PROXIMATE AND ULTIMATE ASPECTS OF PHENOTYPIC PLASTICITY IN TIMING OF GREAT TIT BREEDING IN A HETEROGENEOUS ENVIRONMENT

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Abstract.—Using the theoretical framework of phenotypic plasticity, we studied the timing of breeding in great tits (*Parus major*), combining proximate questions about its physiological causation and ultimate questions about its fitness consequences. The plasticity observed in the timing of breeding can be explained either as an adaptation to the best time for rearing young or as determined by changing environmental conditions prior to laying. We related the variation in timing of breeding and breeding success to local temperature and food abundance. For the most part, spring temperature (but also caterpillar abundance and low temperature around the expected start of egg laying) as well as the presence of the birds in their breeding territories during the previous winter explained within-population variation in timing. Intraindividual variation in timing showed a plastic response to changes in environmental conditions prior to laying, but the plasticities did not differ among individuals. Birds raising their young when food was most abundant were the most successful breeders. The most productive laying date differed significantly among years because unpredictable yearly fluctuations in environmental conditions after the birds started laying still affected the development of caterpillars. In addition to being affected by changes in environmental conditions early in the season, the laying dates of experienced tits were affected by the difference between their timing and the caterpillars' timing in the previous year. Thus, great tits adjust their timing to the best time for rearing young, but variation in environmental conditions will maintain variation in timing.

Many traits of organisms show a phenotypic plasticity (see, e.g., Stearns 1989), that is, the same genotype forms different phenotypes in different environments. This implies that differences in phenotype among individuals may be caused by any combination of differences in genotype, differences in ontogeny, and differences in environment (Stearns 1989, 1992; van Noordwijk 1989). The measurement of an individual's trait (phenotype) at a given moment may be explained proximately, by an interaction of the genotype with environmental conditions during the expression of that trait, as well as ultimately, by an interaction of the genotype with the environmental conditions under which selection for that trait occurs. However, the expression of a phenotype and the selection thereon will often be separated in time and/or space. In consequence, the environmental con-

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ditions affecting phenotype formation and selection acting on that phenotype may differ to any degree. One may distinguish contingent plasticity, which can only be explained proximately, from adaptive plasticity, which has an ultimate as well as a proximate explanation (van Noordwijk and Müller 1994). Therefore, to understand phenotypic plasticity of a trait, we have to combine proximate questions about the causal mechanism and ultimate questions about the functional significance.

Here we will consider the plasticity of the timing of breeding in the great tit (*Parus major*). The abundance of food available to raise nestlings usually varies seasonally. Thus, there is a most advantageous breeding date for raising young, when the highest demand of the feeding parents coincides with the highest food abundance (Lack 1968). Since the time of maximum food abundance varies considerably both in time and space (Perrins 1979; and see Study Area and Methods), the birds must rely on some flexible mechanism to time their reproduction correctly to the seasonal pattern in food abundance. Thus, the absolute timing of breeding in the great tit varies among years and habitats (Perrins 1979; van Noordwijk et al. 1981).

The timing of breeding has important fitness consequences. For several bird populations, a seasonal decline in reproductive success has been reported (Perrins 1965, 1970, 1991; Newton and Marquiss 1984; Nilsson and Smith 1988; Verhulst and Tinbergen 1991; but see van Noordwijk et al. 1981). Although earlier laying seems to be selected for in some populations, and laying date can be heritable (van Noordwijk et al. 1981; Boag and van Noordwijk 1987), it is a paradox that earlier breeding has not evolved (Price et al. 1988). Clearly, the evolution of the birds' breeding season is not yet fully understood. Two main explanations for the timing of breeding have been put forward. The bird's breeding season might be adapted to the time of appearance of caterpillars needed later for the young (Lack 1954, 1955), or the timing might be constrained early in the season by a limited supply of energy needed by the female for egg production (the energy limitation hypothesis; Lack 1966; Perrins 1970). In other words, the plasticity in timing of breeding might be adaptive or contingent, respectively. In the former case, the success of the breeding attempt depends on how reliably the environment prior to egg laying relates to the environmental conditions in the critical nestling period 4–5 wk later.

We studied a breeding population of great tits (*P. major*), their most important prey during the breeding season (caterpillars), and temperature over 5 yr at several localities in a heterogeneous forest. In this article we will determine which factors in the prelaying period influence the timing of breeding of great tits, expressed as the date on which a bird lays its first egg (laying date). We analyzed both inter- and intraindividual differences in laying date as a plastic response of that trait to a shift in measured local environmental conditions (temperature and food abundance). We then investigated the extent to which reproduction was timed correctly to the seasonal pattern in food abundance, that is, if the response to the environmental conditions early in the breeding season is adaptive.

