

A Comparative Study of the Breeding Ecology of the Great Tit *Parus major* in Different Habitats

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A COMPARATIVE STUDY OF THE BREEDING ECOLOGY OF THE GREAT TIT *PARUS MAJOR* IN DIFFERENT HABITATS

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1. INTRODUCTION

The Great Tit *Parus major*, a territorial songbird of woodland, occupies a wide range of habitats, both during and outside the breeding season. In his review of the breeding habitats of Eurasian tits, Snow (1954) described the Great Tit as "in many areas the most euryoecious species". On the other hand, he stated that coniferous forests tend to be avoided. Deciduous woods form the main breeding habitat over most of its range.

An analysis of the extensive literature on breeding densities in relation to habitat (Chapter 3) shows that the breeding densities of Great Tits in deciduous forests are several times higher than those recorded for coniferous forests. Moreover, Kluyver & Tinbergen (1953) have found that a mixed habitat (i.e. with both deciduous trees and conifers) is preferred by settling Great Tits to a pure coniferous stand. This probably also applies to pure deciduous woods as opposed to coniferous woods. The question arises whether such habitat selection is adaptive, i.e. whether the requisites for successful reproduction are in short supply in the non-preferred type of habitat. The main requisites to be considered in this case are: the availability of suitable nesting holes, and a food supply sufficient for the energy demands of reproduction.

The importance of nesting holes becomes apparent from the literature on breeding densities in several types of habitat, with or without the provision of artificial nesting sites (nestboxes). In Chapter 3 it will be shown that woods almost uninhabited by Great Tits are occupied after the introduction of nestboxes. By this means Great Tits can be tempted to settle in a variety of places where the density would otherwise be at most very low. This applies at least to the present-day habitats in Western Europe, which are heavily influenced by man and are consequently poor in tree holes.

Even when a sufficient number of nestboxes is available, the breeding density in coniferous woods never reaches the level in deciduous woods (p. 6). This suggests that the preference for a certain type of habitat is not based on the availability of nesting holes, but on other factors in the environment. Feeding conditions during the breeding season have long been suspected

to be the ultimate factor (cf. Gibb & Betts 1963, Kluyver 1963, Lack 1955, 1958, 1966). Evidence for the operation of this ultimate factor can be obtained by studying the proximate effects of food on breeding success and related aspects of the breeding ecology. In this paper the effects of feeding conditions during the breeding season of the Great Tit are treated systematically by comparison of the reproductive cycles in two contrasting habitats, oak- and pinewoods. These two types of habitat were chosen because it was apparent from the literature that they represented a very favourable and a relatively unfavourable habitat for the breeding of Great Tits.

2. STUDY AREAS

The observations reported here were carried out in four woodland areas, two oakwoods on fertile soil, representing the preferred habitat-type, and two pinewoods on poor sandy soil, where the natural breeding density is extremely low. One of these areas is situated in the southern part of The Netherlands (Liesbosch, near Breda), the other in the central part, near Arnhem. Short descriptions of the areas are given below.

H o g e V e l u w e : the total area with nestboxes covers about 320 ha in the southern part of the National Park "Hoge Veluwe". The main work was done in the northwestern part of this area (part A, 160 ha with c. 95 nestboxes). The vegetation consists of 50–80 year old plantations of Scots Pine *Pinus sylvestris* with locally very poor undergrowth, while in other places birches *Betula* ssp. and American Bird-cherry *Prunus serotina* provide much more undergrowth. Regularly some of these plantations have been felled and replanted with young conifers, locally mixed with deciduous shrubs, but these areas were not included for the computation of tit densities. Nestbox inspection was started in 1955, when the inhabitable area of part A measured 83 ha (70 boxes); this part was enlarged to 122 ha (100 boxes) in 1956, and to 138 ha (96 boxes) in 1959; the inhabitable area later decreased slowly, due to fellings, to 122 ha in 1966 (92 boxes).

The adjoining area (part B, about 160 ha) has a mixed vegetation of Scots Pine, birches, oaks (*Quercus robur* and *Q. borealis*) and some Beeches *Fagus sylvatica*. In part B the nestboxes were introduced in the autumn of 1958. The inhabitable area varied from 111 to 125 ha in the period from 1959–1968, the number of nestboxes from 121 to 159.

Unless otherwise stated, reference to Hoge Veluwe means the pine part A, and reference to pine means *Pinus sylvestris*.

I m b o s c h : uniform plantations of Scots Pine. Of the total area, c. 80 ha with 41 boxes, 70% consists of mature pinewood (about 65 years old in 1965), the remainder being younger (planted in 1919–1932). This area was studied from 1961 to 1966.

Oosterhout: a small deciduous wood with mature oaks predominant, situated on rich loamy soil near the Waal River. Shrubs and herbs form a dense undergrowth. In 1956 there were 12 nestboxes (on 4 ha), increasing in 1957 to 24 boxes on 9 ha, in 1959 to 29 boxes on 11.4 ha, in 1964 to 48 boxes, in 1965 to 78 boxes, and in the autumn of 1966 to 147 boxes (11.4 ha). The wood is surrounded by meadows, arable land, and orchards, and is isolated from other woods.

Liesbosch: mature oakwood, with many beeches and clumps of conifers locally. This area too is situated on fertile soil. Size about 190 ha, but only small parts are used as nestbox areas. Part A (18 ha) has carried 63 boxes since 1955 and 97 boxes since autumn 1957. This part can be characterised partly as *Violeto-Quercetum*, partly as *Querceto-Carpinetum* (Leys 1965). In a second part (B: 16 ha) 70 boxes were introduced in the autumn of 1959. The vegetation is more varied than in A, but oak is still the most numerous tree. In another part of the wood (C) about 25 boxes are distributed over a large area with similar vegetation (c. 50 ha), creating an area with a low breeding density. Most of the observations were done in part A, but in Chapters 6 and 9 results from part C will be compared with those from part A.

In all areas nestbox inspections were performed at least weekly during the breeding season. This provided us with data on breeding density, dates of egg laying, clutch-size, and numbers of young hatched and fledged. All parent tits in the Hoge Veluwe and Liesbosch woods were caught and ringed from the start of the study and in Oosterhout from 1964 onward.

3. BREEDING DENSITY

Because of the frequent visits to the nestboxes and the identification of the breeding tits by capture on the nest, the number of breeding pairs in the study areas is known exactly. The number of Great Tits breeding outside the nestboxes is known to be negligibly small.

Table 1 shows the breeding density in the study areas, and demonstrates the great differences between the densities found in a rich oakwood and a poor pine plantation. The mean density in the mixed wood on sandy soil (5.8 pair per 10 ha) is significantly * higher than that in the adjoining pine plantation (2.2 pairs), but does not approach the high densities found in the two rich oakwoods, where the mean density is about 23.

The differences in breeding density cannot be caused by differences in nestbox density, for there were usually sufficient numbers of unoccupied boxes, especially in the pinewoods (cf. note c).

* The value for significance has been taken throughout the paper as $P < 0.05$. In this case Student's t-test was used.

Table 1. Breeding density, in number of pairs per 10 ha, over a 10-year period.

Year	Hoge Veluwe		Imbosch	Oosterhout	Liesbosch
	A	B			A
1959	2.5(34)	4.8(58)	—	12.3(14)	28.9(52)
1960	1.3(17)	4.8(57)	—	7.0(6)	17.2(31)
1961	3.7(50)	8.6(101)	2.8(22)	14.0(16)	34.4(62)
1962	1.2(16)	3.9(46)	2.8(22)	11.4(13)	25.0(45)
1963	1.1(14)	3.9(46)	0.9(7)	10.5(12)	18.3(33)
1964	1.2(15)	4.0(47)	1.3(10)	14.9(17)	24.4(44)
1965	3.7(45)	7.8(88)	2.3(18)	24.6(28)	30.6(55)
1966	2.0(25)	5.7(63)	1.5(12)	22.8(26)	17.2(31)
1967	2.3(28)	7.1(85)	—	24.6(28)	16.7(30)
1968	3.4(42)	7.1(89)	—	19.3(22)	19.4(35)
Mean density	2.2	5.8	1.9	22.8	23.2

- Notes :
- Values between parentheses indicate the number of pairs.
 - In Oosterhout there was a shortage of nestboxes up to 1965; the mean density was therefore calculated for the years 1965-1968.
 - In some years, when in some woods almost all the boxes were occupied by Great Tits and other species, some Great Tit pairs may not have been able to occupy a nest site and the potential density may therefore have been higher. This applies to 1961 (Hoge Veluwe B, Liesbosch), 1965 (Hoge Veluwe B, Liesbosch) and 1967 (Hoge Veluwe B). This factor is, however, unlikely to play an important role, for the Great Tit is known to be dominant over the other species in the competition for nest sites. In any case the operation of this factor could only increase the difference in mean density between oak- and pinewoods.
 - With the publication of these values the approximate figures given by Kluyver (1963, 1966, 1971) are supplemented and partly corrected.

These density figures have been compared with data from the literature, collected from habitats similar to the woods in the present study.

For comparison the following conditions must be fulfilled :

An adequate description of the habitat should be available, to permit comparison with our habitats. The vegetation of the habitat had to be sufficiently uniform, as regards species composition and age of the trees. Since the breeding populations of tits are strongly affected by the availability of nest sites – a subject of indirect interest to this study – information on this point is needed. The most instructive cases are those in which no artificial nest sites are available and those in which nestboxes are present in large numbers, in excess of the total population of hole-nesting passerines. In the latter case the total nestbox area should not be too small (at least 5 ha), otherwise a substantial part of the territories would probably extend beyond the nestbox area. The size of the breeding population had to be given in terms of pairs, individuals, or first clutches, or as the number of singing males. Figures for total numbers of broods were considered an inadequate basis for the cal-

culuation of breeding density when the proportions of first, repeat, and second broods were unknown.

For each area, which could be used for this comparison, the breeding density was calculated as the number of pairs per 10 ha. When data from more than one year are known, the mean density over the period of study is given.

For mature oakwoods on fertile soil the published densities range from 9.6 to 21.7 pairs per 10 ha (Berndt & Franzen 1964, Lack 1958, 1964, 1966), and for mixed deciduous woodland from 14.4 to 22.7 pairs (Lack 1966, Schlegel 1966). This applies to woods abundantly provided with artificial nest sites. The densities found by us are at the upper limit of the range indicated in the literature. Higher densities have been reported from time to time, but these concern very small areas, where it is improbable that the birds would restrict their activities to the small nestbox area and avoid the surrounding area (e.g. Duderstadt 1964, Donner & Höninger 1961).

In similar woods without artificial nest sites the density is considerably lower, ranging from 1.9 to 13.3 pairs per 10 ha (Ferry 1960, Niebuhr 1948, Schlegel 1966, Schütte 1957, Stein 1960, van Stijvendaele 1963). The differences are partially due to a variable supply of natural nest sites (holes in trees), dependent on the age of the trees and on the degree of forestry management applied.

Pinewoods without nestboxes have a very sparse population of Great Tits. The density in pure pinewoods is often nil, and only where there is an admixture of deciduous trees does the density reach 2.0 pairs per 10 ha (Bruns 1959, Glasewald 1933, Kluyver 1951, Rabeler 1950, 1962, Schiermann 1934, Schumann 1947, Siefke 1964, Tinbergen 1949, v. d. Ven & Mörzer Bruijns 1965). The published figures for Scandinavia are in general somewhat lower, and do not exceed a value of 0.7 pairs per 10 ha.

The introduction of nestboxes in pinewoods result in an appreciable increase in density, but the published figures vary considerably (between 1.3 and 11 pairs per 10 ha). The highest figures concern pinewoods with an undergrowth formed by a rich herb layer and deciduous trees. In the poorer types of pine plantations the density does not exceed 4 pairs per 10 ha (Berndt 1938, Berndt & Franzen 1964, Bruns 1959, Kluyver 1951, Over 1958, Tinbergen 1946, 1949, 1960).

Summarizing we may state that in the poor type of pinewood, exemplified by Hoge Veluwe A and Imbosch, the breeding density of Great Tits is practically nil where no nestboxes are supplied, and 1–4 pairs per 10 ha where there is a good supply of nestboxes. Oosterhout and Liesbosch represent the other extreme of a range of habitats, in which the density usually does not exceed 10 pairs per 10 ha in areas without artificial nest sites and amounts to 10 to 23 pairs per 10 ha in areas with a sufficient number of nestboxes.

The areas studied by Dhondt (1970) are intermediate in density between

the two extreme habitats investigated in the present study. Zevergem, mainly oakwood, has a mean density of 17.4, slightly below that of Oosterhout and Liesbosch. In Maaltepark (deciduous park) and Hutsepot (beech wood) the density is considerably lower. The pinewood C.O.O. is much richer in vegetation, including some deciduous trees, than our pinewoods, and has a much higher density of Great Tits (11.0 pairs/10 ha). Where appropriate Dhondt's results will be compared with ours.

4. FOOD SUPPLY

4.1. INTRODUCTION

Because the diet of the Great Tit in spring and summer includes many species of invertebrates, it was obvious from the start that it would be impossible to study the densities of all these species. Moreover, the diet of the adult tits is poorly known (cf. Betts 1955b). We therefore had to confine ourselves to density estimates for the most important prey species fed to nestlings.

The Great Tit generally feeds in the lower levels of the vegetation, including the ground level, but during the breeding season its main feeding stations are in the canopy, at least during the period of maximum caterpillar abundance (Betts 1955b, Gibb 1954, Gibb & Betts 1963, Royama 1970, Tinbergen 1960). Other feeding stations, mainly in undergrowth and herbage, are used after the peak of caterpillar abundance has passed in oakwoods (Royama 1970) and before the peak in *Panolis* abundance in pinewoods (Gibb & Betts 1963, Tinbergen 1960). This situation must be kept in mind when feeding conditions are studied by sampling the canopy fauna.

Several authors have studied the food of Great Tit nestlings in habitats similar to those of the present study (Kluyver 1950, Betts 1955b, Pfeifer & Keil 1959, Henze & Görnandt 1959, Bouchner 1960, Tinbergen 1960, Gibb & Betts 1963, Bösenberg 1964, 1966, Kabisch 1965a, 1965b, Royama 1970). In most of these studies the composition of the nestlings' diet was investigated, and the results were expressed as percentages by number. Most of the authors agree that Lepidoptera taken from the canopy form the bulk of the food. The percentage found in oakwoods (usually in first broods) ranges from 72 to 91 (Bösenberg 1966), and in all studies larvae are predominant in the food. Late oakwood broods have seldom been investigated, but Henze & Görnandt (1959) state that 68.5% of the food in second broods consists of Lepidopterous larvae, pupae and imagines. Royama (1970) observed that after the middle of June a large proportion of the food consisted of herb-feeding caterpillars.

In pinewoods, according to the literature, the situation is rather more variable. In early broods Lepidoptera are not used as food so frequently (cf. Kabisch 1965a, 1965b), but in late broods the proportion of the Lepidoptera is usually high, e.g. from 59 % (Kabisch 1965a) to 68 % (Bösenberg 1964).

Kabisch (1965a) points out that Lepidoptera become still more important when the results are expressed in percentages by weight. Tinbergen (1960) and Mook et al. (1960) observed that during May and early June a large proportion of the food brought in the early morning hours consisted of *Bupalus piniarius* moths, which were picked up from the ground after their emergence.

Most authors agree that there is a preference for caterpillars (and some sawfly larvae in pinewoods) as food, i.e. that the appearance of caterpillars in the habitat is soon followed by its acceptance as food, reducing the importance of the other types of prey.

In view of these considerations it seems justified to judge the feeding conditions for the nestlings by sampling the density of the caterpillars in the canopy, but we should keep in mind that in this way only the preferred types of food are sampled.

The diet of the nestlings in our populations will be reported and the importance of caterpillars as food will be discussed in Chapter 7.

4.2. METHODS

Among several suitable methods preference was given to one requiring less work during the breeding season of the tits, thus enabling us to spend more time on the ornithological aspects of the study. This method, which was also used by Gibb (1950), Betts (1955b) and Tinbergen (1949, 1960), consists of collecting, counting, and weighing the faecal pellets (frass) produced by caterpillars which drop from the tree crowns.* For this purpose we used frass collectors made of cheese-cloth, suspended in a metal frame measuring 50 x 50 cm. Usually 10 to 15 collectors were used in each wood. The collectors were emptied as simultaneously as possible, but the intervals varied due to weather conditions. The contents were stored in paper bags in the laboratory until following winter. By then, the contents of the paper bags were roughly air-dry (5.6% water), and at least did not lose more weight when kept longer (3 years). Thus the moisture content of the sample was uniformly low.

During the winter the contents of the paper bags were sieved, to remove needles, leaves, twigs, and other debris, before weighing. The pinewood samples were examined as a whole, whereas from the larger oakwood samples sub-samples were taken, weighed, and examined. The contents of the samples could be estimated from the weights of the sample and sub-sample. For pinewood samples we used 0.6 mm as minimal accepted diameter of the faecal pellets, following Tinbergen (1960). For oakwood samples the minimal diameter was 0.2 mm, because our observations had shown that pellets smaller than this are produced by the younger instars,

* It should be kept in mind that the frass of a few species living inside buds is not collected by this method (cf. p. 50).

which are rarely fed to Great Tit nestlings. (The minimal diameter differs in the two types of wood because of the size differences in available prey and consequently in the choice of prey; see below). After sieving, the faeces were sorted under a binocular microscope, identified, if possible, and then counted and weighed. The frass from the two main oak caterpillars (*Tortrix viridana* and *Operophthera brumata*) could not be separated, so all faeces from the oakwood samples were taken as a single category. The two species together form the bulk of the caterpillar stock and of the food eaten by the nestlings.

It was possible to identify the frass of most of the species or families in the pinewood samples (cf. Tinbergen 1960). The frass from these species or groups was counted and weighed separately. Frass from *Diprion* species (sawfly larvae) was excluded, as these larvae are rarely fed to the young because of the tit's preference for other larvae (Tinbergen 1960, Prop 1960). *Diprion* faeces rarely formed an important part of the faeces sample. In most years *Panolis flammea* predominated on the basis of both the number and the large size of the faeces.

This treatment of the samples resulted in values indicating the weight of frass falling per day on an area of 0.25 m². The frass weight may be regarded as a quantity directly related to the number and the biomass of the caterpillars in the canopy. It therefore seems justified to use the caterpillar frass weight per day and per area as a measure for the feeding conditions of the tits. It is also possible to use the number of caterpillars or the total biomass of caterpillars per area. The first quantity has a serious drawback, however, because the size of different species (and larval stages) of caterpillars varies enormously, making them more valuable or less valuable as prey. In particular, the most common caterpillars in oakwoods and pine-woods differ in size, those in oakwoods rarely reaching 100 mg, those in pine-woods often reaching 500 mg. To calculate the total biomass of caterpillars from the weight of the collected frass, we have to know the frass production of caterpillars of known weight. Literature on this topic is scarce (e.g. Friden 1958), but the frass production of some species is known in terms of number (or weight) of faeces per caterpillar. These figures were supplemented with the results of rearing experiments, which I made under outdoor conditions, particularly with *Tortrix viridana* and *Operophthera brumata*. The weight of frass collected in the woods could therefore be converted to numbers of caterpillars per area, and by multiplication with the average weight of the caterpillars (taken from our own observations and data in the literature) we could arrive at a first approximation of the total biomass of caterpillars present at a given moment.

4.3. RESULTS

For the rearing of the nestlings to be successful, it is necessary that prey be available in sufficient numbers during the nestling period. Differences in

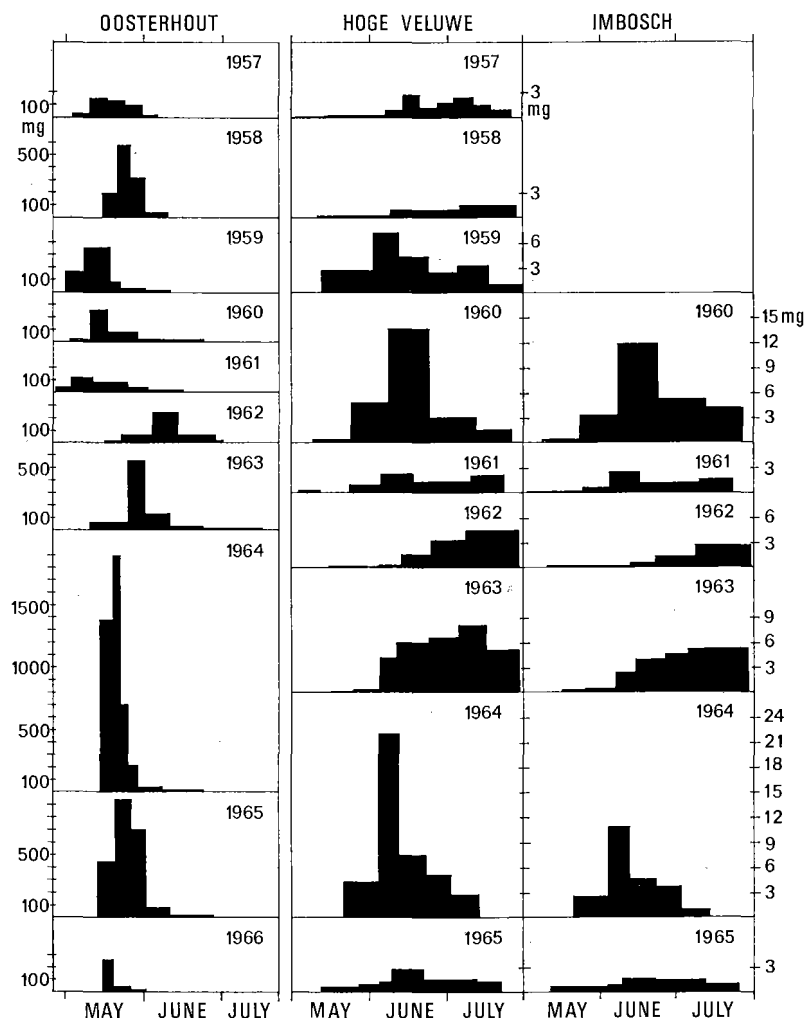


Fig. 1. Weight of caterpillar frass falling per day per 0.25 m², in one oakwood (Oosterhout) and two pinewoods (Hoge Veluwe, Imbosch). Note the large difference in scale. Additional data are available for Oosterhout (1967) and for Liesbosch (1961, 1962).

feeding conditions between oakwoods and pinewoods can be divided into differences in the level of caterpillar density and differences in the period of maximum abundance. Both aspects are shown in Fig. 1, which gives the results of frass collecting that served as the basis for all further calculations. The amount of frass falling in the oakwoods is clearly many times larger than the amount in the pinewoods (note the difference in scale). The level of the annual peaks in frass fall in the different woods is compared in Table

Table 2. Maximal amount of caterpillar frass, in mg per day per 0.25 m²

Year	Oakwoods		Pinewoods	
	Oosterhout	Liesbosch	Hoge Veluwe	Imbosch
1957	153	—	2.7	—
1958	598	—	1.7	—
1959	364	—	7.0	—
1960	264	—	13.6	11.8
1961	119	210	2.2	2.6
1962	240	275	4.4	2.6
1963	550	—	8.1	5.1
1964	1895	—	22.1	10.7
1965	938	—	2.8	1.5
1966	263	—	—	—
mean	538.4	—	7.2	5.7
standard deviation	537.4	—	6.8	4.5
coefficient of variation	99.8%	—	94.3%	78.0%

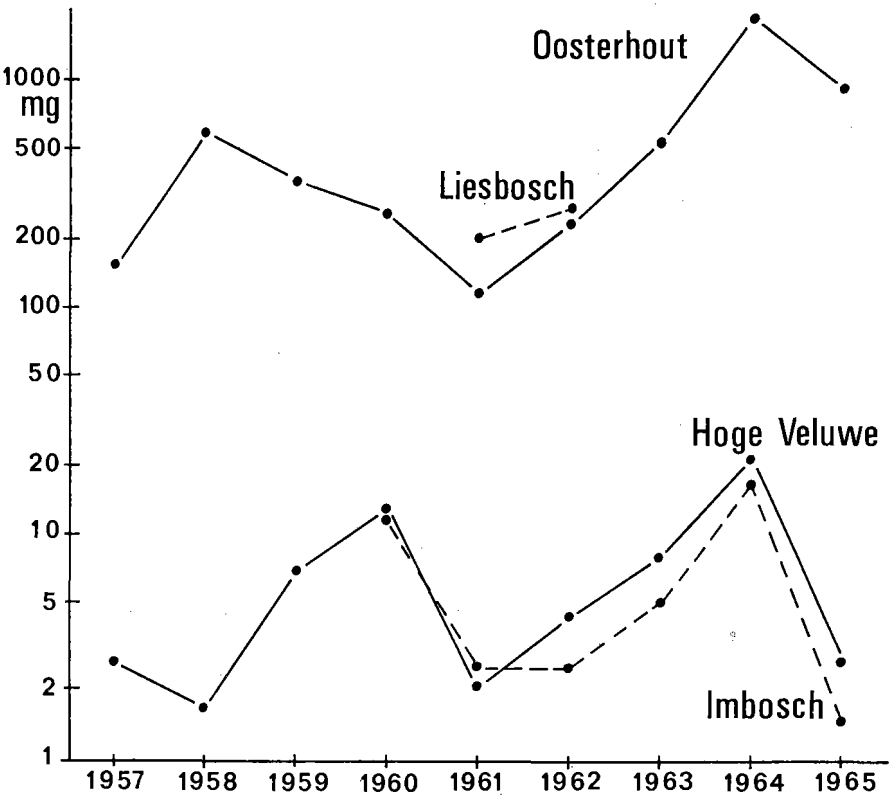


Fig. 2. Size of the annual peaks in caterpillar frass fall in two oakwoods (Oosterhout, Liesbosch) and two pinewoods (Hoge Veluwe, Imbosch); ordinate in logarithmic scale.

