

POPULATION FLUCTUATIONS AND CLUTCH-SIZE IN THE GREAT TIT, *PARUS MAJOR* L.

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INTRODUCTION

History

This study forms part of a long-term investigation of the factors affecting populations of tits; it was started, under the general direction of Dr D. Lack, in 1947. Emphasis has been on the three species great, blue and coal tit, *Parus major*, *P. caeruleus* and *P. ater*, but this paper is largely concerned with work done by the writer, on the great tit, since 1957. Most of the work has been done in Wytham Wood, an area of mixed deciduous woodland, some 2 miles west of Oxford.

In 1946–47 J. A. Gibb put up nest-boxes in the part of the Wytham Estate known as Marley Wood, an area of 66 ac (c. 26 ha), of which about 3 ac are open, marshy, ground, unsuitable for tits and another 8 ac mainly shrubs with no trees. Since the summer of 1947 the number of breeding pairs of great and blue tits has been recorded. The reader is referred to Gibb (1950) for a general description of the breeding biology of these two species.

Since 1957 the writer has used, in addition to Marley, an increasing number of other parts of the wood, as the Marley population was insufficient to provide enough data for various aspects of the study. In addition to those in Wytham there were about 100 boxes in gardens in Oxford from 1958 to 1961, inclusive; the data from gardens provided an interesting comparison with those from Wytham in some respects, but extensive trapping was not practicable in gardens in winter and survival data for the garden birds were not obtained.

Only blue and great tits nest commonly in the boxes in Wytham. For 5 years Gibb (1954a) made careful censuses of the breeding population and found that, while no great tits nested in natural sites, up to one third of the blue tits did so. Hence the population figures for the blue tit, while probably reflecting the numbers present, are not complete.

Wytham Wood

The woodland areas used in this study were all within the Wytham Estate (Fig. 1). The woodland covers some 800 ac, but about 200 ac of this are young plantations, including much conifer, and are less used by the tits. Hence there are some 600 ac (c. 250 ha) of woodland suitable for tits. The wood is privately owned by the University; there was little disturbance, apart from forestry operations.

Except for a few small plantations of mature conifers, the wood is broad-leaved deciduous, very mixed in composition, but of two main types. One consists primarily of oak, *Quercus robur* (L.), with an understorey of varying amounts of hawthorn, *Crataegus monogyna* (Jacq.), hazel, *Corylus avellana* (L.), and elder, *Sambucus niger* (L.), and often a thick ground layer of bracken, *Pteridium aquilinum* (L.) and bramble, *Rubus* spp. The other type is predominantly sycamore, *Acer pseudoplatanus* (L.) and ash, *Fraxinus excelsior* (L.), with a rather clearer forest floor owing to the attention of foresters. However, there is much variation, and other areas range from large, old beech, *Fagus sylvatica* (L.), to impenetrable blackthorn, *Prunus spinosa* (L.), scrub.

Wytham is an island of woodland surrounded by agricultural land and urban areas. While many tits must breed in the surrounding areas it is evident that movement in and out of the wood is limited and to some extent the woodland population can be considered a closed one.

Methods

Each nest-box was visited at least once a week during the nesting season; since the great tit lays one egg per day, it was possible from such visits to get the date when each

clutch was started and completed. Every great tit nest was visited each day from the eleventh day after completion of the clutch until the first young hatched. Thus the date when each brood hatched was known.

On the day of hatching some of the broods were artificially altered in size. For example, if two broods of nine young hatched, three young might be transferred from one brood to the other, making one brood of six and another of twelve. The down of transferred young was dyed with gentian violet, which was normally visible for at least 10 days. This was done mainly to ascertain whether the foster parents discriminated in any way against the strange chicks; they did not. The reason for manipulating the size of broods was that when studying survival of the young in broods of different sizes, Lack, Gibb & Owen (1957) had very few data on the broods of above the normal size. To give some idea

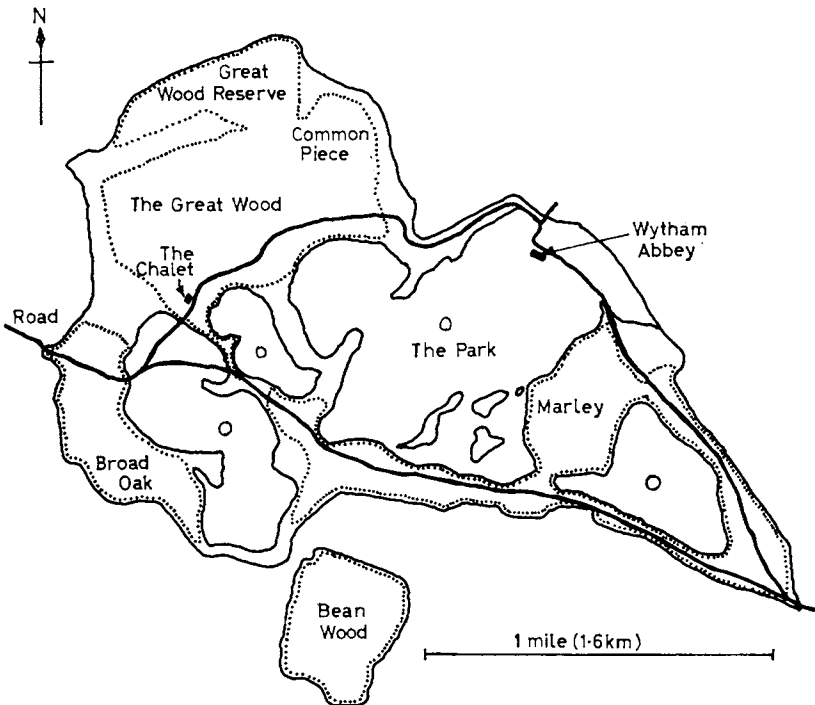


FIG. 1. Wytham Wood. The areas enclosed by dotted lines are those in which there were nest-boxes during this study. Areas marked with an 'O' are open habitats, either fields or young plantations.

of the extent of this operation, some half to one-third of the broods were used for manipulation (excluding late broods); virtually all broods of eleven young or more were artificial.

The young birds were weighed on the fifteenth day after hatching and their weights were recorded against their ring numbers. Thereafter the nests were not visited until well after the time at which the young should have flown (about the nineteenth to twentieth day after hatching) to avoid any possibility of causing the young to leave the nest prematurely. It was nearly always possible at the final visit to ascertain whether the young had fledged successfully or whether they had been attacked by a predator.

From 1961 onwards the females were caught on the nest at night when they were roosting with the young and their age was determined by plumage characteristics.

Once the young have left the nest they can usually be traced for a day or two, but then they go up into the leaf canopy and are difficult to trap. It is not until the autumn that it is easy to catch many of them. By this time they are fully independent of their parents, have undergone their first body moult (though they retain most of their juvenile flight feathers) and do not tend to be in family parties.

Trapping was done to bait (sheep's fat) and an effort was made to keep the food provided to a minimum so as not to assist the birds' survival. In very hard weather bait was not put out. Trapping was originally done in wire funnel traps, but latterly mist nets have been used since they probably catch a more representative sample than is caught in traps. In the winters of 1960–61 and 1962–63 it was difficult to catch birds at bait, owing to the birds' feeding heavily on beech-mast, and most were caught by using nets under the beech trees. The result is that trapping efficiency (as measured by the proportion of the total population trapped) varied markedly from year to year.

Few birds were found roosting at night in the boxes, apparently because much of Wytham contains small, natural holes which the birds prefer to larger nesting boxes. This is in contrast to findings in plantations (with very few natural holes) in Holland

Table 1. *Estimates of total population of great tits in Wytham, 1959–64*

	Winter				
	1959–60	1960–61	1961–62	1962–63	1963–64
Total no. birds trapped	283	538	394	371	300
Total no. birds found roosting	26	44	20	–	–
No. birds found roosting which were also trapped	12	11	15	–	–
Population estimate* based on roosting birds	613	2152	525	–	–
No. birds caught breeding	63	198	152	160	267
No. birds breeding also caught in previous winter	44	66	90	45	109
Population estimate* based on breeding birds	405	1614	665	1319	735

* Population estimates made by Standard Lincoln Index calculation without use of correction factors.

(Kluyver 1950). By examining the proportion of the roosting birds that were also trapped in the winter it was possible to estimate the total population using a simple Lincoln Index calculation. However, it was discovered that the females breeding in the boxes the following summer could be used for this, with the advantage of a much larger sample. The details are given in Table 1.

Comparison of Marley population with those elsewhere

It is important to know how much the variations in a local population, such as that in Marley, reflect the population changes over a much wider area. Fig. 2 shows the number of breeding pairs of great tits since 1947 in Marley, in the Forest of Dean, Gloucestershire, and at the Hoghe Veluwe, near Arnhem, Holland. These latter populations have been studied by Dr Bruce Campbell (*in litt.*) and Dr H. N. Kluyver (*in litt.*) respectively. The Forest of Dean is some 50 miles to the west and the Veluwe some 300 miles to the east of Wytham; all three areas are within a degree of latitude of each other.

If the populations are compared merely to see whether they varied in parallel there is not a striking resemblance in the first part of the study period though there is in the

second. However, in most of the years when one population rose and another fell the variations were small. In the last 8 years, with the exception of Marley in 1959–60 and Veluwe in 1962–63, the three populations have fluctuated similarly, and it was during this period that the two very high levels of population were reached. It may be added that the population in the Great Wood Reserve in Wytham dropped from twenty-two pairs in 1959 to twenty-one pairs in 1960 and thus it is possible that Marley was not, in this year, representative of Wytham as a whole.

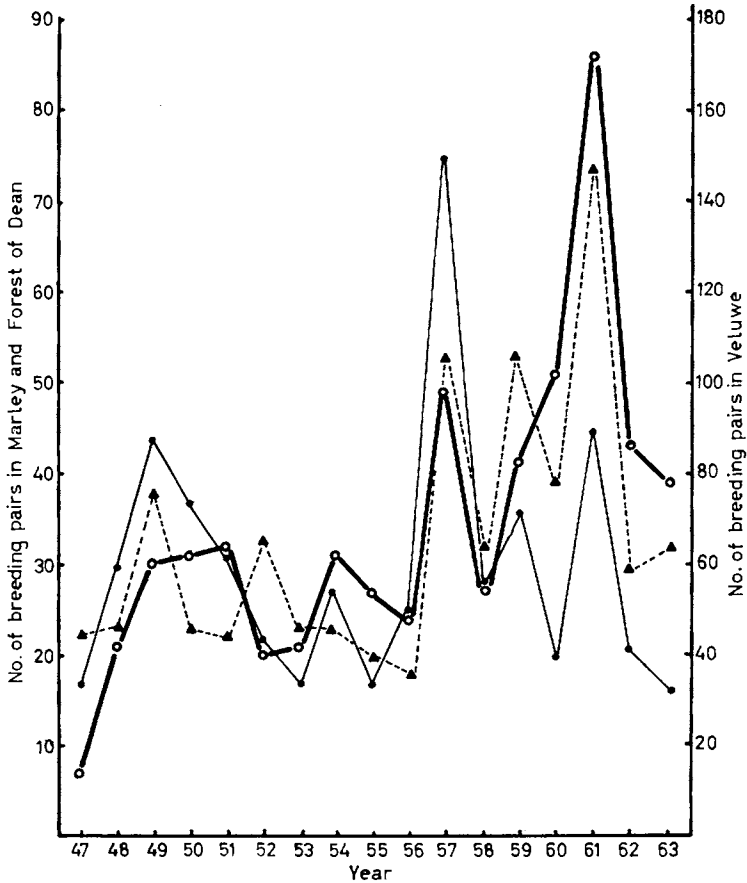


FIG. 2. Great tit: comparison of fluctuations in three nest-box populations. Note that the scale is different for the Dutch population (▲) (shown on the right vertical axis). ○, Marley population; ●, Forest of Dean population.

In spite of the minor variations between the populations, it is clear that the numbers of tits in each area have in general fluctuated in a similar manner. Probably, therefore, the numbers recorded are, within limits, indicative of what is happening over a large part of western Europe.

There is also a close correlation between the populations of great and blue tits in Marley (except in 1963—see discussion below), see Lack (1964, Fig. 3). Hence in general the two species have been affected in a similar way by whatever controlling factors are involved.

Movements of Wytham tits

Cramp, Pettet & Sharrock (1960) have shown that there are, from time to time, large-scale movements of tits in Europe. Sometimes these extend to Britain, but it seems probable that most of the birds involved in these movements are of continental and not British origin.

The writer hopes later to publish an analysis of the movements of tits but there are a few points which affect some of the arguments in this paper. Firstly only very few of the Wytham tits moved further from the wood than adjacent urban areas during the winter. Some of these emigrants are known to have returned to the wood the following summer to breed. Indeed some of the birds appear to be daily visitors to gardens for food, returning to roost in the wood at night. Great tits are known to fly up to 3 km and back daily to feed in German towns (Krätzig 1939) and there is one record of a 2 mile (*c.* 3 km) flight near Oxford. Hence many of the Wytham-ringed tits recovered outside the wood are probably only birds that left the wood each day to feed.

Movements within the wood seem to be very similar to those found by Kluijver (1951). In Holland, more birds settle to breed within 800 m of their birth-place than further away, and most do not wander more than 800 m from their roosting place in the winter. In Wytham, the only important exception is that when there is a crop of beech-mast some birds, particularly young ones, travel greater distances to feed on it. The different behaviour of the old and young birds in this respect probably causes bias in the measurement of the proportions of juveniles to adults trapped during the winter.

Variations in the breeding population and the erection of nest-boxes

The nests of species that breed in holes are safer than those of birds which breed in the open. In 1960 H. Mayer-Gross (*in litt.*) studied the nesting success in Wytham of many species which are not hole nesters. He found that only 12% of the nests were successful, most of the rest being taken by predators. In that year 75% of the nests started in nesting-boxes were successful. These figures do not, of course, reflect the production rates correctly, since a bird that loses its nest will have another attempt and perhaps the majority of the open-nesting species will successfully raise one brood in the course of the summer. The disadvantage of breeding in holes is probably that such a site is often difficult to obtain in competition with other birds.

J. A. Gibb put up 100 nest-boxes in Marley in the winter of 1946–47, and a further 100 in the winter of 1949–50, and there were always many more boxes than there were breeding pairs of tits. There is a tendency for most woodland to be well-managed in England today and for most of the dead wood, with holes, to be removed. Even in the more poorly-managed and therefore more natural parts of Wytham, such as Marley, forestry was practised in the last century and hence most of the trees are relatively young compared with those in primaeval woodland. In forestry plantations it seems likely that the erection of nest-boxes will result in a higher proportion of the tits finding suitable nest-sites, but precisely how much effect the erection of nest-boxes has on the potential breeding population is not known. In Marley there are about three boxes per ac. This is well below the number of holes that would be found in an area of primaeval woodland.

There may have been more pairs of tits than nesting sites in some parts of Wytham in 1961, but it seems unlikely that the number of breeding pairs in Marley has ever been affected by such a shortage. Hence it is safe to conclude that nest sites have not limited the population there. Kluijver has shown that the great tits breeding in his study areas may need two boxes per pair for successful breeding, one for the first brood and one for

the second. However, the birds in Marley do not appear to need more than one box; practically none of the birds roost in the boxes, and extremely few of the Wytham birds have second broods (see later).

Great tits are dominant to blue tits when the two species come into competition for nest-sites, and since in the year of peak population (1961) there were enough boxes in Marley for the blue tits to increase by the same proportion as the great tits, there can be little doubt that there were enough boxes for the great tit. In contrast, nest-sites were scarce in the Great Wood Reserve in 1961. This area had had nest-boxes for the three previous years and they had not been fully occupied. In 1961 the great tits in this area, as in Marley, showed a 60% increase over 1960 but the blue tits increased by only 28%. Hence while great tits may not have been short of nest-sites blue tits probably were. The Great Wood Reserve has about 1.5 boxes/ac (*c.* 4/ha, as compared with 3.0, or *c.* 7.5/ha, in Marley) and at least 117 nests were started in 103 boxes. As soon as one nest was taken by a predator, another was started in the same box. Nests were also built on top of each other, suggesting that one pair were successful in evicting another; this is normally very unusual. Presumably the blue tits also found it difficult to find natural holes at this time. It is not known what happened to the birds which did not find nest-sites. Moving to other parts of the wood would not have helped, since the position was similar in the other nest-box areas except for Marley. Moreover the data in the following paragraphs strongly suggest that the tits do not wander far in search of nest-sites. The great increase in the Marley population could not therefore have been due to immigrants which were unable to find nest-sites elsewhere.