STUDY AREA AND METHODS

The great tit population on Blauen (Ettingen, 10 km south of Basel, northwestern Switzerland, 47°29' N, 07°33' E) has been studied since 1985. The area was

FIG. 1.—A schematic view of the study area on Blauen, with the eight localities indicated by letters A to H. The localities G and H were not sampled in 1988. The unhatched area is forested, and hatched areas are either open field with fruit trees or gardens. Scales are for distances and altitudes.

provided with about 430 nest boxes ranges from 380–780 m above sea level on the northern slope of a ridge in the Jura (fig. 1) dominated by beeches (*Fagus sylvatica*). But oaks (*Quercus* spp.) and hornbeam (*Carpinus betulus*), as well as several coniferous species, are also locally important. There is an average density of between one and eight great tit breeding pairs per 10 hectares. The area is situated on calcareous soil poor in nutrients, and the densities of foliage-eating caterpillars are low in comparison with those of other forests in northwestern Switzerland (H. S. Zandt, personal communication). From 1988 onward, we measured environmental conditions at six (1988) and eight (1989–1992) localities. These localities differ from each other in tree species, altitude, and exposure (fig. 1). A locality included between 10 and 30 nest boxes, depending on local topography.

We measured temperature and food abundance in the center of each locality throughout the breeding season. The general field methods used in this study are described in more detail elsewhere (Nager and Zandt 1994). Mean daily temperatures were obtained by averaging daily readings of three minimum-maximum thermometers per locality that were placed in additional nest boxes made inaccessible to birds. To assess the food abundance, we cut two branches each of between three and five trees per locality each week. The sampled trees were selected to represent the species composition and tree size of that locality (R. G.

Nager, unpublished data). We collected the branches in large plastic sacks and searched them for all potential prey items of great tits (*Lepidoptera* and sawfly larvae, bugs, small beetles, and spiders) in the laboratory within a few days after sampling. Fresh weight of all the items found per branch and the length of the branch were measured. Food abundance was expressed as milligrams fresh weight of prey per 10 m of branch length. Per locality and sampling date, we then calculated the median abundance of all recorded prey items and the median abundance of the caterpillars only. Caterpillars were dominant in biomass at the time of maximum food abundance but accounted for only about 10% of the potential food biomass early in the season during egg laying. The caterpillar peak date per locality and year was defined as the sampling date with the highest median value of caterpillar abundance. The caterpillar peak date varied significantly among the eight localities (fig. 2).

Once great tits start to lay, they produce one egg each day; mean clutch size on Blauen ranged from 7.3 to 9.6 eggs. Therefore, weekly visits of the nest boxes provided an accurate measure of laying date. Around the time of egg laying, many nest boxes at the localities were checked daily, and the actual date the first egg had been laid was observed. Interruptions in the laying of one or more days occasionally occurred, but their effects on the reliability of the measure of laying date are negligible. Clutches that were started more than 30 d later than the first egg was observed in that year and clutches that were suspected to be repeat clutches of already failed attempts were not included in the analysis.

We trapped breeding birds routinely at the nest when the chicks were 7–12 d old and marked them individually. We could identify 79.9% of all the breeding females at our localities ($n = 164$). For nests with at least one fledgling, we identified 97.2% of the females and 90.7% of the males. We aged each bird we caught according to Perrins (1979) as either in the first year of life or older. As a result of extensive nest box inspections in November/December, January/February, and March during the winter nights of 1989/90 and 1990/91, we also obtained information on the presence of individuals in their breeding areas in two subsequent winters. As a measure of breeding success, we counted the number of chicks and measured their fledging weight (weight 15 d after hatching) when the chicks were more or less full grown. Prior to their fledging, we individually marked all nestlings and followed their local survival.

Statistics were calculated with SAS statistical software (SAS Institute 1990). In some analyses, we pooled all data of the various years. To be able to compare between these different years, we used standardized values by subtracting the yearly mean values from the observed values and dividing the result by the standard deviation for that year and trait. The distribution of laying dates was usually not normal, and we therefore standardized it by subtracting the median laying date in that year from the observed laying date. We standardized laying dates separately for the areas below and above an altitude of 500 m since there was a difference in laying date of 4–5 d between these two parts of the study area (R. G. Nager and A. J. van Noordwijk, unpublished data). To model the local recovering probabilities of fledglings to the next breeding season, we used logistic regressions

FIG. 2.—The average seasonal pattern in caterpillar abundance per locality (A, filled circle; B, open circle; C, filled triangle; D, open triangle; E, filled squares; F, open squares; G, filled diamonds; H, open diamonds). Day 0 is the overall mean caterpillar peak date (date of maximal caterpillar abundance), and local peak dates are expressed as the average deviations from the overall mean. The caterpillar peak date differs significantly between localities (Kruskal-Wallis test, $H = 20.75$, $P = .004$), but the caterpillar biomass at the peak date does not ($H = 10.67$, $P = .154$).

(SPSS 1990), entering stepwise weight at day 15 and its square, sex, and hatching date and year as independent variables.