2 and Fig. 2. In the oakwoods the annual peaks vary between 100 and 2000 mg, in the pinewoods between 1 and 25 mg per day per 0.25 m². The yearly fluctuations in frass fall are very large, but they do not differ relatively in amplitude between the two types of wood, as judged from the coefficients of variation (standard deviation as percentage of the mean) in the Oosterhout and Hoge Veluwe data.

Table 3 gives the total biomass of the caterpillars (per 0.25 m²) which produced the annual peak in frass fall. While the maximal amounts of frass in the two habitats differed by a factor of 100, the difference is much larger when frass data were converted into caterpillar biomass, because the pine-wood caterpillars have a higher frass production, in mg frass per mg body weight. Presumably, this is related to differences in digestibility of the food consumed by the caterpillars (pine needles and oak leaves).

Table 3. Maximal biomass of caterpillars, in mg per 0.25 m²

Year	Oosterhout	Hoge Veluwe	Imbosch
1957	1500	6.6	—
1958	5400	4.0	—
1959	4300	18.9	—
1960	2260	34.8	20.6
1961	1180	4.4	6.5
1962	2070	12.6	6.6
1963	4900	18.3	11.9
1964	16190	59.2	30.7
1965	8300	5.2	2.5
1966	2210	—	—
mean	4730	18.2	13.1

Thus, the abundance of caterpillars is far greater in the oakwoods, making this type of wood a much more favourable habitat for rearing young. This conclusion is supported by the results obtained by several authors who studied the Great Tit in one of these types of habitat. Figures on caterpillar abundance in Wytham Wood, measured by different methods, have been published by Gibb (1950), Lack (1954, 1955, 1958) and Perrins (1965). The most complete series, given by Perrins (1965, Fig. 10), shows a peak density varying roughly from 100 to 1300 larvae per m² or 2500 to 32500 mg biomass per 0.25 m², which is about twice the value found for Oosterhout. The figures published by Betts (1955b), on oak caterpillar abundance in the Forest of Dean, work out slightly lower (85 to 307 larvae per m², or 2100 to 7700 mg per 0.25 m²), but during 1950 and 1951, when these measurements were taken, the caterpillar population was unusually low.

Tinbergen (1960) made a long-term study of the relation between tits and insect larvae in a pinewood near Hulshorst (northern Veluwe). The total peak densities he measured were usually of the order of 0.5 to 2.0 larvae per m² (see his Table III). Gibb & Betts (1963) determined caterpillar ab-

undance in the pinewoods of Thetford Chase (Norfolk) during the breeding seasons of 1955 and 1956. The peak value, expressed in mg biomass per m², amounted to 290 and 229 mg in these years, or 72 and 57 mg per 0.25 m², respectively. Since pupae were included, the divergence from our figures is not as large as comparison with the data of my Table 3 suggests.

Fig. 1 shows that the peak in the frass fall in Oosterhout occurs in the early part of the season. With one exception, all the peaks fall before 1 June. This corresponds approximately with the period in which the first broods are reared. A more exact measure of the chronology of the caterpillar season is given by the median dates of frass fall given in Table 4. From this Table it is clear that the median dates in the oakwoods fall between dates 43 and 70, i.e. 13 May and 9 June, and usually in the second half of May. This is in good agreement with the figures for Wytham Wood given by Perrins (1965, Figure 3). The relationship between the period of caterpillar abundance and the tit breeding season in Oosterhout and Wytham will be discussed in section 5.2.

Table 4. Median dates of caterpillar frass fall (dates are numbered from 1 April = 1)

Year	Oakwood		Pinewood	
	Oosterhout	Liesbosch	Hoge Veluwe	Imbosch
1957	50	—	94	—
1958	56	—	101	—
1959	44	—	75	—
1960	46	—	76	82
1961	43	44	85	82
1962	70	71	104	106
1963	60	—	97	100
1964	50	—	71	72
1965	54	—	82	90
1966	49	—	—	—
mean date	52.2	—	87.2	88.7
standard deviation	8.2	—	12.2	12.6

The situation in the Dutch pinewoods studied presents a quite different picture. Here, the median dates of frass fall range from 71 to 106, i.e. from 10 June to 15 July. The collection of caterpillar frass was usually stopped at the end of July. In some years, e.g. 1958 and 1961, the pine looper *Bupalus piniarius* was rather common. This caterpillar has its main growth period in August–October, i.e. outside the tits' breeding season, and is therefore excluded from these calculations.

In Tinbergen's study (1960, Table III) the annual peak of the prey populations usually occurred in June, but occasionally in May, July or August. Furthermore, peak and low years differed between species, which reduced the overall fluctuations in the availability of food. The observations by Gibb & Betts (1963) seemingly contradict our results, because in both years of

their study the caterpillar peak fell in July. Since the caterpillars were rather late in these years (1955 and 1956), both in Wytham and in Hulshorst (1955), I do not regard the results from Thetford Chase as conflicting with our results. It may therefore be said that the caterpillar peak in pinewoods usually occurs in June or July, considerably later than in oakwoods.

The median dates in the two Dutch pinewoods show parallel variations, the Imbosch peak usually falling some days later (Table 4; Kendall rank correlation test, $P < 0.05$). The median dates in oakwoods and pinewoods are also correlated, but not significantly. This phenomenon is probably based on the similar temperature dependence of both groups of caterpillars.

Table 4 shows that the median date of frass fall in the two pinewoods is more variable than the median date in Oosterhout, as judged from the standard deviations. However, the variances of the two samples do not differ significantly (Fisher's F-test, see de Jonge 1960, p. 371). The great variability in time of the caterpillar peak was also apparent in Tinbergen's (1960) study.

In Chapter 5 we will consider the effect of the air temperature on the time of the caterpillar growth period and on the breeding season of the tits. For the moment, we conclude that the maximum food supply in the oakwoods is many times larger than that in the pinewoods, and that the period of maximum food supply occurs much earlier in the former.

5. TIMING OF THE BREEDING SEASON

5.1. INTRODUCTION

In this Chapter we will examine the relation between the period of maximal food requirements and the period of maximal food supply. The question arises whether the breeding season of the Great Tit is adjusted to the feeding conditions in both types of wood in such a way that the nestlings are reared under the best possible conditions. This is an aspect of the general problem of the evolution of breeding seasons, as studied by Lack (1950, 1954) and many other authors (for a recent review see Immelmann 1971). These authors concluded on general grounds that the availability of food for the nestlings is the main ultimate factor in the evolution of breeding seasons.

Gibb (1950) showed for Wytham Wood near Oxford in 1948 and 1949, that the maximal number of Great and Blue Tit broods present in his boxes coincided with the period of maximal caterpillar abundance as measured from the volume of faecal pellets, but he did not consider the changes in food requirements that are connected with the development of the nestlings. The coincidence has been confirmed by the data obtained in later years and published by Lack (1954, 1955, 1958, 1966) and Perrins (1965). These authors characterized the period of peak abundance of the caterpillars by the date of "half-fall" of the winter moth *Operophtera brumata*, i.e. the

date by which half of the larvae of the most abundant caterpillar species has fallen to the ground and thus becomes unavailable to the tits. This date appears to be a good indicator of the peak biomass of caterpillars, since the peak weight of the individual caterpillar is reached shortly before pupation. From the values given by Perrins (1965, Fig. 3) and Lack (1966, Fig. 6) it is clear that the relation between the breeding season and the caterpillar season is not very close and shows wide annual variations. In some years the caterpillars are most abundant when the nestling Great Tits are 2–4 days old, in other years when they are 13–14 days old. This is an important difference, because the food requirements of the nestlings increase considerably with age (see below).

Duderstadt (1964), who studied the insects in an oakwood near Hannover, found that in 1957 the peak in caterpillar abundance roughly coincided with the period in which most hole-breeding species reared their nestlings, but in 1960 the caterpillars were earlier. From his observations (1964, Tables 6 and 7, Fig. 13) it can be calculated that the average hatching date of the Great Tit in 1959 preceded the caterpillar peak by about 4 days, whereas in 1960 the caterpillar peak preceded it by 2–3 days. The latter result deviated appreciably from the observations in Oxford and in The Netherlands (see p. 20).

Altenkirch (1965) concluded from data in the literature that the nestling stage of tits from first broods coincides approximately with the last larval stage of *Operophtera brumata* and the pupal stage of *Tortrix viridana*.

The timing of breeding seasons has of course also a *proximate* aspect. This concerns the factors, including environmental stimuli, that directly determine the onset of laying. Firstly, the increasing daylength in the spring will be important in this respect, but its role in the gonadal development of the Great Tit is not fully investigated. Secondly, the air temperature in the spring is to a large extent responsible for annual variations in the onset of laying (Kluyver 1951, 1952). The influence of the air temperature on the start of laying in our populations must therefore be examined, and it will be interesting to make a comparison with the effect of the air temperature on the development of the caterpillar stock.

Perrins (1965, 1970) has suggested that the timing of the breeding season is determined by proximate rather than ultimate factors. In particular he argued that the female Great Tit produces her eggs as soon as the food supply in the spring permits. Recently, Jones (1972) found that differences in time of breeding show good correlation with differences in body weight between females, small birds laying several days earlier than large ones. According to him small females have lower energy requirements for normal body maintenance, hence they are able to produce eggs sooner, when the availability of food increases in the spring.

5.2. TIMING IN OAKWOODS

In this section the proximate and ultimate aspects of the timing mechanism in oakwoods will be discussed. Emphasis will be on the first clutch, since only a small and variable proportion of the breeding population produces a second clutch. The relevant data, i.e. the mean dates of laying and hatching, as well as other information on the first clutch in Oosterhout, are presented in Table 5. The timing of these phenomena is compared with air temperatures in the period February–June taken from monthly reports of the K.N.M.I. (Royal Netherlands Meteorological Institute).

Table 5. Timing of the breeding season in oakwood: Oosterhout 1957–1966 (Dates counted from 1 April = 1)

1 Year	2 Mean laying date of first egg a	3 Mean clutch -size	4 Mean incubation interval b	5 Mean start of in- cubation c	6 Mean date of oak leaf emergence d	7 Mean hatching date	8 Date of cater- pillar peak	9 Dif- ference between 8 and 7
1957	14.8(9)	8.9	?	?	?	37.8	50	12.2
1958	34.1(8)	10.6	0	43.7	(39)	55.8	56	0.2
1959	18.6(10)	10.6	−0.2	28.0	(33)	40.6	44	3.4
1960	21.0(8)	10.5	?	c. 31.0	36	43.5	46	2.5
1961	14.1(15)	9.9	−1.0	22.0	17	35.3	43	7.7
1962	29.4(10)	9.7	0	38.1	39	51.4	70	18.6
1963	23.5(11)	10.9	+1.0	34.4	34	46.6	60	13.4
1964	22.2(17)	10.7	−1.0	30.9	32	44.9	50	5.1
1965	26.3(19)	9.3	+0.4	35.0	39	48.7	54	5.3
1966	27.2(25)	9.9	−1.0	35.1	31	48.4	49	0.6

- Notes: a. Values between parentheses in column 2 give the number of clutches studied.
 b. The incubation interval (the interval between the laying of the last egg and the start of incubation) was not determined in all years.
 c. Mean start of incubation is the sum of the values in columns 2, 3, and 4, minus one day.
 d. The opening of the oak buds was recorded roughly in 1958 and 1959; in later years large numbers of oaks were observed and the stages of leafing were recorded as 0, 1, 2 or 3. The date on which stage 1 is reached by the average tree is given here in column 6.

The mean hatching date is determined largely by the mean date on which the first egg of the clutches is laid. Annual variations in mean clutch-size are small (from 8.9 to 10.9 eggs), and contribute at most two days to annual variations in hatching date. The date of hatching is also affected by the incubation interval, i.e. the interval between the date of laying of the last egg and the onset of regular incubation. This interval tends to be positive at the start of the breeding season and to shift, as the breeding season progresses, until late and second breeders start incubation several days before the clutch is completed (Zink 1959). The mean incubation interval

in first clutches varied between -1 day and $+1$ day over the 10-year period. The slight annual variation has only a minor effect on the mean date of hatching.

Kluyver (1952) showed that the spring temperature is the most important factor determining the onset of laying, since annual variations in spring temperature, especially in the period from 16 March to 20 April, account for most of the annual variation in the laying date. This was confirmed for British Great Tits by Lack (1955, 1958, 1966) and Perrins (1965). Recently, Dhondt (1970) found that the start of laying in Belgian populations of Great Tits is affected by the air temperature in a more complex way. Laying starts if, firstly, a certain warmth sum has been reached (about 195° starting from 1 March) and, secondly, the daily mean temperature has increased to about 10°C .

I have not applied this approach, but compared the mean laying dates in Oosterhout (Table 5) with mean air temperatures recorded at De Bilt (50 km WNW from Oosterhout), for periods with several starting dates and 20 April as a fixed final date. The correlation with the laying date was significant for all periods studied (see Table 6a), and the closest correlation was found for the period from 1 March to 20 April. This implies that temperatures before 1 March did not contribute to the timing of laying. It is clear that the laying date is determined over a rather long period in spring.

Table 6. Results of Kendall rank correlation analysis. Correlation coefficients (τ) and significance (* = $P < 0.05$, ** $P < 0.01$) are given for correlations with mean air temperature measured during periods ending 20 April

Starting date	a Relation between laying date in oakwood and air temperature	b Relation between caterpillar peak in oakwood and air temperature	c Relation between laying date in pinewood and air temperature	d Relation between caterpillar peak in pinewood and air temperature
1 Jan.	-0.564^{**}	-0.622^{*}	-0.636^{**}	-0.111
11 Jan.	-0.551^{**}	-0.622^{*}	-0.651^{**}	-0.111
21 Jan.	-0.615^{**}	-0.667^{**}	-0.697^{**}	-0.222
1 Feb.	-0.615^{**}	-0.667^{**}	-0.697^{**}	-0.194
11 Feb.	-0.692^{**}	-0.667^{**}	-0.788^{**}	-0.278
21 Feb.	-0.731^{**}	-0.778^{**}	-0.863^{**}	-0.444
1 Mar.	-0.782^{**}	-0.600^{*}	-0.682^{**}	-0.250
11 Mar.	-0.769^{**}	-0.533^{*}	-0.576^{**}	-0.333
21 Mar.	-0.718^{**}	-0.667^{**}	-0.606^{**}	-0.555^{*}
1 Apr.	-0.718^{**}	-0.489	-0.394	-0.361
11 Apr.	-0.410	-0.200	-0.242	-0.528

As mentioned above, the annual variations in clutch-size and incubation interval are slight. Consequently, the start of incubation occurs about 9 days after the laying of the first egg, and shows equally good correlation with spring temperatures. Furthermore the start of incubation coincides approximately but not closely with the opening of the oak buds. The opening of

these buds also depends on the spring temperatures, but this correlation was weak ($r = 0.466$). Moreover, the sensitive period for bud opening covers a few weeks in April and early May, which is considerably later than the sensitive period for egg laying. This explains the poor correlation between these two phenomena.

At the time that the oak buds open, the eggs of several caterpillar species hatch (Schütte 1957, Varley & Gradwell 1962), and the young larvae feed on the buds and young leaves. The abundance of full-grown caterpillars, which form a major part of the nestlings' food, is determined primarily by mortality during the first larval stage (Varley & Gradwell 1962). This implies that the timing of the peak in food supply is fixed at the time of bud opening, but the actual abundance of food at a slightly later stage. It would be profitable for a Great Tit to possess a mechanism reacting to the first signs of bud opening, enabling it to adjust its breeding cycle to the developing caterpillars. In most years, however, the mean laying date of the first egg coincides with the opening of the buds of only the earliest trees. This means that about half of the birds start laying before the opening of the buds becomes visible (to the human observer). Therefore, the tits probably do not depend on a timing mechanism reacting to the opening of the oak buds.

The relation between egg laying and bud opening can be analysed in yet another way. Among oak trees in the same wood, there is wide variation in opening dates, i.e. there are early and late trees, and early and late groups of trees. This enables us to compare the laying date of each clutch with the mean opening date of the ten nearest oak trees. When this is done we find a significant, but weak, correlation in four of the seven years, late clutches being more frequent in sites with late oaks. These small differences in laying date do not necessarily imply a reaction of the birds to the opening of the oak buds, or to the appearance of young caterpillars, but they could partly be due to differences in microclimate.

Besides differences between the oaks of one wood, there are considerable differences in leafing time between different oakwoods, apparently correlated with the height of the trees. In the Hoge Veluwe, large oaks open their buds simultaneously with oaks from Oosterhout of similar size, but smaller oaks are progressively later. As shown in Table 7, this is not accompanied by delayed laying of the tits. On the contrary, the clutches at sites b and c often preceded the Oosterhout clutches by several days. It must be concluded that the opening of the oak buds or the accompanying flush of young caterpillars does not have any direct effect on the tits' laying activity but that the coincidence of both phenomena is probably due to their dependence on the spring temperature. The present results contradict Lack's (1966) view that the tits "presumably respond either to the appearance of fresh green vegetation or to their insect foods".

The incubation period of Great Tit eggs is 12 to 15 days (Gibb 1950). The

Table 7. Time of oak-bud opening and start of egg laying at different localities (Values between parentheses give the number of clutches studied)

Year	Mean date of young oak leaves				Mean date of first egg		
	Oosterhout	Hoge Veluwe			Oosterhout	Hoge Veluwe	
	a	a	b	c	a	a	b+c
1961	17	19	25	31	14.1(15)	15.8(4)	10.5(4)
1962	39	46	50	?	29.4(10)	—	25.6(5)
1964	32	33	34	38	22.2(17)	23.7(3)	21.0(4)
1965	39	40	46	48	26.3(19)	22.0(2)	24.4(5)
1966	31	33	35	38	27.2(25)	23.3(3)	21.3(4)

Notes: 1. Height of the oaks: 20–25 m (a), 10–15 m (b) and 5–12 m (c).

2. In 1963 the opening of the oak buds was not recorded in the Hoge Veluwe.

interval between the mean start of incubation and the hatching date of the chicks (Table 5, columns 5 and 7) is 13.0 days, and varies little between years (S.D. 0.7, computed from the annual means). Consequently, the mean hatching date in each year is also correlated with the spring temperature, as was the case for the start of laying and the onset of incubation.

Next we will examine the relationship between the caterpillar peak at Oos-

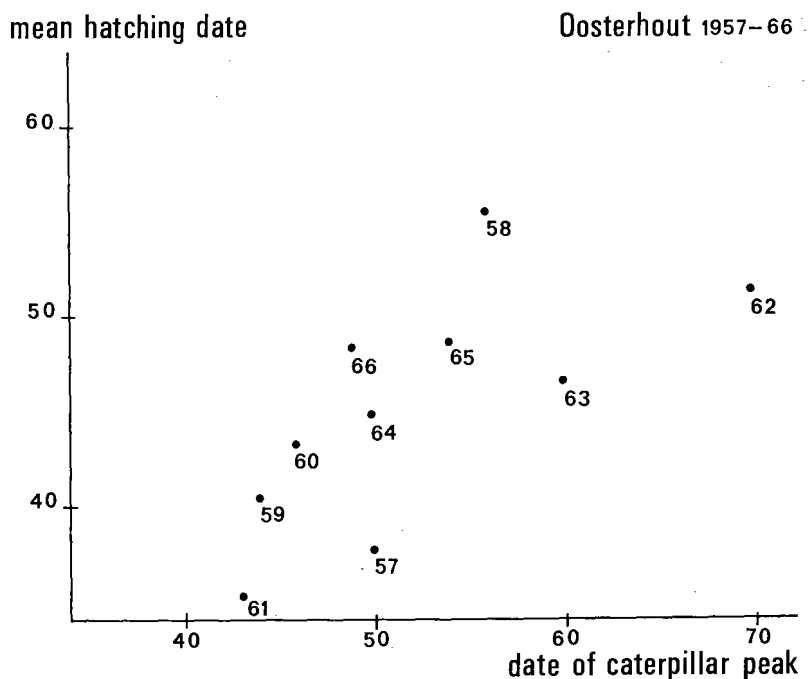


Fig. 3. Relation between the mean hatching date of the first brood and the date of the caterpillar peak in oakwoods. Oosterhout, 1957–1966. Dates counted from 1 April = 1. Numbers refer to years.

terhout and the air temperatures in spring. In this connection we studied the mean temperatures in a number of periods, with starting dates between 1 January and 21 April and ending between 20 April and 31 May. For a comparison with the timing of egg laying the temperatures before 20 April are most important. It appears (Table 6b), that the largest correlation coefficient is found the period 21 February – 20 April, roughly coinciding with the period during which the air temperature affects egg laying.

This implies that the tits, by reacting to the air temperature during the months before egg laying, roughly adjust the hatching date of their young to the date of the caterpillar peak. In fact, the two phenomena are significantly correlated (see Fig. 3; $P = 0.01$), but the interval between them is very variable, ranging from 0.2 to 18.6 days (see Table 5). This is due to the fact that temperatures after 20 April also contribute to the timing of the caterpillar peak. The correlation coefficients increase in size when temperatures after 20 April are included, e.g. $r = -0.933$ for the period 21 February – 10 May.

The mean interval between the hatching date of the nestlings and the date of the caterpillar peak is 6.9 days (S.D. 5.8, see Table 8). Possibly the interval is somewhat shorter in early than in late seasons, 5.3 versus 9.4 days, respectively. From the correlations with air temperature mentioned above, it follows that in years with a warm April and May, when the development of the caterpillars is accelerated, the interval between the mean hatching date of the tits and the caterpillar peak will be very short, and that in cold springs the interval will be long.

Table 8. Interval (in days) between the mean hatching date of the Great Tit and the date of the caterpillar peak

	Early years		Late years		All years		
	n	\bar{x}	n	\bar{x}	n	\bar{x}	S.D.
Oosterhout	6	5.3	4	9.4	10	6.9	5.8
Wytham	7	8.6	9	10.7	16	9.8	2.9

Notes: 1. Early and late years were judged from the date of the caterpillar peak.
2. Values for Wytham taken from Perrins (1965, Fig. 3).

Comparison with data for Wytham Wood (taken from Perrins 1965) shows a situation rather similar to the one in Oosterhout (see Table 8). The difference in mean interval between the two woods (6.9 versus 9.8 days) may be due to the fact that the estimates of caterpillar abundance were not done strictly in the same way, as explained on p. 14. In Wytham the interval was also longer in late than in early years. The situation in Wytham also differs in the much smaller variability of the mean interval, as expressed in the standard deviation. In 11 out of 16 years the interval lasted from 8 to 12

days. It is not clear whether this difference is due to the difference in the method of estimating the caterpillar peak.

Now, we will consider the ultimate aspect of timing and try to answer the question of whether the hatching of the young tits, on the average 6.9 days before the caterpillar peak, is adequately timed with regard to their food requirements. For this, we need to know at what age the food requirements are maximal.

During the nestling stage we distinguish a period of rapid increase in body weight, lasting from hatching to an age of about 10 days (see Figure 24), and a period of feather development from about 7 days until after fledging. It is not clear beforehand which of the two processes demands most energy. It is also conceivable, for several reasons, that the food requirements are largest after fledging. The activity of the young increases after fledging and moreover they no longer roost collectively in a nestbox, protected from low temperatures. Both aspects contribute to an increase in food requirements.

There are no data in the literature, which show at what stage the young tits require most food. We tried to obtain this information in two ways. The first is a direct method, i.e. determination of the food consumption in a number of well-fed, normally developing broods, without mortality. In anticipation of the discussion in section 7.3.2.4. (Table 17) we may mention that the food consumption, hence the food requirements, increases from day 0 (the day of hatching) to day 8, and remains on a high level until fledging.