On 5 April 1961, sixty-one boxes were put up in Bean Wood, an outlying, previously unboxed, area of some 40 ac (16 ha) on the south side of Wytham. Within 11 days of the boxes being erected, twenty-five of them contained nests with eggs and occupation of the others followed rapidly. Only three boxes were not used. The average date of the first egg of twenty-one pairs of great tits in Bean Wood was 20 April, actually a day earlier than in Marley! Also, although the sample was small, there was little difference between the proportions of young and older birds breeding in Bean Wood and in the rest of Wytham. Thus the birds breeding in these newly erected boxes were not just wandering juveniles in a year of high population. Two of the first-year birds were already ringed, both having been caught at the closest trapping site to Bean Wood in the previous winter. Had the birds been wandering, more of them should have been ringed, since it is believed that about a quarter to a third of the tits in Wytham were caught during the winter. Many tits were heard singing in the wood on the day that the boxes were erected and were presumably holding territories. Presumably those birds that bred in the boxes either had not previously found a nest-site or else had had a less suitable one.

Hence the birds in Bean Wood did not have suitable sites, yet did not move into areas where there were nest-boxes, for instance Marley. Presumably if boxes had not been put up, at least some of these birds would not have succeeded in breeding. Hence one of the factors limiting the tit population in planted woods in Wytham could be the number of nesting sites available to the birds. It does not follow, however, that the tits are ever limited by nest-sites in truly natural (*primaeval*) woodland, a point requiring study elsewhere. It is also very unlikely that the Marley population was ever limited by nest-sites 1947–63, or that it acts as an overflow area which absorbs homeless birds from elsewhere. The latter point is also supported by the fact that the birds breeding in Marley in 1961 had been trapped in or near to Marley in the previous winter and not elsewhere.

Hence in modern British woodland the erection of nest-boxes may lead to more

successful breeding, but the Marley population during this study has been limited by something other than nest-sites.

Survival of the young after they leave the nest

With the exception of a few large broods (particularly in 1961), it was unusual for many blue or great tit chicks to die in the nest in Wytham unless they or their parents were attacked by predators. Most of the deaths occur at the beginning of the nestling period, and usually affect the last young to hatch. Losses of nestlings are much greater in gardens and coniferous woods (see later, and Gibb & Betts 1963).

Most of the mortality of the young tits occurs after they leave the nest. As mentioned, after this time the young birds become extremely difficult to study, and it is not until the leaves start falling from the trees (November) that the birds can be caught again in large numbers. The results of the trapping in winter show that some classes of young birds (for example the heavier rather than the lighter young) are recovered* in much higher proportions than others. Trapping biases could not produce such results; therefore, either the birds from the classes that are recaptured in lower proportions are dying in greater numbers or they are leaving the wood.

Kluijver (1951) has suggested that the later young to hatch have a greater tendency to emigrate. However, his evidence is far from conclusive and he notes that the German and Swiss recoveries do not support it. The late young in the Dutch studies are mainly in pinewoods, and Kluijver showed that there is more wandering from pinewoods than from oakwoods. In any case Kluijver's late young are not really comparable with the Wytham ones since they are from late second broods, much later than most young found in Wytham.

Those birds that are recovered outside Wytham appear to be a random sample of those that are alive in the wood, not of those that are missing. There is no evidence that the surviving young that were trapped did not come at random from the broods of their class.

Lastly, most of the survival figures are presented in terms of the percentage of the young recovered from particular classes. These percentage figures should be used for comparison only with other percentages from the same year, because trapping efficiency varied from year to year (due partly to differing conditions of both the weather and the wood, and partly to the writer's increasing knowledge of the wood and of trapping tits). Therefore the figures are not necessarily comparable between years, although the figures in Table 1 could be used to obtain some idea of the overall survival each year.

THE BREEDING SEASON

Period of food abundance

Following Lack (1955) and Kluijver (1951), the mean date of the laying of the first egg by each pair has been taken as the measure of the date of the breeding season. As shown by Gibb (1950), the tits lay their clutches at a time which will result in many of their young being in the nest when food is most abundant. Both blue and great tits feed their young largely on the caterpillars on oak trees. These insects are being studied in Wytham by Professor G. C. Varley and by G. R. Gradwell (*in litt.*) who kindly made their data available.

* The term 'recovered' as used in this part of the paper is not quite the same as that in normal bird-ringing usage. Here a recovered bird is one that is known to be alive at least 3 months after fledging; it is really equivalent to surviving. It is believed that all the young that reach this stage stand a more or less equal chance of further survival with all the other young birds.

Fig. 3 shows the dates of 'half-fall' of the most abundant species of caterpillar, the winter moth *Operophtera brumata* (L.), in all years of the tit study except 1947, when no observations were made. The 'half-fall' is the date by which half the larvae have fallen to the ground, where they bury themselves and pupate. Gibb (in Lack 1955) showed that the half-fall of the winter moth was 1 day earlier than the peak abundance of all species, which he measured by the rate of fall of their frass (excreta). Fig. 3 shows that the dates on which the broods of great tits in Marley were, on average, 11 days old* show some correlation with the data for the half-fall of the winter moth, although the spread of dates when the tit broods were 11 days old (as shown by the 'boxes' in the figure) is considerable. Hence, while caterpillars are most abundant at this time, half the winter moth larvae have already disappeared, and thereafter food will rapidly become sparser. It

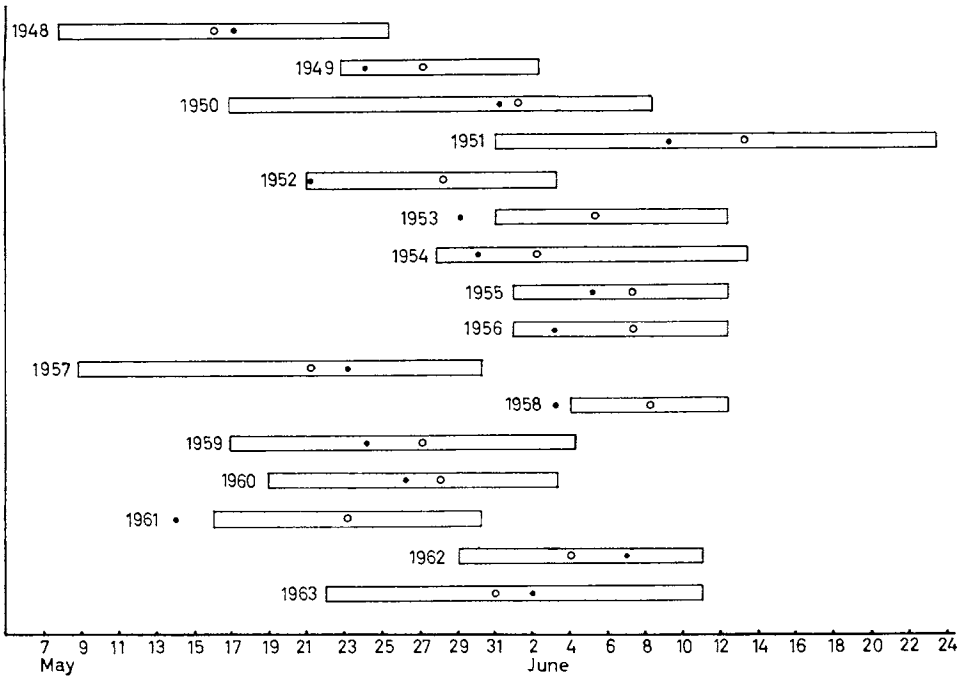


FIG. 3. Breeding season of great tits in Marley in relation to time of abundance of winter moth. ○, Mean date of great tits being 11 days old (box shows spread of dates); ●, date of 'half-fall' of winter moth.

does not necessarily follow that the day on which the maximum amount of food is taken to the nest is the day on which the parent birds have to search hardest for food. Earlier there are more caterpillars, but they are smaller and perhaps harder to find and provide less food when found; later, the fewer caterpillars are larger and more valuable as food.

Hence, though the evidence is suggestive, it is not possible to prove with certainty that all the tits are breeding at the most opportune time with respect to their food supply, though some certainly breed close to that time. This point will be covered more fully in the discussion.

* The eleventh day was chosen solely because it is the day on which Betts (1955a) observed the highest feeding frequency. Since the food items are larger later in the nestling period, feeding frequency and maximum amount of food are not precisely correlated.

Temperature

Tollenaar (1922) and Kluijver (1951) have shown that the breeding season of the tits is closely correlated with the spring temperature. Following Kluijver, Fig. 4 shows for the period 1 March to 20 April the warmth average (equal to day-degrees C—calculated by summing the mean temperatures for each day), plotted against the mean date of the first egg in the year. There is a clear, though not very close, correlation between the temperature and the date of breeding. That the correlation is not closer is due partly to the method of analysis; since the mean date of first egg has varied by about a month, the temperature over a fixed period is not a satisfactory way of measuring the earliness of the spring, since in early seasons, e.g. 1948, the birds were all breeding before the end of the period used for the temperature record, and so could not have been influenced by the later temperature concerned. Indeed, since a tit needs about 4 days to produce an egg (Kluijver

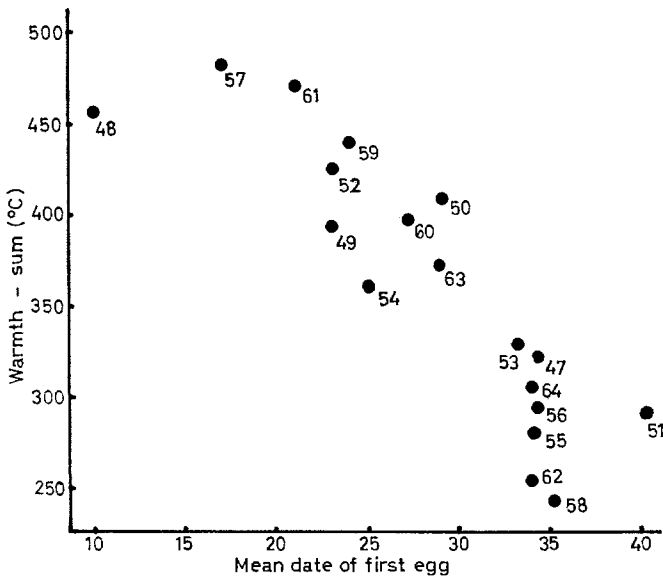


FIG. 4. Great tit: date of breeding in Marley in relation to spring weather. Date of breeding is the mean of the dates of the first egg (1 April = 1, 5 May = 35) laid by each pair in each year; the index of spring weather is the sum of the mean of the maximum and minimum temperatures (°C) for each day from 1 March to 20 April.

1951) many of the birds breeding in 1948 were hardly influenced by any April weather at all. Early April was not warm in this year and so the warmth sum for 1948 appears relatively colder than the actual period which affected the breeding season of the tits. Again, in 1958 there was an exceptionally fine February, and it seems possible that this caused the birds to breed earlier than would have been expected from the March temperatures.

However, the breeding season of the tits can be fairly closely correlated with weather in March and early April and perhaps also in February. The times of appearance of the caterpillars on oaks vary in parallel, and thus are available to the tits for their young earlier in a warmer spring than in a cold one. It seems possible that, as Lack (1954) suggested, the tits come into breeding condition primarily in response to the increase in day-length during the spring, but that their response is modified by temperature so as

to bring them into breeding condition at such a time that their young will be in the nest when the caterpillars will be most numerous. However, it is not clear in what way the tits respond to temperature. It seems likely that they do not do so directly. Great tits kept by Suomalainen (1937) in continuous illumination during January and February came into breeding condition (as judged by gonad size), while other tits kept in natural day-length did not. One half of each of these two groups was kept at around 0° C and the other at 15–19° C. The temperature made no apparent difference to gonad size and hence temperature, at that time, probably has no direct effect in bringing the birds into breeding condition in the wild state.

In Germany, Löhrl (1957) has shown that the warmer the weather in April the earlier the collared flycatcher, *Ficedula albicollis*, breeds. The collared flycatcher is a migrant and does not arrive in Europe until late April, and yet its time of breeding is still affected by the temperature on the breeding ground before it gets there. Here the collared flycatcher cannot be responding directly to temperature, but it may be to some phenomenon such as the opening of the leaves or the number of insects available, which may be directly correlated with the temperature of the preceding period. The great tit may well do the same.

Table 2. *Age of female great tits in relation to date of laying*

	Age of bird (years)	No. of birds	Mean date of first egg (April)
1961	1	122	22.4
	2	19	17.7
	3	15	17.8
1962	1	52	33.2
	2	40	32.3
	3	12	30.2
1963	1	54	30.0
	2	32	26.7
	3	28	26.4
	4	8	26.1

The date is counted from 1 April, e.g. 33 = 3 May.

Age of breeding

It is known that, in many species, females breeding for the first time lay slightly later than older birds. For most species these differences have been shown only between birds breeding for the first time and birds that have bred before. However, in some species, e.g. the yellow-eyed penguin, *Megadyptes antipodes* (Hombron & Jacquinet) (Richdale 1957), it is known that the average laying dates become progressively earlier over at least the first 3 years of breeding.

Kluijver (1951) has shown that second-year great tits lay, on average, 2.1 days earlier than those that are breeding for the first time. In addition Kluijver had data for eight 3-year-old birds and these bred 3.8 days earlier than his 2-year-old birds. Comparable data are available for the Wytham great tits only since 1961. Table 2 shows that the first-year birds bred on average 4.7, 0.9 and 3.3 days later than the 2-year-old birds and 3-year-olds 0, 2.1 and 0.3 days earlier than 2-year-olds.

The difference in the date of laying of the different age groups will modify somewhat the mean date of laying of the whole population in different years. If the year is one when there is considerable increase in the breeding population, there will be proportionately more young birds present than in a year when the population has decreased.

However, the greatest effect that this is likely to have had on the mean date of laying is to alter it by 1 day either way.

It is not known whether the age of the males influences the date of laying. This could happen if the older males courted more vigorously or started earlier than the younger males and so brought the female to the point of breeding earlier. Unfortunately the data on this point are not available for Wytham. Kluijver notes that he could find no such effect.

Habitat

Lack (1955, 1958) showed that the tits breed at different times in different habitats, in particular that blue and great tits breed earlier in scots pine, *Pinus sylvestris* (L.), than in corsican pine, *P. nigra* (Arnold), and earlier in gardens than in woodland. In both cases the birds bred first in the more open habitat.

Table 3 shows the mean dates of laying in Marley, the Great Wood Reserve and the

Table 3. *Mean date of laying in different areas*

	Mean date of first egg (1 April = 1)		
	Marley	Great Wood	Gardens
GREAT TIT			
1958	35.1	35.8	31.6
1959	23.9	21.2	17.6
1960	27.1	23.0	23.0
1961	21.0	20.1	15.7
1962	34.5	32.1	—
1963	29.7	28.6	—
BLUE TIT			
1958	34.3	30.7	32.0
1959	21.8	18.4	22.5
1960	19.9	18.9	20.8
1961	18.7	12.4	17.8
1962	32.2	31.0	—
1963	32.4	30.6	—

The date is counted from 1 April, e.g. 33 = 3 May.

gardens at Oxford. The great tits in gardens were the earliest by an average of 3 days over those in the Great Wood Reserve and nearly 5 days over those in Marley. Lack showed that blue tits bred about 2 days earlier in gardens than in woodland, but at Oxford they started about the same time as the birds in Marley and about 3 days later than those in the Great Wood Reserve. The tits laid consistently earlier in the Great Wood Reserve than in Marley (Table 3). The only exception was in the Great Wood Reserve in 1958, perhaps because this was the first year that boxes were provided.

