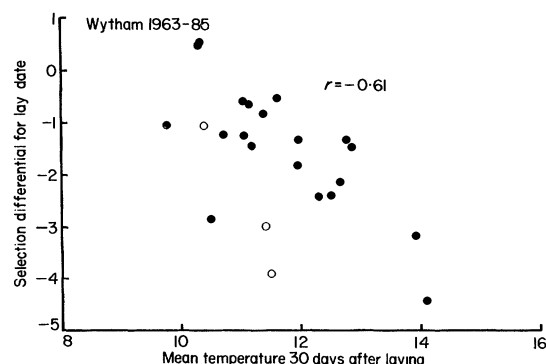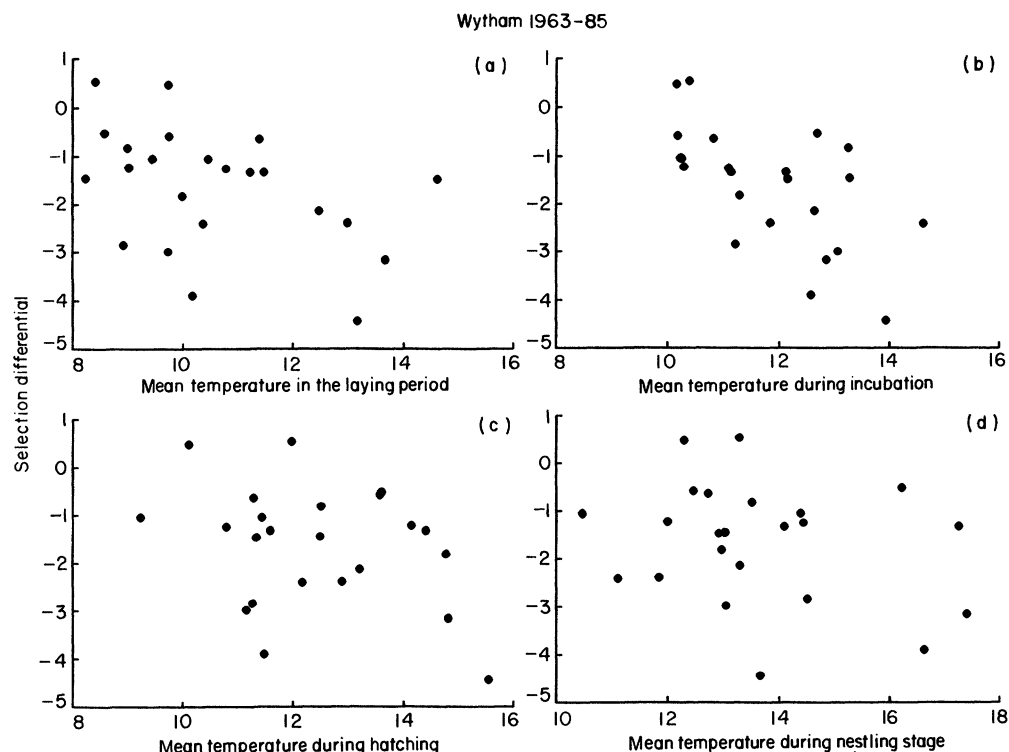

Fig. 6. The correlation between the selection differential for laying date in the great tit and the mean temperature in the period 30 days after the mean laying date ($r = -0.61, n = 23$, $P = 0.002$). The correlation is stronger if years are omitted in which the selection differential is based on less than 50 recruits ($r = -0.71$, $n = 20$, $P = 0.0004$) or omitting years producing less than 60 recruits ($r = -0.77$, $n = 15$, $P = 0.0008$). Data for Wytham 1963–85.

incubation has started there is little that can be done towards speeding up or slowing down the reproductive process. This leads to two predictions. If the birds cut short laying, a smaller mean clutch size is expected when the temperatures during the mean laying period are high. If they delay incubation in cold weather, or if other mechanisms play a role that let the birds adjust their timing during the laying period, but not during the incubation period, it is expected that the effects of temperature during the laying period are compensated for and hence do not lead to selection for laying earlier or later. Thus, it is expected that the selection differentials show a higher correlation with the temperature during the incubation period than with the temperature during the laying period. Using data based on population means is a very crude way of assessing these relationships. We defined the laying period as the 9 days following the mean laying date, and the incubation period as the next 9 days. This was done to avoid problems of comparing correlations with temperatures over periods with different lengths. The correlation in the temperatures over these two periods was 0·022 ($n = 39$, 1947–85, all years) and 0·245 ($n = 23$, 1963–85, years with data on recruitment), respectively. Our first prediction did not hold. There was no correlation between mean clutch size and the temperature during the laying period ($r = 0·031, n = 23$).