The second method is an indirect one. In 1966 I attempted to measure the energy requirements of nestlings in Oosterhout from the nocturnal weight loss of nestlings of different age classes. Since the nocturnal weight loss of a resting bird is probably a function of its basal metabolism, this weight loss serves as a measure of the energy required for body maintenance. Hence, we suppose that large requirements during the day are accompanied by a large loss in body weight when the input of energy ceases during the night. The nocturnal weight loss also depends on environmental factors, e.g. the air temperature, and probably also on the behaviour of the female (whether she broods the nestlings) and on the behaviour of the nestlings during the night. We found that the female continues brooding until the nestlings are about 14 days old, and therefore after this age we may expect a higher consumption of energy. The results of these weighings are given in Table 9. The nestlings were weighed at about 22.30 hours, and again at about 3.30 hours, between 23 and 31 May. The first weighing was done about two hours after the last feeding, hence most of the large and variable initial weight loss occurring at the beginning of the night, had already taken place. The remaining weight loss clearly depends on the age of the nestlings (Table 9), and increases up to the age of 11–12 days. The young in these age classes were all weighed under similar environmental conditions, and all of them were brooded by the female. Conditions change when nestlings older than

Table 9. Nocturnal weight loss of nestling Great Tits; Oosterhout 1966

Age (days)	Number of birds weighed	Body weight in evening (grams)	Weight loss per hour (grams)	
			mean	S.D.
5- 6	11	10.22	0.055	0.010
7- 8	24	13.37	0.078	0.018
9-10	22	15.10	0.094	0.015
11-12	23	16.33	0.110	0.014
13-14	26	17.87	0.109	0.024

14 days are studied. Only two older broods (14 nestlings, age 15-16 days) could be weighed; these had an evening weight of 17.43 grams and a weight loss of 0.147 grams per hour, appreciably higher than in the younger age classes. Since, in addition, tits roosting solitarily in a nestbox in winter, at temperatures above freezing, lose only 0.080 grams per hour (van Balen 1967), it is clear that heavy weight losses occur in the last few days before fledging. This may be due to the nestlings' imperfect insulation, because their feathers are not yet fully grown.* If this is the cause of the large weight loss, conditions should be worse after fledging, because the imperfect insulation, combined with increased activity and solitary roosting must put a heavy strain on the fledglings. Support for this hypothesis has been provided by recent observations (van Balen, unpubl.) on the survival after fledging, which show that mortality is heavy during the first 4-5 weeks after fledging, and that the survivors undergo heavy weight losses during this period.

The heavy weight loss shortly before fledging could also be due to the activity of parasites. The larvae of *Protocalliphora azurea*, which suck nestlings' blood, presumably affect their condition by reducing the haemoglobin level in the blood (observations by C. W. Eshuis-van der Voet, in: van Dobben 1971). If this holds for our population too (nothing is known about the abundance of *Protocalliphora* in Oosterhout), conditions must improve considerably after fledging, because the parasites remain in the deserted nest. From this point of view the period before fledging would be the critical one.

Royama (1966b) suggested that the food requirements of fledglings are almost as high as those of adult tits and probably three or four times those of nestlings.

In our view the period shortly before and several weeks after fledging is critical for the survival of the young tits. I suggest that it would be favourable if there were an ample food supply during that period.

* Mertens (pers.comm.) has drawn my attention to the fact that in his experience a considerable part of the nocturnal weight loss is in fact water loss connected with the thermoregulation of the brood. This process may offer an alternative explanation for the increased weight loss of the older nestlings. Since nocturnal water loss would be compensated for by the intake of food (water being mainly obtained by way of food), this should not seriously weaken our argument.

Returning to Table 8, which showed that the food supply in the oakwood has a peak 7 days after the hatching of the tits, it now seems probable that hatching occurs considerably later than would be necessary for a good coincidence of the period of maximal food abundance and the period of maximal food requirement. This might imply that the availability of food for the young is not the most important ultimate factor determining the timing of the breeding season.

Another ultimate aspect, possibly operating in the timing of breeding seasons, may be the condition of the adults. During the reproductive season there may be a critical period in which food requirements are maximal and an ample food supply is of particular importance to the adult tits. Inaccurate timing has consequences for the survival of the adults and for their contribution to subsequent generations. Indications for the validity of this view were obtained from the well-known weight loss of adult birds during the breeding season. In the Great Tit, the females show a continuous loss of body weight from the time of egg laying up to the fledging of the young. The amount of weight lost during the breeding season was studied by repeated weighing of individual females in Oosterhout. The birds were weighed at a fixed time (at night), which eliminated the influence of weight fluctuations within one day.

The weighings were grouped in four periods :

- Period 1. The first few days of incubation (on the average 3.7 days after the last egg was laid).
- Period 2. The last days of incubation (on the average 9.4 days after the last egg was laid).
- Period 3. The first half of the nestling period (on the average 6.7 days after hatching).
- Period 4. The second half of the nestling period (on the average 13.9 days after hatching).

These four weighing periods divide the period of parental care into three intervals, a, b and c, as indicated in Table 10.

The mean daily weight loss shows considerable fluctuation and is largest in interval b, i.e. in the period including the hatching of the chicks. In spite of the small number of observations the weight loss in interval b differs

Table 10. Weight changes in female parent Great Tits; Oosterhout 1965 and 1966

Interval between weighings	Number of birds weighed	Daily weight loss (grams)	
		mean	S.D.
a. Incubation period	10	0.11	0.058
b. Transition incubation-nestling period	14	0.18	0.063
c. Nestling period	18	0.06	0.068

significantly from the weight loss in interval a ($P < 0.05$) and interval c ($P < 0.001$).

During the nestling period the weight loss is always small; some birds do not lose weight at all or show a slight increase. This suggests that the females do not exhaust themselves in rearing their young. This is also indicated by the well-known fact that the feeding frequency can be raised considerably (at least for a period of several hours) when the food requirements of the young increase suddenly. This happens, for instance, when extra young have been added to a brood in experiments, after heavy rains, and after other disturbances which interfere with feeding (cf. Kluyver 1961, Keil 1963). This means that under normal conditions the parents do not make a maximum effort. In general, the nestling period will not be a critical period for the parents.

The causes of the fluctuations in weight loss shown in Table 10 are unknown. It is a priori improbable that the demands made on the female are greatest in the middle period, because the food requirements of the young chicks are still small and the male parent provides most of the food they require. The female spends only a small part of the day in feeding herself, however. Royama (1966a) has shown that male tits provide a substantial part of the females' food, both during the egg-laying and the incubation period. During incubation, most of this food is passed when the female is off the nest and the length of these intervals should determine the amount of food fed by the male to the female. Since the total amount of time spent off the nest decreases from about 5 hours daily at the start of incubation to about 3 hours in the second week of incubation (observations made in 13 first broods in Oosterhout), it seems possible that the females have difficulties in obtaining sufficient food toward the end of incubation. During the first few days after hatching, when a considerable amount of incubation is still needed, the situation is similar. All this suggests that this is a critical period in the life of the female Great Tit.

If these considerations are valid, there are two critical periods during the reproductive season, one for the adults (at least the females), and one for the juveniles. The breeding season is timed in such a way that the first critical period coincides with the caterpillar peak in some years (see Table 5, column 9), but usually falls 1–2 weeks earlier, while the second critical period usually occurs later than the caterpillar peak, only coinciding in one year (1962). The fact that the caterpillar peak usually falls between the two critical periods could mean that during the evolution of the breeding season a compromise between two conflicting selective factors has been reached. In the mechanism that affects timing proximately, the air temperature plays an important role, as mentioned above (p. 17).

A different explanation is given by Perrins (1965, 1970) and supported by Lack (1966). According to these authors there is a selective pressure towards early breeding because the earliest breeding birds produce the most surviving

offspring, but the availability of food for egg production acts as an opposing proximate factor, preventing part of the population from laying at the most appropriate time. More information about the energy requirements of the tits during the breeding season is needed to show which explanation is correct, but it is also quite possible that both mechanisms contribute to the timing of the breeding season. This point will be discussed further in Chapter 10.

5.3. TIMING IN PINEWOODS

Relevant data on the timing of the breeding season in pinewoods are given in Table 11, which concerns the situation of the first broods in Hoge Veluwe A; the situation in Imbosch was very similar in all the years of the study (1960–1965). These data will be treated in the same way as the Oosterhout data, and the results obtained in the two types of habitat will be compared.

Table 11. Timing of the breeding season in pinewood: Hoge Veluwe A. 1957–1966. (Dates counted from 1 April = 1; values between parentheses give the number of the clutches studied)

1 Year	2 Mean laying date of first egg	3 Mean clutch-size	4 Mean hatching date	5 Date of caterpillar peak	6 Difference between 5 and 4
1957	20.2(37)	9.2	43.6	94	50.4
1958	33.5(17)	9.4	55.4	101	45.6
1959	15.2(26)	10.2	36.8	75	38.2
1960	20.6(15)	9.7	43.8	76	32.2
1961	16.0(42)	10.1	37.2	85	47.8
1962	28.8(13)	10.2	51.7	104	52.3
1963	26.0(13)	11.2	49.6	97	47.4
1964	21.5(13)	11.5	46.0	71	25.0
1965	23.3(44)	10.3	47.2	82	34.8
1966	20.9(21)	11.0	44.3	?	?

The start of egg laying in the pinewood was found to be equally dependent on the spring air temperature. In this case the best correlation was obtained for the period from 21 February to 20 April (see Table 6c), which is very similar to the finding for the oakwoods. This explains why the average laying dates in both woods, and consequently the mean dates of hatching, do not differ significantly (sign test, $P > 0.10$).

Several investigators have compared egg-laying dates in different habitats; most of them concluded that egg laying coincides in most habitats, but not in gardens, where it occurs earlier, and in Corsican Pine plantations, where it occurs later than in the other habitats (Kluyver 1951, Lack 1955, 1958, Perrins 1965). Recently, Dhondt (1970) established significant, although very small, differences in laying date between several populations near Gent, including the oakwood Zevegem and the pinewood C.O.O. In the Dutch

populations differences in laying dates between different habitats (except the early start in gardens) have not yet been demonstrated.

In Chapter 4 we mentioned that in pinewoods the peak of caterpillar abundance falls very late. In various years the peak date came between 10 June and 15 July. The effect of the spring temperature on the timing of the caterpillar peak was studied as in the oakwoods. The results differed considerably from those found for the oakwood, since the correlations in the periods up to 20 April were weak and usually not significant (Table 6d). Good correlations were obtained with temperatures in May and June, especially the former ($r = -0.833$). In late years, temperatures during the period from 1 to 20 June also appeared to be effective. These periods are much later than the period in which the breeding season of the tits is determined (21 February to 20 April). Hence, we cannot expect good correlation between the mean hatching date in pinewoods, and the period of the caterpillar peak. In fact, this correlation was not significant ($P = 0.075$). The relation between these two phenomena, as shown by Fig. 4, is such that a delay of 10 days in the caterpillar peak is accompanied by a delay of about 5 days in the hatching of the young tits. The interval between the two increases with the lateness of the season.

On the average, the interval between the hatching date of the first broods and the caterpillar peak amounts to 41.5 days (S.D. 8.3 days) which is

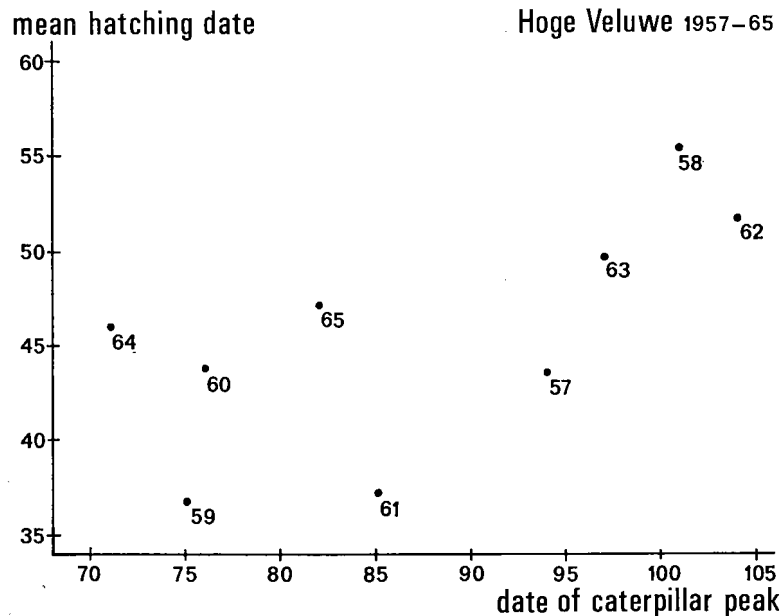


Fig. 4. Relation between the mean hatching date of the first brood and the date of the caterpillar in pinewoods. Hoge Veluwe, 1957-1965.

much larger than the interval found in oakwoods. The lateness of the caterpillars in the pinewoods implies that the young tits cannot profit from the peak of food abundance during their growth period. During the critical period for the parents (see above), feeding conditions are still far below the maximum. During the critical period of the young (shortly after fledging), feeding conditions are much better. In some years (e.g. 1964, see Table 11, column 6) we may expect relatively good survival of fledgings, because the caterpillar peak coincides with the critical period. In many years, however, the caterpillar peak falls later than the presumed critical period. Moreover, the level of caterpillar abundance is much lower than that in the oakwood. The effect of feeding conditions on the survival of the nestlings will be discussed in Chapter 8.

As already mentioned (p. 25), the start of egg laying coincides in the two habitats, and egg laying in oakwoods is adequately timed, with the result that the hatching date in oakwoods shows good correlation with the date of the caterpillar peak (p. 20). From these considerations it follows that the mean hatching date in pinewoods should be correlated with the date of the caterpillar peak in oakwoods. These two phenomena are indeed clearly correlated, as shown by Fig. 5 ($P < 0.002$). Taken together, all these considerations suggest that the timing mechanism, determining the start of the breeding season in both habitats, is an adaptation to the feeding conditions in oakwoods.

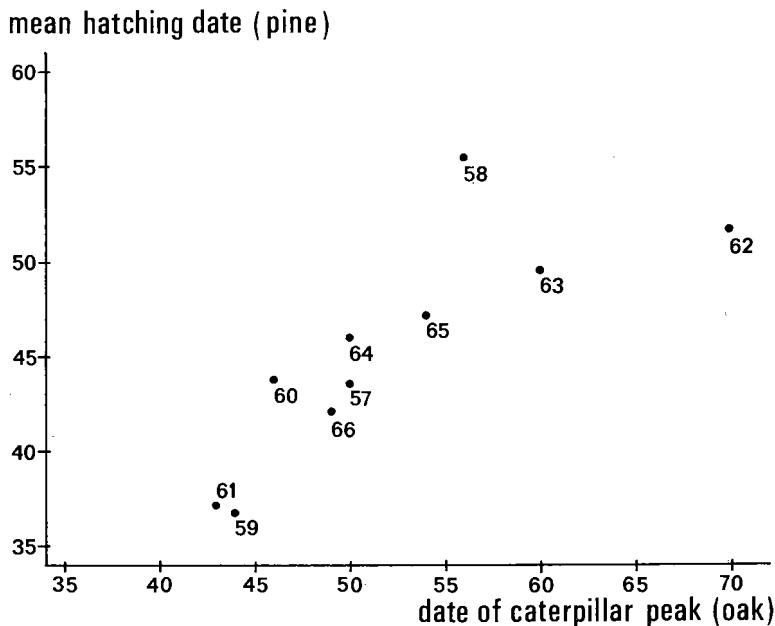


Fig. 5. Relation between the mean hatching date of the first brood in pinewoods and the date of the caterpillar peak in oakwoods (Hoge Veluwe and Oosterhout).

6. CLUTCH-SIZE

6.1. INTRODUCTION

The relation between habitat and clutch-size has been studied by many investigators of Great Tits, sometimes with conflicting results. Part of the disagreement is certainly due to the failure of some authors to eliminate the confusing effects of other factors influencing clutch-size.

Berndt (1938) was one of the first to notice differences in breeding season and clutch-size between deciduous and coniferous woods, which he thought to be related in some way to feeding conditions.

Kluyver (1951) was unable to find local differences in clutch-size apart from those due to variations in population density. Since the coniferous woods had low densities, the clutch-size was usually larger than that in densely populated deciduous woods. The effects of habitat and breeding density could not be separated.

According to Lack (1955, 1958, 1966) the clutch-size in British populations of Great Tits is highest in Scots Pine plantations, slightly lower in deciduous woods (including pure oakwoods), and considerably lower in plantations of Corsican Pine and in gardens. In Lack's view both habitat and breeding density affect clutch-size in such a way that in the most favourable habitat clutch-size is not maximal due to the high density.

Perrins (1965) was able to show significant differences in clutch-size between various parts of Marley Wood, clutches being largest in areas with many tall trees. In his calculations allowance was made for variations in breeding density and laying date.

Krebs (1970) re-analysed the clutch-size data from Marley Wood. His results deviate from Perrins's in that the areas with high and low clutch-sizes did not always overlap, and were not characterized by the type of vegetation. However, his analysis was not based throughout on the same years as those used by Perrins, so their results are not completely comparable.

In von Haartman's (1969) study area in Southern Finland no significant variations of clutch-size with habitat could be found.

Dhondt (1970) studied Great Tit populations in a number of woods and parks in the vicinity of Gent (Belgium). The areas differed in suitability as breeding habitat, but not to the same extent as in the comparable Dutch habitats. The average clutch-size varied in parallel with breeding density, the difference between the two most favourable habitats (mixed deciduous wood and park) and the remaining habitats (pinewood, beechwood, and urban park) being significant. Dhondt also examined the relation between breeding density and clutch-size within the same habitat, but did not compare clutch-sizes at equal density in different habitats.

This review of the literature indicates how necessary it is to make allowance for the effect of several factors on clutch-size. The effects of these factors on clutch-size and their relevance to the present problem must therefore

be analysed next. In the literature the following factors are mentioned as influencing clutch-size in the Great Tit: the age of the female, the breeding density, the date of laying, and the food supply. The study of these factors is usually confined to the first clutches. This approach will also be used in the present study.

6.2. AGE OF THE FEMALE AND CLUTCH-SIZE

Several authors have studied the relation between the age of the female and clutch-size, and in most cases only first clutches were considered. Kluyver (1951) was the first to show that yearling females (i.e. females born in the preceding calendar year) have smaller clutches than older females. This difference, amounting to approximately 0.6 egg, was apparent in 8 out of 9 years, but was rarely significant. Donner & Mayer (1964) reported a similar effect from a deciduous wood in Austria. The average clutch-size over a period of seven years amounted to 9.5 eggs in yearlings, 10.4 in two-year-old birds and 10.1 in three-year-old birds. A similar trend in clutch-size, increasing up to the second breeding year and then decreasing, was found by Perrins (1965). At Lemsjöhölm, von Haartman (1969) found that the difference in clutch-size between yearling and older females was on the average 0.37 egg. Dhondt (1970) calculated a difference of 0.7 egg between these two categories. Neither author differentiated between two-year-old and older females. All these studies indicate that yearling females have a smaller clutch than older ones, and that the difference is larger than would be expected from the slightly later laying dates of the yearlings.

Table 12. Effect of female's age on clutch-size in four areas

Area	Age of female (years)			
	1	2	3	4
Liesbosch A	9.78 (290)	9.96 (96)	10.22 (27)	9.90 (20)
Oosterhout	9.63 (63)	9.79 (33)	10.32 (22)	10.13 (16)
Hoge Veluwe B	9.95 (381)	10.44 (133)	9.93 (58)	10.50 (26)
Hoge Veluwe A	10.25 (168)	10.28 (40)	10.27 (15)	9.50 (8)

Notes: Mean clutch and sample size are given. Only first clutches are included, usually from 1959–1968, in Oosterhout from 1964–1970.

That the results for the older age classes should not be generalized as applying to other populations, is shown by Table 12. In none of our four areas does the clutch-size consistently follow the trend described by Donner & Mayer (1964) and Perrins (1965). In all areas there is a small increase from the first to the second year, but only for Hoge Veluwe B is the difference significant (*t*-test, $P < 0.01$). This also applies to the difference between the first year and all later years combined. Trends in clutch-size after the second

year vary from place to place, but the differences are insignificant except for the decrease from the second to the third year in Hoge Veluwe B. There is an indication that the oldest birds again have smaller clutches. In general, the differences between the age classes are small and can hardly have any effect on the comparison between oakwoods and pinewoods, in spite of the fact that the average age of the breeding population is higher in oakwoods than in pinewoods.

6.3. BREEDING DENSITY AND CLUTCH-SIZE

The effect of the density of breeding pairs on clutch-size has been investigated by Kluyver (1951). In 5 out of 6 areas the average size of the first clutches decreased with increasing density, but the correlation coefficients were not significant. Lack (1955, 1958) found a similar trend in the combined data of three deciduous woods in England. In this case the average clutch-size decreased by 0.06 egg for each additional breeding pair. Perrins (1963a) studied a larger series of years in Marley Wood, and found a significant correlation. Clutch-size decreased with 1.54 eggs per additional pair per acre, which corresponds with 0.62 egg per pair per hectare. In the regression analysis allowance was made for the mean date of laying. In Finland von Haartman (1969) found no relationship between clutch-size and breeding density. In Dhondt's (1970) study areas clutch-size was negatively correlated with breeding density.

When the annual mean clutch-size in our areas is plotted against the breeding density (Fig. 6), a clear relationship is not apparent at first sight. To eliminate other factors obscuring the trend of decreasing clutch-size with increasing density, a multiple regression analysis was performed with the annual means of clutch-size, breeding density, and laying date as variables. The results (see Table 13) showed that in all areas clutch-size was inversely related to breeding density, but only for Oosterhout was the regression coefficient significant. Nevertheless some importance is assigned to these coefficients, since our results are in good agreement with the results reported in the literature. A negative relation between clutch-size and breeding density seems to be a widespread phenomenon in Great Tit populations.

Table 13. Relation between breeding density and clutch-size: results of regression analysis (n.s. = not significant)

Area	Years	Mean density	Regression coefficient	Significance
Liesbosch A	1955—1970	22.6	—0.028	n.s.
Oosterhout	1959—1970	15.4	—0.074	P < 0.05
Hoge Veluwe B	1959—1968	5.8	—0.158	n.s.
Hoge Veluwe A	1955—1968	2.1	—0.216	n.s.

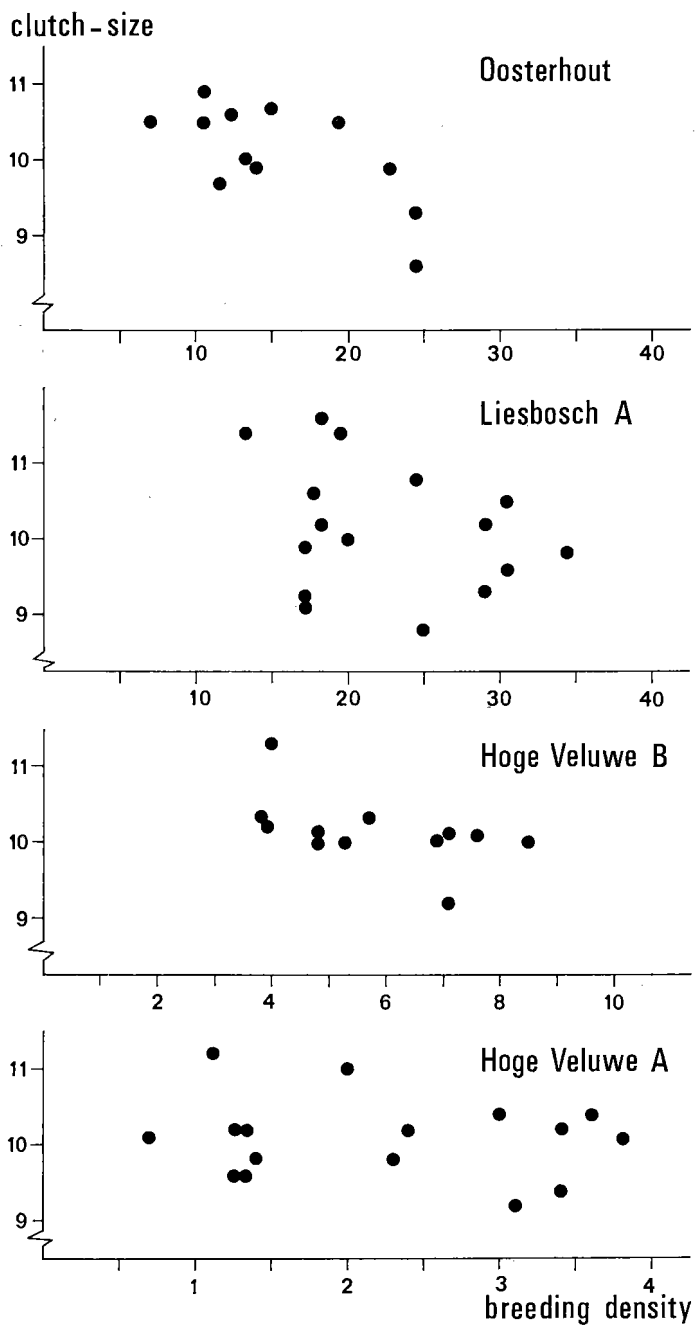


Fig. 6. Relation between the annual means of breeding density and clutch-size in four areas. First clutches only. Density in pairs/10 ha.