There is some evidence that the caterpillars in the Great Wood Reserve are a little earlier than those in Marley, the average difference being about 1 day (Gibb, in Lack 1955). The only obvious difference between the two areas is that the former lies a little lower, being on average about 250 ft above sea-level whereas Marley is about 350 ft above sea-level. However, the long series of data for Marley, which runs up the side of a hill, shows no variation in date of laying with altitude.

The Great Wood Reserve would seem the best habitat for tits which has been examined during this study. Evidence provided later shows that the clutch-size is highest here and

that nestling mortality is lowest. In addition there appears to be a higher density of blue tits here than in Marley.

If the Great Wood Reserve is a habitat with a good food supply then the birds might breed earlier there because they can get into breeding condition earlier. The earlier breeding of the tits in scots pine than in corsican could also be explained on this basis since Gibb (1960) showed that there is usually more insect life in scots pine, endemic in northern Europe, than in the introduced corsican pine.

However, this does not explain why great tits should be able to breed earlier in gardens whereas blue tits do not do so, and a good explanation has not been given.

It is of interest to note that Kluijver (*in litt.*) tried to influence the breeding season of the great tit in Holland by putting out trays of mealworms, *Tenebrio molitor* L., for them in early spring. While the birds ate them in the winter they ignored them in the spring and concentrated on their natural foods. This suggests that the birds did not need the extra

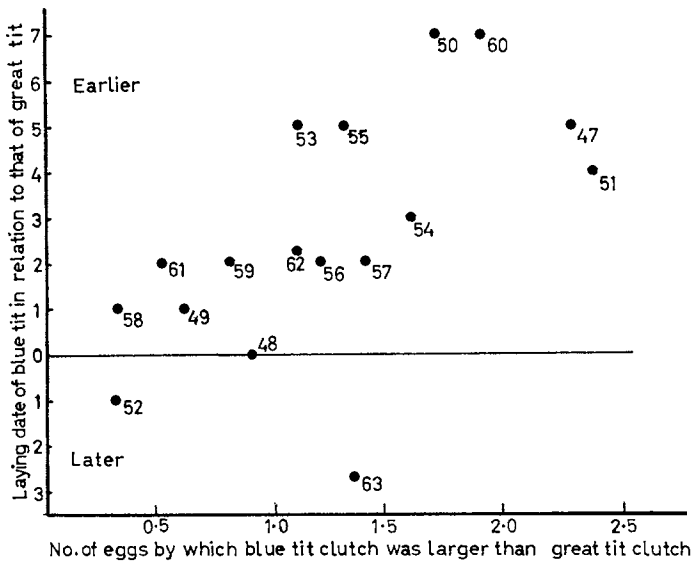


FIG. 5. Relation between time of breeding and mean clutch-size of great and blue tits in Marley in different years.

food in the spring and thus the supply put out by people in gardens at this time may be similarly unimportant.

Specific differences

Lack (1955) has shown that, in woodland, the blue tit lays a little earlier than the great tit. This was explained by Gibb (in Lack 1955) on the grounds that, as the blue tit lays more eggs than the great tit, unless it started earlier it would not be as well-timed as the great tit to the period of caterpillar abundance.

It seems unlikely that this is the whole story. Fig. 5 shows the relationship between the mean dates of laying and the mean clutch-sizes of the two species, based on all the Marley data for each year. The date on which the blue tits started to lay in Marley has varied from about 7 days earlier than the great tit to about 2 days later. The clutch of the blue tit has varied from 0.3 eggs to 2.4 eggs more than that of the great tit. Those blue tits

which lay up to a week earlier than the great tits, do not lay clutches which are seven eggs larger. The relationship is nearer to a third of an egg larger for each day earlier.

It will be shown later that it is advantageous for the great tit to breed as early as it can; it is likely that this also holds true for the blue tit. Therefore the differences in date of laying between the two species are due to some factor which is influencing one species more than the other, or to which they react differently.

Such a factor is unlikely to be one that is affecting Marley as a whole, such as the weather, nor can it be due to some delaying factor such as competition for nest-sites, since there has always been a surplus of nest-boxes in Marley. Since, except in 1962–63, the numbers of the two species have always fluctuated in parallel, it is likely that they will have been affected similarly by density-dependent factors. There is no sign that the difference in laying dates of the two species is more marked in early or late seasons.

However, Hartley (1953) has shown that, in most months of the year, blue and great tits feed in different niches in the wood, the great tits feeding much more on the ground, especially in February and March. But 'in April came a sudden change. The great tits had now gone upwards, leaving the ground and now did not differ in their feeding level from the blue tits'. He did not give the precise date at which the change-over occurred; presumably this varied from year to year. Betts' (1955b) study of the gut contents supported Hartley's observation. It is not until April that much of the great tit's food comes from the twigs, buds and leaves of the trees and then only 10% compared with over 90% for the blue tit. In May and June 70% and 80% respectively of the food of the great tit comes from the twigs, buds and leaves.

Perhaps the food which the two species take just prior to breeding is the factor which affects the time at which they breed in relation to each other, in some years one species having a better food supply than the other. In one year (1962–63) the blue tit population rose while the great tit population dropped slightly. There were thus relatively more blue than great tits in this year, and therefore possibly relatively less food for blue than for great tits. 1963 was also the year when the blue tits in Marley bred latest in relation to the great tits. 1963 was also the only year (out of six) when the great tits started to lay, on average, before the blue tits in the Great Wood Reserve.

CLUTCH-SIZE

While several factors will be shown to affect the size of the great tit's clutch to varying extents, the average clutch in Wytham is usually about nine or ten. Lack (1947) developed the theory that the clutch-size of birds was adapted to the largest number of young which could be raised successfully; Lack *et al.* (1957) gave some evidence that this was true for the great tit. It is now possible to examine the situation further.

Gibb (1955) showed that the larger the brood the more often the parents feed the young, but they are not able to increase the rate of feeding in proportion to the increase in the number of young. 'A member of a small family therefore received more food per day than did one of a larger family' (Gibb 1955). This situation has been recorded for many species of bird (e.g. Moreau 1947; Kendeigh 1952). As might be expected, the result is that the young of the large broods are lighter in weight; Table 4 shows the range. (It will be shown below that young in later broods are lighter than those in early ones and that brood-size decreases with season. Hence large broods occur most commonly when young tend to be heaviest and so the weights in this table are biased in favour of the large broods and the difference, at any given time of the season, is actually greater than that shown.)

Table 4. *Great tit—weight in relation to brood-size*

	Brood-size																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
1958																	
No. of broods	1	-	-	3	3	8	5	2	3	3	7	5	3	-	-	-	-
Mean of mean weights (g)	17.0			19.4	20.2	20.1	19.8	19.1	18.6	18.8	17.8	18.5	16.2	-	-	-	-
1959																	
No. of broods	-	1	3	12	12	13	10	6	13	8	9	11	6	1	-	-	-
Mean of mean weights (g)	-	18.5	19.1	19.8	19.9	19.6	19.6	19.2	19.0	18.7	18.6	18.3	18.2	16.0	-	-	-
1960																	
No. of broods	1	1	4	7	12	17	7	12	4	13	10	3	1	-	-	-	-
Mean of mean weights (g)	19.0	20.1	20.5	20.0	19.4	19.6	19.5	19.0	19.3	18.9	18.6	18.1	18.2	-	-	-	-
1961 (Marley)																	
No. of broods	-	1	4	4	6	7	5	9	3	-	3	8	9	-	-	-	-
Mean of mean weights (g)	-	19.9	18.9	19.4	18.4	18.3	18.5	18.0	17.5	-	15.1	17.4	16.9	-	-	-	-
1961 (rest of Wytham)																	
No. of broods	-	4	11	12	15	18	21	17	11	6	8	5	1	-	-	-	-
Mean of mean weights (g)	-	19.3	19.0	19.1	19.2	18.8	18.6	19.0	19.2	18.3	18.6	17.9	13.6	-	-	-	-
1962																	
No. of broods	2	2	8	10	25	19	14	21	16	11	10	3	1	-	-	-	-
Mean of mean weights (g)	21.3	20.0	19.1	19.1	19.0	18.5	18.5	18.2	18.3	16.9	16.6	16.5	18.4	-	-	-	-
1963																	
No. of broods	1	1	2	13	8	13	18	21	22	26	14	6	3	-	1	2	-
Mean of mean weights (g)	19.5	20.5	19.9	19.3	20.1	19.3	19.0	19.1	19.6	19.1	18.8	18.3	18.6	-	18.7	18.5	-

Brood-size here is the number of young weighed, except for Marley 1961 (where many of the large broods lost several young); there it is the total number of the young originally present.

In Wytham, omitting nests destroyed by predators, 90–95% of the young leave the nest successfully, regardless of their weight. Many of these young are caught during the following winter and analysis of these in relation to their weight (Fig. 6) shows that more of the heavy than of the light young survive. Hence proportionately more of the young from the smaller broods survive than those from the large broods. Although an analysis has not been made, heavy young are usually quite plump, and presumably some of their weight is fat which is available as a food store in the difficult period when the birds are learning to fend for themselves.

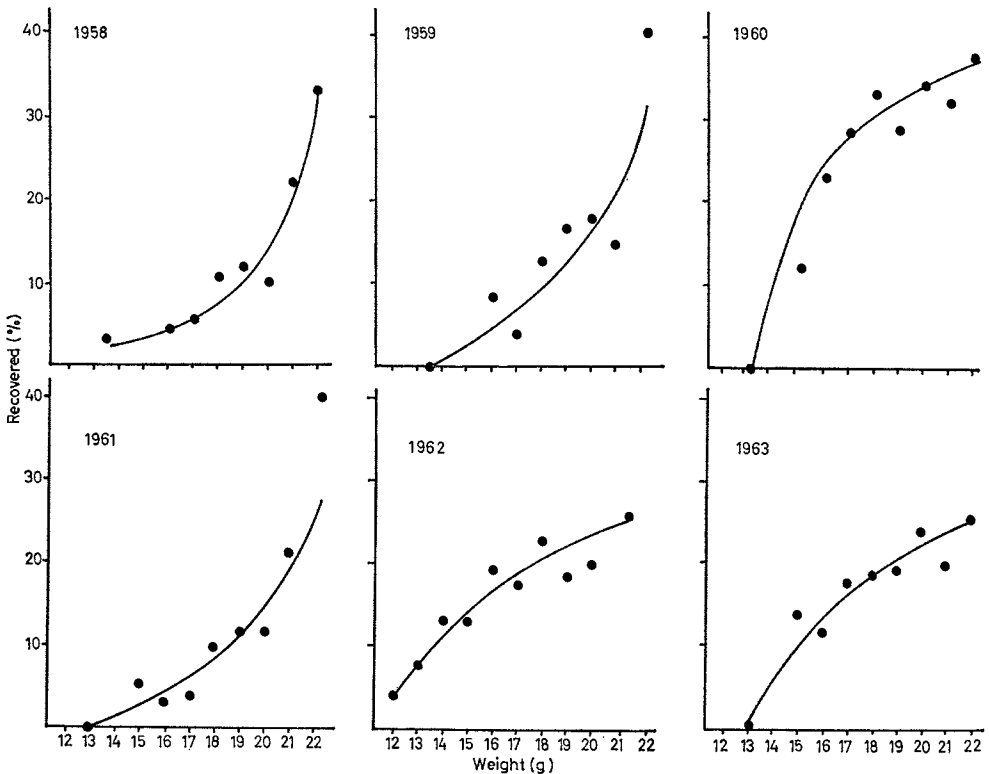


FIG. 6. Survival of great tits in relation to weight on the fifteenth day. Any bird which was known to be alive 3 months after fledging was counted as having survived. Owing to the very small numbers of recoveries of birds of 15 g or less, in most years information for the birds of 12–15 g has been lumped and presented as one point. Since the weights of the young form a normal distribution, data on the very light and the very heavy are fewer than those of the more average weights. The lines are drawn through the points by eye.

Table 5 shows the recoveries in terms of the number of surviving young per brood (the important measure from the evolutionary point of view). The large broods do not always produce proportionately more surviving young than those of normal size. Table 5 shows the survival rate in relation to brood-size for the blue tit, where the same holds true. The figures given here include broods that were taken in the nest by predators since predators tend to take larger broods (Table 6). (The reason for dividing the season into two halves will become apparent in the following section.)

There is little doubt that the large broods are taken more frequently by predators because they are hungrier and calling more. The predators are chiefly weasels, *Mustela*

nivalis, grey squirrels, *Sciurus carolinensis*, and great spotted woodpeckers, *Dendrocopus major*. The two mammals enter the box by the hole, the weasel being able to get through a hole large enough for a great tit, the grey squirrel having to enlarge it. The woodpecker provides additional evidence that it is finding the young by sound. It makes a hole into the box through one of the sides just at the level of the calling young, a little less than an inch above the level of the nest. It seems likely that it is gauging the level of the young by ear. In addition to the loss of the young about 20% of the females seem to be taken with their broods, thus increasing the disadvantage of raising a large brood, since these females will not get a further opportunity to breed.

Table 5. Recoveries of great and blue tits in relation to brood-size

	Brood-size	Great tit				Blue tit	
		No. broods	No. young	Recovered (%)	No. recovered /brood	No. broods	No. recovered /brood
1958	2-5	4	17	11.7	0.50	1	0
	6-8	16	109	12.5	0.87	9	0.44
	9-11	14	142	8.4	0.85	32	0.69
	12-14	12	153	6.5	0.83	6	1.67
1959	1-5	28	120	15.8	0.63	3	0
	6-8	42	286	13.3	0.90	27	0.59
	9-11	31	308	13.6	1.36	71	0.89
	12-14	21	264	7.5	0.95	16	0.47
1960	1-5	33	124	27.5	1.03	5	0
	6-8	36	257	25.7	1.83	22	0.74
	9-11	21	211	27.9	2.81	67	1.09
	12-16	12	152	30.3	3.83	37	1.49
1961 (All Wytham except Marley)	2-5	41	157	10.2	0.39	10	0.10
	6-8	67	467	8.6	0.60	80	0.28
	9-11	32	312	12.8	1.25	77	0.42
	12-15	8	100	8.0	1.0	8	0.13
1961 (Marley)	2-5	20	80	7.5	0.30	(The above entries (1961) are for Wytham incl. Marley)	
	6-8	28	179	6.7	0.43		
	9-11	9	91	3.3	0.33		
	12-13	17	212	1.9	0.23		
1962	1-5	38	168	13.7	0.61	5	0.25
	6-8	44	316	15.8	1.14	18	0.56
	9-11	50	494	12.8	1.26	73	0.67
	12-14	25	349	7.2	1.25	23	0.48
1963	1-5	16	70	20.0	0.88	1	0.00
	6-8	35	262	25.2	1.89	13	0.46
	9-11	75	742	15.4	1.52	85	1.20
	12	7	84	21.4	2.57	43	1.60
	13-16	14	209	12.4	1.86	34	1.12

Table 5 is biased in favour of the large broods. The great majority of the broods of eleven or more in the great tit are artificial in that, as mentioned earlier, the broods were increased by three or more young at hatching. These broods appear to be reared in a perfectly normal way by the parents. However, they differ from natural broods of the same size in that, had the parents laid a clutch of that size, they would either have had to start laying earlier (for which they might not have had enough food) or the clutch would have been completed later, and consequently hatched later, by 3 or 4 days. Such delay would have been accompanied by lower survival since, as will be shown later, the date of hatching markedly affects the survival of the young. Hence the young in these artificially

increased broods, had they been natural, would have hatched later and survived less well than the figures show by perhaps 15%.

Hence the commonest brood-size is that which normally produces the most surviving young. A larger brood results, on average, in fewer rather than more surviving young. Further, I think that the variations in clutch-size which will be demonstrated in the following section can also be looked at in this light.

