

## LAYING DATES AND CLUTCH SIZE IN THE GREAT TIT

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**ABSTRACT.**—During the course of 40 years of observations, we found that the mean date at which a population of Great Tits (*Parus major*) starts to lay varies from 10 April to 10 May. Clutch size is shown to decline with laying date and such an effect is apparent between as well as within seasons, with birds laying larger clutches in early seasons than they do in late ones. Clutch size also declines with increasing density of both Great Tits and Blue Tits (*P. caeruleus*). Breeding success decreases seasonally and the decline can be very marked in some years. The laying bird, therefore, has the “choice” of whether to lay more eggs, and suffer the reduced success of having them hatch later, or of stopping laying sooner and hence having a smaller brood but gaining the advantages of having them hatch earlier. The relative advantages of these two options are discussed, and it shown that the seasonal decline in nesting success is insufficient to explain why birds lay the smaller clutches observed; differences in individual bird quality are also involved.

The aim of this paper is to examine factors affecting the timing of breeding and clutch size of the Great Tit (*Parus major*). A number of factors have been shown to affect these aspects of breeding, and these are re-examined here with a larger set of data. Some comparisons are made with data for the Blue Tit (*P. caeruleus*). The breeding biology of the Great Tit is probably better known than that of any other wild bird. It is convenient for study purposes for a number of reasons. It is common and usually nests in broad-leaved deciduous woods at densities of approximately one pair per ha or more. It largely is sedentary, thus studies can be continued through the winter. Also, many of the nestlings raised in a study area breed there in later years. Above all, it is a hole nester, accepting nest boxes readily. Normally, virtually all Great Tits nesting in a woods will use nest boxes if these are available. Furthermore, over much of Europe, it is one of only two abundant hole nesters, the other being the Blue Tit; since the latter species is much smaller (10–12 g as opposed to 18–20 g), the Great Tit normally wins disputes for nest boxes. Therefore, the numbers nesting in boxes closely reflect the number of breeding pairs present.

Long-term studies have provided much of the basic data. The first, started in the Netherlands in 1912 by H. Wolda, subsequently was made famous by the works of H. N. Kluijver (Kluyver 1951). The present paper is based on some analyses from the long-term British study begun in 1947

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by Lack and Gibb in Wytham Wood, a wood owned by the University of Oxford (e.g., Lack 1966). We now have data for 42 consecutive years. The original work was carried out in a 26.7-ha subsection of Wytham Wood called Marley Wood, and it was not until 1958–64 that the study was expanded to cover the whole woods, an area of some 230 ha (e.g., Perrins 1979, Minot and Perrins 1986). The data for Marley Wood are less extensive but cover more years, whereas those for the whole wood are more extensive but only cover a period of a little over 20 years. Further, many of the areas outside Marley Wood contain a lower density of nest boxes, and at least at times of high breeding numbers, not all the Blue Tits are able to obtain a box. In this paper, we use mainly the data for Marley Wood, but for some analyses we have used the more extensive data for the whole forest of Wytham.

#### Definitions

The following conventions are used in this paper: (1) *Laying date*. The annual laying dates given are the means of the dates on which each pair in the population laid their first egg. Since Great Tits usually lay one egg per day throughout their laying period, the date on which the first egg in a clutch was laid can be extrapolated from weekly visits to the nesting boxes. There are, however, some potential sources of error in calculating mean laying dates. Because some nests fail during the laying period, usually due to predation, and because the parent birds lay a replacement clutch, more clutches are started than there are breeding pairs in the wood. A replacement clutch of an early pair may be laid before the first clutches of later pairs. Since the identities of the birds are not known at this time, we do not know the status of all nests, with the result that the decision as to which are first clutches and which are replacements (second broods are rare and come much later) is inevitably somewhat subjective. However, the status of only a small number of nests is in doubt, and their inclusion or exclusion rarely affects the mean date of laying by more than a day. (2) *Clutch size*. Certain nests in which eggs were laid were excluded from the calculations; these included those where the female never got as far as incubating. They were mostly incomplete or late nests (i.e., those excluded on the basis of their date of laying). All nests of four or fewer eggs were also excluded, even though they may have been incubated; such small clutches are rare and probably usually incomplete. (3) *Recruits*. We have used as our measure of breeding success the number of young which survive long enough to breed in the nest boxes. The number of such recruits does not fully reflect the total number of young which survive to breed, since some emigrate from the study area and breed elsewhere (McCleery and Perrins 1985). There is, however, no reason to suppose

that the number of recruits is not an accurate indication of the relative success of the different classes of nests.

### Variations in Laying Date

Both the clutch size and the laying date of the Great Tit are very variable. In our study area, the mean date of laying has varied from 10 April to 10 May, while the annual mean clutch size has varied from 7.7 to 12.1. These year-to-year changes are the result of all birds in the population "tracking" the annual changes. This was clearly shown in 1986 and 1987, respectively, a very late year and a fairly early one. Ninety-four Great Tits bred in both these seasons, and their laying dates and clutches in both seasons are shown alongside those for the population as a whole (Table 1).