RESULTS

Variation in Timing

A great tit that laid early in one year was also among the earliest ones to lay in the next season (fig. 3; repeatability of standardized laying date [$\pm$ SE]) was

FIG. 3.—The absolute laying dates of females laying in two successive years on Blauen. Day 1 is April 1. The dotted lines indicate equal laying dates in both years. The great tits' timing relative to each other remains about the same (for all correlation coefficients, $P < .05$), but the absolute timing of the same individual may well differ among years.

0.43 ± 0.095 , $n = 66$ females). However, the repeatability of absolute laying date was lower (0.34 ± 0.082) because the laying date of the same individual (same genotype) could differ from one year to the next (different environmental conditions) by 10–15 d (fig. 3). The repeatabilities were calculated according to Lessells and Boag (1987) and the standard errors according to Becker (1984).

We now want to examine which environmental factors are correlated with differences in timing among years and localities. Table 1 shows the correlations between the median local laying date and mean temperature measured at that locality over several time intervals prior to laying. The highest correlation coefficient (r) was found for the interval from March 17 until April 15, and the mean local temperature during this interval has been used in the subsequent analyses. The relationship between laying date and local temperature prior to laying still holds when corrected for year effects and did not vary among years (ANCOVA, table 2; see also fig. 2 in Nager 1990). Great tits lay later at localities with lower spring temperatures (fig. 4). A decrease of 1°C in mean spring temperature corresponds to a delay of 3.84 d in the start of egg laying. Recalculating the regression including only clutches laid in boxes closest to the thermometers (boxes to which

TABLE 1

PEARSON'S CORRELATION COEFFICIENTS (r) BETWEEN LOCAL SPRING TEMPERATURE OVER DIFFERENT TIME INTERVALS AND LAYING DATE AND CATERPILLAR PEAK DATE

	MARCH 1 UNTIL			MARCH 17 UNTIL		
	April 15	April 20	April 28	April 15	April 20	April 28
Laying date:						
r	-.549	-.551	-.400	-.638	-.496	-.278
n	31	31	31	37	37	37
P	.001	.001	.026	<.001	.002	.096
Caterpillar peak date:						
r	.0254	-.259	-.259	-.212	-.382	-.408
n	30	30	30	36	36	36
P	.176	.167	.166	.215	.022	.014

NOTE.—No temperatures are available for March 1–15, 1988. Only values for which $P < .008$ should be considered as significant (Bonferroni transformation).

TABLE 2

EFFECTS OF YEAR (4 LEVELS, WITHOUT 1990) AND AGE (YEARLING OR OLDER) ON THE RELATIONSHIP BETWEEN LAYING DATE AND TEMPERATURE

	Sums of Squares	df	F Statistic	P Value
Effect of Year	.085	3	.05	.987
Temperature	2.503	1	3.97	.048
Year $\times$ temperature	.144	3	.08	.973
Error	115.19	115		
Effect of Age	.034	1	.04	.846
Temperature	26.422	1	29.92	.0001
Age $\times$ temperature	.19	1	.22	.643
Error	127.586	115		

NOTE.—The relation between laying date and temperature follows the same lines for different years and age classes. The cold spell during the laying period in 1990 led to a larger spread of laying dates in that year than in the other years (see fig. 3; Bartlett's test for homogeneity of variances, $\chi^2 = 24.81$, $df = 4$, $P < .001$).

a thermometer box was added or the one next to it) yielded a similar relationship ($\pm$ SE): $Y = -2.77 (\pm 1.231) \times X + 41.013 (\pm 10.244)$ ($n = 25$, $P = .03$, $R^2 = 0.18$; t -test of differences of slopes, $t = 0.75$, NS). Since great tits had already laid in early April in some years (1990, 1991), the calculations of the correlations in table 1 include the temperatures of days on which some great tits had already completed their laying. In 1990 the great tits started laying very early as a result of the mild weather in March, but after many females at the early localities had started laying, a period of cold weather of several days occurred with mean daily temperatures close to 0°C. This cold spell decreased the mean temperature between March 17 and April 15, although the median laying date was early that year. This explains the three points in figure 4 for which the tits laid around April 5 although the mean temperature was only 8°C.