The large variation in size of the regression coefficients is striking. The size of the regression coefficient appears to be related to the average breeding density in the four woods. In the oakwoods, with a dense breeding population, the effect on clutch-size is much smaller than in sparsely populated woods. This is presumably due to the fact that the addition of 1 pair per 10 ha in a sparsely populated area implies a large (c. 50%) increase in density, whereas in densely populated areas the addition of one pair causes only a small increase in density (c. 5%). A large percentage increase in density means that the size of the territories decreases considerably, and perhaps implies that the frequency of contacts with neighbours is raised equally.

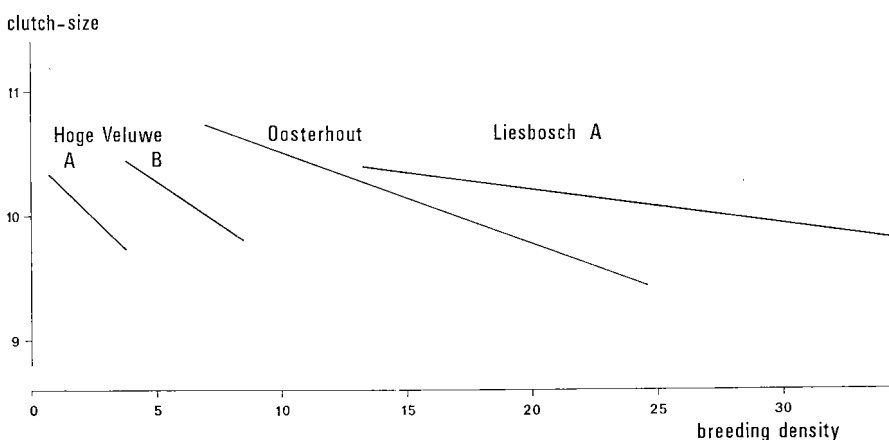


Fig. 7. Relation between breeding density and clutch-size (see text, p. 32).

The effect of breeding density on clutch-size will be discussed further in the next section. The relation between breeding density and clutch-size is shown for the four woods in Fig. 7, constructed from the regression equations with the assumption of a constant mean date of laying (24 April). Differences in the slope of the lines, due to the regression coefficients discussed above, are apparent. The effect of habitat on clutch-size can be examined on the basis of this Figure, as will be shown in section 6.6.

6.4. LAYING DATE AND CLUTCH-SIZE

Variations in clutch-size in relation to the date of laying have been described for many bird species. This phenomenon is generally studied by adding data from several years (and often from a large area), and computing a general trend of clutch-size during an average breeding season. The results provided by this method can be classified under several types (for a thorough discussion, see the review by Klomp, 1970): in the most common type clutch-size decreases from the start of the laying season until the end; the other types show a peak. The peak in clutch-size may occur shortly after the start,

around the middle of the laying season or near the end. In the Great and the Blue Tit *P. caeruleus* the clutch-size is maximal at the beginning of the season (Kluyver 1951, Lack 1955, 1958, 1966, Von Haartman 1969, Balat 1970). The seasonal decline in clutch-size is usually considered to be ultimately related to the number of young that the parents can raise successfully.

Lack (1958) pointed out that the decline in clutch-size during any given season is due to :

- a. A substantial decrease from first broods to later (repeat- and second) broods of individual females.
- b. A slight decrease during the main laying period of the first broods. When several years are combined, a third difference appears:
- c. First clutches are larger in early than in late years.

The first of these trends can be distinguished in all the Great Tit populations studied so far. The second trend was found in Oranje Nassau's Oord (Kluyver 1951) and was also analysed for Marley Wood, where Lack (1958, p. 102) found that it occurred in less than half of the years concerned. The third trend has puzzled several authors, because it could not be understood in terms of the action of natural selection on the survival of the young (cf. Lack 1966, p. 28).

The data from our study areas were classified as indicated at the beginning of this section: clutches from all years were grouped in periods of three days according to the laying date of the first egg, and the average clutch-size for these periods was computed. To obtain sufficiently large samples longer periods than 3 days had to be taken at the start and the end of the breeding season. Fig. 8 shows the seasonal trend of clutch-size in four woods. In both parts of the Hoge Veluwe, clutch-size decreased right from the start of the breeding season, but in Liesbosch there seems to be a peak near the end of April. The situation in Oosterhout is intermediate between those in Liesbosch and the Hoge Veluwe.

The differences between the seasonal trends of clutch-size in the different woods become more distinct when the average clutch-size is taken for the first clutches of each pair. This can be done because the identity of most of the females is known. Fig. 9 shows the seasonal trend of clutch-size for all first clutches. In addition to the four woods discussed above, data for the thinly populated oakwood Liesbosch C are included. In this wood and in both parts of the Hoge Veluwe the clutch-size decreases significantly with the date of laying, in Liesbosch A there is a significant increase, and in Oosterhout the data do not show any trend (Kendall's rank correlation test).

The striking difference between the two parts of Liesbosch suggests that differences in the seasonal trend of clutch-size are not linked with the habitat but are due to differences in breeding density. The magnitude of the correlation coefficient (r), which is a measure of the correlation between clutch-size and laying date, is distinctly related to the breeding density, as

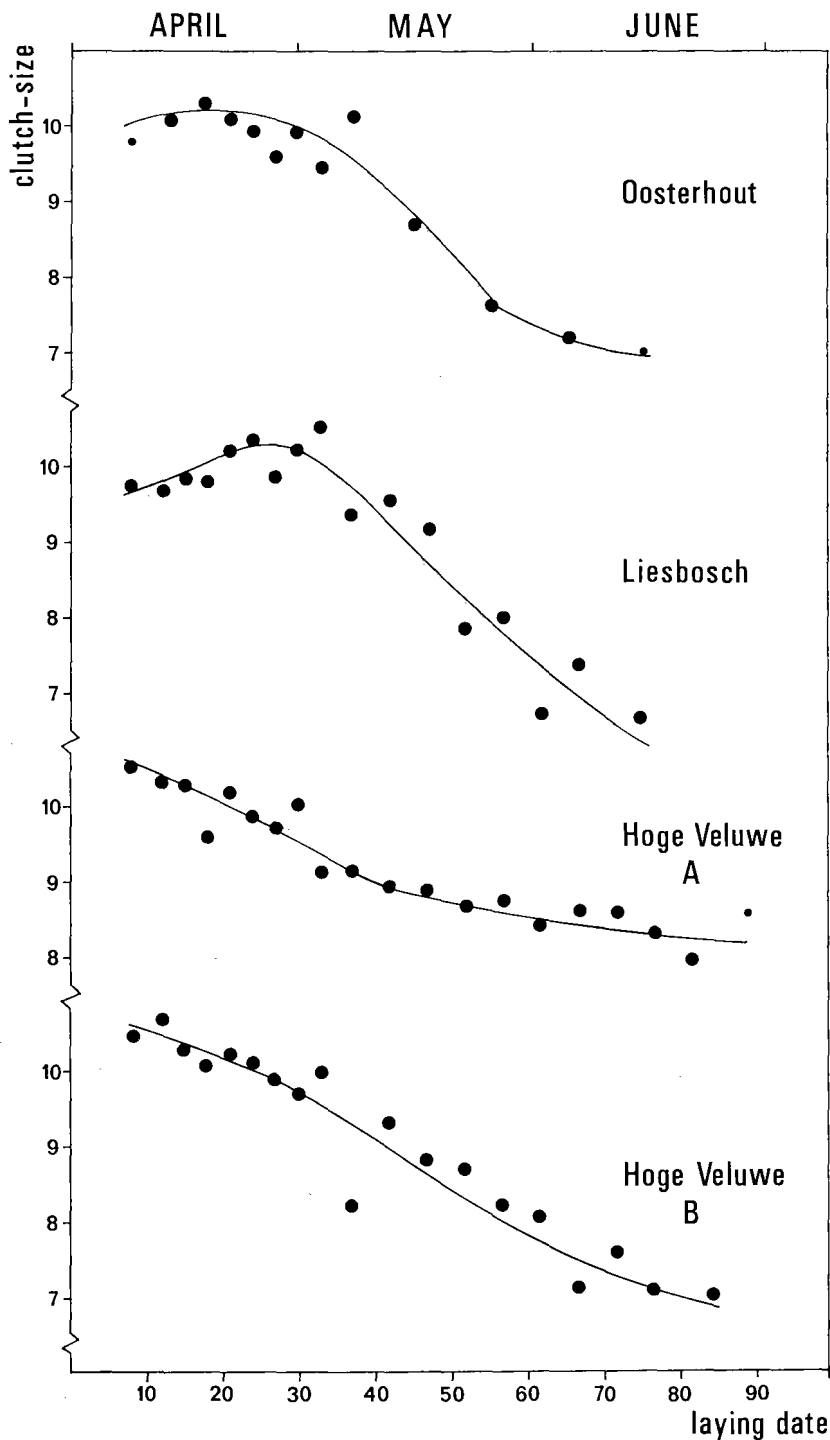


Fig. 8. Relation between laying date and clutch-size. All clutches up to 1968. Small dots are based on less than 10 clutches. Lines drawn by eye.

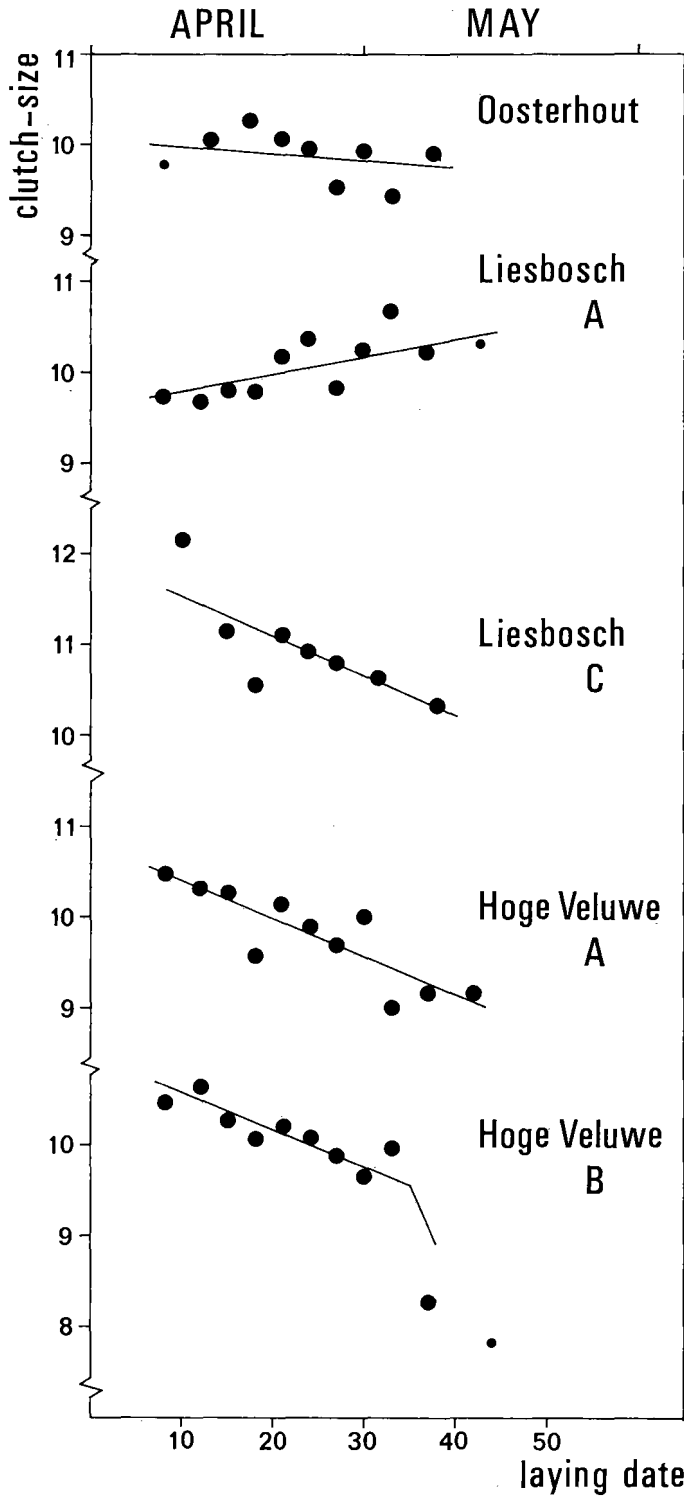


Fig. 9. Relation between laying date and size of first clutches. As Fig. 8.

Table 14. Relation between clutch-size and laying date, expressed as the correlation coefficient r , compared with mean breeding density

Area	Mean density	r
Liesbosch A	23.2	+0.46
Oosterhout	16.1	—0.18
Liesbosch C	c. 6	—0.44
Hoge Veluwe B	5.8	—0.50
Hoge Veluwe A	2.2	—0.66

shown by Table 14. With decreasing density the positive correlation gradually changes into a negative correlation.

When the lines for Liesbosch A and C in Fig. 9 are compared, it becomes apparent that the effect of breeding density is operative at the start of the breeding season, whereas after 30 April clutch-size is similar in the two habitats. Thus, high density causes a substantial reduction in the size of the earliest clutches. This effect of breeding density is understandable if it operates through territorial behaviour and if territorial behaviour is most intense, and therefore most effective, in early April or even earlier. This is probably the case, since Kluyver (1951) states that territorial fighting reaches its climax at the end of March, and Hinde (1952) mentions a maximum in the intensity of reproductive fighting during the weeks before the breeding season. Similarly, Dhondt (1970) states that territorial behaviour reaches its climax in the second half of March. Moreover, Kluyver (pers. comm.) observed that the female Great Tits participate in territorial defense until the clutch is completed. Hence, a high breeding density, involving numerous territorial contacts, could reduce the amount of time spent in feeding, and therefore the amount of food available for egg production (cf. Krebs 1970).

The tendency for mean clutch-size to be larger in early than in late years (p. 33) is not confirmed by our data. Fig. 10 shows that the annual means of clutch-size and laying date are neither positively nor negatively related. This is confirmed by the results of the regression analysis, referred to above. The regression coefficients obtained, representing the change in mean clutch-size when the mean laying date changes by one day, varied from -0.033 (Hoge Veluwe A) to $+0.036$ (Liesbosch A), and were all non-significant.

Dhondt (1970) did not find any correlation between mean clutch-size and mean laying date either. Apparently, the phenomenon seems to be a peculiarity of populations of British Great Tits *Parus major newtoni* which are distinct from continental Great Tits at the subspecies level.

6.5. FOOD SUPPLY AND CLUTCH-SIZE

Most of the variations in clutch-size are usually interpreted as adaptations to the food supply available for rearing young. This applies to the seasonal decline in clutch-size and to the relation with breeding density.

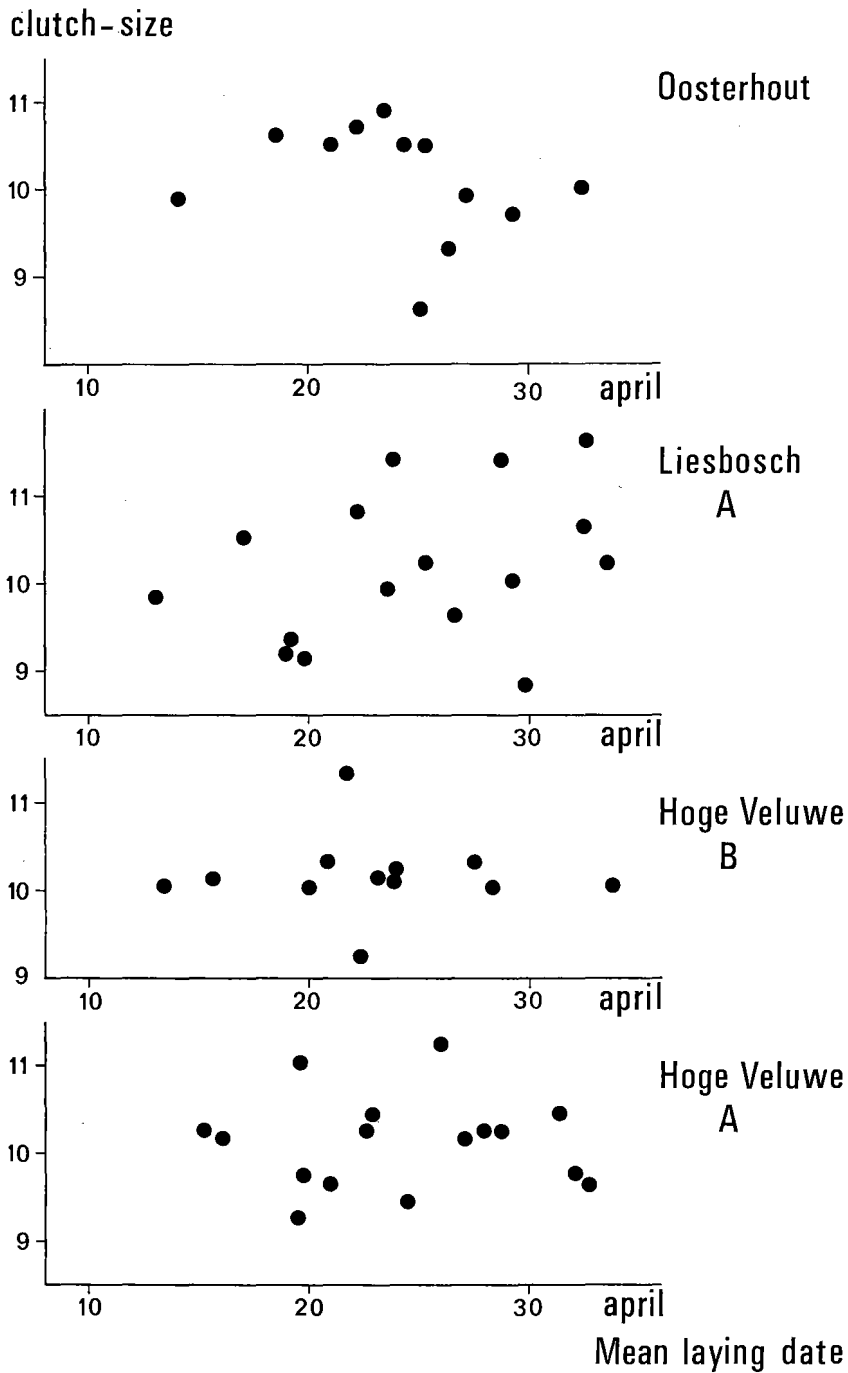


Fig. 10. Relation between annual mean laying date and annual mean clutch-size of first broods.

Annual variations in clutch-size can also be due — apart from the effects of breeding density and laying date — to variations in the food supply. Either the food available to the female during the period of egg formation may affect the size of the clutch proximately, or the size of the clutch may be ultimately adapted to the food supply during the period of rearing young, or both mechanisms may operate together.

In the literature a proximate effect of food on clutch-size is usually considered improbable (Perrins 1965, Klomp 1970), since in most areas the clutches decrease in size during a period of rapidly increasing insect biomass. This is not the case in Liesbosch A, but the increase in clutch-size in this wood has been explained above as an effect of the breeding density.

For an ultimate determination of clutch-size operating through the food supply for the nestlings, the parents should react to some stimulus connected with the food supply several weeks before the nestlings hatch. One of the possible stimuli could be the food supply in the period of egg formation. In section 5.2 we concluded that the start of incubation, which is usually the same as the end of egg laying, roughly coincides with the mean date of bud opening of the oaks. Since the clutch-size is probably determined some days before the laying of the last egg and the abundance of large caterpillars is determined shortly after the opening of the oak buds (5.2), a close correlation between clutch-size and the abundance of large caterpillars is not to be expected.

This problem can also be approached by comparing the annual mean clutch-size with the annual peaks in caterpillar abundance. This method was put forward by Lack (1955) and further used by Perrins (1965, p. 628), who concluded from a regression analysis that the apparent correlation between clutch-size and caterpillar numbers in Wytham was accidental, and that the correlation coefficient was not significant. A similar analysis was performed with the data for Oosterhout. In addition to the data on breeding density and laying date referred to above, the maximum values of caterpillar frass production (Table 2) were used. The regression coefficient with caterpillar density, indicating the change of mean clutch-size corresponding to an increase in frass production of 10 mg per 0.25 m², was only -0.005, which is not significant ($0.10 < P < 0.20$).

In Hoge Veluwe A (pinewood) the size of the first clutches was likewise not related to the caterpillar frass fall in May, June or July.

The size of second clutches in pinewoods was also investigated in relation to the caterpillar frass fall during the laying period, but no relationship was apparent.

6.6. HABITAT AND CLUTCH-SIZE

The size of the first clutches from different habitats can now be discussed with allowance for the effect of other factors. It is clear from the foregoing

that especially the effects of laying date and breeding density have to be taken into account. This can be done by computing from the regression equations the expected clutch-size at a fixed density of, for example, 8 pairs/10 ha and a fixed laying date of 24 April. The results, shown in Table 15, indicate that at this level of density the clutch-size in the oakwoods is about 1.8 egg larger than in the pinewoods, with the mixed habitat intermediate. The same is evident from Fig. 7, which shows the differences in clutch-size over a wide range of densities, viz. the lowest and highest density observed for each wood. Comparable figures can be computed for Marley Wood (Oxford) from the data given by Lack (1966; Table 2). The expected clutch-size in this mixed deciduous wood is 10.47 at 8 pairs/10 ha, which is similar to the clutch-size in the Dutch oakwoods.

Table 15. Expected clutch-size at a fixed breeding density and laying date (computed from the regression equations, assuming the density = 8 pairs/10 ha and the average laying date = 24 April)

Area	Expected clutch-size
Liesbosch A	10.53
Oosterhout	10.64
Hoge Veluwe B	9.77
Hoge Veluwe A	8.75

Figures on clutch-size are available for two more areas, but these are not in sufficient quantity to permit regression analysis. The following data concern the average clutch-size of all first clutches. In Liesbosch C, where the density is probably about 6 pairs/10 ha, the mean clutch-size is 10.91 which corresponds with the results from the other oakwoods. In the pine-wood Imbosch a mean clutch-size of 10.13 was found, which – at a density of 2 pairs/10 ha – fits remarkably well in the line for Hoge Veluwe A (see Fig. 7). Thus, the size of the first clutches in all the deciduous woods studied is very similar, and in the mixed habitat (Hoge Veluwe B) and the pinewoods it is considerably smaller at equal density. The difference in clutch-size between populations in different habitats can be detected only when the effect of breeding density is allowed for, since the average clutch-size is more or less similar at the densities occurring normally in each of the woods.

7. NESTLING FOOD

7.1. INTRODUCTION

For a study of the breeding ecology of the Great Tit in different habitats, primary importance is assigned to measurements of the food brought to the nestlings. The relation between the composition of the diet and the seasonal trends in caterpillar populations is interesting (7.3.1.). The amount of food

the nestlings receive also requires study, not only in relation to the food supply available in the wood but also in relation to brood-size and to the survival of the nestlings (7.3.2.).

Several authors have measured the feeding frequency in Great Tit broods. Most of them based their conclusions on material from one or a few broods (Hinde 1952, Bartkowiak 1959, Bouchner 1960, Keil 1963, Deckert 1964). Kluyver (1950) presented figures for 8 broods from several habitats and studied several aspects such as the daily rhythm, the division of feeding between the sexes, and the relation of feeding frequency to prey size and brood-size. Gibb (1950, 1955) made a comprehensive study of feeding rates and reached conclusions on the feeding conditions of large v. small and early v. late broods, but lacked information on prey size.

Studies on the composition of nestling food have already been discussed in 4.1. and need to be mentioned here.

Gibb & Betts (1963) made detailed observations on the nestling food of 4 species of tits in a British pine plantation. Feeding frequencies of Great Tits were obtained in 8 early and 5 late broods, but observations on food weight were available from only one early and one late brood. Daily these broods received per nestling 4.66, and 7.28 g of food respectively.

Royama (1966b), who studied feeding rates and food consumption of *Parus major minor* in a Japanese Larch wood, particularly stressed the insufficiency of feeding frequencies as a basis for the study of food consumption. This aspect will be further discussed in 7.3.2.3. In a later study (1970) he investigated hunting behaviour and food selection in Wytham Wood (mixed broad-leaved woodland).

7.2. METHODS

Observations on the feeding frequency and on the nature and size of the prey were done in selected broods in oak- and pinewoods (Oosterhout, Imbosch).

Most of the methods commonly used for the study of feeding habits are unsuitable for our purpose. The analysis of stomach contents would not give a quantitative picture of the food of tits without impairing the population seriously. The use of neckcollars (cf. Kluyver 1933) does not give reliable quantitative results with Great Tits. We observed during our study that the parent tits tend to remove large preys from the gullet of the nestlings when the collar prevents them from swallowing the prey, and when part of the prey projects from the nestling's bill. As a result of this behaviour the large preys take a smaller share in the food samples and, in addition, the normal feeding frequency is lowered considerably.