Many birds breed earlier in warm springs than in cool ones. This holds true for the tits. Previous studies of the Great Tit, (Kluijver 1951 [with some modifications 1952], Dhondt 1970, van Balen 1973) have shown that the laying date markedly is affected by spring temperature. This correlation has been demonstrated in a variety of ways; in particular, Kluijver (1951) and van Balen (1973) showed that the spring temperatures (as measured by the sum of the mean of the maximum and minimum temperatures for each day = the "Warmth-Sum") have a major effect on the date at which laying starts. Although Kluijver (1951) thought that temperatures as early as January might affect the date of laying, he later decided that the period from mid-March onward was the most important (Kluijver 1952). van Balen (1973) showed that the period with which, statistically, the date of laying is most closely correlated is 1 March to 20 April. He thought that temperatures before 1 March did not contribute to the timing of laying. This analysis of the Wytham Wood data supports this conclusion in that mean laying dates of the Great Tit are not correlated significantly with the sum of the maximum and minimum temperatures for February. In the case of the Blue Tit (which lays a few days earlier than the Great Tit), February temperature has a small but statistically significant effect on the laying date:

Blue Tit laying date =  $53.1 - 0.0239 \text{ Feb-Warmth-Sum}$ ,  $P < 0.01$

The March/April Warmth-Sums explain almost 70% of the variation in laying date in both species, showing spring temperature to have a very strong effect on the timing of breeding in the tits. Indeed, it is probably stronger than these analyses suggest, because there are a number of ways in which such analyses are not entirely satisfactory. The most important of these is that, since the laying date varies by a month between years, any fixed period of time will not coincide closely with the onset of laying

TABLE 1  
CHANGES IN LAYING DATE (L-D) AND CLUTCH SIZE (C-S) OF THE SAME BIRDS IN  
SUCCESSIVE YEARS, 1986 AND 1987

	1986			1987		
	N	L-d	C-s	N	L-d	C-s
Total population <sup>a</sup>	193	38.4		228	22.3	
	188		8.73	225		10.00
Known to breed 1985	61	39.0	8.57	61	21.6	10.33
in both years 1984	33	38.1	9.06	33	22.1	9.91
Combined	94	38.7	8.75	94	21.8	10.18
Shift (in total)		L-d	16.1	C-s	1.27	
Shift (in 94 birds)		L-d	16.9	C-s	1.43	

<sup>a</sup> The first two rows show laying data and clutch size for all birds in both years. In rows 3 and 4 the 94 birds are divided by whether they were breeding for the first time in 1986 (1985 = born in 1985, 1984 = born in 1984 or earlier), since the laying dates and clutch size of first-year birds are usually later and smaller (respectively) than those of older birds. In this case, none of the differences between the two age groups is significant, though clutch size in 1986 approaches significance ( $P = 0.08$ ). Also note that the total population in 1987 will have contained many young birds, while all the 94 were at least two years of age by then; hence the latter group would be expected to have a slightly larger clutch size than the whole population.

in all springs; for example, in one year (1948) the mean date of laying occurred ten days before the end of the period over which the Warmth-Sums are measured, while in others (1979, 1986) a full 20 days elapsed between the end of this period and the mean laying date.

Second, as pointed out by both Kluijver (1951) and Dhondt (1970), the relationship between laying date and spring temperature is not a simple one; more than a single factor is involved. Dhondt suggested that the daily mean temperature had to reach at least 10°C before the birds would start to breed. Kluijver suggested that the birds were affected by two factors. First the Warmth-Sum had to reach a threshold (of about 32°F) by the beginning of April if breeding was to start early, but if the birds were delayed from starting then, the Warmth-Sum required for breeding to commence falls as the spring progresses. In other words, breeding would start relatively earlier with regard to any given Warmth-Sum, the later the date. Kluijver suggested that some other factor such as day length held the birds in check earlier in the season, but that after the temperature threshold had been reached, this second factor ceased to act. Clearly temperature is not the only factor affecting the birds at this time; among other things, the days become progressively longer. Comparing the two extremes of the starting dates in Wytham Wood (10 April and 10 May), there is an increase in daylight of almost two hours between them (a 12.6% increase in feeding time or a 19% reduction in fasting time). Hence, even if all other environmental conditions (especially food and temper-

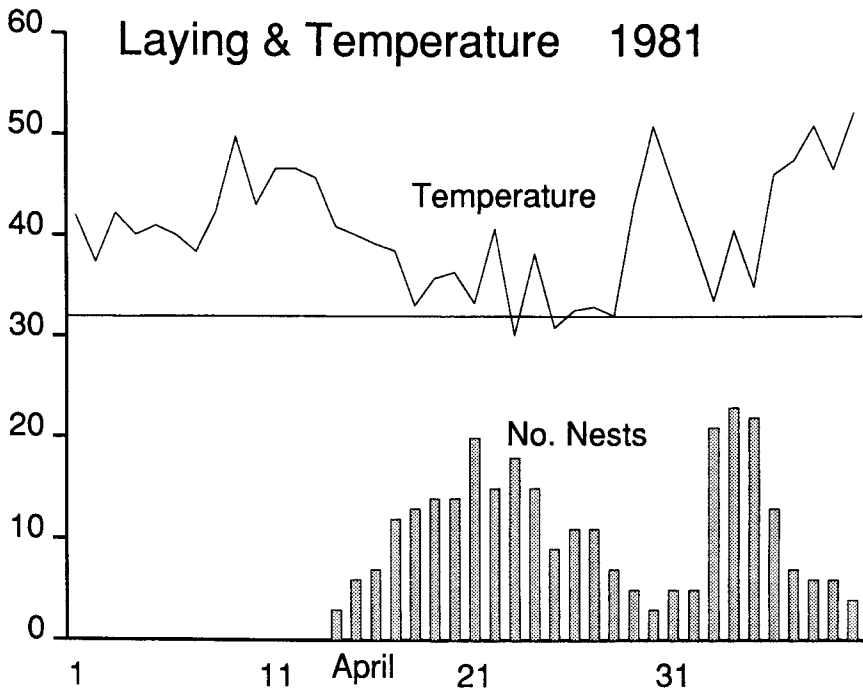


FIG. 1. The effect of cold weather during the laying season on the number of nests started each day. Upper graph shows minimum daily temperatures (vertical axis = °F), horizontal line freezing point, and the histogram shows the number of nests started each day. Laying normally starts four days after an increase in temperature. In this year (1981) a cold snap discouraged many birds from laying and they did not start until four days after the weather improved again.

ature) were identical, birds should find it easier to start breeding in cold conditions in May than in April—they then would have longer in which to gather food.