After correcting for the effect of local spring temperature on laying date by

FIG. 4.—Great tits lay later at localities with lower mean temperatures. The regression of the median local laying date (day 1 is April 1) on mean local temperature ($^{\circ}\text{C}$) from March 17 until April 15 is $Y = -3.84 (\pm 0.726) \times X + 47.911 (\pm 6.015)$; $P = .0001$, $R^2 = 0.45$, $n = 37$. There are data for eight localities and 5 yr; no temperature was measured at localities *G* and *H* in 1988; and no great tits bred at locality *F* in 1989). This regression is not only due to differences among years but also holds within years (table 2). Note the data points for three localities that laid around day 5 at a mean temperature of about 8°C (see text).

using the residuals from the regression line in figure 4, we found that additional environmental variables influenced laying date. Localities where the great tits started egg laying earlier than predicted by spring temperature (negative residuals) had higher caterpillar abundance early in the season than at localities where the great tits laid later than predicted (positive residuals; $P = .02$; table 3). However, there was no difference in total food abundance (including all potential prey items; table 3). In addition, the temperature a few days prior to the predicted laying date may also influence the onset of laying (von Haartman 1990), since egg formation in great tits starts about 4–5 d before the actual laying of the first egg (Walsberg 1983). At the localities where tits laid relatively late, the mean temperatures during the 3–6 d prior to the predicted onset of egg formation were lower than at the localities where the tits laid as predicted ($P = .02$; table 3).

Another factor affecting laying date in great tits is the age of the female (Perrins and McCleery 1985; Dhondt 1989). In the sample of the great tits breeding at the various localities, first-year females laid an average of 4.2 d later than older birds (on the standardized laying date, see the section titled Study Area and Methods; t -test, $t = 4.08$, $\text{df} = 118$, $P = .0001$). However, age did not influence the relationship between laying date and temperature (ANCOVA; table 2). In 1990 and 1991 there was a marked difference between first-year and older breeding females depending on whether they had been caught at least once at that locality

TABLE 3

COMPARISON OF THE LOCAL LAYING DATES CORRECTED FOR DIFFERENCES IN LOCAL SPRING TEMPERATURES (RESIDUAL VALUES FROM THE REGRESSION IN FIG. 4) WITH FOOD ABUNDANCE AROUND THE PREDICTED LAYING DATE AND TEMPERATURE 3–6 d PRIOR TO THE EXPECTED LAYING DATE

	Laying Earlier than Predicted (Residuals < 0) (<i>n</i> = 20)	Laying Later than Predicted (Residuals > 0) (<i>n</i> = 13)	Wilcoxon Paired-Samples Test
Food abundance (mg fresh wt per 10 m of branch length):			
All prey items	8.1 (0–45.1)	5.3 (0–29.6)	<i>Z</i> = −.61 (NS)
Caterpillars only	.8 (0–8.1)	0 (0)	<i>Z</i> = −2.32*
	Laying within 2 d ^a of Predicted Date (<i>n</i> = 13)	Laying > 2 d after Predicted Date (<i>n</i> = 10)	Wilcoxon Paired-Samples Test
Temperature (°C)	10.65 (5.0–13.7)	8.45 (4.5–11.6)	<i>Z</i> = −2.26*

NOTE.—Values shown are mean and range.

^a Arbitrarily chosen interval.

* *P* = .02.

during the previous winter. Of 156 identified females, 12 (7.7%) were never caught as roosting birds, although they were known to have bred in the same area before. These females were not included in the following analysis. Older females (> 1 yr) were more often caught in the previous winter (66%) than were yearling females (21.7%, $\chi^2 = 5.88$, *df* = 1, *P* = .015). Older females already roosting in their future breeding area the previous winter laid, on average, 3.83 d earlier than first-year females also already roosting in their future breeding area, although the difference was not significant (*t* = 2.08, *df* = 23, *P* < .1), but laid significantly earlier than yearling females not caught in their breeding area in the previous winter (on the average, 6.87 d, *t* = 3.54, *df* = 30, *P* = .001).

Phenotypic Plasticity of Laying Date

If the timing of breeding in great tits is a plastic trait, we would expect that individual females change their laying date from year to year according to changes in environmental conditions. In the previous paragraph, we have seen that more than one environmental factor influenced the laying date. To combine these on a common environmental axis, Falconer (1989) proposed to calculate an environmental value as the mean performance of all genotypes in that environment. All great tits breeding at the same locality are supposed to share the same environment. We calculated the environmental value as the median laying date per locality (each time excluding the individual female we were interested in from the calculation of the environmental value) and plotted it against individuals' laying dates (fig. 5). Laying date increased with environmental value (factorial ANCOVA, *F* = 19.94, *df* = 1,1, *P* < .0001), with an overall slope of 0.548 d per

FIG. 5.—Illustration of the range of responses of different females to changing environmental conditions. The laying dates of individual great tits are plotted against the mean laying date of other great tits laying at the same locality (with the same environmental value, see text). Points of the same individuals are connected by lines. Laying date increased with environmental values (factorial ANCOVA, effect of covariate, $P < .001$), but there is no difference in response among individuals (interaction term, NS).

unit of environmental value. There were significant differences among individuals ($F = 3.01$, $df = 1,30$, $P = .001$) but no interaction between individual and environmental value ($F = 0.71$, $df = 1,30$, NS). Moreover, the differences in an individual's laying date between two seasons increased with the differences in environmental value between those two seasons (fig. 6). Thus, intraindividual differences in laying date are plastic responses to changes in environmental conditions around egg laying. To understand to what extent these responses are adaptive, we now have to turn to the relationship between the timing of breeding and the environmental conditions in the nestling stage.