Table 6. *Predation on great tit nests in Wytham in relation to brood-size and time of season, 1959-63*

1959						
Brood-size	Up to 13 May			After 13 May		
	No. nests	No. lost	%	No. nests	No. lost	%
3-6	9	0	0	25	1	4.0
7-10	23	0	0	14	3	21.4
11-15	17	0	0	20	5	25.0
1960						
Brood-size	Up to 15 May			After 15 May		
	No. nests	No. lost	%	No. nests	No. lost	%
2-5	13	1	7.7	20	3	15.0
6-8	24	2	8.3	34	5	14.7
9-14	28	5	17.8	21	6	28.6
1961						
Brood-size	Up to 10 May			After 10 May		
	No. nests	No. lost	%	No. nests	No. lost	%
2-5	22	2	9.1	33	7	21.2
6-8	43	0	0	43	9	20.9
9-13	35	6	17.1	26	6	23.1
1962						
Brood-size	Up to 23 May			After 23 May		
	No. nests	No. lost	%	No. nests	No. lost	%
2-7	31	1	3.3	42	5	11.9
8-10	30	3	10.0	26	4	15.4
11-14	20	3	15.0	19	4	21.1
1963						
Brood-size	Up to 26 May			After 26 May		
	No. nests	No. lost	%	No. nests	No. lost	%
0-9	70	0	0	23	4	17.4
10-16	65	2	3.1	4	1	25.0

Each year is subdivided so that approximately half the data will fall into each half of the season. Similarly brood-sizes are chosen so that similar numbers of nests will fall into small, medium and large broods. The data are biased in favour of large broods as the very late broods suffer the heaviest predation and most of these broods are small. In 1963, with very few losses, the season is not divided into two halves, but into main and late; all four losses of broods of 0-9 occurred after 15 June and were second broods.

FACTORS AFFECTING CLUTCH-SIZE

Date of laying

The size of the clutch becomes progressively smaller as the breeding season progresses, as demonstrated by Tollenaar (1922) and Kluijver (1951). In Marley the reduction in clutch-size is 0.09 eggs (S.E. 0.039) for each day later that breeding begins.

Gibb (1955) showed that the individual young in early broods are fed more often than those in late broods. This is presumably correlated with the food supply, which he showed was abundant for only 2-3 weeks, after which it rapidly diminished. The weight of the young decreases as the season progresses. This fact is partly obscured since brood-size decreases with season, and weight decreases with increasing brood-size. A regression

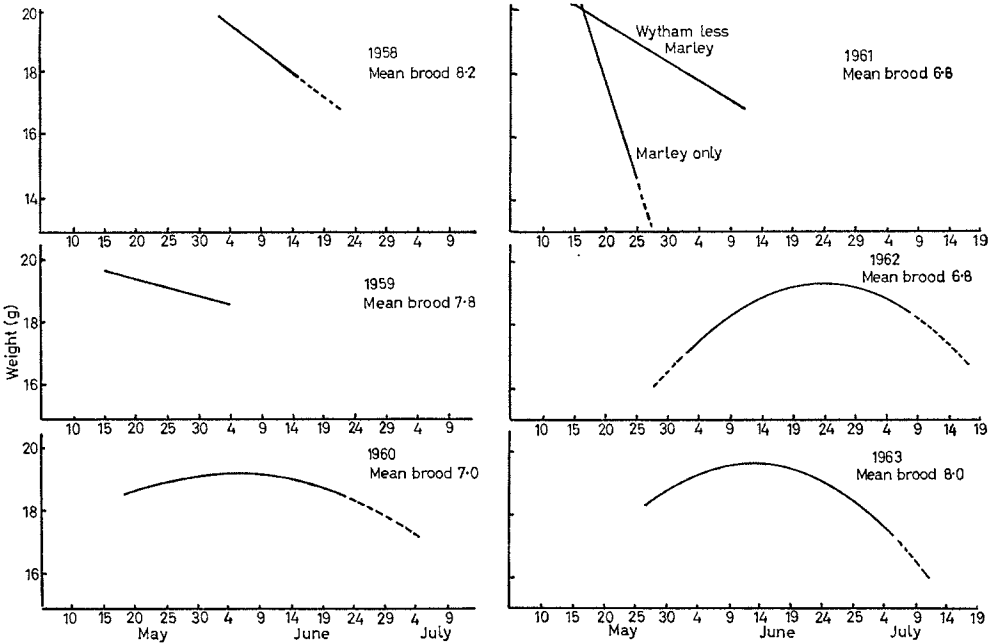


FIG. 7. Regression lines showing differences in weight of young great tits hatched at different times in the season. The weights are plotted against the date of weighing although, of course, they hatched 2 weeks earlier. The lines are dotted where there are particularly few data. The unusually low weights in the early part of 1962 were due to the very cold weather; the females had to brood the small young to keep them warm and so could not go and collect food for them; associated with this, weights were low and mortality in the nest was high (Table 8).

Table 7. Nestling mortality of great tits in relation to date of hatching, Marley, 1961, and all Wytham, 1962

Marley 1961			
Date of hatching	No. broods	No. young	Died (%)
3-6 May	3	28	0
7-8 May	9	76	9.2
9-11 May	26	202	10.4
12-14 May	13	83	34.9
15-19 May	2	14	64.3
All Wytham, 1962			
Date of hatching	No. broods	No. young	Died (%)
13-27 May	113	916	23.1
28 May to 17 June	27	200	9.0
18-30 June	5	28	39.3

analysis in which brood-size was allowed for, made by Dr J. F. Scott, showed that there was usually a highly significant reduction in weight as the season progressed, though the young in the earliest broods were also sometimes lighter than those a little later. The resulting regression lines are shown in Fig. 7. Even by rearing a smaller brood, the parents that breed later are not usually able to feed the young sufficiently well to produce young as heavy as those reared earlier in the season. Hence it seems clear that the reduction in clutch-size with date is an adaptation to a steadily worsening food supply for the young which reduces the chances of raising many well-nourished young.

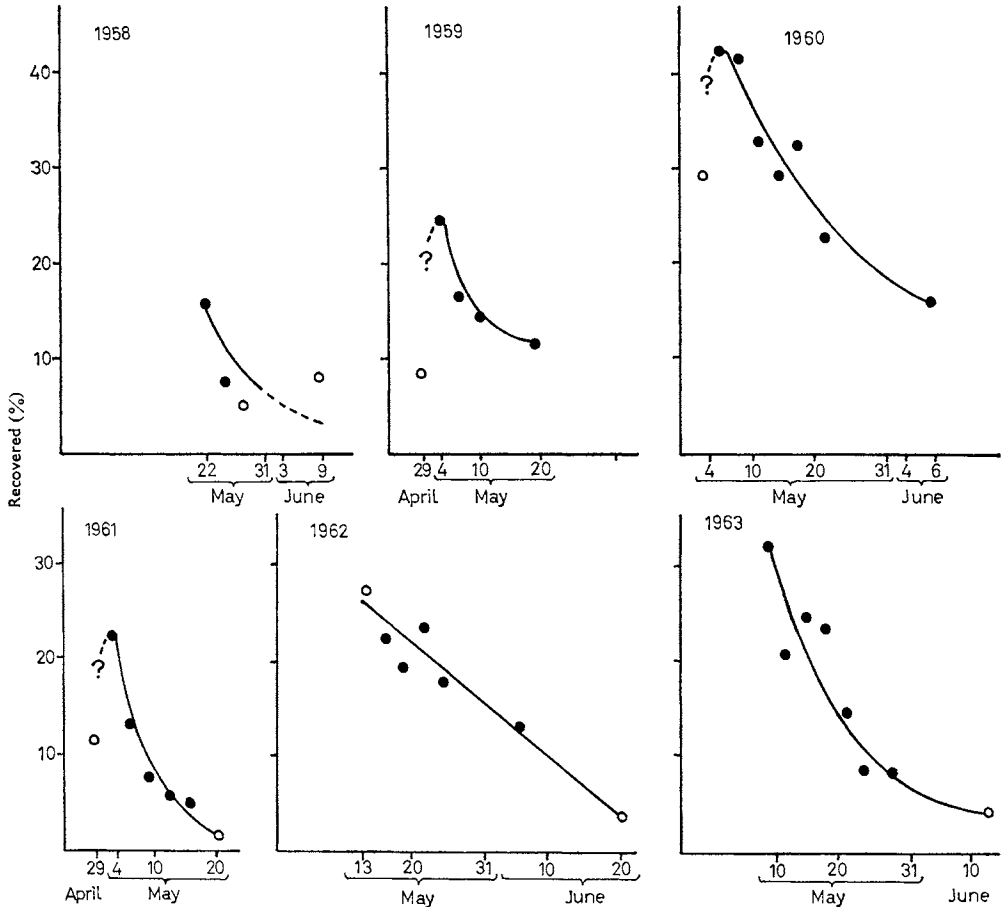


FIG. 8. Survival of young great tits in relation to date of hatching. Again survival means that the birds were known to be alive 3 months after fledging. Data are lumped into 3-day periods at the beginning of the season, but into longer periods at the end when there was less information. Points marked by open circles are based on less than five recoveries. Lines are drawn through the points by eye.

There is a higher proportion of predation in the later part of the season (Table 6). The young of the later broods are lighter and more noisy than the early ones, and this is probably the main reason that they are more vulnerable to predators. It is also possible that predators require more food at the time. In either case there will be selection for earlier breeding since it results in smaller losses of females and young in the nest.

There is some other evidence that the parents cannot easily raise their young later

in the season. Table 7 shows the mortality in the nest in relation to date of hatching in 1962 and in Marley in 1961; these are the two instances when more young than usual were lost during the nestling period.

Fig. 8 shows how rapidly the chances of survival for the young decrease from the start of the season. Since the figures are percentages and the earlier broods are larger than the later, the advantages of early breeding in terms of production of young are even more marked than is apparent from this figure.

As might be expected from the data in Fig. 8, there is some evidence that the weight of the chicks is less important to their survival at the beginning of the season than later. Hence while a 17 g young may stand an almost equal chance of survival with a 20 g one if it hatches at the beginning of the season, it has a much lower chance of surviving later in the season. This effect is particularly noticeable in 1962 when many of the early young were quite light, but they survived as well as the heavier young that were raised a little later.

Table 8. *Survival of young great tits in relation to the part of the season in which they hatched*

Year	First half of season					Second half	
	Early part		Remainder		Total	No. young	Recovered (%)
	No. young	Recovered (%)	No. young	Recovered (%)	Recovered (%)		
1947	27	7.4	48	14.8	12.9	88	6.8
1948	68	11.8	90	18.6	15.8	209	10.9
1949	46	8.7	231	9.1	9.0	200	7.0
1950	15	6.7	56	3.6	4.2	115	3.5
1951	22	0	51	7.8	5.5	83	7.2
1952	30	16.7	41	2.4	8.4	77	6.5
1953	39	15.4	46	8.7	11.8	89	4.5
1954	35	8.6	95	7.4	7.7	100	2.0
1955	19	5.3	59	3.4	3.8	100	8.0
1956	29	10.3	74	5.4	6.8	70	4.3
1957	28	3.6	89	6.7	6.0	99	4.0
Total	358	9.61	880	8.52	8.80	1230	6.42

Similar results are shown in Table 8 for the years 1947–57, though here, with many fewer data, the breeding season was divided into only two parts. It will be seen that, in general, the young survived better in the first half of the season, while in the two apparent exceptions the data were very sparse. There is no clear evidence that the very first birds to breed in the season are at a disadvantage. Table 8 also shows the success of the earliest broods compared with the rest of the broods in the first half of the season. Overall the survival from the earliest broods was the same as that from the others. Hence the survival figures show that there must be strong selection for breeding in the first part of the season and, in addition, that there is no clear sign that those that breed first of all are at either an advantage or a disadvantage. In 1962, but in no other year, cold weather forced the females to brood and not to feed the young and so caused high mortality and low weights among the early broods. This disadvantage was not enough to outweigh the advantage of early breeding and does not seem to occur at all frequently.

Density of breeding pairs

Clutch-size decreases as the population increases, as shown in Fig. 9. When the population doubles in size the clutch is reduced by 2.02 eggs (S.E. 0.39). In all 69% of the variation

in clutch-size can be accounted for by the effects of date of laying and density. It is difficult to provide evidence that this variation is an adaptive behaviour since feeding conditions and nesting success vary so much from year to year. However, in 1961, there was a considerable difference in the breeding densities in different parts of Wytham. The full reasons for this are not clear, but it may have been due partly to Marley having more than

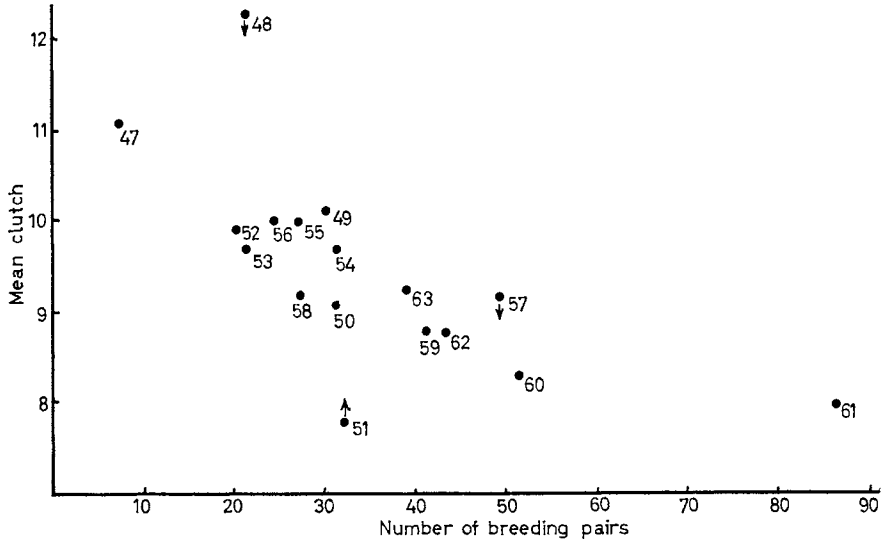


FIG. 9. Clutch-size of great tit in relation to density of breeding pairs in Marley. Arrows mark points which were particularly affected by the date of breeding, i.e. breeding was late in 1951 and clutch-size would have been larger if the birds had bred at the normal time, clutch-size would have been smaller in 1948 and 1957 if the birds had not bred so early.

enough boxes and Great Wood insufficient. There is no reason to suppose that in 1961 the initial food supply was poorer in Marley than in Great Wood, the caterpillar populations tending to be similar over large areas of woodland due to the aerial dispersion of the winter moth in its first instar.

In Marley mortality in the nest was abnormally high (for deciduous woodland) and this was markedly affected by brood-size (Table 9). Fig. 7 shows that in 1961 the

Table 9. *Nestling mortality of great tits in relation to brood-size, Marley, 1961*

Brood-size	No. broods	No. young	No. died	Died (%)
2-4	9	28	1	3.6
5-7	19	112	9	8.0
8-10	11	93	16	17.2
11-13	14	170	40	23.5

difference in weight between the early and the late young was much more marked in Marley than in the rest of Wytham. In addition breeding stopped earlier in Marley, there being a tendency for birds in other parts of Wytham to lay repeat clutches later than those in Marley. Not only did the young in the nest in Marley fare worse than those in the other parts of Wytham, but there was a significant difference in the survival after fledging between the young in the two areas (Table 10). Even comparing young of equal weight, survival was poorer in Marley than elsewhere.

The reason that the tits raised fewer young in Marley than in Great Wood could well have been that tits have greater difficulty in raising young at high than at low density, because there is less food per pair. I therefore suggest that the habit of laying fewer eggs at a higher density has been selected as a result of the individual birds producing, under these circumstances, more surviving young from small than from large clutches. This is in contrast to the suggestion of Wynne-Edwards (1962) that lower production at

Table 10. *Breeding success of great tits in Marley and Wytham Great Wood, 1961*

	Marley	Wytham Great Wood
Density (pairs/ac)	1.3	0.60
Mean weight of young on fifteenth day	18.0	19.0
Nestlings died (excluding those taken by predators) (%)	16.4	3.0
Broods taken by predators (%)	29	8
Fledged young recovered after 3 months (%)	6.6	12.4
No. young recovered per brood after 3 months	0.44	0.96

high densities is an adaptation which prevents over-population. The reduction in clutch-size is not nearly proportional to the increase in the number of breeding pairs, so that it is difficult to understand how the latter system works in the great tit.