Third, temperature also has short-term effects. A sudden period of warm weather may stimulate laying, or a sudden cold snap may deter it. This means that the weather of the moment may override more general trends of the Warmth-Sum. This may even happen after the first birds have laid; a cold snap may deter the rest from starting (Fig. 1). As a result, the spread of laying can be quite variable between years. Not surprisingly under these conditions, the laying date of the first quarter of the population is more closely correlated with the Warmth-Sum than is that of the population as a whole.

Fourth, taking the mean of the maximum and minimum temperatures may not be the best way of measuring what is happening in the environment. Kluijver first made this point, in fact his Warmth-Sum discounts temperatures below freezing, counting all such temperatures as 32°F. The Wytham data also show a closer correlation between laying date and temperature if this is done. There is, of course, no reason why freezing point should be the critical temperature above which the Warmth-Sum should be calculated. It may be that it is the accumulated warmth above some other level that is important. Some analyses of the timing of bud-burst in forest trees have shown a complex relationship with low temperatures in winter and temperatures above 5°C (41°F) in spring (Cannell and Smith 1983). However, using 41°F as the lower threshold for the Warmth-Sum gives a much lower correlation with laying date than does the Warmth-Sum with a 32°F threshold. Similarly, using a more recent model for bud-burst of oak trees (Nizinsky and Sangier 1988) does not improve the correlation between laying date and temperature. Nevertheless, some effect of the warmest weather seems likely to be important in the tits, since an analysis of the Wytham data against only the sum of the maximum temperatures gives an even higher correlation than that between the laying date and Warmth-Sum in both Great and Blue tits; these are shown in Fig. 2. Not surprisingly, the laying dates of the two species are closely correlated with each other ( $r = 0.880$ ,  $P < 0.001$ ).

The timing of laying in the tits is also correlated closely with the shifts in abundance of their main prey, the caterpillars which feed on the leaves of oaks (*Quercus*). The most common species of prey, the winter moth (*Operophtera brumata*) was studied intensively in Wytham Wood for a number of years (Varley et al. 1973). When it is fully grown, the winter moth larva drops from the tree and pupates in the ground after which it is no longer available to the tits. In Wytham Wood, the mean date of pupation of the winter moth caterpillars has varied from 14 May in 1948 to 8 June in 1951 and 1962. Like the tits' breeding season, the caterpillars' season is closely correlated with the Warmth-Sum. The date at which half the caterpillars have fallen is well correlated with the laying date of the tits (Fig. 3). The tits' laying date does not seem to be correlated with the numbers of caterpillars present (Fig. 4). Although there is a statistically significant correlation, this is heavily dependent on the one outlying point, and its removal makes the correlation non-significant. What is not immediately apparent from the between-species correlations is that there is considerable variation in the timing of one species compared with the other (Fig. 5). Although, on average, the Blue Tits tend to lay 2–3 days before the Great Tits, they have laid as much as 10 days earlier and as

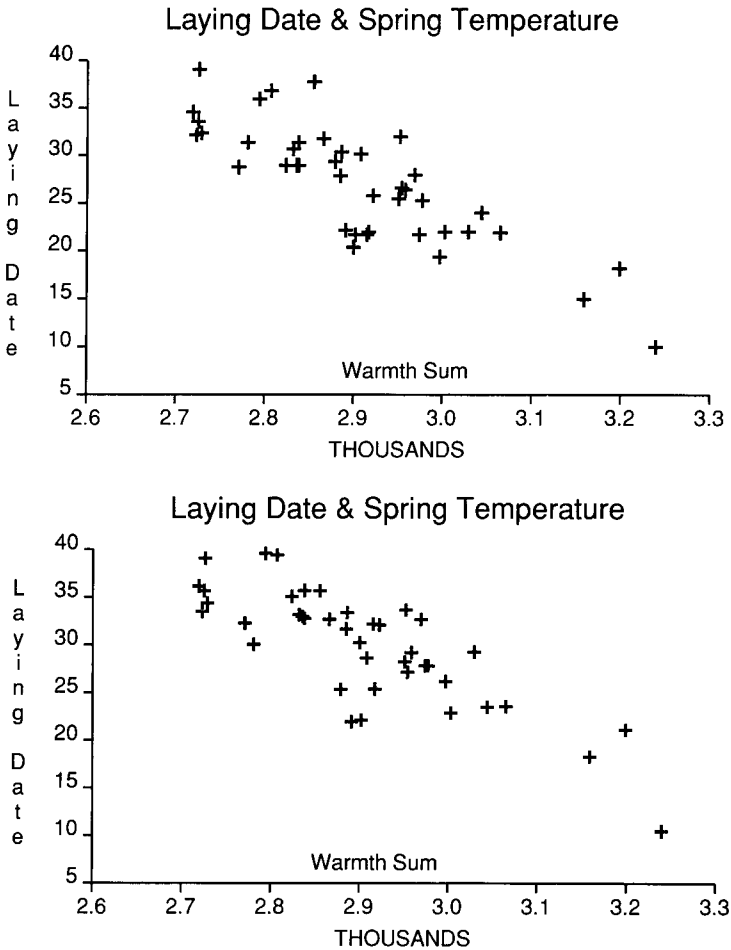


FIG. 2. Correlation between the sum of the daily maximum temperatures 1 March to 25 April and the mean laying dates for Great Tits (above) and Blue Tits (below); both regressions are highly significant ( $P < 0.001$ ).

much as four days later than the Great Tits. This variation does not seem to be associated with breeding densities or earliness or lateness of season although it is correlated significantly with February temperatures. The higher the February temperatures, the more the Blue Tits lay in advance of the Great Tits. For the present, in spite of the problems in such analyses, one can safely conclude that laying date is very strongly influenced by spring temperatures, specifically those in March and April.