Timing and Breeding Success

Breeding success might be related to the absolute timing of the birds, expressed as laying date, or their timing in relation to the seasonal pattern in caterpillar abundance, expressed as synchronization, that is, the difference between caterpil-

FIG. 6.—The differences in laying date of individual great tits between two successive breeding seasons are correlated with differences in the local environmental conditions in the prelaying and laying period during these two seasons. The environmental conditions are expressed as environmental values, as in fig. 5. The equation of the regression line is $Y = 0.492 (\pm 0.123) \times X - 1.171 (\pm 1.094)$; $P = .0003$, $R^2 = 0.29$, $n = 42$.

lar peak date (see the section titled Study Area and Methods) and the middate of the birds' nestling stage (day 7; day 0 = day of hatching). By that time, the workload of breeding birds has already reached its maximum level (Betts 1955; van Balen 1973), and food abundance at that time affects the growth of the young (Henrich-Gebhardt 1990; Keller and van Noordwijk 1994). The most important components of avian breeding success are the number of young fledged and their survival until they breed (Clutton-Brock 1988; Newton 1989). Breeding pairs that had 7-d-old nestlings more than 1 wk before or after the caterpillar peak date produced fewer fledglings than the pairs with the best synchronization with the caterpillar peak date, although the difference was not significant (table 4). However, this measure does not take the quality of the young into account. The fledging weight gives an indication of the quality of the young; great tits that are heavier at leaving the nest are more frequently recovered as breeding birds (Perrins 1965; Dhondt 1971; Garnett 1981; Tinbergen and Boerlijst 1990; Gebhardt-Henrich and van Noordwijk 1991). Indeed, birds with the best synchronization with the caterpillar peak date raised the heaviest nestlings (table 4). A combination of the quantity and quality of young produced would be given by the number of recruits (birds born in a study area and reported breeding in a later year). However, in most cases it is only possible to estimate the probability of locally

TABLE 4

COMPARISON OF THE BREEDING SUCCESS OF GREAT TITS BREEDING WITHIN 1 WK OF THE CATERPILLAR PEAK DATE, MORE THAN 1 WK BEFORE THE CATERPILLAR PEAK DATE, OR MORE THAN 1 WK AFTER THE CATERPILLAR PEAK DATE

	More than 1 wk before Peak Date	Within 1 wk of Peak Date	More than 1 wk after Peak Date	Kruskal-Wallis Test
Number of fledglings	-.20 ± .23 (21)	.09 ± .14 (52)	.05 ± .12 (63)	$H = 1.76$ (NS)
Mean fledging weight	-.51 ± .28 (11)	.43 ± .11 (40)	-.27 ± .17 (44)	$H = 13.58^{***}$
Potential recruitment rate	-.29 ± .21 (21)	.28 ± .14 (52)	-.08 ± .12 (63)	$H = 7.88^*$

NOTE.—Since we sampled caterpillar abundance only once a week, the estimate of the caterpillar peak date will have a precision of 1 wk at the best, and we therefore look at effects on this time scale. Given are standardized values (corrected for differences among years) ± SE, with the sample size of various measures of breeding success in parentheses (see text).

* $P = .019$.

*** $P = .001$.

recovering young as breeding birds. This does not take dispersal into account. From 1988 to 1991, only 43 birds (24 males and 19 females) of 1,035 young fledged from first broods were recovered locally as breeding birds. Thus, the actual numbers of local recruits of the subsample of birds breeding at the localities are too small to be able to compare the number of recruits and their synchronization with caterpillar peak date. Alternatively, we can estimate local recovery probabilities for fledglings with logistic regression analysis (see the section titled Study Area and Methods). Fledging weight was the only significant factor in our model ($P = .003$). The square of fledging weight, year, hatching date, sex, and all possible interactions had no significant influence on local recovery rate. Since there was no sex bias in the sample of recovered birds ($\chi^2 = 0.39$, NS), the effect of weight was not simply a consequence of the lighter females dispersing further than the heavier males. We used these recovery rates to estimate the potential recruitment rate per brood that takes the number as well as the quality of the young produced into account. Birds with the best synchronization with the caterpillar peak date had the highest potential recruitment rate (table 4).

Analogously, breeding attempts were grouped into three subsamples of approximately the same sample size according to their standardized laying dates. We found no differences in potential recruitment rates between early (over 3 d before the median laying date), intermediate, or late (over 3 d after the median laying date) laying birds (Kruskal-Wallis test, $H = 0.02$, $df = 2$, NS). Thus, the above analyses suggest that the synchronization with the caterpillar peak date is more important than simply laying early.