Therefore, we turned to a method first used by Promptov & Lukina (1938), and elaborated by Tinbergen (1949, 1960), Betts (1955b), and Royama (1966b), viz. observing the events in a glass-backed nestbox, attached to a

portable observation hide. This method enabled us to observe the feeding process at close range and to determine the kind and the size of the preys. A similar technique was used by Haftorn (1965, 1966) to study the behaviour of tits at the nest. Good alternative or supplementary methods for the study of nestling food are the collection of food samples with an 'artificial nestling gape' (Promptov & Lukina 1938, Betts 1954, 1956), and photographic recording of the preys (Royama 1959, 1966b).

In each of the two woods three observation hides were used simultaneously. These hides were erected near selected nests with clutches in the incubation stage. Then the nestbox was lowered in two or three phases until it hung on the front of the hide. Next, the nest with eggs was transferred to the observation box on the hide. This last step occasionally caused desertion by the tits, especially in the pinewood. Otherwise, the birds quickly became accustomed to the new situation.

During part of the incubation period and throughout the nestling period the visiting frequency in all observed broods was automatically recorded with a Fuess chronograph. Entries and exits were recorded separately, and the number of visits per unit of time could be computed easily. These results could be checked by comparing the number of visits recorded with the number counted by the observer during the observations.

During each observation period, notes were made for each visit by a parent tit on the following points: time of entry, sex of the bird, type of the prey, estimated weight of the prey, and some details on the behaviour of parent and nestlings during feeding. The observer attempted first of all to estimate the weight of the prey as accurately as possible. With some training this appeared to be successful. The observer's accuracy in estimating prey weight was checked repeatedly by comparing the estimated weight of insects collected from trees or from neck-collar samples with their actual weight. All food observations were done by the author.

Because the process of feeding proceeds quickly and primary attention was paid to the size of the prey, it was often impossible to determine the prey species (or genus) exactly. However, in most cases we could assign a prey to one of the following categories: caterpillars, pupae, Lepidoptera imagines, Diptera imagines, other insects, spiders. For about 15% of the preys, the type remained unknown. Usually, this was due to the behaviour of the tits, for instance when the parent entered the nestbox very quickly and turned around prior to feeding the nestlings, or when, during the last days before fledging, the nestlings received their food through the entrance hole, without the parent entering the nestbox. Another category of objects fed to the nestlings, consisting of pieces of egg-shell or snail shell and beakfulls of earth, occurred mainly in the pinewood and with very low frequency. This category is not included in the calculations of the composition and the weight of the food.

Food observations were usually made on alternate days during the whole

nestling period. An observation period generally lasted from 1 to 2 hours, depending on the frequency of feeding. The observations were continued until the average estimated prey weight remained constant. This was usually the case after 1 to 1½ hours, but incidentally it took more time, especially when the parent tits changed from one main type of prey to another type during the observation period. In addition, the observation periods of each brood were distributed over a large part of the day. By this procedure possible differences in prey size during the day were highly diminished.

The preys observed during an observation period were regarded as a representative sample of the preys brought to the brood on that day. By multiplying the average weight of the observed preys by the number of visits with food during the day recorded by the chronograph, we obtained a figure representing the total amount of food brought to the brood on a given day.

Food observations started in 1959, but some of the results of the first year had to be discarded, because the technique was not yet sufficiently standardized. During 1960–1963, observations were spread over the entire breeding season, and in 1964 and 1965 additional observations were done on some first broods. In all 32 broods were studied in the oakwood (20 first, 3 repeat, and 9 second broods), and 37 in the pinewood (24 first, 3 repeat, and 10 second broods).

7.3. RESULTS

7.3.1. Composition of the food

7.3.1.1. Introduction

The composition of the nestling food, as grouped in the rather large categories mentioned above (7.2), was determined separately for each observation period. Percentages by number and by weight were both computed, but only the latter were used for further calculations. This was necessary because the average weight of the different types of prey differed considerably, and the biomass of the preys is more important than numbers of preys in the economy of a tit brood.

The percentages obtained for each observation period were grouped according to the date of observation, and mean percentages were calculated for each five day period, giving equal weight to the constituent percentages. In this way a detailed survey of the food composition in the course of the breeding season was obtained.

7.3.1.2. Food composition in oakwoods

Fig. 11 shows the composition of the nestling food in Oosterhout for 1962. The share of the caterpillars increased steadily, reaching a peak in mid-June. After a short gap in the observations (between the fledging of the latest first

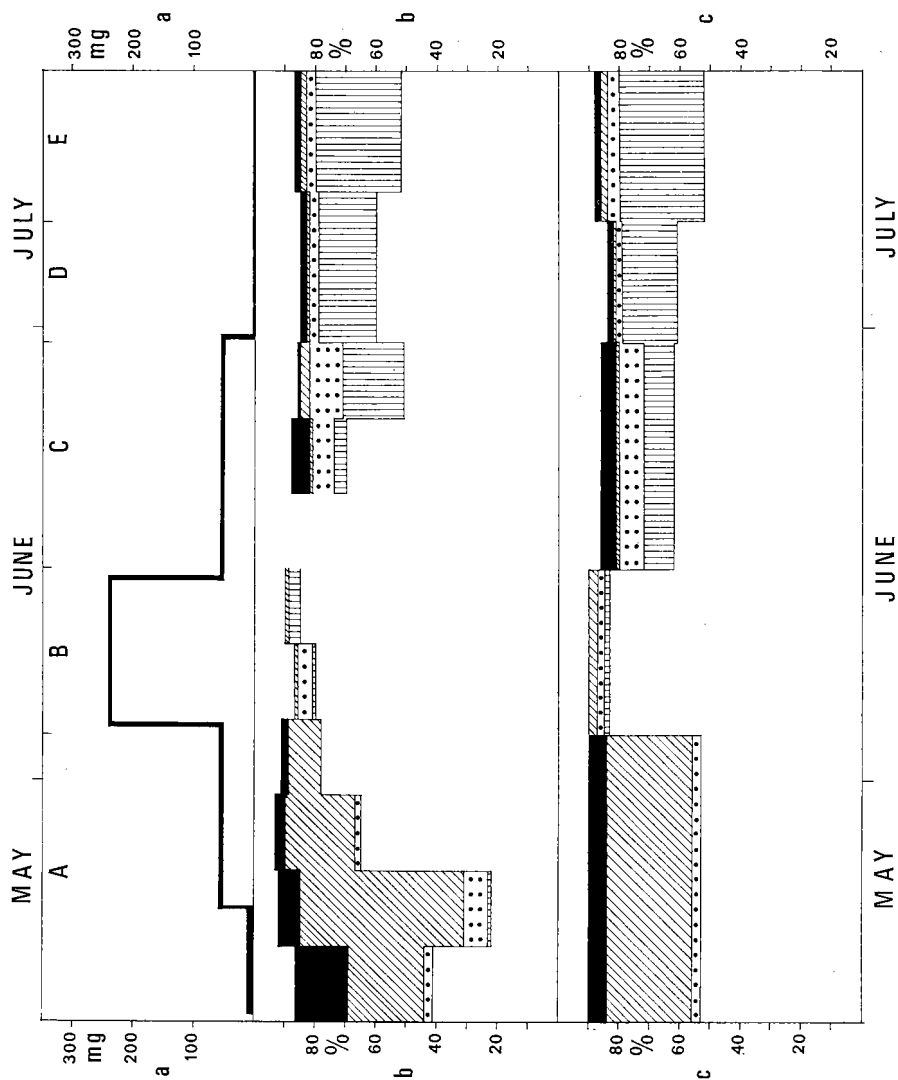
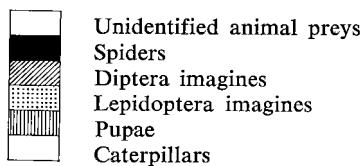


Fig. 11. Composition of nestling food in Oosterhout, for 1962, in relation to caterpillar frass fall.
 a: caterpillar frass fall in mg per day per 0.25 m² (cf. Fig. 1).
 b: percentage of prey categories in nestling food, legend see below.
 c: as b, over larger periods (see text, p. 44).



broods and the hatching of the second broods), the caterpillars became less important preys and the share of the pupae increased steadily. Diptera were common preys in May, and butterflies and moths were fed in small numbers over much of the season. Spiders were fed especially to small young, in both first and second broods (cf. Royama 1970).

For comparison of the results of different years and analysis of the relation between the composition of the food and the seasonal trend in the caterpillar population, each season was divided into 5 periods (A to E), according to the curve of caterpillar frass fall in the year concerned. In each year the peak of frass fall fell in period B, period A represented the period of increase, and C to E the longer period of decrease (see Fig. 11a). An example of the results is shown in Fig. 11c, for Oosterhout 1962. During the peak in frass fall, 83% of the food consisted of caterpillars (mainly *Tortrix viridana* and *Operophtera brumata*) and 2% of pupae (of *Tortrix viridana*, which pupates in the canopy or in the undergrowth).

Comparable figures for all years are given in Table 16a, which shows that from the start of the breeding season caterpillars form the main food for the nestlings. During period A, which can be further divided into two equal parts, the share of the caterpillars increases from 41% in the first to 72% in the second half. This increasing importance as food is largely due to the increasing weight of the caterpillars concerned, due to growth. Second in importance in period A are Diptera (32% and 13% in the two parts of A), and third are spiders (10% and 5%). With the increasing percentage of caterpillars from the start of A until B, the percentages of all other types of prey decreased to a very low level. Within all years (except 1960), the percentage of caterpillars in the food was maximal in period B, coinciding with the peak in frass fall. The percentage of caterpillars in period B varied from 64–92%. The possible explanation of this variation will be discussed below.

During periods C to E, when the biomass of the caterpillars in the canopy drops – at first quickly, later more slowly – the share of caterpillars in the food generally decreases, but the general level varies widely from year to year. Alternative food is presented by pupae, butterflies, and Diptera. In period C caterpillars are still most important, with pupae in the second place. The share of the pupae generally increased from C to E, but only in 1965 did the pupae reach first place. In two years (1959, 1963) butterflies and moths became the most important prey during the last period, and only in one year (1965) did the percentage of Diptera reach any importance.

Annual variations in food composition may be due to annual variations in the density of the types of prey concerned, or to variations in timing of the tit's breeding season in relation to the period in which the different types of prey are most numerous. Both possibilities can only be examined in relation to the main type of food, i.e. caterpillars, as information on the density of other types of food is lacking. In Fig. 12 the percentage of caterpillars in the

Table 16. Composition of nestling food in percentage by weight

a. Oakwood (Oosterhout)

Year	1959				1960				1961					1962					1963					1964	1965			
Period	B*	C	D	E	B*	C	D	E	A	B*	C	D	E	A	B*	C	D	E	A	B*	C	D	E	C	B*	C	D	E
Caterpillars	82	60	42	20	64	74	66	56	54	75	69	36	50	53	83	62	61	52	69	83	(72)	75	32	83	(92)	87	28	11
Pupae	1	25	6	3	3	5	16	12	3	0	17	23	24	0	2	10	18	28	0	1	(8)	0	3	3	(0)	4	56	51
Lepid.imag.	2	4	31	68	0	4	3	18	1	2	2	9	5	3	2	8	2	4	1	1	(0)	8	40	4	(0)	0	3	4
Dipt.imag.	1	2	7	2	0	2	5	0	7	6	1	7	1	28	13	1	1	2	18	6	(3)	2	11	1	(2)	0	4	18
Spiders	10	2	5	1	19	3	2	1	23	4	0	2	2	6	0	5	2	2	2	0	(0)	2	1	1	(3)	1	0	1
Unknown	4	7	9	6	14	11	9	12	13	13	13	23	18	10	10	14	17	12	10	9	(8)	13	13	10	(2)	8	9	16

b. Pinewood (Imbosch)

Year	1960					1961					1962					1963					1965	
Period	A	B	C*	D	E	A	B	C*	D*	E	A	B	C	D	E*	A	B	C	D*	E*	A	B
Caterpillars	56	70	89	83	76	52	71	71	75	46	49	44	73	56	75	53	46	(48)	83	74	73	45
<i>Panolis</i>	0	12	82	68	57	0	0	25	47	16	0	0	0	30	70	0	0	(21)	60	58	0	0
Pupae	14	5	0	0	6	8	3	3	3	3	3	5	4	1	2	1	7	(4)	1	0	4	1
Lepid.imag.	2	1	2	8	1	12	6	4	3	21	9	2	7	24	4	15	11	(16)	2	7	2	23
Dipt.imag.	0	0	0	0	0	11	4	0	3	1	7	5	1	0	0	2	2	(3)	0	5	3	6
Coleopt.imag.	1	0	0	0	0	0	0	0	0	0	0	10	0	0	0	3	0	(0)	0	0	0	0
Spiders	13	6	2	5	6	5	2	7	7	4	11	10	2	8	9	5	3	(1)	3	2	3	1
Unknown	15	18	7	5	12	12	14	14	10	25	21	24	13	11	10	21	29	(29)	11	12	15	24

Notes: Explanation of periods A-E in text, pp. 44 and 48. Asterisks denote period of peak frass fall. Figures between parentheses are based on only 1 or 2 observation periods. Figures for *Panolis* are included in figures for caterpillars.

food is compared with the relative density of caterpillars, expressed as the weight of their frass. It is clear that over a large range of densities (from 40 mg of frass upward), caterpillars are the main food of the nestlings. In general, the percentage of caterpillars increases asymptotically to a level of about 90%, but the relation between the percentage in the food and the density in the trees varies in the periods concerned. For period A, no conclusions can be drawn. During period B the percentage of caterpillars in the food is clearly not related to density, and even in years with a relatively low caterpillar density the percentage in the food is very high. Coupled with the high level of food provision in this habitat (see p. 56), this suggests that even in a poor caterpillar year the food supply during the peak period is sufficient, and that in most of the years the caterpillar level is in excess of the amount necessary for rearing a brood.

A definite positive correlation was obtained for period C, the period of rapidly decreasing caterpillar biomass. In years with a high density during period C (1964 and 1965, cf. Fig. 1) the percentage in the food remained over 80, whereas in the other years values ranging from 60 to 70% were

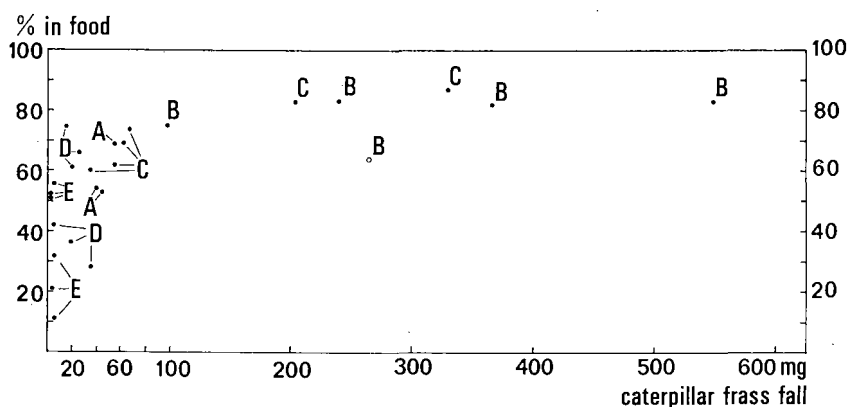


Fig. 12. Relation between percentage of caterpillars in the food and caterpillar frass fall in corresponding periods. Oosterhout, 1959–1965.

Frass fall in mg frass per day per 0.25 m².

A, B, C, D, E: explanation in text, p. 44.

obtained. Since the percentages of caterpillars and pupae in the food during period C were negatively correlated, the annual differences in percentage of caterpillars in this period may be largely due to a variable pupation rate. This applies especially to the larvae of *Tortrix viridana*, which pupate in the canopy, and whose pupae are available for predation during several weeks. The sum of the percentages of caterpillars and pupae accounts for 72–91% of the food in period C, and is not related to the caterpillar density. Hence, the conclusions drawn for the period of peak density apply equally to the

period of decreasing caterpillar density, in which caterpillars and pupae together provide plenty of food for the nestlings.

During periods D and E, large variations occur in the percentage of caterpillars in the food, and these variations are not related to the density as measured by frass fall. In most of the years caterpillars and pupae together still form the bulk of the food, in spite of the relatively low densities measured. The density of alternative types of prey, especially butterflies and moths (other species than the caterpillars common earlier in the season), may play a part in determining the food composition, but no information on their density is available.

Royama (1970) reported that after 15 June many of the caterpillars taken as preys, were herb-feeders. No information is available on the source of these preys in the present study, but if Royama's observations also apply here, they could explain the discrepancy between the high percentage of caterpillars in the diet and the low density measured in the canopy during the second half of the breeding season.

A further comment is desirable in connection with Royama's (1970) study on food selection by Great Tits in Wytham Wood (mixed deciduous forest). In his study area the major tree species was the oak *Quercus petraea* but many other deciduous trees were present. The caterpillar fauna was composed of many species, and was probably much more varied than in the oakwoods studied here. The composition of the nestlings' diet in Wytham Wood differed accordingly, the main divergence from our results being the low predation on small-sized caterpillars like *Operophtera brumata* and *Tortrix viridana*. While many of the preys observed in the present study could not be identified as to species, the high percentage in the diet from these two species is beyond doubt. Similarly, other workers (Betts 1955b, Pfeifer & Keil 1959, Henze & Görnandt 1959) have reported *Operophtera brumata* and/or *Tortrix viridana* as the main prey species for early broods of Great Tits in oakwood. These species often reach plague densities in continental Europe, but there is no information on the densities (in pure oakwood) of the larger prey species mentioned by Royama. I suggest that the composition of the diet, which Royama uses to illustrate the operation of his concept of profitability, is typical for mixed habitats with a varied prey fauna, but that in pure oak habitats, where a few small species are superabundant, these species are preyed upon primarily. Predation on these species could be made profitable – extending Royama's reasoning – by shortening the handling time for each prey. This is accomplished by bringing more than one prey item at a time, and by searching the immediate surroundings of the nest, thereby shortening the transportation time for each prey item and increasing the feeding frequency considerably. Both phenomena were observed in this study. When preying on *Tortrix viridana* larvae, the tits may bring 2–3 larvae at a time. The overall average is 1.16 larvae per feeding visit, while with other types of prey this average lies very

close to 1 larva per visit. The principal means for the efficient exploitation of abundant small-sized prey is to increase the feeding frequency. The average number of feeding visits in first broods is 730 per day, which is considerably more than the feeding rates reported by Gibb (1955) for Wytham, which were of the order of 500–600 per day. Frequencies of 800–1200 visits per day are quite common in Oosterhout, and up to 1535 visits per day have been recorded. By this means the tits succeed quite well in raising a large brood of nestlings on small preys (cf. Chapters 8 and 9).

7.3.1.3. Food composition in pinewoods

The preys observed in the pinewood were grouped in the usual categories (section 7.2). In some cases Coleoptera were also fed, especially the longicorn beetle *Rhagium bifasciatum*. Often caterpillars could not be identified as to species, except the conspicuous larvae of *Panolis flammea*. Fig. 13 gives an example of the result obtained in 1962, a year with a very late caterpillar peak. As in most years the bulk of the frass during the peak was produced by *Panolis* (Fig. 13a), and the availability of *Panolis* is clearly reflected in the food (Fig. 13b).

For comparison of the results from different years, each season was divided into 5 periods (A to E), but the variable timing of the caterpillar peak prevented us from arranging the periods in such a manner that the caterpillar peak coincided with the same period in each year. Therefore, each season was divided into 5 equal parts, as a result of which the caterpillar peak coincided with period C in 1960, which C–D in 1961, with D–E in 1963 and with E in 1962 (see asterisks in Table 16b).

The results for all years, given in Table 16b, show that caterpillars are the most important type of prey during all periods. It should be remarked that some of the preys included in this group were in fact sawfly larvae (Hymenoptera), such as *Acantholyda nemoralis*. The frass of this species is treated as caterpillar frass, and hence is included as such in Fig. 13a. In spite of the very much lower overall caterpillar density in the pinewood as compared with the oakwood (cf. Table 3) caterpillars are equally important as nestling food in the two habitats.

In general, the composition of nestling food is rather similar in the two habitats. The share of the pupae is appreciably lower in the pinewood, which can be explained by the absence of species that pupate in the canopy. Lepidoptera, Diptera and spiders were equally common preys in both habitats. In addition to these types of prey, in the pinewood Coleoptera were fed on some occasions, and in early June of 1962 a few tits fed pine-seed to their young.

The percentage of caterpillars in the food is maximal when the biomass of caterpillars in the canopy has its annual peak. This is due to the frequency of *Panolis* in the food, which reaches very high values when *Panolis* is the

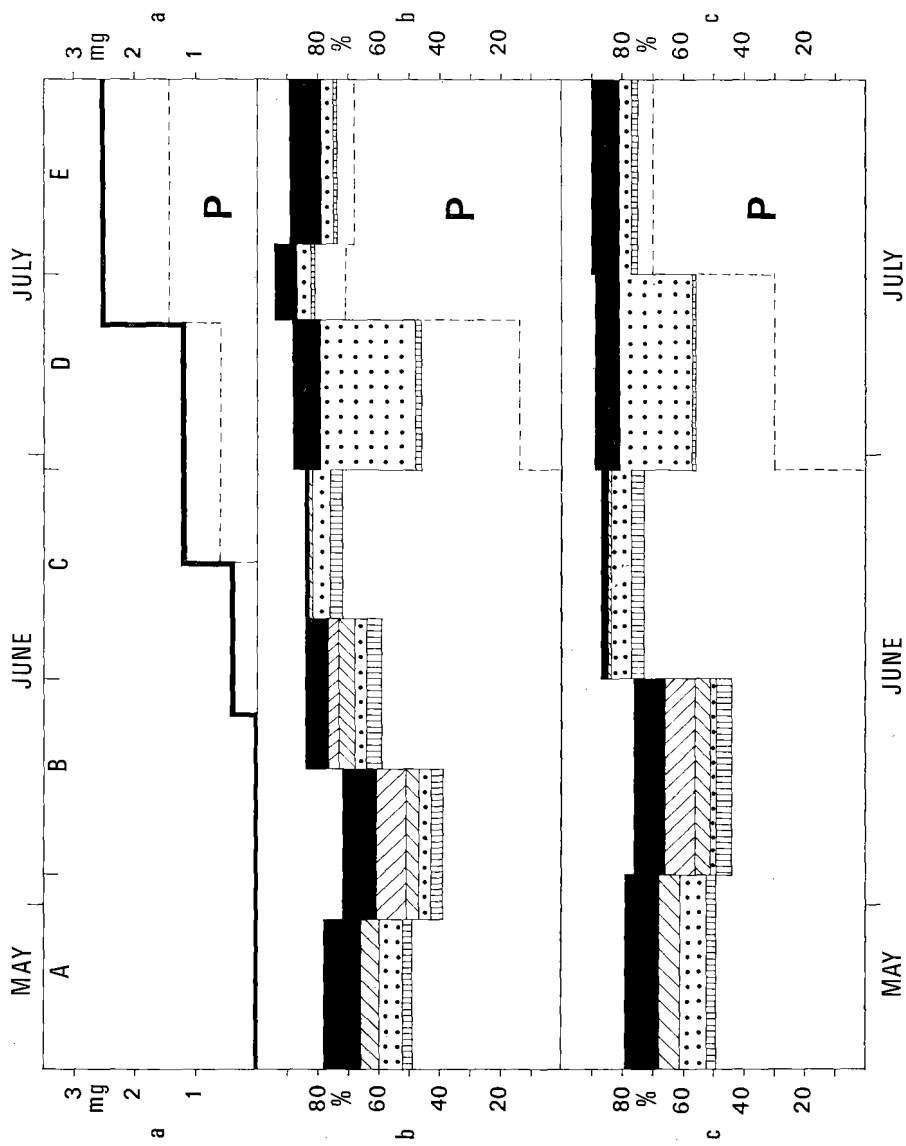


Fig. 13. Composition of nestling food in Imbosch, for 1962, in relation to caterpillar frass fall. Legend see Fig. 11.

P = *Panolis flammea*.  Coleoptera imagines.