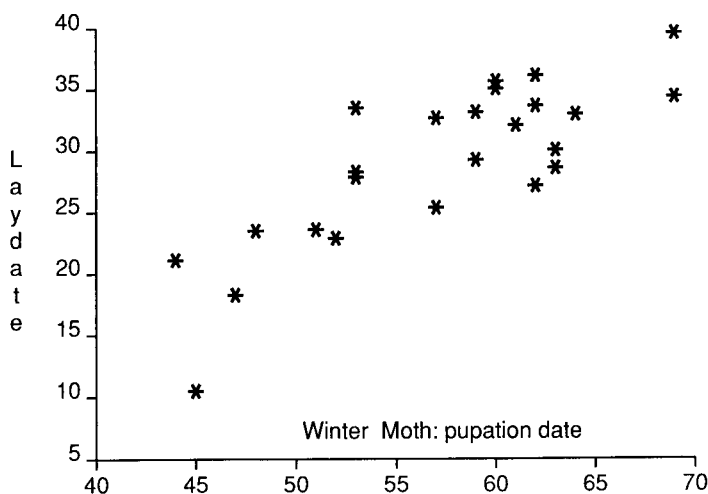


FIG. 3. Correlation between mean laying dates of the Great Tit and mean pupation date of winter moth (on both axes 1 = 1 April). The correlation is highly significant ( $P < 0.001$ ).

### Variations in Clutch Size

It has long been known that the Great Tit's clutch size is affected by the laying date and also by the density of the breeding pairs (Kluijver 1951, Lack 1958). This is likewise true of the data examined here, but other factors also seem to be involved. The factors with which clutch size is correlated significantly are shown, for both Great and Blue tits, in Table 2.

*Laying date and food supply.*—As in previous analyses, clutches are smaller in years when the breeding season is late (Table 2). This is borne out in the present analysis which shows clutch size declining by almost 0.07 eggs for each day's delay in the mean laying date (where April 1 = 1):

$$\text{Clutch size} = 11.0 - 0.0675 \text{ Laying date} \pm 0.02243, \quad P < 0.01$$

We have data for the years 1947–71 on the densities of the winter moth, and there is a significant correlation between clutch size and caterpillar density (Fig. 6), which is still present if the one year of very high caterpillar density is removed. There is also a significant tendency for there to be more caterpillars in early springs than late ones, although again, as with the correlation between laying date and caterpillar numbers, this correlation is heavily dependent on the one year. Hence, the correlation between clutch size and laying date seems likely to be one of food supply rather than laying date per se. Nonetheless, the relationship between clutch



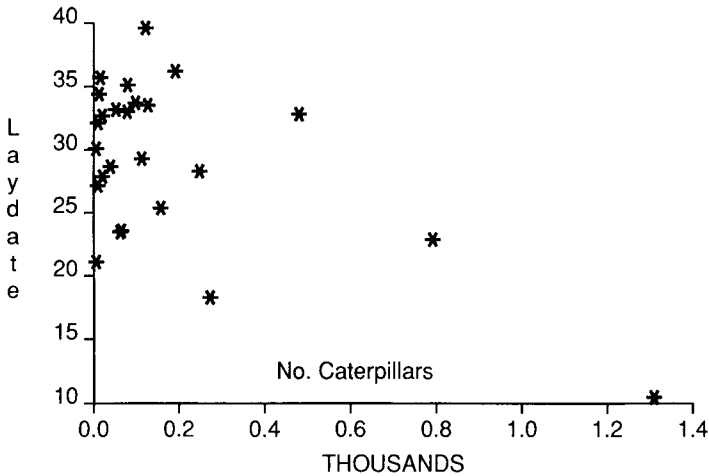


FIG. 4. Correlation between mean laying dates of the Great Tit and the number of winter moth caterpillars per m<sup>2</sup>. The correlation is not significant if the highest density year is excluded.

size and the food supply is more complex when the two species are considered together, since as is shown in Fig. 5, their clutches vary considerably in relation to each other between years. Therefore, either clutch size is not closely related to the food supply or the two species must be taking different prey.

*Breeding density of Great Tits.*—Overall, there is a strong correlation between breeding density and clutch size (Table 2). Clutch size decreases by 0.026 of an egg for each extra pair of Great Tits breeding in the wood.

*Breeding density of Blue Tits.*—If the presence of other Great Tits leads to a reduction in clutch size, is such an effect purely intraspecific or do other species have an influence? The most abundant species, for which we have similar data, is the Blue Tit; breeding numbers of Blue Tits also have a significant effect on the clutch size of the Great Tit, which decreases by 0.016 of an egg for each extra pair of Blue Tits in the woods. The clutch size of the Blue Tit is similarly affected by the densities of both species (Table 2).