Synchronization with the caterpillar peak date is related to the standardized laying date (fig. 7). The significant effect of year means that during the study period in some years, early laying birds raised their young when food was most

FIG. 7.—The synchronization of the great tit's breeding season in relation to its main prey, the caterpillars, is related to standardized laying date (ANCOVA, $F = 44.58$, $df = 1, 119$, $P = .0001$). Laying date is standardized by expressing it as the deviation from the yearly median laying date, and the synchronization is the difference between the midpoint of the tits' nestling stage and the date of maximal caterpillar abundance. The laying date with the best synchronization (and the highest breeding success; table 4) differs among years (ANCOVA, effect of year, $F = 31.16$, $df = 4, 119$, $P = .0001$; interaction, $F = 1.25$, $df = 4, 118$, NS). Symbols represent the different years (1988, filled circle; 1989, open circle; 1990, filled triangle; 1991, open triangle; and 1992, filled square).

abundant (e.g., in 1988), whereas in other years birds laying late in the season reared nestlings when food was most plentiful (e.g., in 1991; fig. 7).

Temperature and Peak Date of Caterpillar Abundance

The laying date of great tits is correlated with spring temperature over various time intervals (table 1). However, the outcome of breeding success then depends on environmental conditions 4–5 wk later; that is, success depends on the synchronization of the birds' nestling stage with the caterpillar peak date. Since the development of caterpillars also depends on temperature (Perrins 1979), the caterpillar peak date might also be predictable from the temperatures during the same time interval to which the great tits' laying date is related. However, this was not the case, since the caterpillar peak date did not correlate with spring temperature (table 1).

Nonenvironmental Changes and Individual Laying Dates

A substantial part of the variation in laying date can be explained from local environmental conditions early in the season. However, because of unpredictable

FIG. 8.—The influence of previous experience on the laying date. The nonenvironmental change of laying date is the intraindividual change in laying date between two seasons independent of changes in environmental conditions; these are the residuals from the regression in fig. 6. Synchronization is defined as in fig. 7. Females rearing their young before (negative values of synchronization) or after (positive values of nonenvironmental changes in laying date) the peak date of caterpillar abundance delayed or advanced their laying date the following year, respectively ($r = -0.559$, $n = 34$, $P = .0006$).

fluctuations in environmental conditions after the birds started laying, this same environment predicts only weakly the environment at which laying date is selected on. But there were significant differences in the timing of caterpillars among the localities over the 5-yr study (fig. 2). This allows for the interesting possibility that birds with local experience may be able to adjust their decisions of when to start laying to the local environmental circumstances.

Laying date of great tits with at least one previous breeding attempt can be predicted if local environmental conditions in both seasons are known (fig. 6). The difference between this predicted laying date and the observed one (residual values from the regression in fig. 6) then measures the change in laying date independent of changes in environmental conditions (later called the nonenvironmental changes in laying date). Birds that had reared no fledglings in the previous breeding season had larger absolute values of nonenvironmental changes in laying date than birds rearing at least one fledging in the previous season (t -test, $t = 2.25$, $df = 40$, $P = .03$). Nonenvironmental changes in laying date also correlated negatively with the female's synchronization with the caterpillar peak date in the previous season (fig. 8). This correlation could be due to an asymmetry in the probability of changes in laying date between early and late laying birds. Birds laying very early in one season might be more likely to delay laying the next year, and these would also usually be the birds that had raised their young before

the caterpillar peak date in the previous season. An analogous argument applies to birds that lay very late. Therefore, we simulated the nonenvironmental changes in laying date of a population in which the probabilities of advancing and delaying breeding in the next year were different for early and late laying birds. Laying date was allowed to change randomly from year to year with a mean and a variance as observed in our study population. But if such a simulated laying date fell outside the range of observed laying dates (seen as the minimal and maximal possible laying date), it was set equal to the limit it had passed. However, these nonenvironmental changes in laying dates simulated with asymmetric changes to advance and delay breeding for early and late birds alone could not produce a pattern similar to that found in figure 8. The correlation coefficients between simulated nonenvironmental changes in laying date and synchronization between tits and caterpillars in the preceding season were not different from zero ($r = 0.054 \pm 0.134$, $t = 1.27$, NS) but were significantly different from the r (-0.559) in the real data ($t = -14.47$, $P < .001$). That means that locally experienced tits that had previously reared young after the caterpillar peak date seem to advance their laying date to correct for environmental differences between years. And females that reared their nestlings before the caterpillar peak date seem to delay laying the following year to correct for environmental differences between years. Moreover, the observed changes in laying date resulted in a better synchronization with the current caterpillar peak date than the changes in laying date predicted by the relation in figure 6 (matched-pair t -test, $t = -2.44$, $n = 38$, $P = .02$).