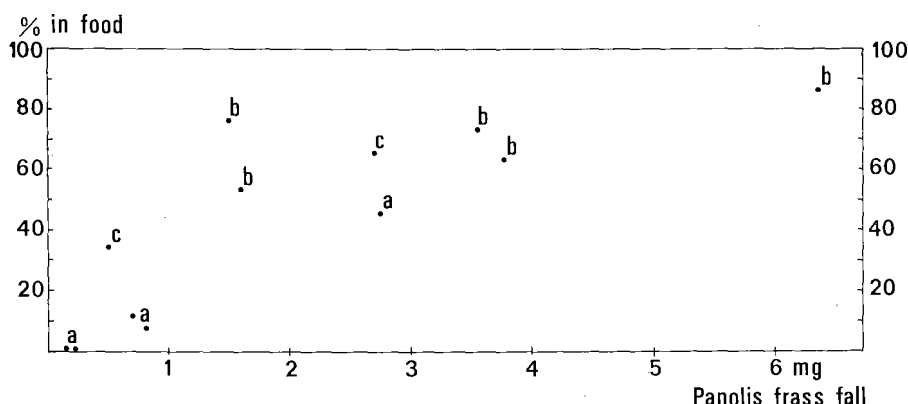


Fig. 14. Relation between percentage of *Panolis* larvae in the food and *Panolis* frass fall in corresponding periods. Imbosch 1960–1965. Frass fall in mg per day per 0.25 m². Percentage of *Panolis* calculated over all identified preys. a = before, b = during, c = after peak in frass fall.

most common caterpillar in the canopy. The relation between the percentage of *Panolis* in the food and the amount of *Panolis* frass is given in Fig. 14, which shows that in the lower range of densities the percentage in the food increase with increasing density.

During the first half of the season, before *Panolis* appeared in the food, the percentage of caterpillars was higher than expected. The amounts of frass collected during this period were usually very small (Fig. 1), and most of it was produced by Geometrid larvae (e.g. *Ellopija prosapiaria*), which were found in the food of the early broods to some extent. However, some of the larvae fed to the nestlings came from species living inside pinebuds (e.g. *Rhyacionia buoliana*). The frass of these larvae does not fall down, and thus was not collected by our trays. The graphs presented in Fig. 1 therefore do not give a complete picture of the availability of caterpillars in the course of the season. According to the literature (e.g. Lange & Bogenschütz, 1970), *Rhyacionia* larvae are mostly found in young pine plantations. There are plantations of suitable age adjacent to one side of the study area, and presumably some of the larvae found in the food were taken in that area. It is impossible to give exact percentages for the share of *Rhyacionia* in the food, because part of the larvae remained unidentified, but in 1960–1962 about 20% of the food in period B consisted of these larvae. As soon as *Panolis* appeared in the food, the percentage of *Rhyacionia* dropped to a very low level. In general, *Ellopija* and related species predominated in period A, *Rhyacionia* in B, and *Panolis* during the rest of the season.

A few deciduous trees (oaks) are found in the Imbosch pine plantations. Moreover at one of the corners of the study area there is a large group of oaks. These oaks show retarded growth compared with oaks on a more

fertile soil, but presumably they still carry more insect food than the pine trees. On several occasions the tits fed oak caterpillars (e.g. *Tortrix viridana*) to their nestlings. This was mostly done by pairs living near the oak trees, and only during a limited period (mostly in B). These observations agree with the conclusions drawn by Gibb & Betts (1963, Table 12), who found that Great Tits in a pine plantation at Mousehall (Thetford Chase, East Anglia) collected about 25% of the food for early broods from broadleaved trees. Presumably, the percentage for Imbosch is lower, because smaller numbers of deciduous trees are present.

Similarly, Kabisch (1965a) observed that Great Tits breeding in a birch wood collected large numbers of *Tortrix viridana* larvae and pupae from an adjoining strip of oaks.

The high percentage of caterpillars in the food, in both oakwoods and pine-woods, and the relationship between the amount of caterpillar frass and the percentage in the food, suggest that caterpillars are the preferred food during the breeding season.

In view of the large difference in caterpillar density in oakwoods and pine-woods it is of great interest to compare the total weight of food and the condition of the nestlings in the two habitats.

7.3.2. Weight of the food

7.3.2.1. Introduction

The weight of the food brought daily to a tit brood was calculated from the feeding frequency (recorded automatically) and from the average weight of the preys observed during part of the day.

Firstly, the two components will be discussed briefly.

7.3.2.2. Prey weight

The average prey weight is a quantity varying considerably between broods on the same day, between successive days, and between first and second broods in one season. Thus, only some general trends can be indicated.

As shown in Fig. 15, there is a general trend for prey weight to increase with the age of the nestlings, at least during the first week. Superimposed on this trend, variations occur in connection with the availability of different types of prey. In the oakwood (Fig. 15A), prey weight decreased among the older nestlings of first and repeat broods, coinciding with a high percentage of small *Tortrix* pupae in the food. Similar phenomena in the pine-wood (Fig. 15B) are connected with the succession of large *Ellopia* and small *Rhyacionia* larvae during the first brood of the tits, and with the high percentage of large *Panolis* larvae in both repeat and second broods. Kluyver (1950) and Gibb & Betts (1963) found similar differences in prey weight between early and late broods in pinewoods.

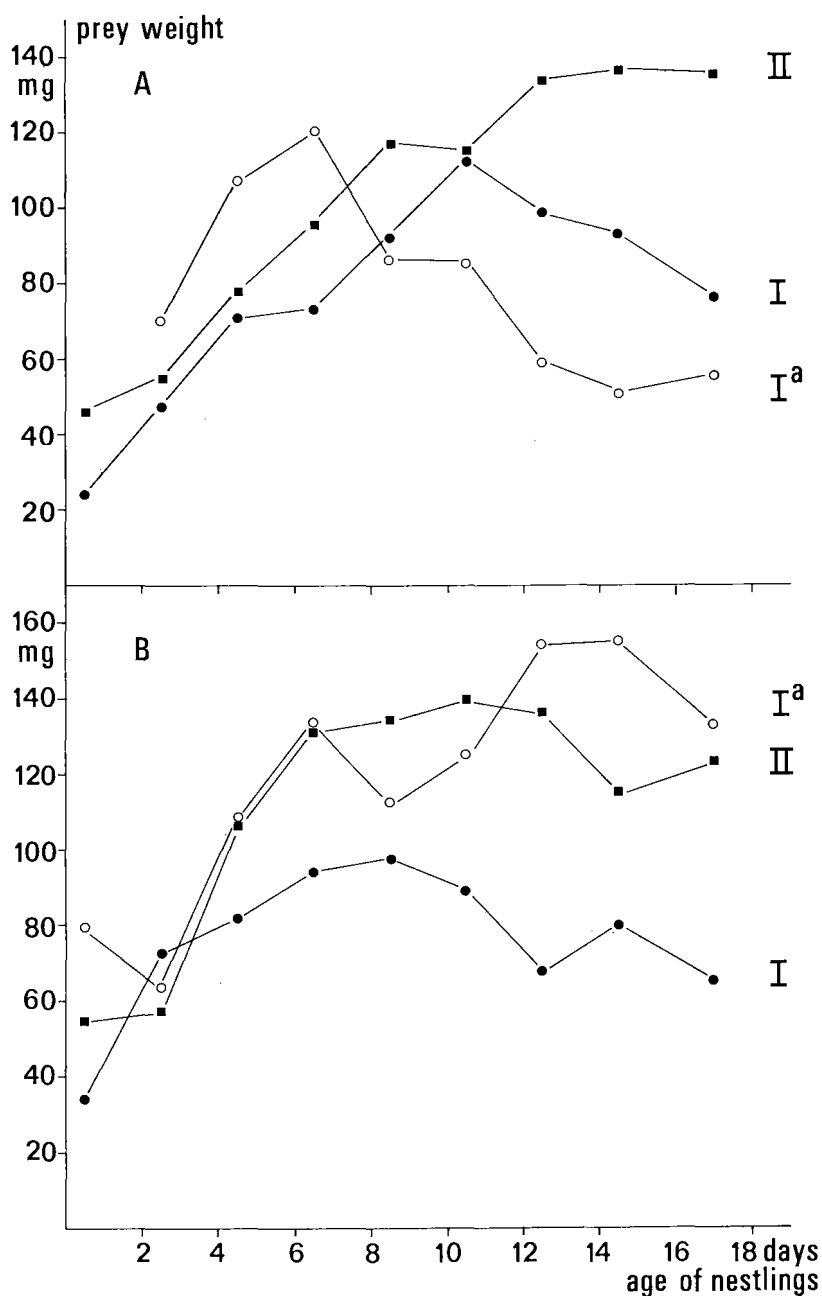


Fig. 15. Average weight of preys in relation to age of the young in oakwood (A) and pinewood (B).
I, Ia, and II: first, repeat and second broods.

7.3.2.3. Feeding frequency

In many studies on parental care in birds the assumption has been made that the feeding frequency is a useful index of the total amount of food provided by the parents. Gibb (1955) pointed out that feeding frequencies are not a good measure of food consumption, because of the variations in prey size. Since we were convinced that both feeding frequency and the size of the preys were extremely variable quantities, we tried to measure both quantities and studied the relation between the two. Royama's (1966b) observation that feeding frequency and size of the prey are inversely related, was confirmed in the present study. As an example, Fig. 16 shows this relation for all broods in the oakwood. Apparently, the relation between feeding frequency (per nestling) and prey weight is well described by a hyperbole, which means that the product of $a \times b$, i.e. the daily weight of food per nestling, is more or less constant. This result can be understood by assuming that the feeding frequency is such that for a given prey weight, the food requirements of the nestlings are satisfied.

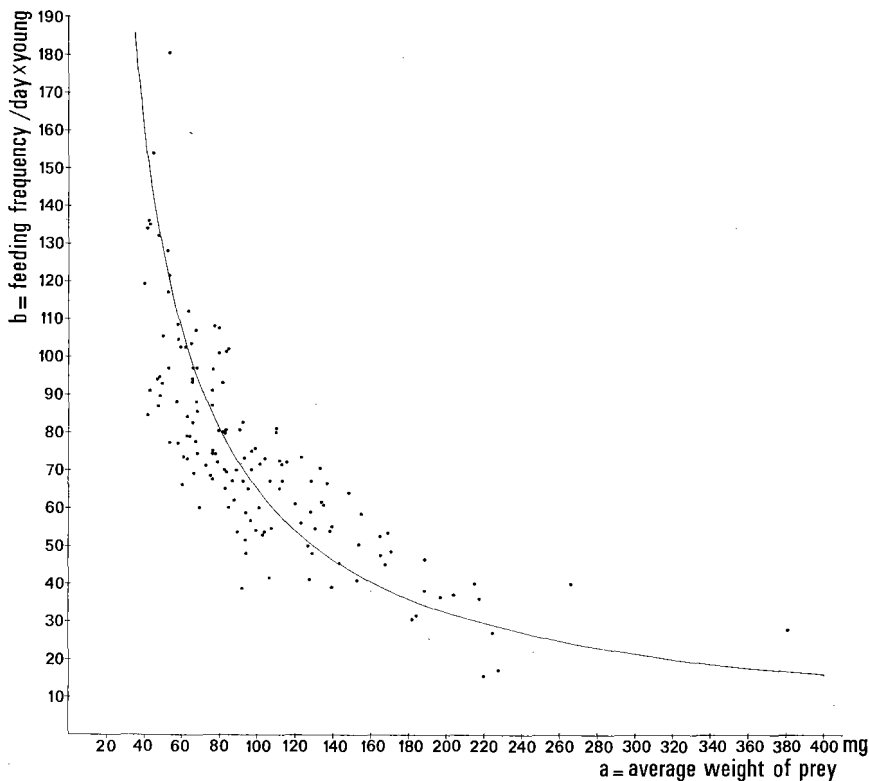


Fig. 16. Relation between prey weight and feeding frequency in all broods from oakwoods. Nestlings 8–17 days old. The line represents the hyperbole $a \times b = 6487$ mg per day per young.

Deviations from the hyperbole are due to differences in food requirements of nestlings in small or large broods (cf. p. 61).

The curve in Fig. 16 is applicable to nestlings from 8 to 17 days old. For younger nestlings parallel curves were found, at lower values of a and b .

In view of these results it is understandable that the trends of feeding frequency in the course of the season are inverse reflections of the trends in prey weight described in 7.3.2.2.

7.3.2.4. Daily food consumption

From the foregoing discussion it has become clear that the product of feeding frequency and weight of prey, i.e. the total weight of food fed daily to a brood (or a nestling), is the most useful index of food consumption. For an overall comparison of food consumption in oak- and pinewoods the average of the products of $a \times b$ (from Fig. 16 and the equivalent curve for the pinewood) may be taken. The average daily food consumption per nestling amounted to 6487 mg in the oakwood and 6126 mg in the pinewood for 8 to 17 days old nestlings (difference insignificant at the 5% level).

In a more detailed study of food consumption in oak- and pinewoods the effect of other factors on food consumption must be taken into account. Among these factors the age of the nestlings, brood-size, and season are the most important. For a comparison of food consumption in the two habitats the consumption per brood is most important. At a later stage the food consumption and food requirements per nestling will be discussed.

The dependence of food consumption on the nestling's age is shown in

Table 17. Daily food consumption (per brood) in first broods from oakwood

Age of nestlings	Number of observation days	Daily food consumption (grams)	
		Mean	Standard error
0	6	3.1	0.80
1	5	7.2	1.31
2	9	11.0	1.80
3	7	20.5	3.23
4	5	29.4	5.89
5	7	36.0	5.45
6	5	42.1	5.16
7	6	49.8	4.95
8	5	63.0	11.64
9	7	65.1	5.34
10	5	66.9	9.09
11	10	75.3	11.18
12	4	63.0	11.79
13	11	65.4	5.72
14	9	63.2	6.01
15	7	66.9	9.49
16	6	66.2	7.96
17	8	60.4	5.03

Note: Data from 20 broods with an average size of 10.10 (S.D. 1.94).

Table 17 for all first broods in the oakwood. The daily consumption increased sharply during the first week of life, but from day 8 a level was reached around which small fluctuations occur. This trend was shown by all broods with good survival, only the level reached depending on the size of the brood. The period from day 8 to day 17 seems most suitable for the study of food consumption in relation to brood-size, season and habitat.

The picture gained from Table 17 is typical for broods reared under good feeding conditions. These broods have a very high nestling survival (Chapter 8), and attain a high body weight (Chapter 9). Hence the food consumption measured in these broods can be considered to represent the food requirements of the young. The observed trend corresponds with the findings reported in section 5.2 (Table 9), on the nocturnal weight loss of nestlings.

The initial brood-size in oak- and pinewoods is more or less equal, but nestling mortality in late oakwood and all pinewood broods (cf. Chapter 8), is responsible for a reduction in brood-size (often irregularly) during the nestling period. The food consumption of these broods changed accordingly, as is demonstrated in Fig. 17.

The figures have been averaged over two days to reduce day-to-day fluctuations. In early oakwood broods hardly any mortality occurred. These broods, with an average of 10.1 young, received 60 to 70 grams of food per day during the period from day 8 to day 17. Late oakwood broods were divided into broods without mortality (brood-size 7.3) and broods with mortality (initial size 7.5, at fledging 5.2). Since most of the mortality occurred before day 8, the low level of food consumption is not surprising. The relation between mortality rate and food consumption can be examined in more detail with the pinewood material. Fig. 17B shows the daily food consumption in pinewood for five groups with different percentages of mortality, and the brood-sizes at hatching and fledging. Groups a, b, and c did not differ in consumption up to day 7. The mortality in b and c occurred mostly between days 4 and 8, and from day 8 the level of food consumption was appreciably lowered in these broods. In groups d and e the level of food consumption was still lower, and deviated from group a at an earlier stage, in accordance with the early mortality in these broods. The relation between food consumption and mortality is further discussed on p. 60.

In Chapter 8 it will be shown that nestling survival hardly differs in early and late pinewoods broods. Moreover, the food consumption of pinewood broods was generally not related to their earliness or lateness. This is rather unexpected, since Kluyver (1950) and Gibb & Betts (1963) have found that second broods in pinewood receive much more food (due to increased prey size) than first broods. Since Gibb & Betts' conclusions are based on observations on only one early and one late brood, both from 1956 when the caterpillar peak occurred very late (see 4.3), I do not regard these results as representative of the situation in British pinewoods. As regards the Dutch situation, Kluyver's results too came from only two broods, both from

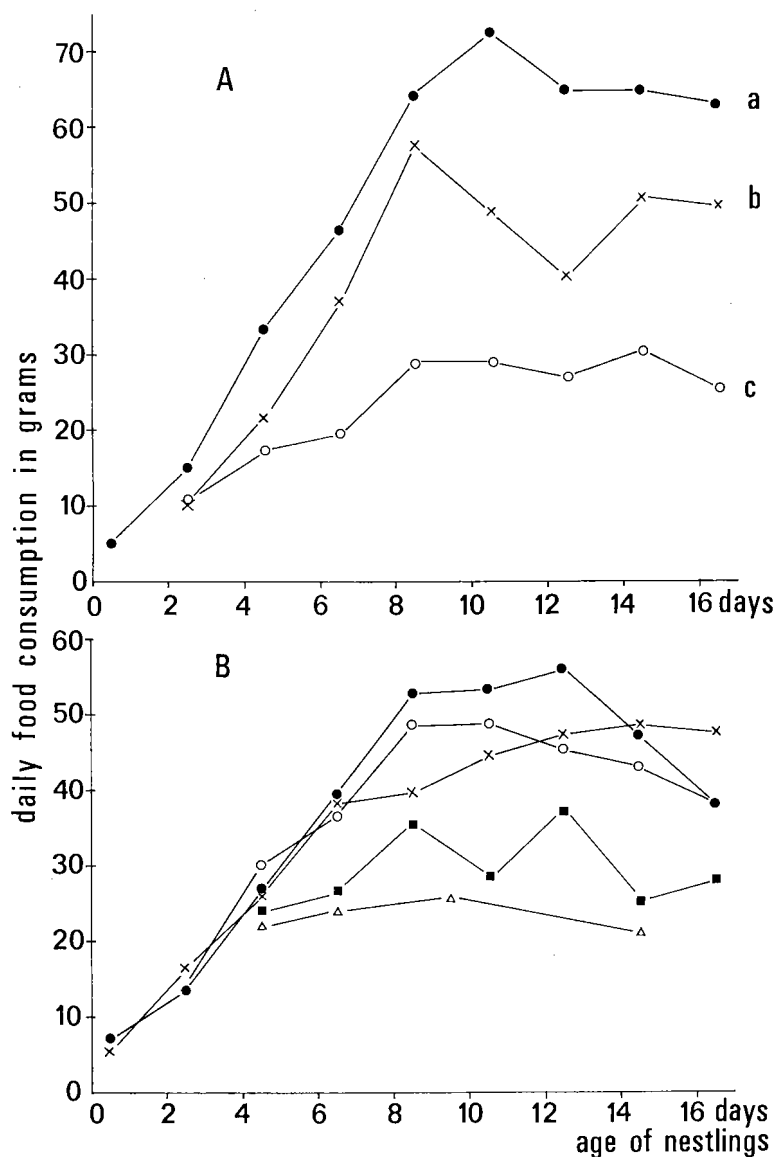


Fig. 17A. Daily food consumption (per brood) in oakwoods.
 a: all first broods (no mortality).
 b: repeat and second broods without nestling mortality.
 c: repeat and second broods with nestling mortality.
 B. Daily food consumption (per brood) in pinewood.

- a: —●— no mortality; brood size 8.3
 b: —x— 1–20% mortality; brood size 9.1→8.0
 c: —○— 21–40% mortality; brood size 8.9→6.4
 d: —■— 41–60% mortality; brood size 8.0→4.0
 e: —△— 61–90% mortality; brood size 7.0→1.3

1937. This might have been an atypical year as far as the food supply is concerned, but no observations on caterpillar abundance are available. In section 4.3 we concluded that the caterpillar peak in Dutch pinewoods usually occurs in June or July, coinciding with repeat or second broods. This means that in some years first and second broods have more or less equal chances, whereas in other years second broods meet better feeding conditions than first broods. The effect of feeding conditions on nestling survival will be discussed in Chapter 8.

So far we have examined the food consumption of broods with different mortality rates resulting in differences in brood-size. A more exact picture of food consumption in relation to brood-size is given by Fig. 18. Whereas in Fig. 17B each brood contributed to one of the groups a to e, here the data of each brood contribute to several brood-size classes, according to the number of young surviving at the observation day. From this graph it can be seen that over a large range of brood-sizes the consumption was slightly higher in the oakwood than in the pinewood. Among broods of 6 to 9 nestlings the difference in consumption is only 7%. Even in the larger broods (10 to 13), where the food consumption was 11.3% higher in the oakwood than in the pinewood, the difference is not significant ($P = 0.06$).

It could be argued that the slightly higher food consumption in the oakwood is due to a greater effort made by the parent tits. A suitable measure of the effort spent by the parents is the length of the feeding day, i.e. the time elapsed between the first feeding visit in the morning and the last one in the evening. The numerous measurements made during this study indicate that the length of the feeding day is affected by the date of observation (= day length), the age of the nestlings (= food requirements) and the habitat. At comparable dates and ages the pinewood tits had longer feeding days than the tits in the oakwoods (Fig. 19C). This difference is due to a slightly earlier start by the pinewood tits, but mainly to extended feeding in the evening, suggesting that they had difficulties in satisfying their young (Fig. 19A en B).

The difference in the length of the feeding day was largest in May (about 35 minutes), decreased to zero in the middle of June, and increased again to 30 minutes in July. This corresponds with the fact that the feeding conditions in the pinewood are best in the middle of the breeding season (cf. 4.3 and 8.3).

The observations on food consumption and on the length of the feeding day show that the pinewood tits were unable to satisfy their young completely, in spite of the longer time spent in searching for food.

At first sight, the small difference in food consumption between broods from oak- and pinewoods does not seem consistent with the large difference in mortality (cf. Chapter 8). This raises the question of whether feeding conditions in the pinewood are really as good as the food consumption suggests. The answer is that days with a low food consumption are usually

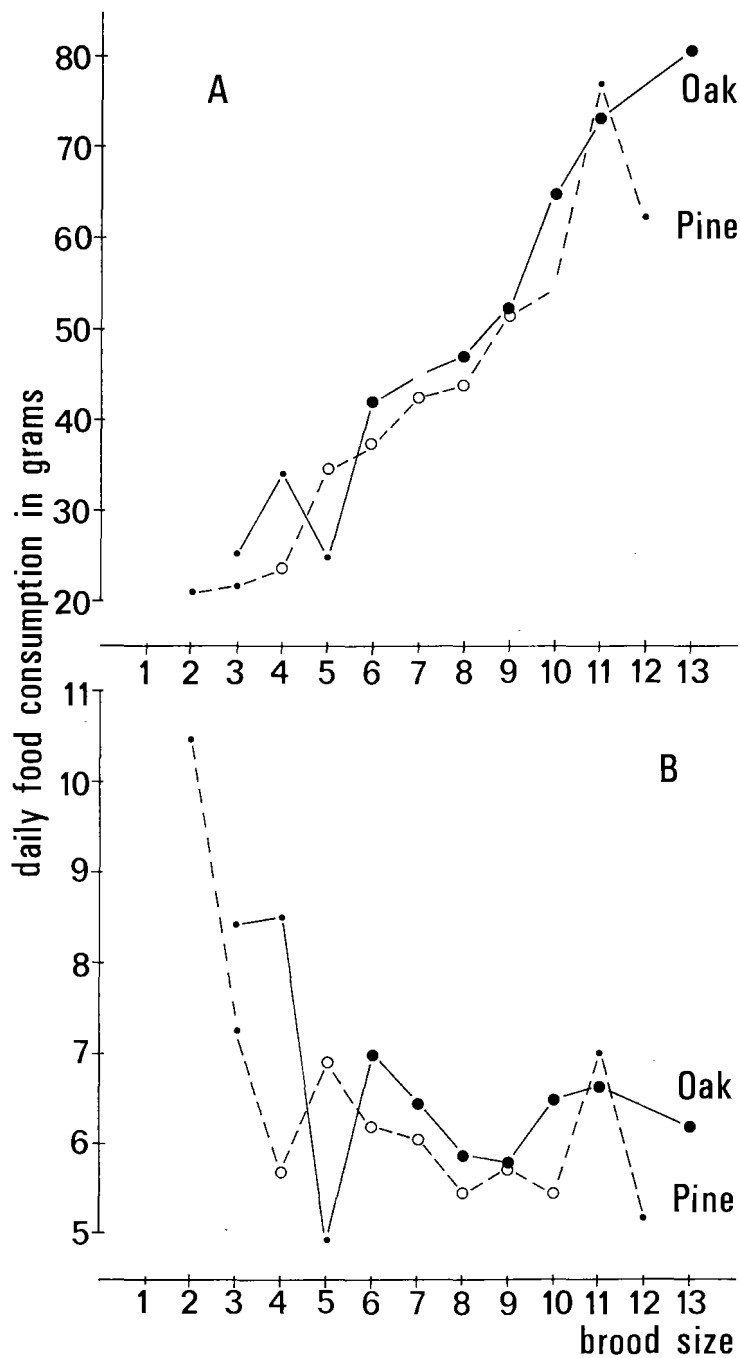


Fig. 18A. Daily food consumption in relation to brood-size. Nestlings aged 8-17 days. Small dots are based on less than 10 observation days.
B. Daily food consumption per nestling, otherwise as in A.