*Between year effects.*—We have found one further factor with which the clutch size seems to be correlated and that is the clutch size in the previous year (Table 2). There is no significant autocorrelation over periods longer than one year. Since clutch size is negatively correlated with population size, one possibility could be that this correlation results from

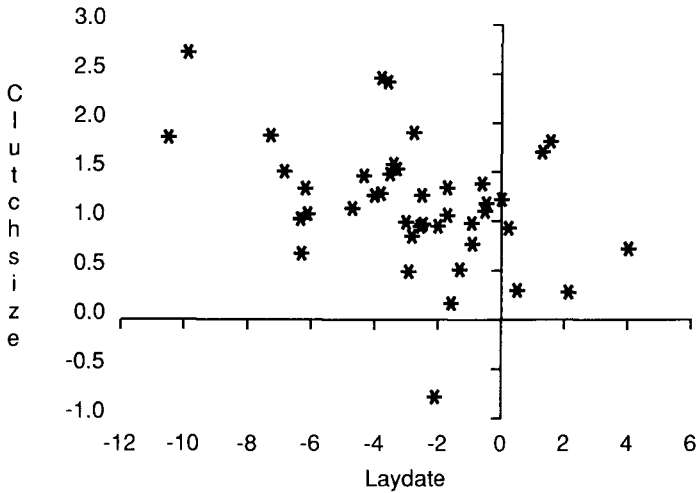


FIG. 5. Relationship between the mean laying dates and the mean clutch sizes of the Great and Blue tits. Both axes show the annual mean for the Blue Tit minus the annual mean for the Great Tit. The earlier the Blue Tit breeds in relation to the Great Tit, the larger is the difference between their mean clutch sizes.

TABLE 2

REGRESSION OF DENSITY OF GREAT TITS AND BLUE TITS, OF MEAN LAYING DATE AND OF CLUTCH SIZE THE PREVIOUS YEAR ON CLUTCH SIZE OF GREAT TIT AND BLUE TIT

	Correlation coefficient	SD	P
<b>Great Tit</b>			
Constant	9.780	1.257	<0.001
Density of Great Tits	-0.027	0.008	<0.01
Density of Blue Tits	-0.016	0.006	<0.001
Mean date of laying	-0.059	0.0159	<0.01
Previous year's clutch	0.276	0.105	r <sup>2</sup> 59.2%
<b>Blue Tit</b>			
Constant	10.519	1.570	<0.001
Density of Great Tits	-0.029	0.009	<0.05
Density of Blue Tits	-0.016	0.006	<0.01
Mean date of laying	-0.052	0.019	<0.05
Previous year's clutch	0.255	0.011	r <sup>2</sup> 51.5%

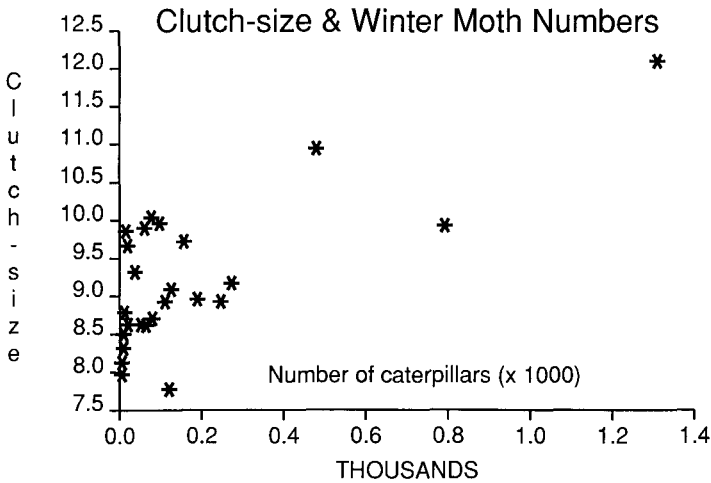


FIG. 6. The correlation between the clutch size of the Great Tit and the number of winter moth caterpillars per  $m^2$ .

between-year correlations in population size. However, these are very weak and do not appear to be the explanation.

One way in which such a correlation might arise would be if individual cohorts laid, on average, slightly different clutch sizes. This is possible since clutch size is an inherited characteristic (Perrins and Jones 1974), and there are shifts in selection from year to year (van Noordwijk et al. 1981). On average, in any year about 50% of the breeding population is made up of one-year-old birds which, since they have a survival rate of about 50%, make up roughly 25% of the birds of the following year. Thus, the presence of the same cohort in their first and second years of life provides a common component between years. However, we do not have sufficient data for Marley Wood alone from the early years to analyze for this. Using the much larger data set for the whole of Wytham Wood (but for a shorter run of years), we were not able to find either a between-year correlation or significant differences between the clutch sizes of different cohorts. Hence, we cannot explain why this between-year correlation occurs. It is, however, also apparent in Blue Tits.

Overall, these four factors, i.e., food supply, numbers of breeding pairs of Great Tits and of Blue Tits, and the between-year correlation, are all significant, and in combination they explain 51.5% of the variation in Blue Tit clutch size and 59.2% of the variation in Great Tit clutch size.

There is, however, a problem with these analyses. As reported elsewhere for the effect of density on clutch size (McCleery and Perrins 1985), the

strength of the effect of all four of these factors on clutch size has varied with time. Clutch size was strongly correlated with all four variables in the first part of the study, barely at all with any of them in the middle period, and strongly again in the most recent period. The combined  $r^2$  for each of the four periods (1947–57, 1958–67, 1968–77, and 1978–88) were 90%, 9%, 21%, and 82%, respectively (the comparable figures for Blue Tits are 41%, 13%, 65%, and 91%). We have no explanation for this.

*Within season variation in clutch size.*—Clutch size is also correlated with laying date within breeding seasons. Although the slope differs greatly between years, a seasonal decline in clutch size is apparent in almost all years (Fig. 7). The reason for this decline is almost certainly associated with the fact that late nests are less successful than early ones. Fig. 8 shows the number of young per nest which survived to breed in later years as a function of the date on which laying started in each nest. Again there is great variation, but overall the penalty for being late is very severe; for each day's delay in starting (and hence in hatching the young) the number of survivors produced decreases by an average of 3.7% (range 0.5%–10.6%).