DISCUSSION

In this article we addressed the question about the dependence of the expression of laying date on the local environment. We analyzed data of both inter- and intraindividual variation in laying date in relation to measured local environmental conditions. However, we did not regard environmental measurements as defined conditions but treated them as deviations from the average condition or from the condition birds had experienced previously. Following this procedure, the analyses were quite powerful in detecting effects of local environmental conditions on the phenotype in a heterogeneous environment. Local variation in timing was related to local differences in temperature over a period of the second half of March and the first half of April. Abundance of caterpillars, and not total food abundance, as well as low temperature around the time of the predicted onset of egg formation modified this pattern. In addition, young females, and particularly those that were not present in their breeding area during the previous winter, laid later than older females already established in the breeding area.

Proximate Factors of Laying Date

Many studies so far have shown significant correlations between birds' timing of breeding and the temperature in early spring (song sparrows, Nice 1937; great tits, Kluyver 1952; Perrins 1965; O'Connor 1978; Dhondt and Eyckerman 1979; Schmidt 1984; Nager 1990; finches, Newton 1964; sparrow hawks, Newton 1986).

This relationship could arise because low temperature either increases the female's costs for body maintenance at the expense of egg formation or affects the food abundance, resulting in an energy supply early in the season that is too low to allow both body maintenance and egg formation (energy limitation hypothesis; Perrins 1970). Experimental advancement of the laying date by a few days through supplemental feeding (in tits, Källander 1974; von Brömssen and Jansson 1980; Clamens and Isenmann 1989; Nilsson and Svensson 1993; R. G. Nager, unpublished data; but see Blondel et al. 1990, P. J. Jones, unpublished data) is usually interpreted as supporting the energy limitation hypothesis. However, experimental manipulation of overnight temperature in the prelaying and laying period of tits and thereby their energy demands for thermoregulation did not affect the laying date, although the egg formation process has been affected by the treatments (Nager and van Noordwijk 1992; Yom-Tov and Wright 1993). These latter experiments show that temperature is not a causal factor of laying date, but their results are in contrast with the energy limitation hypothesis.

Alternatively, the birds might not be energetically limited in their egg formation but may rely on a signal indicating that the favorable period for rearing young is approaching (Lack 1954, 1955). This factor cannot be temperature, as has been shown experimentally (Nager and van Noordwijk 1992). Other candidates for the proximate factor might be bud burst, which correlates with the appearance of the caterpillars in spring (P. J. Jones, unpublished data; but see van Balen 1973) or the appearance of the first small caterpillars. At the localities where tits started to breed later than expected by temperature alone, we found no caterpillars early in the season; however, the caterpillar abundance (but not the much higher total food abundance) was significantly higher at localities where tits laid before the date predicted by the local temperature (table 3). Experimentally supplemented food not only provides additional energy but might also act as a trigger for the onset of egg laying or at least might allow the bird to respond more quickly to the factor containing the appropriate information from the environment (Högestedt 1981). Thus, supplemental feeding experiments cannot distinguish between these two alternatives. Experimental manipulations of the energy costs of body maintenance independent of the food supply failed to affect laying date (Nager and van Noordwijk 1992; Yom-Tov and Wright 1993). This suggests that the laying date of great tits is usually not energetically limited but may instead depend on some signal(s) from the environment that contains information about the appearance of their main prey, the caterpillars.

When the temperature around the expected time of laying dropped, the great tits on Blauen delayed their onset of egg laying, which is in agreement with other observations (Kluyver 1952; Perrins 1979; von Haartman 1990). Perrins (1979) attributed these postponements of the onset of laying to a shortage of energy available to laying females. However, females that had already started laying before the weather turned unfavorable usually continued laying. It has been demonstrated (van Noordwijk et al. 1995) that temperature after the period of egg laying has a strong effect on the selection differential of laying date. Therefore, it might also be possible that delaying breeding when the weather turns unfavorable represents a strategy of the tits to adjust their time of peak energy requirements

to the new conditions. A fine adjustment of the reproductive decisions to changes in the current environment could be an important strategy for a bird to improve its breeding success.

Selection Acting on Laying Date

Lack (1968) predicted that, in general, birds breeding at an intermediate date are the most successful ones. However, several studies have reported on a seasonal decline in breeding success (Perrins 1965; Newton and Marquiss 1984; Nilsson and Smith 1988; Perrins 1991; Verhulst and Tinbergen 1991). Such a seasonal decline in fitness will shift the most productive breeding time before the peak date in caterpillar abundance (Daan et al. 1989). The breeding success of the great tit population on Blauen, however, did not show a seasonal pattern. Birds raised young most successfully around the time the caterpillars were most abundant (table 4), as Lack (1968) predicted. However, there was no particular laying date that synchronized best with the caterpillar peak date over all study years (fig. 7).