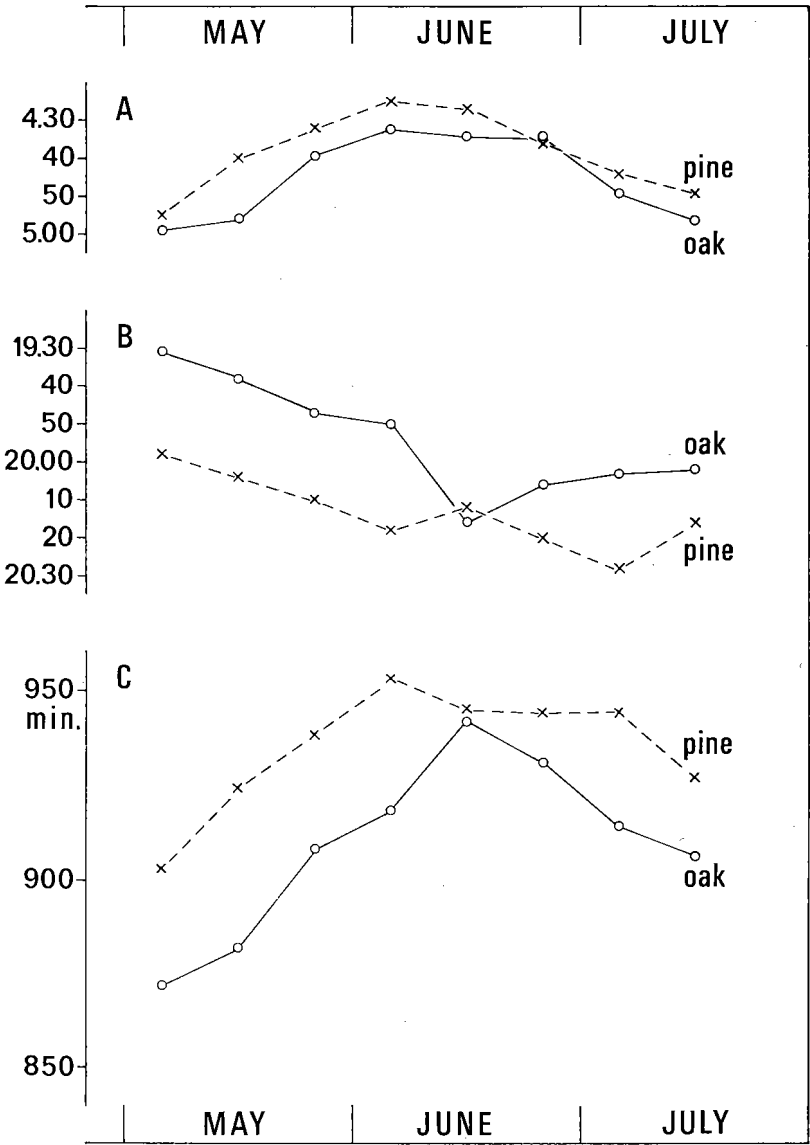


Fig. 19. Average time of first (A) and last (B) feeding visit (hours M.E.T.), and average duration (C) of feeding day (in minutes) in the course of the breeding season.

followed by mortality, which brings the number of nestlings into balance with the amount of food that the parents can provide. Evidence for this view is presented in Table 18, which shows the relation between daily food

consumption per nestling and subsequent mortality. All cases in which one or more of the young died within two days have been scored as +. For the calculation all broods in oak- and pinewoods with 4–13 young were included, since the food consumption per nestling is roughly constant over this range of brood-size (see p. 61). The Table shows that low food consumption is often followed by the death of one or more nestlings. In all age classes there is an inverse relation between food consumption and percentage mortality. Comparison of the two oldest groups shows that the mortality decreases with age, at comparable food levels. Presumably food shortage during the last stage of the nestling's life is likely to manifest itself in a lowered condition at fledging, e.g. a low body weight.

Table 18. Relationship between food consumption and subsequent mortality. Frequency of death (+) and survival (—) within two days after measurement of food consumption

Daily food consumption per nestling (grams)	Age 4–5 days			Age 6–7 days			Age 8–12 days			Age 13–17 days		
	+	—	% mort.	+	—	% mort.	+	—	% mort.	+	—	% mort.
2.00— 2.99	5	17	23	2	3	40	—	—	—	—	—	—
3.00— 3.99	2	16	11	5	9	36	2	3	40	2	6	25
4.00— 4.99	0	6	0	4	13	24	6	20	23	1	17	6
5.00— 5.99	0	2	0	0	6	0	3	29	9	3	45	6
6.00— 6.99	—	—	—	0	5	0	1	28	3	1	30	3
7.00— 7.99	—	—	—	—	—	—	0	22	0	0	17	0
8.00— 8.99	—	—	—	—	—	—	0	14	0	0	10	0
9.00— 9.99	—	—	—	—	—	—	0	5	0	0	3	0
10.00—10.99	—	—	—	—	—	—	—	—	—	0	4	0
Total	7	41	15	11	36	23	12	121	9	7	132	5

The conclusion on the relation between food consumption and mortality holds for all four age groups in Table 18, whereas in Fig. 18 only the two oldest groups were considered. Possibly still another factor plays a role in the food provision of the younger age classes. When the data on the relation between food consumption and mortality rate are analyzed separately for the two habitats, it appears that the above-mentioned relation exists in both habitats (and in all age classes), but that the mortality rate of the younger nestlings (up to 7 days) is higher in the pinewood than in the oakwood, at comparable food levels. This suggests that the quality of the food in the pinewood is inferior.

The level of food consumption per nestling in broods of medium size is on average about 5.5 to 7.0 g fresh weight per day (Fig. 18B). These results may be compared with the few data published by other workers. From Kluyver's (1950) results the food consumption per nestling can be calculated as 3.4 and 7.5 g per day in an early and a late pinewood brood. As already mentioned (7.1), Gibb & Betts (1963) found a daily food consumption

of 4.66 and 7.28 g fresh weight in two similar broods. These values fall within the range for the individual broods studied by us. Royama (1966b, Fig. 6) determined the food consumption of the Japanese race, which is 3–4 g lighter than the European races. For young of 12 to 14 days old the food consumption amounted to 0.9 g (dry weight) daily, or 3.6–4.5 g fresh weight. In relation to body weight the Japanese nestlings received about 6% (dry weight) or 25–31% (fresh weight) of food, assuming that the moisture content of the food was 75–80%. For our birds, with an average body weight of about 16 g (cf. Fig. 23), these percentages are higher, viz. 7–11 (dry) and 34–44 (wet weight). The level of food consumption of nestlings is low compared with the 18% (dry weight) determined by Gibb (1957) for captive adults, but part of this difference should be attributed to the difference in air temperature during Gibb's winter feeding trials (4.4°C) and during May–July in our study area (about 15°C). As Royama (1966b) pointed out the low level of food consumption by nestlings is made possible by the heat-conserving properties of brood and nest.

We mentioned above that the food consumption per nestling was more or less constant over a large range of brood-sizes (cf. Fig. 18B). To study the food requirements of nestlings from different brood-sizes, an attempt was made to collect all data from broods in good conditions. This was achieved by discarding all data from broods with a low mean body weight (under 17.0 grams on the 16th day) and all data from days with subsequent mortality within two days. The remaining material from the oak- and pine-woods was added, and the results are given in Fig. 20A. Apparently, the food consumption of nestlings in broods with 2 and 3 young shows an increased value in relation to the general level in the larger broods.

The relation between food consumption per young and brood-size was first studied by Royama (1966b), who found that food consumption in the period from the 7th to the 13th day was inversely related to brood-size. The range of brood-sizes he tested was 3 to 13 young. He argued that the rate of heat loss is much greater in small broods, due to the large surface-volume ratio of the brood as a whole. Fig. 21A shows Royama's results, recalculated by me from his Fig. 15. The shape of his curve is clearly different from mine (Fig. 20A). Whereas in Royama's birds the food consumption increased with decreasing brood-size over the whole range, in our birds this occurred only in the smallest broods. Royama's extreme values (3 and 13 young) are based on only one brood each, and hence are less reliable. Nevertheless, there is some discrepancy between his and mine results in the medium range of brood-size.

Mertens (1969) measured the heat production of Great Tit nestlings (10 days old), and found an inverse relationship with brood-size at 12°C and no dependence on brood-size at 18°C, except when the brood was reduced to one nestling. His results are included in Fig. 21. Comparison of Fig. 20A and 21 shows that my results are similar to Mertens' findings at 18°, while

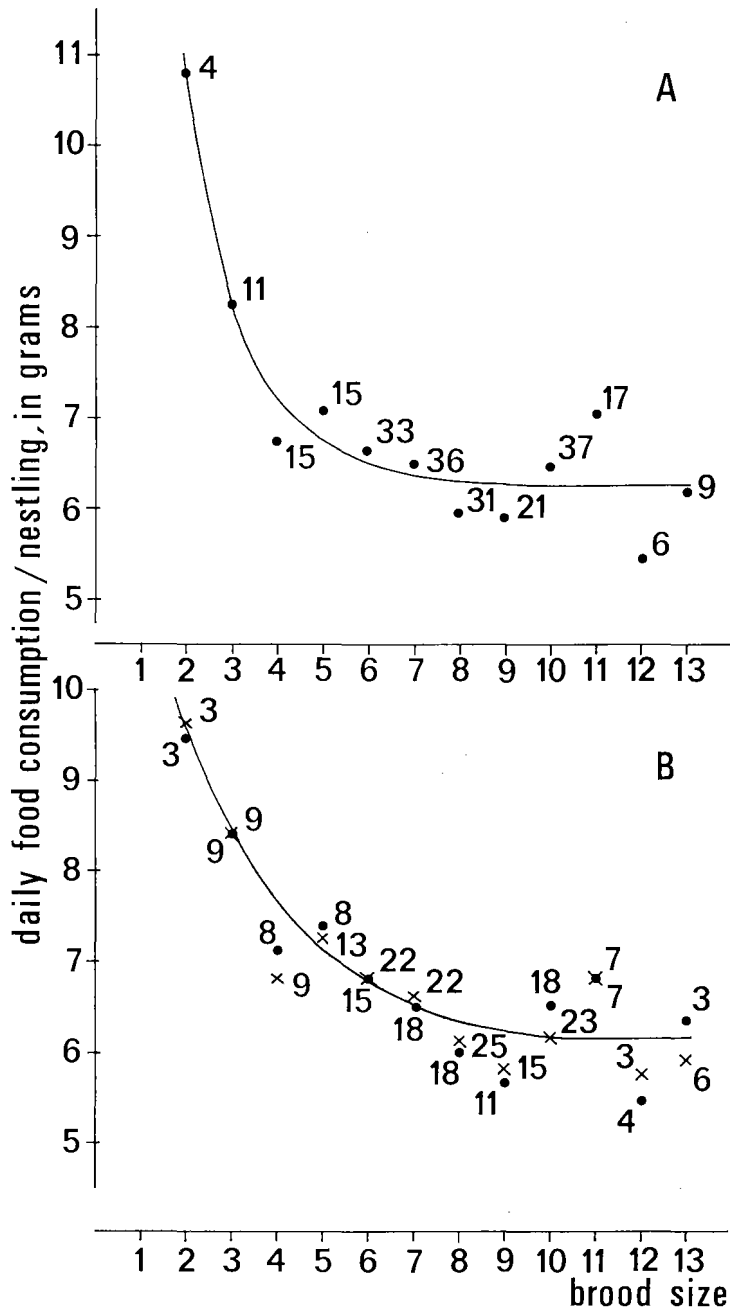


Fig. 20A. Relation between food consumption per nestling and brood-size. Age 8-17 days. Broods in good condition (see text, p. 61). Figures denote the number of observation days.

B. As in A, but from medium range of air temperature (see text, p. 63). Dots: day temperature 13°-18°. Crosses: morning temperature 11°-17°. Lines fitted by eye.

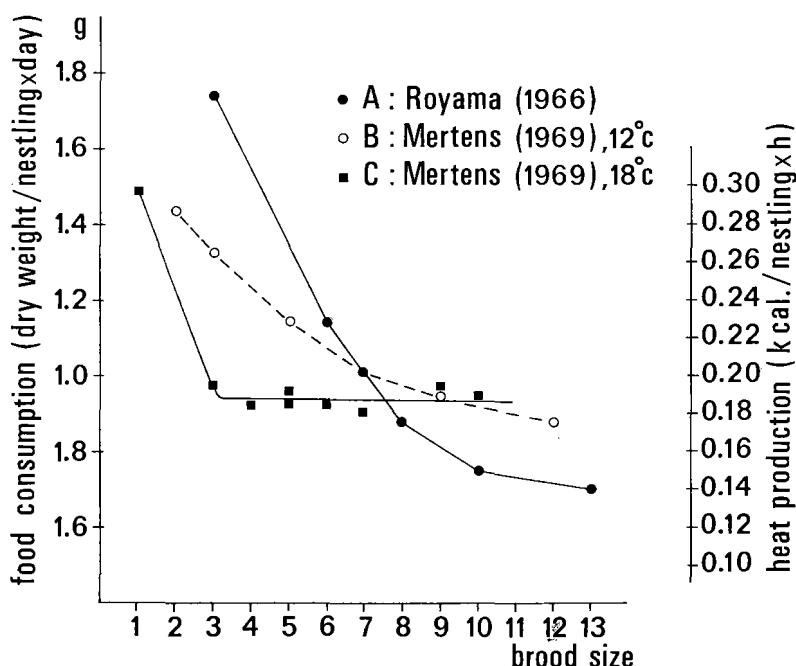


Fig. 21. Relation between brood-size and food consumption (or heat production) according to Royama (1966b) and Mertens (1969).
 A: data from Royama (1966b, Fig. 15); age 7–13 days, temperature unknown.
 B: data from Mertens (1969, Table 3); age 10 days; temperature 12° C.
 C: as in B, but temperature 18° C.

Royama's results resemble, and show an even steeper curve than Mertens' results at 12°.

Examination of the effect of air temperature on food consumption in my material showed that over a large range of temperatures food consumption was unaffected. At daytime temperatures under 12°, food consumption increased; and at daytime temperatures over 23° or morning temperatures over 17°, food consumption decreased. For the study of food consumption in relation to brood-size it is advisable to use the data from the medium range of temperatures, i.e. daytime temperatures of 13–18° or morning temperatures of 11–17°. As Fig. 20B shows, both procedures give similar results, and the resulting curve indicates a more gradual increase of food consumption with decreasing brood-size than the overall curve in Fig. 20A. Moreover, the shape of the curve is intermediate between Mertens' curves at 12° and 18°, in agreement with the temperature range used by me.

The main conclusions from section 7.3.2 are that the total amount of food brought to first broods in oakwood amounts to 60–70 g daily (days 8–17),

and that in all other broods the level of food provision is much lower. The amount of food provided affects mortality in such a way that a low food consumption is quickly followed by mortality in a larger number of cases, and this adjusts the number of young to the feeding capacity of the parents.

8. NESTLING SURVIVAL

8.1. INTRODUCTION

In Chapter 7 the mortality of nestlings was mentioned repeatedly, and the relationship between food consumption and subsequent mortality was discussed. Here, a general survey of nestling survival in relation to habitat will be given, and the results will be compared with those in the literature.

Many authors discuss this subject on the basis of breeding or nesting success (percentage of young fledged from eggs laid), but our high frequency of nestbox inspection enabled us to assess the fledging success (percentage of young fledged from young hatched). The number hatched was determined either by counting directly, or could be computed within narrow limits from the clutch-size, the number of young ringed, and the number of unhatched eggs and dead young found in the nest. The number of fledged young was usually determined from the number ringed, usually at the age of 7 days, and the number found dead after fledging. In many cases this was confirmed by inspection shortly before fledging (e.g. for weighing). All cases of total brood mortality were excluded from the calculations, to avoid the possible influence of predation on parents or young.

In the study of nestling survival in the course of the breeding season, the broods were classified according to the day of hatching, irrespective of the distinction between first, repeat and second broods.

8.2. HABITAT AND NESTLING SURVIVAL

A general survey of nestling survival in the four main study areas is given in Table 19.

Table 19. Survey of nestling survival in oakwoods (a) and pinewoods (b)

Area	Years	Period	Number hatched	Number fledged	% Survival	Number fledged per brood
a. Oosterhout	1956—1970	early	1603	1507	97.9	9.02
Oosterhout	1956—1970	late	420	333	79.3	5.95
Liesbosch A	1955—1967	early	3522	3382	96.0	8.90
Liesbosch A	1955—1967	late	1009	810	80.3	6.04
b. Hoge Veluwe A	1955—1970	early	2108	1494	70.9	6.50
Hoge Veluwe A	1955—1970	late	1982	1450	73.2	5.64
Imbosch	1960—1965	early	390	306	78.5	7.29
Imbosch	1960—1965	late	348	248	71.3	5.64

Note: Early broods hatched up to May 29, in most years this includes all first broods. Late broods, hatched from May 30, include repeat and second broods.

In the two oakwoods the survival of the early broods was very high, in some years even 100%. Among the late broods survival was considerably lower, i.e. about 80%. The difference in survival between early and late broods occurred in all years, and is highly significant ($P < 0.001$ in both oakwoods). Differences in survival between Oosterhout and Liesbosch are very small and not significant.

Accurate assessments of nestling survival in the literature are scarce. Many authors merely calculated nesting success or productivity per pair, both parameters that cannot be directly compared with our results.

The data given by several authors for oak and mixed broad-leaved woodland at Wytham (Oxford) correspond in general with the results for the Dutch oakwoods. In first broods, nestling survival normally amounts to 94–98% (Perrins 1965, Lack 1966), but during 1958–1963 in Marley only 89% of the nestlings survived. This last period included one year (1961) with very high numbers of tits and a low level of caterpillar abundance. In repeat and second broods, which are rare in Britain, 53% of the nestlings survived (Lack, Gibb & Owen 1957), which is considerably lower than the figure found for the Dutch oakwoods. It seems likely that feeding conditions in the British oakwoods deteriorate during the season to a greater extent than in our oakwoods.

In the oakwood Zevegem near Gent conditions for the nestlings are evidently not as favourable as in the above-mentioned habitats, since Dhondt (1970) states that nesting success in early and late broods is 76.2% and 71.5% respectively, which is equivalent to 75–80% nestling survival, if hatching success is put equal to the hatching success in the Dutch oakwoods.

Nestling survival in our two pinewoods is on average much lower than in the oakwoods (Table 19). The difference is significant in early as well as in late broods ($P < 0.001$).

Differences in survival between the Hoge Veluwe and Imbosch are small and not significant in both early and late broods. At the Hoge Veluwe late broods seem to have a slightly better survival rate, but the difference is not significant. At Imbosch the early broods have more success; in this case the difference is hardly significant ($P < 0.05$).

These findings are similar to the results obtained by Dhondt (1970) in a pinewood near Gent, where nesting success amounted to 69.4% and 65.9% in early and late broods respectively, equivalent to a nestling survival of about 72%. On the other hand our results are not in good agreement with the figures published by Lack (1958, 1966) for pinewoods in Thetford Chase (Norfolk), where nestling survival amounted to 62% in first and 87% in second broods. Seasonal variations in nesting success have generally been explained as the consequence of variations in food availability. Indeed, during two years the caterpillar stock in Thetford Chase increased from May to July, in parallel with increasing nestling weight and survival (Gibb & Betts, 1963). In the Dutch pinewoods this increase in caterpillar abun-

dance is found in some years (e.g. 1962; see Fig. 1), but in other years the caterpillar peak occurred earlier, in June. The seasonal trends in nestling survival could be due to this difference in food availability. In the next section the effect of food on nestling survival will be examined further on the basis of the annual and seasonal variations, in some detail.

8.3. ANNUAL AND SEASONAL VARIATIONS IN NESTLING SURVIVAL

In the oakwoods the survival in the early broods varied only slightly from year to year. For Oosterhout the annual percentages range from 94.1 to 100 (S.D. 2.3) and for Liesbosch they range from 91.3 to 98.6 (S.D. 2.4). This indicates that feeding conditions in this type of habitat are extremely reliable, at least during the first half of the breeding season.

One of the possible relations is the one between nestling survival and breeding density. A negative correlation between the two is to be expected if the effect of breeding density on clutch-size has adaptive significance (cf. Klomp 1970, p. 104). Indications for the existence of such a relation were obtained in Marley (Oxford), where in 1961, at an extremely high breeding density, nestling survival and body weight were much lower than in more normal years. In The Netherlands, however, this is not the case, since nestling survival (in the first clutches in oakwood) showed only slight annual variations unrelated to breeding density. For the late broods the annual variations were much larger (S.D. 7.5 to 15.2%), but they are not related to the breeding density or to the number of second broods either.

Both early and late broods in pinewoods showed large annual variations in nestling survival, with standard deviations of the means ranging from 8.7 to 17.8%. Under these conditions, where the parents obviously meet with difficulties in rearing young, it could be expected that high breeding densities reduce nestling survival, but this was not the case. Among early broods, no

Table 20. Seasonal trends in nestling survival

Period of hatching	Oosterhout		Liesbosch A		Hoge Veluwe A		Imbosch	
	number of young hatched	% fledged	number of young hatched	% fledged	number of young hatched	% fledged	number of young hatched	% fledged
20— 29	10	(100.0)	33	(100.0)	42	(88.1)	—	—
30— 39	213	96.2	814	95.6	597	74.0	78	85.9
40— 49	1060	98.4	1713	97.0	680	71.3	154	76.0
50— 59	313	97.6	971	94.5	789	67.2	158	77.2
60— 69	112	83.4	349	87.4	399	81.0	56	62.5
70— 79	120	77.0	288	77.1	287	78.0	47	(83.0)
80— 89	152	80.5	315	76.5	559	69.6	145	72.4
90— 99	38	(69.3)	57	73.7	620	70.2	100	69.0
100—129					117	67.5		

Notes: 1. Periods of hatching are given numerically, on the basis of 1 April = 1.
2. Percentages in parentheses are based on less than 50 young.

relation between nestling survival and breeding density could be found; among late broods, survival was not affected by the number of late broods (i.e. the density of parents starting a second brood), and only slightly and not significantly by the density of first broods. This implies that so far the adaptive value of the effect of breeding density on clutch-size has not been demonstrated. This problem will be examined further when the body weight of the nestlings is discussed (9.3.3.).

Table 20 gives a detailed survey of the seasonal trends in nestling survival. In the two oakwoods, nestling survival remained at a high level until the end of May, after which it was significantly lower until the end of the season. In Liesbosch there was a significant downward trend in survival from May to July. At the Hoge Veluwe (pinewood) the survival of the earliest broods and of the broods hatching between 60 and 79 April (30 May – 18 June) is significantly higher than for the broods hatching in the other periods. In the other pinewood, for which the available data are rather scanty, the same trends can be distinguished, but they are not significant. The seasonal trends in survival generally correspond with the trends in food availability, described in Chapter 4, where the peaks in caterpillar density were found to occur early each year in the oakwood, and often in the middle of the season in the pinewood.*

For a more detailed comparison of seasonal trends in nestling survival and caterpillar density we must allow for annual differences in the timing of the caterpillar peak. Hence, the material was divided into years with an early, medium, or late caterpillar peak (cf. Table 4) and the seasonal trends were studied separately for these groups of years. Fig. 22 shows that in the oakwood nestling survival exceeded 90% during the peak and part of the decline in caterpillar density. Only when the caterpillar abundance drops to very low levels, the nestling survival appears to be affected.

In the pinewoods the caterpillar peak occurred either late or in the middle of the season. The survival of the nestlings was strongly affected (Fig. 23). In early broods (hatched from 30 to 59 April) survival was significantly higher in medium than in late peak years. For broods hatched in the middle of the season, survival was similar in medium and late peak years. For the latest broods (hatched from 80–110 April) survival was significantly higher in years with a late caterpillar peak. Clearly, nestling survival in pinewoods is positively correlated with the feeding conditions during the nestling stage.

The low nestling survival in the pinewoods and the relation between survival and caterpillar abundance show that feeding conditions are often quite unfavourable, even at the time of the annual caterpillar peak. Hence,

* The good survival of the broods that hatched between 60 and 79 April, and consequently grew up in the period of maximum daylength, suggests that nestling survival in pinewoods is related to daylength. However, from the evidence presented below, on the effect of the time of the caterpillar peak on nestling survival, the conclusion arises that the daylength is unlikely to play an important role in affecting survival.