The pattern is more complex than this, as can be seen from Fig. 9 which shows the data for all years combined (but thereby loses the variation between years). There are four points to note. First, there is an inverse relationship between clutch size and the proportion of the season over which that size of clutch is laid. Very large clutches are laid only during the first third of the season. Second, the seasonal decline in success is not linear, the very first clutches laid are less successful than those started a few days later (this is certainly very variable between years, with the very first clutches faring well in some years and quite poorly in others). Third, the success of large clutches decreases more sharply with season than does that of small clutches. Fourth, although not clearly visible in this projection of the data, there is a slight, but statistically significant, decrease in survival rate per young with increasing brood size, such that the number of survivors does not increase proportionately with increasing brood size.

#### DISCUSSION

Why should these birds show such marked variations in laying date and clutch size? The general answer to this is probably fairly easy, although the details are elusive. Tits have very large broods; indeed, as far as is known, the Blue Tit lays the largest clutch of any nidicolous bird in the world. Tits feed their young primarily on caterpillars, which in our study area were mainly ones collected from oaks. The birds are dependent on being able to get very large numbers of caterpillars for their large broods. When feeding large young, both Great and Blue tits may bring caterpillars

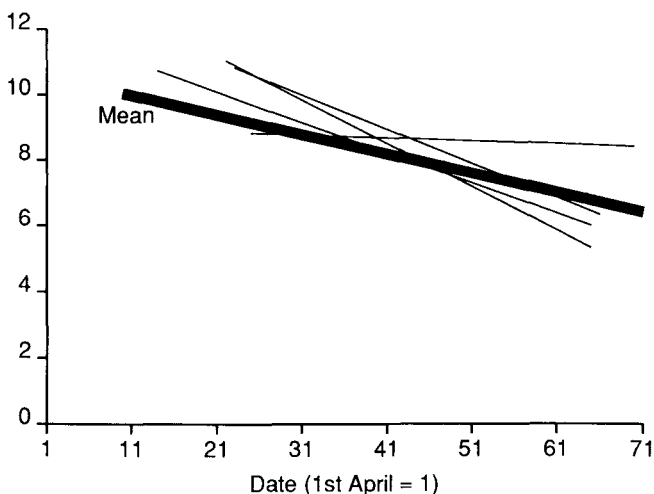


FIG. 7. The mean clutch size in relation to the date of laying within years. The thick line shows the average for all years; the thin lines a range of individual years. Based on data for the whole wood for the years 1960–87.

to the nest at the rate of one per minute throughout the whole of a 16-h day, almost 1000 caterpillars per day. However, the caterpillars vary markedly in the time of year when they are present and in their numbers; in particular, they develop very rapidly, and they may only be present in any numbers for 2–3 weeks (Gibb 1950).

Ideally, tits should benefit from being able to respond to these changes. Theoretically, they need to be able to cope with two rather different problems. First, they might benefit from knowing how many caterpillars there will be. Second, and perhaps more crucial, they need to have their young in the nest as early as possible in relation to the short period of caterpillar abundance; as we have shown, later nesting birds do much less well.

We suggest that the variations in laying date are made so that the birds can match these shifts in the food supply and that the variations in clutch size are made so as to take into account variations in the quantity of food available. If this is indeed the case, how well can they do this? The answer seems to be only moderately well. There are some things that they simply cannot do. First, we have emphasized that it is crucial for them to get their timing right. However, they cannot do this precisely since the time taken by the caterpillars to develop (from hatching to pupation) varies by more than two weeks between years as a result of temperatures *after* the birds have laid (Perrins 1973).

*Laying date.* — Laying date is clearly and markedly related to the spring

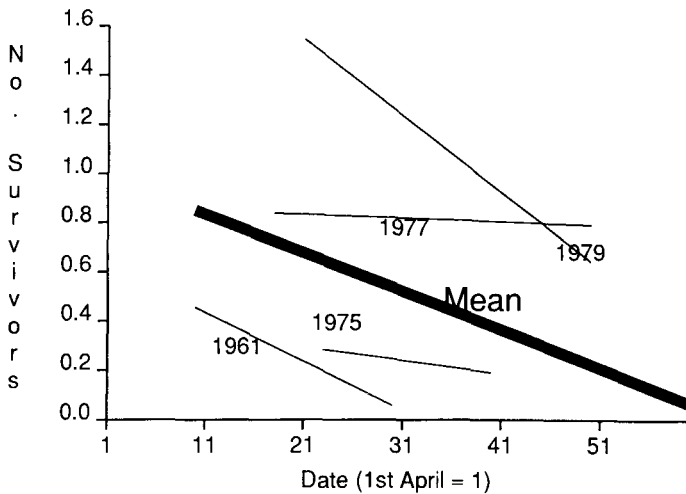


FIG. 8. The number of survivors per brood (=recruits) in relation to date of laying. The thick line shows the average for all years, the thin lines a range of individual years. Based on data for the whole wood for the years 1960–87.

temperature, and these mirror the progress of spring. Plainly, plentiful food is available to the tits earlier in a warm spring than in a cold one. In their turn, the caterpillars must be able to move their season to match that of the bud-break of the oaks, since they grow much better on a diet of newly emerging leaves; these also develop earlier in warm springs than in cool ones.

One could, therefore, argue that in every year the birds are merely breeding as early as they can and that their laying date is just a reflection of the time when the food becomes abundant enough for them to be able to start breeding. However, the situation is probably not as simple as that since the laying dates of the two species vary so much in relation to each other.