Age of birds

Kluyver (1951) has shown that, on average, birds breeding for the first time have smaller clutches than older birds. Table 11(a) shows that this is also true for Wytham great

Table 11. (a) *Mean clutch-sizes of yearling and older great tits*

	All Wytham, 1961		All Wytham, 1961		Marley, 1961		All Wytham, 1962		All Wytham, 1963	
	No.	Mean	No.	Mean	No.	Mean	No.	Mean	No.	Mean
Yearlings	32	7.9	128	7.7	41	7.9	54	8.5	54	9.4
Older birds	24	8.5	77	8.3	24	8.1	93	9.1	100	9.8

No. = No. clutches; Mean = mean clutch.

(b) *Mean clutch-size and age of great tits in Wytham*

Age	1961		1962		1963	
	No.	Mean	No.	Mean	No.	Mean
Yearlings	128	7.7	54	8.5	54	9.4
2	18	8.5	43	9.0	33	10.0
3	14	8.3	12	8.8	29	9.7
4			5	8.2	9	9.7
5			1	8.0	2	9.5
6					1	9.0

tits. There does not seem to be any further change in clutch-size with further increase in age (Table 11b); rather, the opposite appears to be the case. Older birds breed slightly earlier than the younger ones, thus part of the difference in clutch-size will be due to this. However, the mean difference in laying date is not enough to account for all the difference in clutch-size.

In years of population increase, there will be proportionately more young birds in the population than in years when there has been no increase, since increases occur mainly when large numbers of young birds survive. Hence the reduction in the size of clutch at higher densities will be exaggerated by the higher proportion of young birds, particularly if the change in population is large. The reverse is also likely to be true, in that when the population decreases the proportion of older birds is larger. However, these effects are usually only very small, and unlikely to be greater than 0.2 of an egg.

The figures in Table 12 show that not only did the older birds produce a slightly higher percentage of surviving young, but since their broods were also larger they produced considerably more surviving young per brood. Presumably natural selection must favour the laying of a rather smaller clutch in the first year, since those individuals which do so must, on average, raise more young.

It seems unlikely that the time of year which is most favourable for the breeding of experienced adults would not also be the best time for the younger birds. The most reasonable suggestion is that the birds cannot get into breeding condition earlier, and that

Table 12. *Survival of young great tits in relation to age of female parent*

	1960		1961 (excluding Marley)		1961 (Marley only)		1962		1963	
	Year-ling	Older	Year-ling	Older	Year-ling	Older	Year-ling	Older	Year-ling	Older
No. hatched	160	234	489	359	278	194	349	745	476	875
No. broods	23	29	73	48	37	22	45	87	52	94
Mean brood	6.9	8.1	6.7	7.5	7.5	8.8	7.8	8.5	9.1	9.3
No. recovered	40	75	45	45	11	12	55	110	66	163
Recovered (%)	25.0	32.0	9.2	12.5	4.0	6.2	15.8	14.8	13.9	18.6
No. recovered per brood	1.74	2.59	0.62	0.94	0.30	0.55	1.22	1.26	1.27	1.73

An analysis of variance done by P. H. Leslie, on the above data, showed that the differences in survival between the two age classes were significant at the 5% level.

first-year birds, not being so experienced in collecting food, are unable to get into breeding condition as early as older, more experienced birds.

Habitat

Both Lack (1955) and Kluijver (1951) have shown that the clutch-size of the great tit is affected by the habitat in which the clutch is laid. The same is true for the blue tit (Lack 1955). Since the differences were consistent there can be no doubt that they were due to some aspect of the habitat itself. This argument is strongly supported by the fact that, in both studies, the largest clutches were found in rich oak woodland and the smallest in gardens or open parkland.

These variations in clutch-size can be explained only on the basis of some form of reaction of the bird to the environment. However, the food which the birds utilize for their young is not available at the time of laying so that the birds cannot be responding to this (see also below). Hence it seems more likely that the tits respond to the general appearance of the vegetation in some way, perhaps to the number of large trees in the surroundings or to some other indicator of what the later food supply will be like. It is conceivable, though not known, that those habitats, in which there was most food for the young, were also those in which there was more early spring food for the adults; if this were true then clutch-size could be affected adaptively by the food supply for the parents.

However, since the laying dates and clutch-size do not vary in parallel in different habitats, food supply cannot be the factor influencing both.

Many of the differences shown by Kluijver and Lack were for areas of woodland situated far apart, but even within the Oxford area there is a marked difference between the mean clutch-sizes found in gardens and in woodland (Table 13). These two areas are too close to be seriously affected by different local climatic conditions and are at the same altitude. The smaller clutches in gardens cannot be due to a higher density there, at least for the great tit, since the territory size seems to be about half as large again as that in Marley during the 4 years shown. Even within Wytham, there seem to be consistent differences between the mean clutch-sizes of blue tits laying in areas of oak woodland and those laying in areas of more mixed woodland (Table 13) though this does not hold for the great tit. Perhaps the most significant point about these small differences is that they are in the same direction as those shown by Lack and Kluijver in other woods.

Table 13. *Clutch-size in relation to habitat*

	Gardens		Marley		Great Wood	
	No. pairs	Mean clutch	No. pairs	Mean clutch	No. pairs	Mean clutch
GREAT TIT						
1958	15	7.6	25	9.2	10	9.3
1959	17	7.7	41	8.8	8	8.6
1960	22	7.2	51	8.3	11	8.6
1961	39	7.8	86	8.0	21	7.9
1962	—	—	43	8.8	13	9.1
1963	—	—	39	9.2	9	9.3
Average of means		7.6		8.7		8.8
BLUE TIT						
1958	9	8.3	12	9.5	16	10.6
1959	14	9.3	20	9.6	16	10.9
1960	18	8.8	23	10.2	28	11.1
1961	17	8.9	51	8.5	32	9.8
1962	—	—	21	9.9	14	10.7
1963	—	—	41	10.6	15	12.1
Average of means		8.8		9.7		10.9

Clutches are in fact larger in good oak woodland than in poor woodland and larger in poor woodland than in gardens.

In view of this, the main types of woodland in Marley were mapped with respect to the nest-boxes. When this had been done it proved possible to separate seven areas, each being reasonably homogeneous within itself. Examination of these areas showed that three of them, A, D and G, had a large number of big trees (these being oak in A and G and wych elm, *Ulmus glabra* (Huds.), in D) with much undergrowth of nettles, *Urtica dioica* (L.), bracken and brambles, whereas B, C and E had fewer large trees and were predominantly stands of hazel with dog's mercury, *Mercurialis perennis* (L.), as a herb layer. Area F was, in profile, rather similar to the latter group though the shrub layer was of close stands of hawthorn and elder, some of which had nothing growing under them. At first it was uncertain whether F, which has a few oaks, and G, which has a few stands of blackthorn among the oaks, might not have been grouped together as intermediate between the other two groups. Plate 1, taken in A and B, gives some idea of the differences.

As it has been shown that both the density of breeding bird and the date of laying influence the mean clutch-size, both of these factors were allowed for in the analysis of the mean clutch-size in these areas; the very large multiple regression analysis was made by Mr J. F. Scott. Using the formula

$$y = a_i + bx + cz$$

where y is the clutch-size, x the number of pairs per ac, z the number of days to the laying date after 30 March, b is -1.54 , c is -0.074 and a_i is a constant specific to the i th area and thus measures the average clutch-size after adjustment for density and date, mean clutch-sizes for the great tit were derived, adjusted for 0.60 pairs per ac (1.48 pairs per ha) and a laying date of 27 April, as follows:

Area	A	B	C	D	E	F	G
Adjusted clutch-size	9.99	9.07	9.28	10.14	8.97	9.13	10.21

It will be seen that the clutch-size in area G suggests that this area is, in fact, similar to areas A and D while the clutch-size in area F suggests that this area is similar to areas B, C and E. Thus the seven areas will be treated as if they form two groups, those with many large trees and those with fewer large trees. It will be seen from the above figures that the latter have average clutch-sizes of 8.97–9.28, whereas the areas with large trees have average clutch-sizes of 9.99–10.21. The differences are highly significant ($P = 0.001$). The complete data are deposited at the Edward Grey Institute.

Apart from the tendency for the areas with larger trees to be those in which the tits lay, on average, larger clutches (as found by Kluijver (1951) and Lack (1958)) there is only one other trend in these data. This is that in areas A and D the birds start to lay slightly later than those in areas B, C and E. No satisfactory reason can be given for this.

One point slightly reduces the validity of the above differences; the analysis was done assuming that each clutch was independent of all the others. This is, of course, not so as many of the birds must have contributed clutches laid in 2 or more years. However, as most of the birds were not individually recognized, this factor could not be allowed for. In any case there are several reasons for believing that it is not important.

Firstly, the analysis extended over 15 years; only about half the adults alive in one year are alive the next, so that very few indeed will have been responsible for clutches in as many as 5 different years. There is no sign that the magnitude of the differences between the areas has altered over the period of the study, as would be expected if the differences were due mainly to particular individuals.

Several factors might produce these results. If, for example, birds bred in the habitats in which they were reared and there were inherited differences in clutch-size, small differences such as those shown might continue to be apparent for a very long period whether they were advantageous or not. Alternatively, older birds lay larger clutches than those breeding for the first time and, if such birds showed a tendency to move into the areas where there were more larger trees, larger clutches would be expected in such places. However, there is no sign that either of these possibilities actually occurs.

Again, it seems likely that these variations are adaptive, since oak woodland appears to be the habitat in which the tits can most easily raise a large number of young. In gardens, in spite of the smaller brood-size, the young are much lighter than those in Wytham. Over the 4 years 1958–61 the mean brood-size on the fifteenth day after hatching was slightly less than 9.0 in Wytham and 5.1 in gardens, and the mean weight of the young 19.0 g in Wytham and 16.1 g in gardens. (The mean weight of garden broods would



(a) Taken in area A (see text). Many large trees, mostly oak, with a large amount of open space and rich ground vegetation, mostly bracken and bramble. Clutches of great tit are larger here.

(b) Taken in area B (see text). Rather few large trees, but many hazels. Ground vegetation mostly rather poor, much dog's mercury. Clutches of great tit are smaller here.

(Photographs by D. A. Kempson.)

(Facing p. 626)

be even less than this if it were not for the fact that many of the lighter young had already died and therefore could not be weighed.)

Table 14 shows that, in gardens, both blue and great tits lose a great number of their nestlings while those in Wytham do not. The most striking point is perhaps that there is a consistently higher mortality of young blue and grey tits in Marley than in the Great Wood Reserve. The garden losses shown here are considerably higher than those given by Lack (1955); one of the main reasons for this may be that the Charterhouse gardens (one of the main areas used in Lack's analysis) are more richly wooded than the Oxford ones, many of the gardens backing on to oak woodland.

Table 14. *Numbers of chicks lost in different habitats*

	Great tit				Blue tit			
	No. broods	Mean brood-size	No. young	Lost (%)	No. broods	Mean brood-size	No. young	Lost (%)
GREAT WOOD								
1958	17	9.2	156	5.0	27	10.1	272	4.8
1959	22	8.6	189	5.8	33	10.3	340	4.4
1960	14	6.0	83	4.8	40	10.5	419	5.0
1961	25	7.8	197	3.0	36	9.1	329	2.7
1962	18	7.7	123	11.4	10	9.6	96	4.2
1963	15	9.3	140	6.4	17	10.8	183	7.1
			888	5.9			1639	4.6
MARLEY								
1958	18	9.2	166	9.6	10	8.9	89	7.9
1959	27	10.5	284	2.5	19	9.1	173	11.6
1960	37	8.1	303	9.6	21	9.0	189	9.0
1961	53	7.5	403	16.4	41	8.0	330	4.8
1962	34	7.5	256	13.7	19	9.2	175	7.4
1963	34	8.6	293	14.7	34	10.6	360	5.3
			1705	11.3			1316	7.0
OXFORD GARDENS								
1958	11	7.3	80	38.8	8	8.2	66	30.3
1959	14	7.5	105	40.0	12	8.6	103	34.0
1960	20	7.1	143	31.5	15	8.0	121	19.9
1961	24	8.1	194	58.8*	12	8.4	101	40.6*
			522	44.4			391	30.8

* The losses for gardens in 1961 are minimum figures, some boxes were not visited often enough to establish that other young had not died in addition to those given above.

For both species the mortality was significantly higher in gardens than in Marley, and in Marley than in Great Wood (at the 1% level on the overall figures).

Some of the garden broods lose all their young, but they are lost gradually over the whole of the nestling period. In these cases the chicks are always thin and squeaking and have all the signs of dying of starvation. It seems very unlikely that any of the garden losses were due to the parents feeding the young on insects poisoned by insecticides. Firstly most of the nest-boxes were on Headington Hill, in large rather poorly tended gardens where there is little, if any, spraying, especially of trees. Secondly, the way in which the young die, in ones and twos throughout the nestling period, the smallest ones dying first, suggests gradual starvation of the broods. If the young birds were dying of poisoning it might be expected that the whole brood would have died more or less simultaneously.

In gardens in Wytham village in 1961, six pairs of great tits nested in some sparrow boxes. One pair lost all eight young, but since the box was taken over by sparrows within a week of the last young dying it is just possible that the sparrows were responsible for the losses and so the data for this brood are excluded. The remaining five broods lost twenty of the thirty-four young which hatched. In the one blue tit nest in the same area at least two of the eight young died. These losses are thus very similar to those in the Oxford gardens. However, these village boxes were some 400 yd from Marley and other woodland and there are several large isolated oaks nearer at hand. From what is known of great tits it is unlikely that the parents of these nests in Wytham village would have been driven out of Marley during the period when they were collecting food for their young, since the tits are not very territorial at this time. Hence one of two factors, or possibly both, account for the low nesting success of these birds. Either they were not flying the 400 yd to Marley, or the better feeding conditions they could find there were of little value since they took so long to get there.

Within Marley it was shown that there were consistent differences in clutch-size between the different habitats. In most years there are so few nests and so few recoveries that it is difficult to measure the survival rates in the two habitats. However, the average size of sixty-one broods in the areas where there were many large trees was 8.2, and 0.79 young were recovered per brood, while in 149 broods in the areas with fewer large trees the average brood-size was 7.5 with 0.70 recoveries per brood. The difference is not significant. Hence, although the adaptive nature of the different clutch-sizes in the different areas of Marley has not been demonstrated, it seems clear that the variations of clutch-size in different habitats is related, at least roughly, to the number of young which the parents can raise in the different habitats.

Food

The trends in clutch-size discussed have been explained as adaptations which enable the birds to raise the greatest number of young. This must depend on the amount of food that the parents can find for them.

Fig. 10 shows the clutch-size of the great tits in Marley for each year since 1947 and the number of caterpillars per m². A brief glance suggests that there may be some correlation at both the beginning and the end of the period, but little from 1951 to 1958. It seems certain, however, that the apparent correlations were accidental and they can be explained on the basis of trends in clutch-size in relation to the density of pairs and the date of laying that have already been established. Hence clutch-size was high in 1947 because the birds were so sparse, high in 1948 because breeding was so early, low in 1951 because breeding was so late and low in the years 1959–61 owing to the steadily increasing density of breeding birds. This was checked by a regression analysis by Mr J. F. Scott. There was no significant indication that either the caterpillar population or the clutch-size showed a serial correlation. This greatly simplified the analysis as it was then possible to do a straightforward regression on the data. When the clutch-size was adjusted for date of laying and density of pairs (see earlier), the correlation coefficient with the density of caterpillars was only -0.12, which is, of course, nowhere near significance. These findings are in agreement with Lack (1958), correcting Lack (1955).

Survival of parents in relation to the size of brood they rear

The parents which raised the largest broods did not always produce as many surviving offspring as those which raised slightly smaller broods. It was also noted that a propor-

tion of the females were killed when their broods were taken by predators and, since more large than small broods were taken by predators, fewer of the parents of such broods would live to breed again.

Kluyver (1952) has shown that both parents lose weight while raising young and that they are at their lightest in June and July. It seems likely that this is due to the strain of raising a brood; similar loss of weight during breeding has been recorded for several species. The greatest strain presumably will be imposed on those birds which are endeavouring to raise the largest broods, though this point does not seem to have been examined.