The second prediction, however, was tenable. The correlation between temperature in the laying period and the selection differential for laying date was weaker than the correlation with temperature during the incubation period (Fig. 7). These results suggest that a third of the variation in selection differentials can be explained from the temperatures on days 10–18 after the mean laying date. The temperatures in each of these two 9-day periods were equally correlated with the temperatures over the 30-day period /that we had used previously. There was thus a suggestion that the birds change their timing to some extent while they are still potentially able to do so, or alternatively that the second period has a larger effect on caterpillar development than the former. An alternative explanation for these correlations would be that the very first broods already have nestlings during at least the later part of the second 9-day period. This possibility was investigated by examining the correlations of the selection differentials with the mean temperatures over the next two 9-day periods: days 19–27 and days 28–36 after the mean laying dates. Clutches started on the mean laying date will hatch in the middle of the third period and they will have nestlings of about 10 days at the end of the fourth period. Caterpillar half-fall is usually on one of the first days of the fourth period.

If temperature has a direct effect on the nestlings rather than through their effect on caterpillar developmental rates, a high correlation between selection differentials and mean temperatures in the third and

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Fig. 7. The correlations between the selection differential for laying date and the mean temperatures in four 9-day periods after the mean laying date. (a) In the period between the mean lay date (mld) and mld + 9 days most females will mainly be laying eggs ($r = -0.43$, $n = 23$, $0.01 < P < 0.05$). (b) In the period mld + 9 to mld + 18 most females will be incubating ($r = -0.61$, $n = 23$, $P = 0.002$). (c) In the period mld + 19 to mld + 27 most clutches will be hatching ($r = -0.33$, $n = 23$, NS). (d) In the period from mld + 28 to mld + 36 most broods will have nestlings ($r = -0.26$, $n = 23$, NS). Thus, temperatures in the second 9-day period show the strongest correlation with the selection differential. Although the correlations with temperatures in the first and third period are stronger if only years with larger samples are considered, the second period still shows the strongest correlation (20 years with n $\geqslant$ 50 recruits: $r = -0.54$, -0.60, -0.49, -0.14, respectively, for the four periods; and 15 years with n $\geqslant$ 60 recruits: $r = -0.58$, -0.69, -0.41 and -0.25, respectively).

fourth period would be expected. The data in Fig. 7 show an absence of such correlations. This is summarized in Table 1, giving the correlations of the selection differentials with the mean temperatures over 30 days after the mean laying date, and the mean temperatures over four consecutive 9-day periods following the mean laying dates. It is clear that the temperature over the 30-day period was equally correlated

with the three periods that were part of it, but that the selection differential did not correlate with the temperatures in the third and the fourth period.

Discussion

We considered neither the variation in laying dates among individual birds, nor any variation in environmental conditions, such as caterpillar timing among trees or local temperature differences. Nevertheless, we found strong correlations between selection differentials and the difference in the mean timing of caterpillars and birds. There is a considerable variation among individual trees in leaf emergence and in peak caterpillar abundance (e.g. Crawley & Akhterruzzaman 1988), where leaf emergence may vary by up to 4 weeks and the caterpillar peak up to 2 weeks, depending on the weather. The variation in laying dates in the tits stretches over a similar period of up to 3 weeks. Whereas there is some evidence for a synchronization of tits to their local surroundings (Nager 1990; Nager & van Noordwijk 1992), such local tuning could be detected with the analyses we report here.

We assumed that it is important to have caterpillar half-fall coincide with 7-day-old nestlings, but the

Table 1. The correlations between the selection differential for laying date and the mean temperature over various periods

	Seldiff*	T_{total}	T_{lay}	T_{incub}	T_{hatch}
T_{total}	−0.61				
T_{lay}	−0.43	0.77			
T_{incub}	−0.62	0.65	0.24		
T_{hatch}	−0.33	0.68	0.24	0.30	
T_{nestl}	−0.26	0.31	0.09	0.15	0.22

* Seldiff is the selection differential for laying date.