It is interesting to speculate about how the birds are able to respond. Kluijver (1952) suggested that the birds laid earlier in warm springs, compared with cool ones, because females preparing to breed in warm weather would need less food to maintain themselves and could therefore get into breeding condition more quickly. However, while it is doubtless true that warm weather has such a proximate effect on a bird, we suspect that the weather has an even more important effect on the timing of the food supply.

One reason for thinking that it is the food supply to which the tits are responding, rather than the direct effect of the temperatures on themselves, is that other birds show similar changes in the timing of their breeding

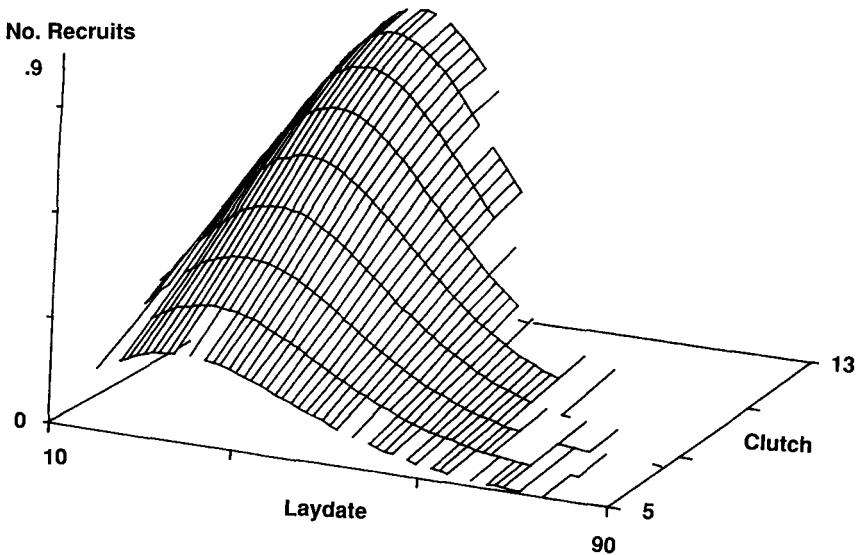


FIG. 9. The number of survivors per brood (=recruits) in relation to date of laying and clutch size. The distribution is based on a Poisson model with square terms for both clutch size and laying date and cubic terms for laying date, all of which significantly affect the model.

season in relation to spring temperature. One of these is the Pied Flycatcher (*Ficedula hypoleuca*) (Löhrl 1957). However, unlike the tits, this species is migratory and is not in Europe during March, so it cannot experience the actual temperatures which might affect its laying date. In this species, the temperatures can only affect the birds indirectly, presumably through effects on other environmental factors such as their food supply.

More direct evidence that laying date is influenced by food availability comes from experiments where artificial food has been supplied to some birds but not to others (Källander 1974, von Bromssen and Jansson 1980). In these experiments on Great Tits and other tit species, the fed birds laid earlier than the controls, though the differences were only a matter of a few days rather than a month as observed here. These feeding experiments indicate that the birds will lay earlier when given extra food at the time of laying. However, there is no convincing correlation between laying date and caterpillar numbers. Further, one might expect that, when they were preparing to lay, the birds would find natural food supplies more difficult to come by, and so breed later in years of high than years of low density. There is no sign that laying date is affected by breeding density in either species. Hence, under natural conditions, the laying date

of the birds does not seem to be affected by the size of the natural food supply.

Clearly, spring temperatures affect date of laying. We suggest that this is largely via its effect on the food supply. This is in contrast to Kluijver (1952) who thought that it was mainly due to direct effects on the birds but in agreement with Tollenaar (1922) who thought that the effects were indirect.

*Clutch size.*—In contrast to laying date, clutch size is affected by a number of different factors. We suggest that all these responses are best seen as attempts by the tits to maximize the number of fledglings that they produce.

Clutch size is correlated with caterpillar numbers over the smaller run of years from which we have data. Since there is also a significant tendency for there to be more caterpillars in an early season than a late one, this may explain why there is a correlation between clutch size and laying date. However, there may be a separate advantage of breeding in an early spring, which is independent of caterpillar numbers. Since, on average, the weather gets warmer as the spring progresses, the caterpillars tend to encounter cooler weather in early seasons than in late ones. As a result, they develop more slowly in early than in late seasons; their prolonged presence should be of considerable advantage to the tits (Perrins 1973). What is perhaps surprising is that feeding experiments show that providing extra food results in a marked shift of laying date but not of clutch size. This could be because the birds are monitoring the natural foods in order to determine their clutch size and are only taking advantage of the extra food provided by man in order to be able to breed earlier.

For a long time it was thought that the caterpillars were so abundant that competition for them by tits raising broods was negligible. The observations of Minot (1981) show that this may not be the case. By removing nestling Blue Tits from an area of woodland, Minot was able to show that the Great Tits were able to feed their young better and fledge them at higher weight than those Great Tits breeding in other areas nearby where Blue Tits were also busily collecting caterpillars for their young. The presence of large numbers of both species depresses clutch size, perhaps for the same reason: the more pairs there are present, the more difficult it is for the parents to raise their young so the better it is to start with smaller broods. If this is indeed the case, it is not surprising that the clutch sizes of both species are affected by the breeding densities of both species. As far as we know, this is the first time that it has been suggested that there may be interspecific effects of density on clutch size. One would like to know how general a phenomenon this is and whether the clutch size of the tits is affected by the density of other species in the same guild and vice-versa.



Early pairs raise more young than later ones; these chicks are heavier and survive better. Fig. 9 shows how survival goes down the later the birds breed and that this decrease in survival rate is more marked the larger the brood size.