Our measurement of breeding success takes only the quantity and quality of the fledglings of first broods into account. On Blauen, repeat and second clutches of great tits are not common in most years and are often not successful (R. G. Nager and A. J. van Noordwijk, unpublished data). In some populations, early fledglings have a higher local survival than late-fledging young (Dhondt 1971; Kluyver 1971), but not in others (Tinbergen and Boerlijst 1990; this study). The date dependency partly reflects differences in survival but also differences in dispersal (Dhondt and Olaerts 1981). It has been suggested that date dependency of local survival of fledglings (independent of weight) is not important when considering only first-brood nestlings and/or populations with low densities of great tits (Tinbergen and Boerlijst 1990), conditions that also apply to the present study. We may therefore conclude that our estimates properly describe the seasonal breeding success.

The repeatability of laying date in our study population is 0.34–0.43, which is in close agreement with the observations of other populations (van Noordwijk et al. 1981; Boag and van Noordwijk 1987). This could allow for a significant heritability of laying date, and it would be possible for selection to act on laying date. However, we have seen that there are consistent differences over years among the localities in the earliness of the caterpillars (fig. 2). As the same female usually breeds at the same locality in successive breeding seasons, some portion of the repeatability will be due to a common environment. Selection will not act on the form of the phenotypic plasticity (Stearns 1992) because of the absence of a genotype-environment interaction (fig. 5).

Local temperature in early spring was strongly correlated to laying date but not to the caterpillar peak dates. Therefore, the environment at which the phenotype is formed and the environment at which that phenotype is selected on 4–5 wk later are not tightly linked. If, for example, weather turns unfavorable after the start of egg laying and delays the caterpillar peak date, early clutches will suffer a low breeding success (van Noordwijk et al. 1995). It has been proposed that if a female cannot predict whether a year is going to be a good or a bad year

for early laying, selection may favor a trait value different from the one that is, on the average, most productive (Boyce and Perrins 1987). That may explain the absence of evolution in laying date in spite of an apparent selection for laying earlier. In addition, there are differences in timing of caterpillars among forests (van Balen 1973) as well as within forests (see fig. 2), and gene flow among habitats may make it impossible for local populations to evolve a laying date suitable for a particular habitat (Perrins 1990; Zandt et al. 1990).

Intraindividual Variation in Laying Date

In many species, including great tits, older birds start laying eggs earlier and breed more successfully than young birds (Perrins and McCleery 1985; Dhondt 1989; Perdeck and Cavé 1992). Similarly, we have also found a later start of egg laying in younger females, but that might have been confounded by the settlement pattern of the birds in the previous winter. Birds that were not yet caught in a nest box in the winter in their future breeding area had a later start of egg laying (see also Dhondt and Schillemans 1983). This delay was largest for unsettled yearling females compared with settled older females. It therefore might be that older great tits lay earlier than 1-yr-old females because they do not first have to establish themselves in a breeding area in early spring.

Individual great tits changed their laying date from year to year according to changes in environmental conditions (figs. 5 and 6). In addition, in experienced tits the nonenvironmental part of these changes in laying date between years (the residuals in fig. 6) also correlated with the environment at which the previous laying date was selected on (fig. 8). Great tits that reared their young before or after the caterpillar peak date delayed or advanced their laying date the following year corrected for changes in environment, respectively. This correlation cannot only be due to first-year females' laying late in their first year and consequently laying earlier in the following seasons (Perrins and McCleery 1985; Dhondt 1989), since we also find delayed laying dates following years when great tits laid too early. Unequal chances of delaying and advancing laying for very early and late birds are also not sufficient to explain the correlation found in figure 8 (see the section titled Results). Response to previous breeding experience as a factor contributing to intraindividual variation has also been proposed by Gustafsson (1990) for clutch size in collared flycatchers (*Ficedula albicollis*). Therefore, one has to be careful when using intraindividual variation to construct reaction norms, since the expression of a phenotype may depend not only on the current environmental conditions but also on past environmental conditions. Since there are some consistent differences in the caterpillars' timing among localities, tits may use previous local experience to improve their timing in relation to local caterpillar populations. This may also contribute to the commonly observed higher breeding success in older females than in first-year breeders.

Conclusion

Laying date is a phenotypically plastic trait correlated with environmental conditions around the time of laying. However, this correlation is unlikely to be due to an energetic limitation as revealed by manipulation of temperatures in the

prelaying and laying period (Nager and van Noordwijk 1992; Yom-Tov and Wright 1993). The presence of caterpillars early in the season also influenced laying date. Spring temperature will also affect the caterpillar peak date, but unpredictably from the point of view of a prelaying bird. The most successful breeders are those that rear their young when caterpillars are most abundant, but unpredictable yearly fluctuations in environmental conditions will maintain variation in laying date in a heterogeneous environment. The difference in a bird's and the caterpillars' timing in one year also affected a bird's laying date the following year. Thereby, a bird may use predictable differences among habitats to adjust its timing to particular local conditions. Thus, timing seems to be closely linked to seasonal patterns in caterpillar abundance, both proximately and ultimately. Laying date in great tits is therefore best explained as an adaptation to the best time for rearing young.

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