T_{total} = mean temperature (0.5* (minimum + maximum)) from mean lay date (mld) to mld + 30 days.

T_{lay} = temperature over mld to mld + 9 days.

T_{incub} = temperature over mld + 10 to mld + 18 days.

T_{hatch} = temperature over mld + 19 to mld + 27 days.

T_{nestl} = temperature over mld + 28 to mld + 36 days.

Data for Wytham 1963–85.

exact relationship between the half-fall date and the course of the food availability in time is not known. We know that nestling weights are correlated with food availability (below a certain prey density) and that survival after fledging is in turn strongly correlated with fledging weight, but the causal links between chick weight and post-fledging survival are not fully known (e.g. Perrins 1991; Verhulst & Tinbergen 1991). The simplest scenario is that the coincidence of half-fall and 7-day-old nestlings indicates the highest food availability for nestlings, but other more indirect scenarios cannot be excluded.

We also assumed that the differences in temperature during the egg laying and incubation period of the tits have a noticeable effect on the developmental rate of the caterpillars. As illustrated in Fig. 7, we are dealing with differences of about 6 °C over 9-day periods or about 4 °C over 30-day periods (see for example Fig. 2). Experimental data on caterpillar growth show Q_{10} values, the factor by which processes are speeded up per 10 °C, of about 3 in this range of temperatures (see fig. 68 in Perrins 1979). This would imply that the caterpillars need half the time in warm years compared with cold years over the critical 9-day period, or about two-thirds of the time over the 30-day period (which is 24 days compared with 40 days). We know that in some years a difference of 2 or 3 days in hatching can have a very marked effect on nestling weights. Thus, we must conclude that the observed differences in temperature, combined with the effects of temperature on caterpillar growth, are more than sufficient to create differences in nesting success depending on the relative timing of the birds and the caterpillars.

WHY LAYING STARTS TOO LATE

It has been noted that most great tits in Wytham would profit from starting their laying slightly earlier in most years (Perrins 1970; Perrins & McCleery 1989). If there were genetic variation for laying date (Jones 1973; van Noordwijk *et al.* 1981), a consistent selection differential creates a problem. There are, however, at least six alternative explanations for this phenomenon, one of which (number 5) is new and compatible with the analyses presented here.

1. Energetic limitation at laying

Perrins (1970) pointed out that a rapid increase in food availability during the breeding season implies that there is little food at the beginning, which is the laying period. It might thus simply be impossible for a female to produce eggs earlier than she does, because she cannot find enough food earlier. Recent studies of the energetic costs of egg production and incubation suggest that egg production is not as expensive as previously thought, but the energetic cost of incubation is higher than previously believed (Haftorn & Reinertsen 1985; Mertens 1980, 1987). It is therefore

conceivable that there is an energetic bottleneck at the onset of incubation rather than at the onset of laying, but this does not really change the logical status of this explanation. Energetic limitation at laying can also be formulated as a trade-off between the cost to the female of laying earlier with a lower food supply against the benefit of earlier offspring (Drent & Daan 1980). Experiments in which the energetic balance of the female around the onset of egg laying are manipulated (Nager & van Noordwijk 1992) show a considerable effect on egg size, but not, so far, on laying date. The experiments do support the notion that the laying female is close to the energetic limit.

2. Gene flow

The optimal timing differs among habitats; in coniferous woods, the peak in caterpillar abundance occurs several weeks later than in oak woods (van Balen 1973). One may therefore expect that selection for laying date also differs among habitats (e.g. Blondel, Perret & Maistre 1990). This would imply that some immigrants have been selected for later laying dates. Since about 50% of the breeding birds were not ringed as nestlings, there is considerable gene flow and if a substantial proportion of the immigrants comes from habitats with a later optimum laying date, this might maintain genetic variation for laying date without a shift in mean laying date towards the optimum (Perrins 1990). There is some evidence for this hypothesis, but too little to account fully for the phenomenon of breeding later than seems optimal. In Wytham, the laying date of immigrants, corrected for age, is about 0·86 days later than that for residents (C.M. Perrins & R.H. McCleery, unpublished data). This hypothesis predicts a relation between deviation from the optimum laying date and the proportion and source habitat of the immigrants. There is indeed some evidence for such a relation (Zandt *et al.* 1990). Until we know more about dispersal, it is impossible to quantify the role of gene flow in the apparent maladaptation in laying date. There is evidence that great tits lay earlier than profitable in coniferous habitats (van Balen 1973; Dhondt *et al.* 1990). The absence of a net selection differential in two Dutch populations in poorer habitats (van Noordwijk et al. 1981) is consistent with the gene flow hypothesis. This issue is complicated by the occurrence of second broods in habitats with a later maximum food availability.