Gibb (1955) records 'In the second half of the nestling period, activity was usually maintained or increased at small first broods, but slackened off at large first broods.

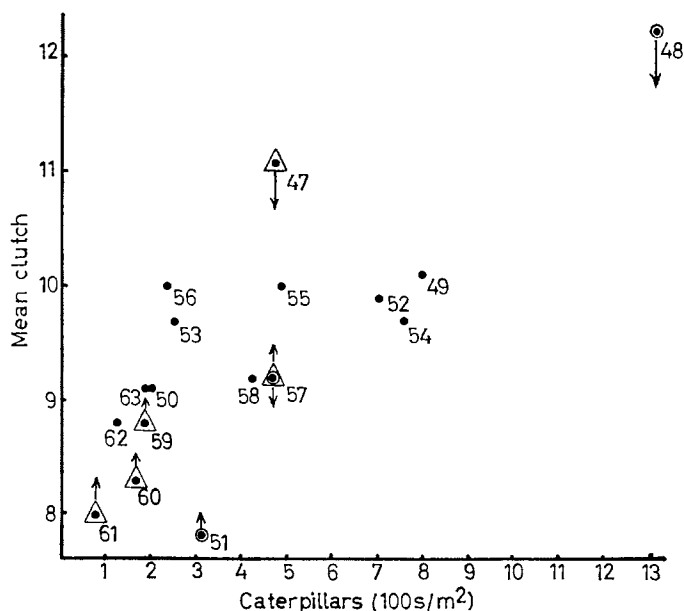


FIG. 10. Mean clutch of great tit in relation to the caterpillar populations. Years when clutch-size was affected particularly by date of breeding season (○) (48, 57 early, 51 late) or density of pairs (△) (47 low, 57, 59, 60, 61 high) are marked, and arrows show direction in which clutch-size would have been altered had conditions been average in these years.

This strongly suggests that parent great tits feeding large broods were becoming tired and so could not maintain their rate of feeding. Arnold (1952) gives a striking case where a female blue tit disappeared half-way through the nestling period. The male at first almost exactly doubled his rate of feeding to compensate for the female's absence, but after the fifteenth day fed very much more slowly. This may be typical of broods where the parent is straining to feed'.

This might be yet another selective factor favouring a smaller clutch-size. The birds that lay larger clutches would, on average, breed fewer times and thus selection would favour the genotypes of parents which laid slightly smaller clutches, but survived to breed again.

Similarly a differential survival rate of parents might be one of the reasons why the birds do not often have late broods. Gibb (1955) has data to show that the parents of late

broods are straining to feed the young, and it will be remembered that the weights of late broods are low and the predation rate is higher. Thus the chances of a parent laying a later clutch and surviving to breed again are lower than those of a parent laying an early clutch. Data to test these factors properly are not yet available, and, while in 1961 there was some evidence that subsequent survival of females laying large or late clutches was lower than that of those laying smaller or early clutches, this did not appear to be true in 1962.

Statistical analysis

Many of the factors affecting clutch-size and survival in the great tit are clearly interacting. A regression analysis was made in an attempt to clarify these interactions, though it does not, of course, show which of the factors are causal. The main points are appended together here rather than scattered through the section.

1. Post-fledging survival of young was more strongly correlated with the mean weight of the brood than with the weight of the individual concerned. This is due to the fact, not mentioned above, that males are heavier than females by about 1 g on the fifteenth day. Since the nestlings could not be sexed, it was not possible to analyse survival of the two sexes separately. Hence a high mean brood-weight means a relatively heavy weight of all young, and a bird below average in such a brood is more likely to be a relatively heavy female with good chance of survival, than a lighter male.

2. The survival of the Marley young was inclined to be different from that of the young from the rest of the wood; this was especially so in 1961. So for these analyses the data for these two areas were kept separate.

3. It was obviously of extreme importance to allow for date while studying survival in relation to brood-size, since both brood-size and survival-rate were smaller later in the season. This is a point that others (e.g. Löhrl 1957; Kluijver 1963) have overlooked. The results of the analysis showed that the larger broods produced more surviving young per brood in 4 of the 6 years in the rest of Wytham and in only 2 of the 6 years in Marley. Since nearly all the large broods were artificial, the data are still biased in their favour, for the reason put forward earlier.

SECOND BROODS

The number of young raised per pair per year is dependent on both the number of young in the brood and the number of broods. Second broods are rare in oak woodland in England, where more than 5% of the pairs raise second broods only exceptionally. In similar (broad-leaved) habitats in Holland the percentage of second broods is about 35 (Kluijver 1951). In pinewoods in both countries there is a higher proportion of second broods, some 28% in England and 76% in Holland (Lack 1958; Kluijver 1951). While the difference between the two countries remains unexplained, the difference between the two habitats is clearly related to the food supply, which is better later in the summer in pinewoods than in oak woodland (see Gibb & Betts 1963).

Kluijver has, therefore, many more data on the occurrence of second broods than it has been possible to obtain in England. He found that second broods occur more frequently (i) in years when the density of breeding pairs is low, (ii) among older birds than younger ones, and (iii) in pinewoods than broad-leaved woods. Under two of these conditions (low density and in pinewoods) second clutches are laid when there is likely to be more food; in the third case they are laid more frequently by the more competent parents.

Thus, like larger clutches, more second clutches are laid when there is a better chance of raising them.

The annual percentages of second broods in Wytham (Table 15) shows that some of the years when second broods occur are those when conditions might have been expected to be particularly favourable; in 1947 there was a very low density of breeding pairs and in 1948 there was an exceptionally early start to the breeding season with the highest caterpillar population of the study.

In recent years there also seems to have been a relationship between the proportion of second broods and the seasonal decline in weight of the young. Thus comparison of the seasonal weight decreases shown in Fig. 7 and the percentage of second broods (Table 15) shows a tendency for second broods to occur in those years when there was less difference in weight between the early and the later broods. Thus the parents lay second clutches in those years when they are able to find more food for their broods.

Nevertheless, although the second broods are produced in those years when there is the best hope of raising them, they are still highly unsuccessful in most years compared

Table 15. *Great tit: proportion of second broods in Wytham*

	No. of broods	Second broods (%)
1947	18	5.6
1948	38	13.2
1949	61	0
1950	35	5.7
1951	35	0
1952	20	0
1953	21	0
1954	31	0
1955	27	0
1956	24	0
1957	49	0
1958	55	0
1959	136	0
1960	147	3.8
1961	256	0
1962	184	3.8
1963	169	7.7

with the earlier broods. Thus it seems likely that there is only weak selection for having them at all in deciduous woodland in England.

SURVIVAL OF YOUNG BIRDS IN SUMMER IN RELATION TO CHANGES IN THE POPULATION

The proportion of young surviving can be estimated by the ratio of juveniles to older birds that are caught in the autumn trapping. Not only does this ratio vary markedly from year to year, but the number of breeding pairs the next year is greatly affected by it. Fig. 11 shows the relationship. It can be seen that there is a close correlation between the age ratios and the changes in population. Since these age ratios are apparent by early November it is clear that they are determined by some factor operating before that.

The data in Fig. 11 make it plain that what happens to the young before the winter is critical in regulating the number of great tits. The ratio of young to older birds present in late autumn has varied between 0.16 in 1961 and 2.0 in 1960. This ten-fold variation

is much greater than that which Kluijver records in 9 different years for the adults in which mortality ranged between 35% and 60%.

It is not known what mortality factors affect the young or exactly when they come into effect. Kluijver believes that the main factor is not direct mortality, but that territorial

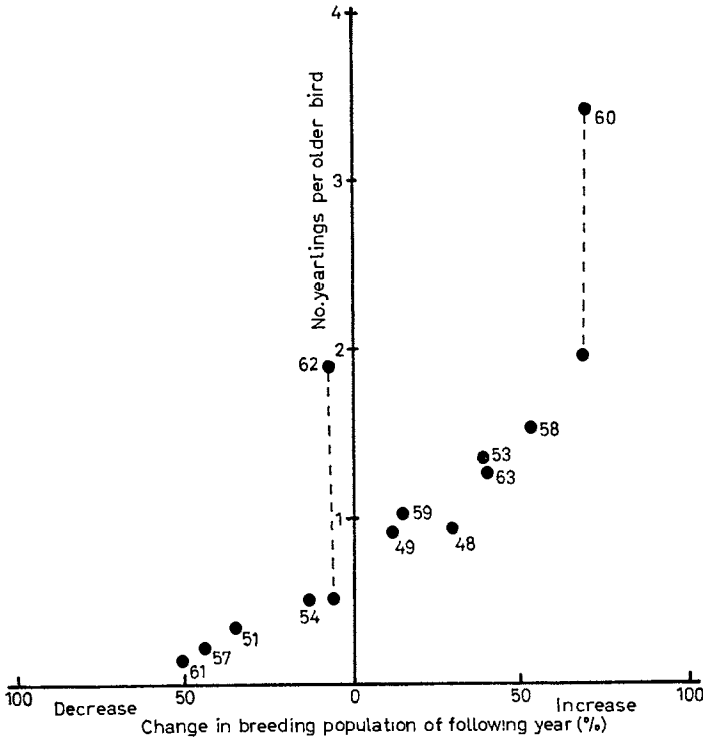


FIG. 11. Great tit: ratio of young birds to older ones in relation to percentage change in the breeding population the following year. The percentage change was calculated as follows: the difference between the numbers breeding in year A and year B was calculated as a percentage of the number in year A. If the population was larger in year B than year A then the percentage was plotted as an increase; if it was smaller as a decrease. In most years there did not seem to be much change between the ratio at the beginning of the autumn and at the end of the winter. This was not so in 1962 when there was an apparently very high mortality of juveniles during the very hard winter. In 1960 virtually all the birds were caught under beech trees, feeding on the seed. More juveniles seem to wander in the winter and come to the beech areas. Thus the number of juveniles is disproportionately high (in fact impossibly so since the birds did not raise seven young per pair in the previous summer). The ratio on a small sample trapped in Marley (i.e. not under the beeches) was only 2.0 young per older bird and there was 1.8 young per older bird breeding in 1961. Hence for 1960 and 1962 two points are shown, that for the high winter ratio and that for the spring. In the text 2.0 has been used as the winter ratio for 1960.

	1948	1949	1951	1953	1954	1957	1958	1959	1960	1961	1962	1963
No. of birds in sample	34	57	31	23	17	22	92	298	515	408	357	300

aggressiveness in September may lead to a large emigration of young birds in years when there is a high density. However, at Wytham there is no evidence that many birds leave and there is suggestive evidence that they do not. Further, the 1960 population was, until then, the highest recorded, and this was followed by the best survival (within the area

of Wytham) of young birds, so that territorial aggressiveness does not seem to have been very important on this occasion.

Few great tits, ringed as nestlings in Wytham, have been recovered outside; those that have been tended to be heavier than the average for their brood. Hence these birds also came from the classes of young that survived within the wood, namely the heavier ones. They were therefore representatives of the classes that were known to be surviving and not of the classes that had disappeared. Since these latter classes, predominantly the light young and those hatched later in the season, were neither present in the wood in the autumn nor outside, it seems clear that they had already died, in the wood, before the autumn.

In 1963, 1252 young great tits were given different colour rings according to their weight on the fifteenth day. Ninety of these birds were seen on 7 days during the second half of July. Care was taken to avoid counting the same bird twice on the same day though, of course, this was not possible between days. The most likely error in the observations was that two adjacent birds wearing the same coloured rings would only be counted as one for fear of duplication. Because of this, and because the birds were usually found travelling through the foliage in small parties, the most likely bias in these observations is weighting in favour of the less common classes. The results are set out in Table 16.

Table 16. *Proportion of young great tits of different weights seen in July*

	Weight class (g)					
	<15.9	16.0-17.9	18.0-18.9	19.0-19.9	20.0-20.9	>21.0
No. fledged	39	182	269	405	268	89
Per cent seen	0	2.7	4.8	8.1	11.2	10.1

While such observations must be repeated it seems likely that since the light young were already relatively less common at this stage, many of them had already died. If this is normally so then a high proportion of the juveniles will be dead at least a month before the time that Kluijver believes that they will be driven out by autumn territorial aggression.

THE IMPORTANCE OF BEECH-MAST TO THE TITS IN WINTER

It was clear that beech-mast was a very important food for the tits in those winters when it occurred. In good years, from late November onwards the birds fed on beech-mast to such an extent that it was not possible to catch many at bait. Accordingly the changes in the tit population were examined in relation to the beech crop, for the data on which I am indebted to Dr J. D. Matthews of the Forestry Commission. The beech crops tend to be consistent over wide areas of Europe so that the data are fairly representative of Holland (there is only one slight inconsistency in 8 years between recorded crops in the two countries). Fig. 12 was prepared as follows. The size of each beech crop as recorded in England was allocated to one of the somewhat subjective categories listed, from nil to abundant. From 1912 to 1947 (excluding 1943 and 1944) the data on the percentage changes in the tits' populations in Holland were plotted against the crop and from 1948 onwards the data from Marley were used.

It is clear from Fig. 12 that the breeding population of the great tit has been considerably affected by the size of the crop. A multiple regression analysis by Mr J. F. Scott on the long series of data from Holland shows that a unit increase in the beech-mast (i.e. from 'poor' to 'poor to moderate') results in about a 7% increase in the tit population, irrespective of other variables.

There are a few minor points to be made. Firstly there are occasional years when the beech crop is not uniformly widespread. Secondly when there is an extended period of snow cover the tits may not be able to get the seed that has fallen. This seems to have been the case in 1962–63, when there was a moderate crop of beech-mast in Wytham and high numbers of young great tits. A considerable increase in the breeding population in 1963 was expected (as it was also by the Dutch workers). There followed the severest winter for more than 200 years, with about a foot of snow covering the ground for 9 consecutive weeks. Instead of the expected increase the great tit population dropped by 10%. By contrast the blue tit population rose by about 30% over Wytham as a whole. Gibb (1954b)

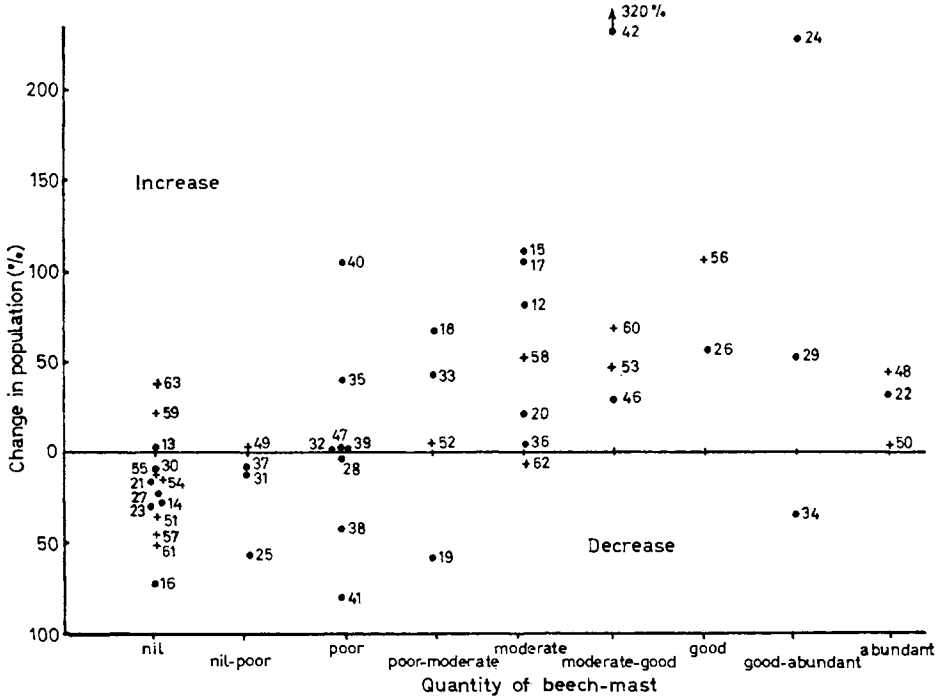


FIG. 12. Great tit: changes in breeding population in relation to the crop of beech-mast. The data for the Dutch populations are from Wolda and Kluijver (Kluijver 1951). The beech crops are given in the categories listed by the Forestry Commission. They are subjective and probably the increase between one category and the next does not represent a constant increase in the quantity of seed. The percentage change in the tit population was calculated in the same way as in Fig. 11. +, Wytham 1948–63; ●, Holland 1912–42, 1946–47.

has shown that the blue tits in winter feed largely on the branches and the twigs while the great tit collects most of its food from the ground. In cold weather these differences between the two species are more pronounced than in mild weather. In spite of the hardness of the winter in 1962–63 there was no whole day in Oxford when there was a complete glazed frost, hence the seed still on the trees would have been continuously available to the lighter, and more agile, blue tits when the great tits could not get it from the ground.