There is, however, a problem here. Although Fig. 9 shows qualitatively that the number of recruits produced decreases markedly with season, this model is not, by itself, sufficient to explain quantitatively why clutch size decreases with season. Suppose a bird has the option of stopping laying today or laying one further egg tomorrow. In the first case, its reproductive output will suffer by having one chick fewer but gain by being able to raise the whole brood one day earlier. In the second, the reverse will be the case; it will gain by having one more chick, but lose by having to rear its brood one day later. Since the average reduction in success is about 3.6% per day, this loss is almost always outweighed by the advantage of an additional chick which is much bigger in percentage terms than 3%; in only the one year when the daily reduction in success reached 10%, was this high enough to counterbalance the advantage of increasing clutch size (for a bird laying ten eggs). Hence, by delaying one day and having the extra chick, the parent birds would almost always raise more young. Of course, this is not true without limit, since increasing brood size also has a deleterious effect on chick survival. At some point, fewer young are raised by having another egg than would be raised by having one fewer. This trend can be seen in Fig. 9, but it has only a small effect.

The reason why the model is insufficient to explain why a bird should stop rather than go on to have a larger clutch is that it is incomplete in one respect. It compares the success of a bird's laying a clutch of nine eggs with that of a bird laying a clutch of ten, and it assumes that if the bird which laid nine eggs had laid ten it would have been just as successful as the bird which actually laid ten. This is not the case. The clutch size of an individual bird is linked closely to the number of chicks which that particular bird can raise (Pettifor et al. 1988). Hence, the slope showing survival in relation to brood size (which is based on information from different individuals) would be much more sharply curved downwards for any one individual.

In conclusion, we emphasize that tits vary their breeding season and their clutch size in ways related to their food supplies. They breed earlier when the caterpillars are early and adjust their clutch size so as to lay larger clutches under those conditions when food is either actually more plentiful or relatively more plentiful because there are fewer birds taking it. They lay smaller clutches when the reverse is the case.

## ACKNOWLEDGMENTS

We are grateful to P. Venters for supplying the temperature data.

## LITERATURE CITED

- CANNELL, M. G. R. AND R. I. SMITH. 1983. Thermal time, days and prediction of budburst in *Picea sitchensis*. *J. Appl. Ecol.* 20:951-963.
- DHONDT, A. A. 1970. De regulatie der aantallen in Gentse Koolmeespopulaties (*Parus m. major* L.). Thesis Rijksuniversiteit. Gent.
- GIBB, J. A. 1950. The breeding biology of Great and Blue Titmice. *Ibis* 92:507-539.
- KÄLLANDER, H. 1974. Advancement of laying of Great Tits by the provision of food. *Ibis* 116:365-367.
- KLUIJVER, H. N. 1951. The population ecology of the Great Tit *Parus m. major* L. *Ardea* 39:1-135.
- . 1952. Notes on body weight and time of breeding in the Great Tit *Parus m. major* L. *Ardea* 40:123-141.
- LACK, D. 1958. A quantitative study of British Tits. *Ardea* 46:91-124.
- . 1966. Population studies of birds. Clarendon Press, Oxford, England.
- LÖHRL, H. 1957. Populationsökologische Untersuchungen bei Halsbandschnapper *Ficedula albicollis*. *Bonn. Zool. Beitr.* 8:130-177.
- MCCLEERY, R. H. AND C. M. PERRINS. 1985. Territory size, reproductive success and population dynamics of the great tit, *Parus major*. Pp 353-373 in *Behavioural ecology* (R. M. Sibley and R. H. Smith, eds.). Blackwell Scientific Publications, Oxford, England.
- MINOT, E. O. 1981. Effects of interspecific competition for food in breeding blue and great tits. *J. Anim. Ecol.* 50:375-385.
- AND C. M. PERRINS. 1986. Interspecific interference competition—nest sites for Blue and Great Tits. *J. Anim. Ecol.* 55:331-350.
- NIZINSKY, J. J. AND B. SANGIER. 1988. A model of leaf-budding in development for a mature *Quercus* forest. *J. Appl. Ecol.* 25:643-652.
- PERRINS, C. M. 1973. Some effects of temperature on breeding in the Great Tit and Manx Shearwater. *J. Reprod. Fert. Suppl.* 19:163-173.
- . 1979. *British Tits*. Collins, London, England.
- AND P. J. JONES. 1974. The inheritance of clutch-size in the Great Tit (*Parus major* L.). *Condor* 76:225-229.
- PETTIFOR, R. A., C. M. PERRINS, AND R. H. MCCLEERY. Clutch-size variation in Great Tits: quantitative evidence for the individual optimisation hypothesis. *Nature* 336(6195): 160-162.
- TOLLENAAR, D. 1922. Legperiodes en eierproductie bij eenige wilde vogelsoorten, vergeleken met die bij hoenderassen. *Meded. Land. Wageningen* 23. Verh. 2.
- VAN BALEN, J. H. 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. *Ardea* 61:1-93.
- VAN NOORDWIJK, A. J., H. J. VAN BALEN, AND W. SCHARLOO. 1981. Genetic and environmental variation in clutch-size of the Great Tit, *Parus major*. *Netherlands J. Zool.* 31: 341-372.
- VARLEY, G. C., G. R. GRADWELL, AND M. P. HASSELL. 1973. *Insect population ecology*. Blackwell Scientific Pubs., Oxford, England.
- VON BROMSSEN, A. AND C. JANSSON. 1980. Effects of food addition to Willow Tit *Parus montanus* and Crested Tit *P. cristatus* at the time of breeding. *Ornis Scand.* 11:173-178.