3. Non-genetic differences in condition

There is a number of different forms of this hypothesis. The basic idea is that an optimum laying date is rather different for different individuals. Even though the individuals that start laying later produce fewer recruits than the earlier birds, these particular individuals would do even worse if they laid earlier. This part of the hypothesis is known as individual opti-

mization (Drent & Daan 1980). To explain the continued existence of genetic variation, we also need a second hypothesis, that there is a genetic component for laying date that is selectively neutral and a non-genetic condition aspect that may shift the actual lay-date forwards or backwards (Price, Kirkpatrick & Arnold 1988). The hypothesis of non-genetic differences in condition is basically an individual form of the energetic limitation hypothesis. However, if the distribution of individual opportunities is skewed (few individuals with good, many with worse conditions), the mean of all individuals starting laying and the mean weighted for the individual prospects of success may well be shifted by a few days, such that the apparent selection is stronger than the actual selection. Although this is theoretically possible, our finding of a very high correlation between the selection differential for laying and the difference in timing between tits and caterpillars makes it unlikely. One special form of this hypothesis is the existence of age-related differences. If young females are both later and less productive in terms of producing recruits, which they are (McCleery & Perrins 1988), this leads to an apparent selection differential for laying earlier. This is then basically an artefact and will not change the genetic composition of the population.

4. Artefact of date-related dispersal

All data on recruitment were incomplete, because there were almost no data on the fate of individuals that had emigrated. It is known from ringing recoveries, and from a Belgian study with many separate study areas, that nestlings from late broods are more likely to emigrate (Dhondt & Hublé 1968; van Balen & Hage 1989). This implies that our data on recruitment are biased towards early broods. If this effect was sufficiently large, a consistent difference between the apparent selection differential and the real selection differential would arise, which would falsely lead to the conclusion that there is persistent selection for breeding early.

5. Asymmetric response opportunities

We have argued that the tits, once they have started laying, have limited possibilities to alter their timing. The correlations with temperature over the various 9-day periods are consistent with the notion that there is more scope for changing the timing in the laying period than during the incubation period. However, the possibilities for adapting the moment of hatching, once laying has started, are asymmetric. The possibilities for retarding the moment of egg hatching are far greater than the possibilities for speeding up the process. Delays may occur during egg laying, between clutch completion and the onset of incubation and even during incubation (Nilsson & Smith 1988; A.J. van Noordwijk, unpublished data). This would lead

to an asymmetric situation, with a net result that the birds are on average too late.

6. A gradual shift in environmental conditions

It is possible that a response to selection is masked by a gradual shift of the environmental conditions in the opposite direction. In the case of the Wytham great tits there is no evidence for such a shift, and this hypothesis remains a theoretical possibility. However, in another example of the absence of an expected response to selection, namely for clutch size in the La Perouse colony of snow geese (Cooke *et al.* 1990), there is good evidence for a gradual decline in environmental conditions due to increased colony size, which might offset the response to selection for larger clutches.

These six hypotheses are not mutually exclusive. In the case of the Wytham great tits, the mean selection differential is 1·65 days (95% confidence interval = 1·18–2·13). A combination of the factors in the first five hypotheses is likely to explain the fact that there is on average selection for laying earlier.

Conclusion

Instead of stressing the fact that there is on average a selection for laying earlier, one might point out that the average tit is never more than a few days away from the optimum timing, which is small compared to the within-year variation among individual laying dates. Given our lack of understanding of the decision rules that individual birds follow in their onset of laying, the fact that a single factor, namely temperature in a short period after the start of laying, explains so much of the between-year variation in selection intensity is remarkable. We are not aware of any examples of natural selection acting on a quantitative trait in a natural population in which such a large portion of the annual variations in selection intensity have been explained by a single environmental factor. This information can be used in seeking mechanisms involved in the onset of laying in the light of the synchronization with peak caterpillar availability. We have thus a single major environmental axis along which we can study the phenotypic plasticity, relative to calendar date, that is observed in the laying dates of great tits.

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