Hence various factors may modify the close correlation between the beech crop and the variation in the tit populations. Further, although the crop records are not quantitative, it looks as if a moderate crop is enough to support the tits throughout the winter,

since tits do not seem to increase more when the beech crop is heavy than when it is moderate. This is supported by the fact that the large population of tits present in the autumn of 1960 were able to feed throughout the winter on a crop estimated by the Forestry Commission as only moderate to good.

It may be doubted whether the correlation is causal because in some areas (e.g. Dean and Veluwe) there are no beech trees, yet here the tits show fluctuations in agreement with those in Marley. However, it appears that many other species of tree (e.g. oak and ash) which also fruit irregularly, fruit synchronously with the beech (see data in Ulfstrand 1963). Since synchronization of the beech crop over wide areas is due to the weather, it is not surprising that other trees may also tend to fruit in the same years. Hence the beech data given in Fig. 12 may also reflect the amount of crop available on many other species of trees. Further evidence is required, but it seems likely that the tit populations in areas where there is no beech may also be able to find more seeds in the years when beech-mast is plentiful than when it is not.

While weather factors affect the crop to a great extent and will presumably be one of the major causes of the synchronization of the crop over wide areas, this is only part of the story. An individual beech tree does not appear to crop in 2 successive years and does not apparently have a heavy crop more than once every 4 or more years. (In Wytham it was noticed that the beech trees which fruited heavily in 1962 were not those which had fruited in 1960 and that none of those that fruited well in 1960 had heavy crops in 1962.) Hence two fine springs in succession do not result in two successive crops of beech seed. The beech crop is widely held to be biennial, but the records show that it tends to crop rather less regularly at intervals of 2 or more years.

It is of interest that Turcek (1955) records a similar situation for the voles and field mice in Czechoslovakia. If there is a beech crop these mammals will be more numerous the following year, if there is no crop they will be fewer. Since small mammals continue breeding in the autumn if there is a good food supply (M. E. B. Smyth, *in litt.*) we are here dealing with a causal connection.

The irregularity of the beech-mast creates a further difficulty in interpreting fluctuations in the populations of tits. Kluijver (1951) summarized the population fluctuations as follows: 'A high breeding population is often found after a low one in the preceding year. This is because, with a low breeding population, the production rate tends to be high and the amount of emigration low. As a result the population curve from year to year tends to be saw-toothed in form, a steep rise being followed by a deep fall'. As already mentioned, Kluijver believed that emigration at high densities is one of the main causes of decreases in the population.

Since the population of tits rises after a beech crop, the population will be high in the year when there is no crop (since the crops do not normally occur in successive years) and the population will fall in the non-beech crop year and be low in the spring prior to the next crop. Hence in many years there will either be large numbers of tits and no beech-mast, or low numbers and beech-mast, and thus the effects of food supply and density are very difficult to separate. Indeed, practically all the major changes in the Dutch great tit population can be closely correlated with the British beech-mast data; in only one case does a major rise in the population occur with a crop of less than 'poor to moderate' and in only two cases does a major decrease occur with a crop of better than 'poor'. It is possible that at least some of the inconsistencies could be caused by bad weather, or to the beech crops being dissimilar in Holland and England.

In Sweden also Ulfstrand (1962) has shown that the beech crop is very important to

the tits. In years when there was a crop many tits remained in the area all winter, but when there was no crop fewer remained and large numbers of tits emigrated from Scandinavia. Thus the presence or absence of the beech-mast greatly affected the migratory behaviour of the tits, large emigrations occurring at times of high density, but also at times when the food supply from the beech was short.

There is one further difficulty in associating movement with high density. In late summer in Wytham it seems that there may, at least at times, actually be more birds in the years when there is a beech crop than in the years when there is a high breeding density and no crop. This is because, in some years, many more young survive in those summers preceding a crop than in those when there is no crop. For example fifty-one pairs of great tits bred in Marley in 1960 and eighty-six in 1961. The juvenile to adult ratio in the autumns of these 2 years was 2.0 and 0.16 respectively. If we assume that there was no adult mortality between the summer and the autumn, then the Marley populations of tits would have been 102 adults and 204 young in 1960 and 176 adults and 28 young in 1961, or 306 birds as opposed to 204. If similar mortality occurs before the autumn in Holland it is possible that there are actually fewer birds alive in the autumn of a year in which there was high breeding density than there are in that of a year of low breeding density. If this were generally true then, obviously, autumn density is not the factor influencing movement.

THE EFFECT OF THE HARDNESS OF THE WINTER ON THE TITS

Kluijver (1951) and Gibb (1960) have shown that the coldness of the winter probably affects the survival of tits, though Gibb was concerned with the coal tit not the great tit. Unfortunately during the Wytham study there has only been one really severe winter (1962-63) so that it is not really possible to measure the effect on the tits. Apart from this year, and presumably due to chance, there has been a tendency for the mild winters to be those when there was a good beech crop and the colder ones to be those when there was no crop. Hence it is very difficult to separate these two factors. However, since in 1962-63 the blue tits survived the winter well while the great tits did not, it seems that the food supply may have been more important than the cold. This suggestion is supported by observations of I. Newton (*in litt.*) working in Wytham in the same winter on bullfinches, *Pyrrhula pyrrhula*. The bullfinches fed mainly on ash seeds which were still on the trees (and therefore not covered by snow). In spite of the large numbers of bullfinches present they survived the winter extremely well and during the whole winter ate only about 0.5% of the available ash seed.

The great tit population in 1963 was only 10% lower than that in 1962, but there were larger numbers than usual alive in the autumn of 1962 and a large increase in numbers was expected. Thus of all the great tits alive in the autumn perhaps 75% died during the winter.

A multiple regression analysis by Mr J. F. Scott on the long series of data from Holland shows that there is some evidence that the doubling of the coldness of the winter (for measurement see below) results in lowering the breeding population by 12%, but this is not significant.

As mentioned, apart from 1962-63, there is no evidence concerning an adverse effect of cold winters in Wytham. Using Kluijver's measurement of the coldness of the winter (the sum of all the average day temperatures below freezing) there were only two cold winters, one of which, in 1946-47 (a year with no mast), may have caused the low

population with which the study started. The other was in 1962–63. A further point is that the winters in Holland seem to be much colder than those in Oxford: the winter cold score in the former is about 80 on average while in Oxford it is only about 40. Hence it is possible that the winter cold may be more important in Holland; only rarely at Oxford is it cold enough to have a serious effect on the tits. This is, of course, to be expected on the basis of the data in Fig. 11 (the relationship between the age ratio and the future population change); if there were large changes in winter numbers due to weather the close correlation demonstrated in the figure would not be apparent.

FACTORS REGULATING TOTAL POPULATION CHANGE

It is clear that the major factor affecting the numbers of breeding tits is the survival of the young in the previous year; survival of adults and movements of birds will modify the changes. Movement does not seem to be important in Wytham.

Kluijver (1951) has shown that adult mortality is much less varied than that of the juveniles in this study. At present there are data on the survival of the adults for only 4 years in Wytham. These are comparable to those shown by Kluijver. The only, tentative, observation that can be made from them is that they were lower in the non-beech years (42% survived from 1961 to 1962, 53% from 1963 to 1964) than they were in winters when there was beech-mast (63% survived from 1960 to 1961 and 61% from 1962 to 1963, the latter in spite of the very hard winter). This would be expected from the data in Fig. 12.

It is the survival of the young birds after fledging that varies so markedly and has considerable effect on the population. Kluijver (1951) has shown that the production of young is partly dependent on the density of the parents; the lower the number of breeding pairs the higher is the number of young raised per pair. The same is also true in Wytham (Lack 1964). Some people (e.g. Wynne-Edwards 1962) have suggested that such behaviour is designed to reduce overpopulation. Two points suggest that this is not true for the great tit. Firstly, the reduction in brood-size is not nearly proportional to the increase in density. In high populations less young are raised per pair, but very many more per unit area. Secondly, the actual production of young to fledging is not closely correlated with the number surviving until the autumn. Indeed there is no significant correlation between the number of young fledged and the change in the following year's breeding population (Lack 1964, Fig. 6). In 2 of the 3 years in which low production of young was followed by a fall in population, one of the main causes of low production was high predation—a factor beyond the control of the birds. It seems true to say that, during this study, the production of young has always been well in excess of what was present in the next breeding season and that the proportion disappearing has not been closely related to the previous density.

Workers differ markedly on what they believe to be the cause of the disappearance of the young. Kluijver believes that they emigrate. The difficulty is that there cannot be emigration from all habitats without numbers increasing elsewhere and so emigration must, in large part, be equivalent to death. Further, the great tit chicks in Wytham in 1963 disappeared much earlier than the time at which they are ever observed moving. Jenkins, Watson & Miller (1963) claim that the disappearance of grouse in late summer is caused by the birds being expelled into areas of unsuitable habitat where they then die. This occurs during a very short period in the autumn.

The main point about the birds that disappear in this study is that they are known to

have been physically inferior to the survivors in that they were lighter, either by virtue of their brood-size or because they hatched at a later date. They are therefore those that would be less likely to survive a period of food shortage. It seems possible that there may be an association between disappearance and food shortage, though more years' data would be necessary to establish this for certain. In the 6 years 1958–63, there was a high disappearance of young in the 3 years when the breeding season was more curtailed (1958, 1959, 1961) and weights of young decreased steadily. The loss of young was less in the 2 years (1960, 1962) when breeding was more extended, late nestling weights were better and second broods were produced; 1963 was rather intermediate. It seems possible to argue that those years when there was enough food late in the season for some parents to have second broods would also be those in which the fledged young from earlier broods would survive best.

Thus there are two major factors which affect the breeding population of the great tit in Wytham, the survival or loss of the juveniles in the late summer or early autumn, due to a largely unknown factor that may be related to the food supply while the young are in the nest, and the survival of both juveniles and adults through the winter which depends to a large extent on whether there is a beech crop or not, the mortality being higher in years without a crop.

DISCUSSION

Selective factors affecting breeding

1. *Date of laying.* The data in this paper show that there is great advantage in being an early breeder, but that many of the great tits do not breed early, and this can only be because something prevents them. The most likely factor seems to be that the birds are unable to get sufficient food to manufacture eggs earlier. It will be remembered the older birds breed earlier than yearlings, perhaps because, being more experienced, they are able to get enough food earlier in the season. The food taken is very varied at this time, but composed mainly of small invertebrates.

Emphasis has been laid on the condition of the female because it seems likely that the production of eggs is a greater strain on the female than the formation of sperm by the male. While the male's gonads enlarge greatly in early spring the energy required for this growth is probably much less than that required by the female to lay a clutch of eggs. Great tit eggs weigh about $1\frac{3}{4}$ g each and, since a female may lay ten to twelve eggs, this means that she will have to produce, over a period of 10–12 days, some $17\frac{1}{2}$ –21 g of eggs—about her own body weight. Kluijver (1952) has shown that the weight of the female increases by about 2 g between mid-March and mid-April. However, in April the variation in weight of the females is very great; presumably this is because some females are in more advanced breeding condition than others. Since there is a great advantage in being an early breeder and no apparent advantage in breeding later, I suggest that the great tits do not inherit a tendency to breed early or late, but only the tendency to breed as early as they can. Hence presumably the variation in the weights of the females reflects the individual abilities and the local food supplies of these birds.

While I have suggested that at least some element of the spring food is sufficiently scarce to prevent many of the females from getting into breeding condition at the time which would enable them to raise the largest number of young, it must be stressed that the evidence is circumstantial. The earlier the tits breed the more young they rear; the tits are lightest in February and early March, but the females increase rapidly in weight from mid-March onwards and need a considerable amount of food to produce

their eggs; finally the older birds manage to breed before the more inexperienced yearlings.

There is one fact which perhaps supports the suggestion that food must be in good supply if the tit is to be able to lay a clutch of eggs. This is that if there is a cold spell after breeding has started those individuals which have not started to lay postpone starting. Those that have started to lay complete their clutches but the rest do not start laying until 4 days after the warmer weather returns.

Insects are likely to be much less active during the cold weather and few emerge during such a period. Thus food supply is much scarcer and collecting enough to make eggs might be difficult. Those individuals that have started to lay continue to do so partly because their behaviour and physiology are arranged so that they tend to complete a clutch once they have started and partly because they have already collected some of the food required to make some of the remaining eggs. It might be expected that those great tits which complete their clutches during a cold spell might lay a slightly smaller clutch. While this is not known, Kendeigh (1952) has shown that house wrens, *Troglodytes aedon* (Vieillot), do lay smaller clutches in cold weather.

In the section on breeding season I noted that there was some difficulty in reconciling the suggestion that the birds were not laying as early as they should with the fact that there is a correlation between the time of the tits' breeding season and that of the caterpillars.

The ultimate factor to which the tits' breeding season is adapted is the food supply for the young, which leave the nest, on average, some 10–12 days after the peak of winter moth abundance. Since those that leave earlier survive much better than those that leave later it is evidently important to leave the nest when food is still plentiful. Yet many of the young leave later than the time when food is most abundant.

Interesting support for this suggestion that the female great tit finds it difficult to collect enough food to manufacture eggs comes from Royama's work in Japan (Royama, in preparation); he observed that the female starts begging for food from the male as soon as she has started laying. From this time onwards the male feeds the female about five times an hour throughout the laying period (i.e. some seventy meals per day and about 30% of the females' daily food). Such feeding has been called courtship feeding, but one would expect selection to have established the habit of the male trying to help the female obtain sufficient food if it is in short supply.

Hence, although there is presumably selective pressure towards breeding at the best time in relation to the caterpillars, the time at which they actually get into breeding condition is not related to the caterpillars' season but to the supply of spring food. (The supply of spring food, like the timing of the caterpillar season, is probably largely affected by the weather. This would explain why the tits' breeding season is approximately correlated to the time of caterpillar abundance (Fig. 3) since both the spring food supply and the caterpillar season are likely to be similarly affected by the spring weather.)

Many points remain to be elucidated before this suggestion can be considered proved but there is, perhaps, one main reason for treating the idea with caution. This is that many other species vary their clutch in the same way as the great tit, the first clutches being largest and a steady decrease in clutch-size occurring throughout the season. It seems likely that, as in the great tit, the largest clutches are laid at the time at which they can be most easily reared, and that selection has favoured the laying of smaller clutches later in the season because it is not possible to rear quite such large broods at this time. Thus the first birds to lay rear the largest number of young and the others would be more successful if they laid earlier.

Not only do other insectivores vary in their clutch-size in this manner, e.g. the collared flycatcher (Löhrl 1957) and the wood warbler, *Phylloscopus sibilatrix* (E. Lack 1950), but so also do some sea-birds, e.g. the kittiwake, *Rissa tridactyla* (Coulson & White 1958). Thus, if my suggestion is correct, it seems likely that many of the individuals of these species are also not breeding at the time which would result in the production of the maximum number of young, but that they are breeding as early as the females can produce their eggs.

Lack (1958) has suggested that 'it is unlikely that the physical condition of the female tits in April could be so critical as to offset the selective advantage of raising as many young as possible'. Nevertheless it has been shown that many of the tits are not breeding at the most opportune time. While I agree with Lack's suggestion that there will be very strong selection for birds to breed at the most advantageous time for the nestlings, it does seem as if many of the birds may not do so, and I believe that some factor is preventing them. If no birds could get into breeding condition by the most opportune time then those birds which bred closest to this time would be the ones that would produce most young. The difficulty remains of explaining the continued presence in the population of a large number of birds which are breeding when the most advantageous time has passed.

As mentioned earlier, the most reasonable suggestion that I can offer is that the great tit does not inherit a tendency to breed early or late, but merely the tendency to breed as early as it can. In this way it is not necessary to postulate an advantage for late breeding, the late breeders being the birds which, had they been able to do so, would have bred earlier.

As early as 1871 Darwin wrote 'there can also be no doubt that the most vigorous, best nourished and earliest breeders would, on average, succeed in rearing the largest number of fine offspring'. R. A. Fisher (1929), quoting Darwin, goes on to say 'whether this is so or not is difficult to say, but it should be noted that the dates of the breeding phenomena of a species could only be stabilized if birds congenitally prone to breed early did not for this reason produce more offspring. The correlation required by Darwin's theory must be due solely to non-hereditary causes, such as chance variations of nutrition might supply'.

2. *Production of young.* Several factors affect the clutch-size of the tits. Although they may not all be influencing the birds simultaneously, usually several of them are affecting the clutch-size at any one time, either directly, or indirectly through the time of laying. Moreover, apart from the factors established, the reasons why, in Marley, the birds that are in the apparently good habitats lay consistently later than the birds in the poorer ones remain to be explained. Thus there must be at least one further factor which is affecting the time of laying. Nor is it by any means clear that all the different times of laying can be explained in terms of availability of food for the adults prior to laying.

In this paper it has been assumed that the birds inherit the ability to vary the size of the clutch within certain limits, the limits being different in genotypes. Thus, a bird which inherits the tendency to lay a large clutch will lay clutches of different sizes in years of high or low density, in good or poor habitats, etc., but in all these conditions its clutch-size will be above average for the conditions prevailing.

It might be supposed that the clutch-size was limited by the physiological requirements of the birds and that the smaller clutches were laid by those birds which failed to get as much food as those that laid the larger clutches. While food supply might limit the clutch-size under exceptional circumstances, such as for instance, unusually cold weather which started after the birds commenced laying, it seems very unlikely that it normally

does so, for the following reasons. Firstly, the later the birds breed the smaller the clutch they lay, in spite of the fact that there is less food for the early breeders and food increases rapidly during the first part of the breeding season. Even if an early breeder (laying a large clutch) loses its clutch and lays a replacement the second clutch is smaller, about the size of the normal for that time of year. Secondly if an early breeder loses its clutch while laying it will move to another box and lay another. The combined total for the two clutches is usually well in excess of the size of a single clutch.

Hence, once food has become sufficiently common for laying to start it seems unlikely that the birds are forced to terminate their clutch by shortage of food, because it is normally becoming progressively more common. It seems more probable that clutch completion is the result of selection for the most productive clutch-size.

From the evolutionary point of view, while it is of selective advantage to rear as many healthy young as possible, in Wytham there is a limit to which clutch-size can be raised without resulting in fewer healthy young being raised (Lack *et al.* 1957). It is believed that a similar situation exists under the other conditions discussed, namely that at some point an increase of one in clutch-size leads, on average, to the production of fewer, rather than more, surviving young. The most productive clutch-size will probably be different in different conditions. At least four factors affect the clutch-size in the Oxford area, namely habitat, date of laying, density of pairs and age of female. In each case, smaller clutches are laid in the conditions that are less suitable for raising a larger one, either when there will be less food or when the parent is less capable.

There is no evidence that the tits can predict the level of the caterpillar populations. It seems likely, therefore, that the tits are not modifying the size of their clutches directly to the food supply for the young, but are adjusting the clutches by reaction to other factors such as, perhaps, the appearance of the habitat. Thus areas of large trees usually carry more food than areas where there are few large trees; nesting at the start of the season means that there will be more food for the young; fewer competitors result in there being more food for each, and so on. By responses of this kind the birds lay clutches which are overall, but not always, well fitted to the conditions.

With this in view it is worth remembering that 1960 was a year in which the overall survival was the best during the study. However, the clutches were only of average size, and it is tempting to suggest that this was a year when the tits could have laid larger clutches, but that they failed to take the opportunity. In 1961 there were exceptionally large numbers of breeding pairs in Marley and although they laid small clutches accordingly, caterpillars were very scarce (the lowest population during the study) and some birds had difficulty in raising even small broods. While the mean clutch was about the normal for oak woodland in Britain, the birds would almost certainly have been more successful with smaller broods still.

Similarly perhaps the great tits in pinewoods, described by Lack (1955) and Gibb & Betts (1963), were responding as they would have in oak woodland. However, they were in pinewood where the food supply is very different from that in oak woodland. In pinewoods caterpillars are relatively scarce at the time when they are most abundant in oak woodland. Nevertheless the pattern of laying of the great tits is the same in pinewoods as it is in oak woods. The first birds to lay have the largest clutches and clutch-size decreases throughout the season. The result is that the first broods are very unsuccessful, the young weighing, on average, 14.4 g on the fifteenth day (as opposed to 19.0 g in Wytham) which is almost certainly too little for many of them to survive. The second broods (more common than in deciduous woodland) fare better partly because they are

smaller anyway and partly because there are more caterpillars at this time. Even so, the chicks of these smaller broods are lighter (17.7 g) than those of the larger first broods in oak woodland.

Thus, in pinewoods, the tits vary their clutches in a similar manner to those in deciduous woodland but, because the food supply is so different, they are not nearly so successful in rearing their young. It must be assumed that the birds respond to factors in pinewood in just the same way as they do in deciduous woodland. Pinewoods are not a natural habitat in England and thus, until recently, the English great tit has had no reason to adapt to pinewood and, even now, no areas of pine in England are large enough for a population of great tits to become genetically isolated there.

The data available lead me to the tentative conclusion that, while the spring food may be of chief importance in enabling the birds to get into breeding condition early, it does not affect the size of their clutch. The latter is determined partly by response to the various external factors like the breeding density, the date of laying and the habitat, and partly by the genetic constitution of the bird.

It has not been explained why the tits which breed in a late season should lay a smaller clutch than those breeding in an early season as shown in both Wytham and Holland. There is no reason to believe that food is shorter in a late season than in an early one, since the caterpillars are as late in hatching as the tits are in starting to lay. Nor is there any evidence that the survival of caterpillars is poorer in a late spring than in an early one. Thus I cannot see any adaptive advantage for laying smaller clutches in a later season. It is possible that there has been such strong selection for reduction of clutch-size within one season that a response has been evolved by which the tits lay a clutch of a certain size at a certain time of year. This might conflict with a possible response which enabled the birds to lay the same size of clutch at the beginning of a season regardless of whether the season was early or late.

Therefore I suggest that there has been strong selection for those birds which could lay a large clutch at the beginning of the season, but laid a smaller clutch if they were not able to start breeding so early. By far the most likely factor to influence the tits is the increase in day-length, a factor well known to stimulate breeding in many species (see Marshall 1961 for review). Indeed Suomalainen (1937) succeeded in getting both sexes of great tits into breeding condition (as judged by gonad size) in February by keeping the birds in artificial light of longer duration than day-length.

In conclusion it is clear that the great tit shows a remarkable series of responses to the external conditions when laying its clutch, although the mechanism by which it does so is not understood. The birds are not able to forecast the food supply directly and their responses are based only on the conditions normal to a given set of circumstances and, while they lay a size of clutch that is reasonably well adapted to local conditions, they sometimes respond inappropriately when these are exceptional. In addition, since conditions for rearing young vary so much from year to year, the most productive clutch-size varies also. Because of this a fairly wide range of clutch-sizes is still found in any population, presumably because each has been the most productive too frequently for it to have been eliminated by natural selection.

Survival of birds after leaving the nest

Some young great tits are more likely than others to survive after leaving the nest, but it has not been possible to show exactly how the mortality occurs. One of the most striking features that has emerged is the great variation in post-fledging survival in different

years, the ratio of young to older birds varying in different winters between 0.16 and 2.0, and the mortality varying between about 90% and 20% or less.

It has been suggested that the heavier young may be carrying more fat than the lighter ones and that it is largely this food store which enables these young to survive better than the lighter ones. In addition, among birds of equal weight, survival was better from the early part of the season than from the later part.

It seems likely that a young bird will stand a much better chance of surviving this critical period in its life if it has an internal food reserve, on which it can survive for a day or two in an emergency, than if it has no food reserve, particularly later in the season.

It seems extremely unlikely that many more of the light, rather than the heavy, young would die from predators or disease until they had become sufficiently weakened by starvation to be particularly susceptible. In other words, much of the predation which occurs after the young have left the nest can probably be looked upon as a side effect of food shortage in the same way as can much of the predation in the nest.

Extra fat on heavy chicks also conveys extra advantage in the form of insulation on cold nights. This seems very unlikely, however, to be of adaptive significance since the period when the young are first out of the nest is in late May or June when the nights are not very cold. Also, the extra weight of the heavy young seems to be of especial advantage to the late young and not the early ones, when it is even warmer.

Another aspect of the survival of the young birds which needs investigation is how well the young in the poorer habitats—gardens and pinewoods—survive after leaving the nest. Their low weights make one doubt whether many of them live long after leaving the nest—in most years at any rate. In Wytham, except for 1960 and 1962, most of the young of these weights did not survive. However, it is possible that the conditions after the young have left the nest are not so bad in gardens as in oak woodland; and the same might also apply in pinewoods where a reasonable food supply is present for much longer than in oak woodland.

Snow (1958) found that blackbirds, *Turdus merula*, unlike tits, were both denser and had better breeding success in gardens than in woodland, but here the main difference in survival between the two habitats was the heavier predation in woodland.

Conclusion

Currently, there are two major theories on the significance of reproductive rates and their relationship to adult mortality. The distinction has been clearly made by von Haartman (1954). One theory (see Lack 1954) is that animals are reproducing as rapidly as they can and, in the case of birds, that birds lay a clutch of such a size that the parents raise the largest possible number of young. By doing so these birds leave the most progeny and their genotype becomes the most common in the population. This von Haartman calls the theory of inter-individual selection. The other theory (Wynne-Edwards 1962) is that a certain number of offspring is needed to compensate for the average mortality of the species. If a group of birds produce more young than is necessary then there will be too many birds, food will become scarce and that population will become extinct. It will be replaced by another population whose individuals, by laying smaller clutches, can maintain an optimum density. This von Haartman, like others, calls the theory of inter-group selection.

One of the critical differences between these two theories is that in the first the birds' numbers are assumed to be limited by food outside the breeding season while, in the second, the birds would starve if there were more of them, but the birds lay fewer eggs to

prevent this happening. The proponents of both theories agree that birds are, ultimately, limited by their food supply, but those holding the first consider that the individual animals are in direct competition for food, while those holding the second believe that the animals have evolved mechanisms which prevent their numbers reaching a level at which any direct competition for food is necessary.

I am of the opinion that the Wytham great tit population shows some tendencies which support the first theory and very few which support the second. Firstly, it is difficult to believe that the tits are not breeding as fast as they can. This does not mean that, in every year, they start with the largest number of young that they could possibly raise, since in some years it seems likely, in retrospect, that they could have raised more than they did. However, it seems probable that the birds are laying a clutch from which they will rear the largest number of healthy young under the average conditions that are found when the young require feeding. There is also strong evidence that the clutch-sizes are adaptively adjusted to various conditions such as habitat, date of laying, density of breeding pairs and age of the individual birds. But some variations do not appear to be adaptive, such as the laying of smaller clutches in a late season, although the tits may not be able to avoid this. Similarly in Britain the great tit in pinewoods responds inappropriately because it is adapted to broad-leaved, deciduous woodland.

In broad-leaved woodland there is clear evidence that in some years the parents of the largest broods do not produce as many surviving young as those birds whose broods are slightly smaller. Thus if the tits had larger broods they would raise fewer, rather than more, young.

Another way in which it would be possible for the tits to raise more young would be to produce more than one brood. This, in oak woodland, they do not normally do. In this paper attention has been drawn to the fact that the birds do not breed as early as perhaps they might. While this difficulty is not finally resolved I have suggested that the birds cannot get into breeding condition any earlier. However, the birds could continue to breed into June and July and rear a second brood at this time. Nevertheless it is clear why, in oak woodland, they do not do this. The late broods are very unsuccessful in most years and second broods would be later and more unsuccessful still. It seems highly probable that the chance of successfully raising a small number of young is not only slight, but is outweighed by the dangers to the adults. The young in the late broods are hungry and noisy and many of the broods are found by predators, and it will be remembered that of the broods taken 20% had the female parent taken also. Probably, on average, those birds which do not have a second brood produce more young because more of them live to breed the next year. Thus second broods are not productive.

It is difficult to believe that the tits are laying only enough eggs to cover their losses. Adult losses are seldom more than 65% yet much larger numbers of young are produced than are necessary to replace them. In many of the years of high density a large proportion of these young probably perish soon after leaving the nest. Since these have presumably depleted the food for the others, this is not an efficient way of keeping the numbers down to a level where the food supply is conserved. For example it is estimated that, in 1961 in Wytham, 400 pairs may have raised about seven young each, only one of which was alive in the autumn; hence some 2000–2500 young great tits died between June and September.

Proponents of inter-group selection also suggest that birds limit their reproductive rate through many individuals not breeding in the first year of life or by their being excluded (by the other birds) from obtaining a breeding site. The first of these cannot

occur in the great tit since they breed when they are 1 year old. Also there is no evidence to suggest that there is normally a non-breeding population.

Further, it is clear that, unless the birds have very varied territorial requirements from year to year, territory size has not imposed a limit to the breeding density in most years. Since the number of pairs in Marley in 1961 was eighty-six then there must, surely, have been room for more pairs in all the other years when there were never more than fifty-one pairs. This suggestion is strongly supported by the fact that Hinde (1952), working in Marley, noted that certain, apparently suitable, parts of the wood were unoccupied. Thus even if the tits were limited by territory size in 1961 (and there is no evidence that this was so) it is unlikely that they were in any other years.

Thus the evidence seems to support the theory of inter-individual selection. The birds are reproducing as rapidly as they can, and they are apparently being limited by the food resources, presumably through competition, at least at times, both in the summer and in the winter.

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SUMMARY

Populations of great and blue tits (*Parus major* L. and *P. caeruleus* L.) have been recorded since 1947 in Wytham Wood, near Oxford; this paper is mainly concerned with the results

on the great tit from 1959 to 1963. The numbers of the two species tend to fluctuate in parallel with each other and with the numbers in other populations.

The breeding season is short, the majority of the birds having only one brood. The date of laying has varied by over a month in different years, this fluctuation being in parallel with that of some of the more common caterpillar species. It seems probable that both tits and caterpillars are affected by a third factor, possibly the opening of the oak leaves, since there is a good correlation between the mean date of laying and the temperatures in spring.

The mean clutch has varied between 12.5 and 7.8 in different years. It is suggested that the mean clutch is usually that which produces the most surviving young, though this is not always so. Four sorts of variations in clutch-size are shown, namely that clutches are smaller later in the season, smaller at higher densities, smaller in habitats with fewer large trees, and smaller when laid by birds which are breeding for the first time. These are all explained on the basis that by laying a smaller clutch when the chances are not so good for raising young the parents are more likely to raise some healthy young which will survive to breed than if they had a larger clutch; hence such modifications have been produced by natural selection acting on the individual through the number of progeny it leaves.

It seems that most of the young tits are normally dead before the winter; the number that are still alive at the beginning of winter is usually a good indication of whether there will be an increase or a decrease in the numbers breeding the next year. The numbers of tits are also influenced to a considerable extent by the size of the beech-mast crop. If there is a large crop more birds survive than if there is not. This may be partly because many other crops fluctuate in parallel with those of the beech.

Attention is drawn to the fact that the earliest breeding birds produce the most surviving offspring. Discussion centres on why, if this is so, most great tits do not breed earlier than they do. The only likely solution seems to be that the birds are unable to get sufficient food earlier in the season to produce eggs.

It is considered that the great tits in Wytham are, usually, rearing as many young as they are able to and that the numbers are greatly influenced by the food supply, both immediately after the breeding season and during the winter.

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