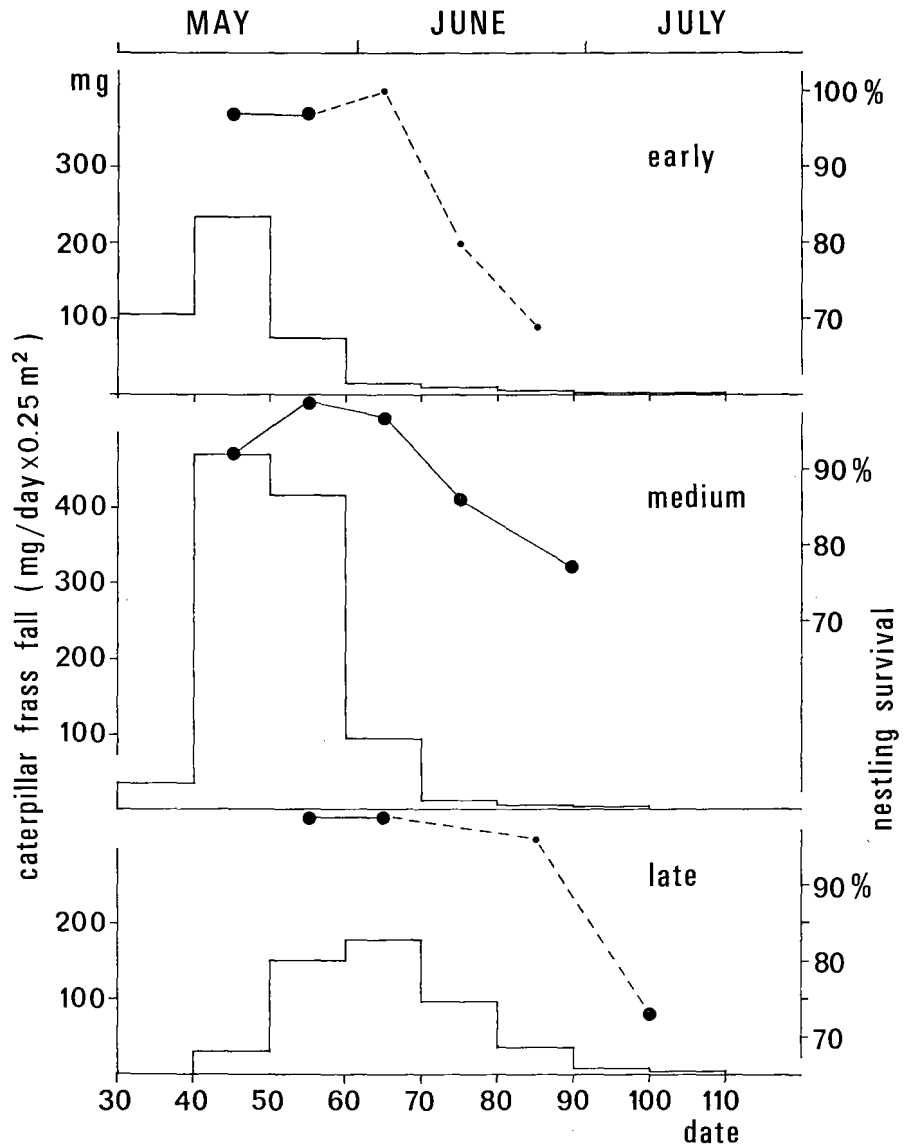


Fig. 22. Relation between caterpillar abundance in oakwood and nestling survival, in early, medium and late years. Small dots are based on less than 50 young. Dates are counted from 1 April = 1.

I can not agree with Kluyver's conclusion that "in pine plantations in Holland a shortage of food is, in general, not probable in June and July" (Kluyver 1971, p. 509).

8.4. MORTALITY AND AGE OF NESTLINGS

The results discussed in the preceding section indicate that nestling survival is positively correlated with the food supply, as measured by the amount of caterpillar frass, which suggests that at least part of the mortality is caused by starvation. This conclusion is supported by the finding, reported in section 7.3.2.4., that a lower than average food consumption is often followed within short time by the death of one or more nestlings. Evidence for the occurrence of starvation is also provided by the body weights of the nestlings (see Chapter 9) and by the temporal distribution of deaths in the course of the nestling period.

Table 21 shows that under good feeding conditions (early broods in oak-woods), when mortality is very low, most of the deaths occur during the first half of the nestling period. It has already been shown (7.3.2.4.) that

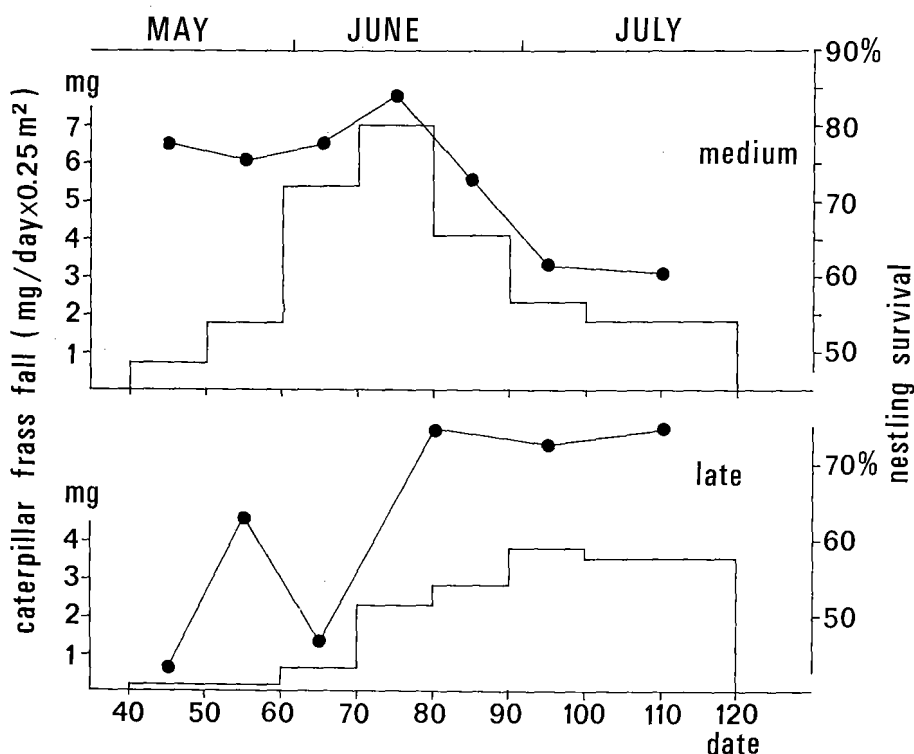


Fig. 23. Relation between caterpillar abundance in pinewood and nestling survival, in medium and late years.

the food requirements increase sharply during the first week of life, and remain on a high level from day 8 until fledging. Since the risk of dying from starvation varies in parallel with the food requirements – other things, such as the food availability and the vulnerability of the nestlings, being equal – starvation is expected to occur during the later part of the nestling period or (in more extreme cases) during the whole period. The early occurrence of deaths in early oakwood broods indicates that starvation here is not the cause of death.

Table 21. Temporal distribution of nestling mortality

Period (days)	Early broods			Late broods		
	number of deaths	% of deaths	number of deaths per 100 hatched	number of deaths	% of deaths	number of deaths per 100 hatched
Oakwood (Oosterhout)						
0—4	9	39	0.8	26	33	6.8
5—9	10	43	0.9	30	38	7.9
10—14	1	13	0.3	6	8	1.6
15—19	3	4	0.1	17	22	4.5
			2.1			20.8
Pinewood (Hoge Veluwe A)						
0—9	135	51	14.8	92	46	12.3
10—19	128	49	14.2	108	54	14.5
			29.0			26.8

- Notes: a. Early and late broods defined as in Table 19.
 b. Day 0 = the day on which the first nestling hatched. Hatching may be spread out over several days, especially in late broods.
 c. In the Hoge Veluwe inspections were not sufficiently frequent to allow division of the nestling period into four parts. For the same reason, figures for 1955—1961 were excluded.

In late oakwood broods and in both early and late broods in the pinewood, where nestling survival is considerably lower, an increasing part of the mortality occurs during the second half of the nestling period, suggesting that starvation does play a major role. However, in the first part of the nestling period the mortality rate is also considerably higher than the value obtained under good feeding conditions. In this connection it must be mentioned that in the late broods the process of hatching is spread out over several days (up to 5), resulting in the presence of young of unequal age within a brood. The smallest nestlings often die within a few days, presumably due to competition for food with their older nestmates (cf. Löhrl 1968). With young of equal age the mortality would probably occur at a later stage.

In the other pinewood, Imbosch, several cases were observed in which a whole brood died at an early age (7–10 days), after being fed mainly on

unsuitable food, such as pineseed, for several days. Otherwise, the mortality pattern in this wood was similar to that in Hoge Veluwe.

In most broods with high mortality, the nestlings of which were weighed periodically, the dying nestlings had a considerably lower weight than their nestmates (Chapter 9).

On the basis of the foregoing it may be concluded that starvation plays a major role in those cases in which nestling mortality occurs.

8.5. NESTLING SURVIVAL AND BROOD-SIZE

In the preceding sections evidence was presented showing that the food supply, as measured by the amount of caterpillar frass, is positively correlated with the survival of the nestlings, and that starvation was a major cause of mortality. These facts lead us to expect that under unfavourable feeding conditions, e.g. in late oak broods and in all pine broods, nestling survival would be negatively correlated with the number of young hatched. Despite the inverse relationship between food requirements per young and brood-size found by Royama (1966b) and confirmed here, the amount of food required per brood increases sharply from small to large broods. Food requirements per brood, calculated from Fig. 20B, range from about 20 g daily in broods of 2 young to about 75 g daily in broods of 11–13 young.

Nestling survival in relation to brood-size was calculated for the two oak-woods (Table 22), and for the Hoge Veluwe pinewood (Table 23). The

Table 22. Relation between brood-size and nestling survival in oakwood

Early broods				Late broods			
Initial brood-size	Number of young hatched	% fledged	Number fledged per brood	Initial brood-size	Number of young hatched	% fledged	Number fledged per brood
Oosterhout							
3—6	71	100.0	5.07	5—6	93	76.3	4.44
7	91	96.7	6.77	7	112	75.9	5.31
8	176	98.9	7.91	8	88	85.2	6.82
9	387	99.0	8.91	9	54	72.2	6.50
10	380	97.4	9.74	10—13	65	84.6	9.17
11	297	98.3	10.81				
12	120	95.8	11.50				
13—14	53	96.2	12.75				
Liesbosch A							
				1—5	93	81.7	3.45
3—6	106	98.1	4.95	6	132	77.3	4.64
7	161	96.9	6.78	7	189	75.1	5.26
8	632	95.6	7.65	8	168	73.8	5.90
9	675	95.4	8.59	9	153	88.2	7.94
10	880	95.7	9.57	10	80	73.8	7.38
11	660	97.0	10.67	11	110	87.3	9.60
12	312	97.4	11.69	12	84	86.9	10.43
13—16	82	93.9	12.83				

Table 23. Relationship between brood-size and nestling survival in a pinewood (Hoge Veluwe A)

Early broods				Medium broods			
Initial brood-size	Number of young hatched	% fledged	Number fledged per brood	Initial brood-size	Number of young hatched	% fledged	Number fledged per brood
3—6	86	70.9	3.59	3—6	78	76.9	3.75
7	126	81.0	5.67	7	112	88.4	6.19
8	280	72.1	5.77	8	160	80.0	6.40
9	531	68.2	6.14	9	180	72.2	6.50
10	470	72.6	7.26	10—12	156	83.3	8.67
11	407	70.5	7.76				
12—13	194	66.5	8.06				

Late broods			
Initial brood-size	Number of young hatched	% fledged	Number fledged per brood
2—5	84	66.7	2.95
6	108	63.0	3.78
7	238	72.7	5.09
8	416	64.4	5.15
9	216	75.5	6.79
10—11	233	77.3	7.83

Tables show that in all woods and during the whole breeding season there is no clear relationship between survival and brood-size. In each group the largest broods were the most productive. These results, though unexpected within the context of this study, confirm the conclusions reached by Kluyver (1951), who found that nesting success in Oranje Nassau's Oord (pine and mixed deciduous woodland) did not vary with clutch-size, except for a slightly higher mortality in the largest late broods. Similarly, Perrins (1963a, 1965) found that in Marley Wood nestling mortality (except that due to predation) is largely unaffected by brood-size, but that differences connected with brood-size occur in body weight and survival after fledging.

Starvation is likely to occur, from different kinds of evidence, but it does not show up in a lower survival among larger broods. This discrepancy can be explained in two ways. Firstly, there is the possibility that differences in feeding conditions between small and large broods result mainly in differences in body weight, as found by Perrins in a situation where little starvation occurs. This aspect will be discussed in Chapter 9. Secondly, the absence of any relation between brood-size and nestling survival may be due to adaptations occurring before hatching, bringing the brood-size more or less into accordance with the expected feeding conditions. This can be accomplished by modifications of clutch-size, adapting the clutch to local food conditions, or to the feeding efficiency of the tits, or both. The relation

of clutch-size to the age of the female is an example of this kind of modification. Now Jones (1972) has found that small females lay earlier than large females, due to their smaller daily energy requirements for normal body maintenance. Similarly, not all Great Tits will be equally efficient feeders. As the supply of insect food increases in spring, first the most efficient and later the less efficient feeders will come into breeding condition. Due to the seasonal decline in clutch-size, the most efficient females will produce the largest clutches. Presumably they also have the greatest abilities to rear the brood successfully.

9. GROWTH AND CONDITION OF THE NESTLINGS

9.1. INTRODUCTION

In the preceding chapters the body weight of the nestlings has been repeatedly mentioned as an aspect worth investigating in connection with the feeding ecology of the Great Tit. The growth rate of the nestlings should be a function of the extent to which food requirements are fulfilled. Moreover, the body weight attained at fledging should be a measure of the energy reserves of the fledgling, and hence be related to the survival after fledging (Perrins 1963b). Since both these aspects are important within the context of this study, one should ideally obtain complete growth curves of a number of broods in both habitats, over a number of years. Because lack of time prevented us from achieving this in more than a few years, we limited our efforts in the other years to weighing as many broods as possible during the last few days before fledging. In the following discussion of growth rate and fledging weight, only the weights of young surviving up to fledging will be considered.

9.2. GROWTH RATE

During 1957, 1958, and 1962, a number of broods were weighed repeatedly, at intervals of two days, in Oosterhout and Hoge Veluwe A. An attempt was made to construct a growth curve for well-fed Great Tit broods. This was done by selecting all Oosterhout broods without nestling mortality and with a growth period coinciding with the caterpillar peak. The results (Fig. 24) show that the growth rate is highest between day 2 and day 9, declines afterwards, and on average falls to zero after day 15. A similar growth curve was obtained by Gibb (1950) for first broods in Wytham. In his case the growth rate was slightly higher and the birds weighed about 18.5 grams at day 15. This corresponds with the higher adult weight of the British subspecies *Parus major newtoni*.

Examination of the growth curves reveals that the increase in weight from day 2 to day 9 is more or less linear, and that the daily increase during this period is a suitable measure of the growth rate. Growth rates per brood were calculated by a linear regression of body weight with nestling's age. The

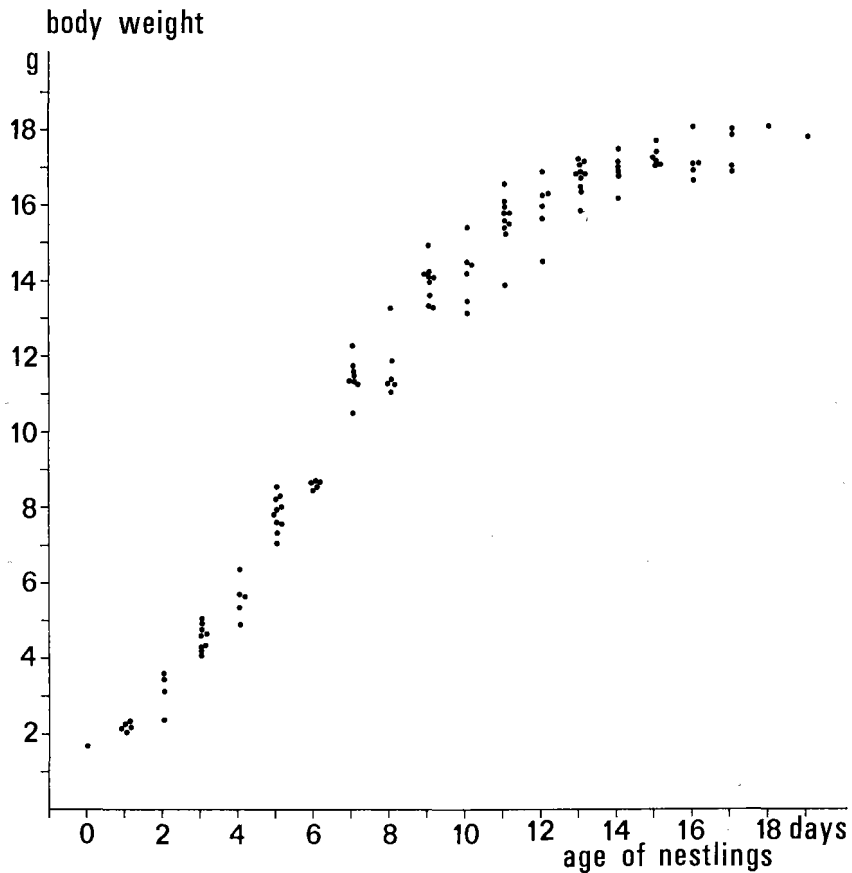


Fig. 24. Growth curve of well-fed Great Tit nestlings. See text, p. 73.

resulting regression coefficients, representing the growth rate in grams per day, varied widely, ranging from 1.208 to 1.707 in the oakwood (mean 1.489), and from 0.557 to 1.920 in the pinewood (mean 1.357). The growth of the nestlings can be affected by several factors, such as the availability of food, the size of the brood and the air temperature during the growth period. The effect of these factors on the growth rate was investigated by regression analysis, in which Y = the growth rate of the brood, X_1 = the weight of caterpillar frass falling daily during the growth period, X_2 = the average number of young present during this period, and X_3 = the mean air temperature during this period.

The results differed for the two areas. In neither area was the effect of the air temperature significant. In Oosterhout, where 30 broods were studied, both food supply and brood-size had significant effects, resulting in the regression equation

$$Y = 1.6945 + 0.0004 X_1 - 0.0323 X_2$$

Here, Great Tit broods grow better when there are many caterpillars in the canopy and relatively few young tits in the nest. For this calculation, both early and late broods were included. When separate calculations are made for early and late broods, it appears that in the early broods both caterpillar abundance and brood-size have significant effects ($Y = 1.6859 + 0.0004 X_1 - 0.0328 X_2$). Similar effects were found for the late broods, but these were not significant, probably due to the small sample size ($n = 11$).

The average growth rates of early and late broods do not differ (1.484 and 1.498 g/day), which is due to the fact that broods decrease in size in parallel with the declining caterpillar abundance.

In the pinewood (Hoge Veluwe A, 29 broods) the effect of brood-size was not significant, so the relation is best described by the linear regression equation

$$Y = 1.1814 + 0.1212 X_1$$

In this habitat, where food is in short supply (cf. Chapters 7 and 8), the availability of food has a profound effect on the growth rate of the nestlings. This becomes even more clear when separate calculations are made for early and late broods. In both groups the growth rate is significantly related to the amount of caterpillar frass. Moreover, the regression coefficient is very large for the early broods, which lived under the worst feeding conditions, at least in the three years in which the growth rate was measured. Table 24 shows that the regression coefficients become progressively larger in the direction from very good to very bad feeding conditions. When caterpillars are very scarce, a slight increase in abundance has a strong effect on the growth rate. Under the worst feeding conditions (early broods in pinewoods) the overall growth rate is very small, but this results from the very bad feeding conditions in the years in question (see Fig. 1).

We conclude that in general in the oakwoods the effect of caterpillar abundance on the growth rate (between day 2 and day 9) was small, and that the overall growth rate in early and late broods was similar. In the pinewoods

Table 24. Effect of caterpillar abundance on growth rate

Area and season	Number of broods	Mean amount of caterpillar frass	Mean growth rate	Regression coefficient
Oosterhout, early	19	189.95	1.4838	+ 0.0004**
Oosterhout, late	11	29.91	1.4983	+ 0.0015
Hoge Veluwe, early	11	0.13	1.2123	+ 9.7297**
Hoge Veluwe, late	18	2.26	1.4454	+ 0.1345*

Notes: 1. Early and late broods defined as in Table 19.

2. * $p < 0.05$, ** $p < 0.01$.

the effect was much stronger, and the growth rate will vary from year to year according to the variable feeding conditions. Under adverse feeding conditions growth is considerably retarded.

It must be kept in mind that the growth was measured for surviving young only; hence, the effects described in this (and the next) section are additional to the mortality discussed in Chapter 8.

9.3. BODY WEIGHT AT FLEDGING

9.3.1. Introduction

Several authors have measured the body weight of Great Tits during the last few days before fledging. Most of them weighed the nestlings on the 15th day, the day on which, according to Gibb (1950), body weight is maximal. In this study, weights of a limited number of broods were obtained up to the 18th day, in some retarded broods even up to the 21st day. After the 15th day some broods decrease in weight, while others remain constant, or even increase up to the 18th day. The latter is most common in broods which were relatively light on the 15th day. Since there was no consistent trend between the 15th and the 18th day, and most broods fledged on the 19th day, any weight obtained between the 15th and 18th day was considered to represent the fledging weight.

9.3.2. Fledging weight and habitat

The average weights in early and late broods from four areas are given in Table 25. As the Table shows, there are differences in body weight between the populations in oak- and pinewoods, but they are small and differ in sign for early and late broods.

Among the early broods, the two oakwood populations have significantly higher weights than the birds from the Hoge Veluwe, and the nestlings in Liesbosch are significantly heavier than those in Imbosch. The late broods

Table 25. Fledging weight in two oakwoods (a) and two pinewoods (b)

Area	Years	Period	Sample size	Bodyweight		
				Mean (g)	S.D. (g)	V (%)
a. Oosterhout	1956—1965	early	723	17.70	1.16	6.5
	1956—1965	late	182	16.89	1.56	9.2
	Liesbosch A	early	672	18.05	1.22	6.7
	Liesbosch A	late	101	16.81	1.46	8.7
b. Hoge Veluwe A	1956—1965	early	626	16.74	1.84	11.0
	1956—1965	late	558	17.23	1.90	11.0
	Imbosch	early	260	17.49	1.92	11.0
	1960—1965	late	179	17.78	1.67	9.4

in the two oakwoods are slightly lower in weight than those in the pinewood populations, but only the difference between Imbosch and the two oakwoods is significant.

Differences in body weight between early and late broods within one wood are significant, except for Imbosch. So far, the results correspond roughly with the trends in caterpillar abundance.

There are also differences in body weight between populations inhabiting woods with similar vegetation. Early young in Liesbosch are significantly heavier than those in Oosterhout. This is also the case when for both woods data from the same period (1958–1964) are taken. The other variables which might be responsible for this difference are food abundance, breeding density, and brood-size. Measurements of food abundance in Liesbosch were made only in 1961 and 1962. In these years the peak density of the caterpillars in Liesbosch exceeded the Oosterhout density by 76 and 15%, but in view of the large annual variations (cf. Table 2) these observations are insufficient to permit the drawing of conclusions about feeding conditions in Liesbosch. From the breeding densities in the two woods one would expect a smaller mean weight in Liesbosch if breeding density has any effect on body weight (see 9.3.4.). Actually, the mean brood-size of the weighed broods was larger in Oosterhout (9.70) than in Liesbosch (8.50), which probably explains the difference found in mean body weight.

Additional weights were collected in the thinly populated area of Liesbosch C. Here, body weights were higher than in the densely populated area, with an average of 18.39 ± 1.10 for the early broods ($N = 173$ young) and 17.57 ± 1.72 for the late broods ($N = 59$). Both these values are surprisingly high, particularly because the mean brood-size (9.58) is larger than in the other Liesbosch study areas (A and B). This result suggests that extreme variations in breeding density have consequences for nestling weight, even under the favourable feeding conditions of the oakwood. The possible influence of breeding density will be discussed further in the next section.

The average weight is significantly higher in the Imbosch population than in the pinewood of the Hoge Veluwe, both for early and late broods. However, since there are considerable annual variations in body weight, it is advisable to use only weights collected in both woods during 1960–1965. When this is done, the average weights in the Hoge Veluwe are 16.81 g for the early and 17.51 g for the late broods. The divergence from the Imbosch data is no longer significant among the late broods, but the early young in Imbosch are still significantly heavier than those from Hoge Veluwe. This difference is not easily explained. Of the factors possibly affecting body weight, breeding density and brood-size are unlikely to play a part, since the breeding densities are almost equal, and the brood-size of the early Imbosch broods is even slightly higher than in the corresponding broods from the Hoge Veluwe (7.12 v. 6.72). Feeding conditions may be slightly better in Imbosch than in the Hoge Veluwe, but the figures on caterpillar

abundance, given in Fig. 1 and Table 2, do not support this assumption. In my view, the food taken from sources not contributing to the measurements of frass fall, such as bud-inhabiting *Rhyacionia* larvae and oak caterpillars (cf. p. 50), must be responsible for the higher weights attained by the early broods in the Imbosch area.

The trends in body weight in the Dutch populations are similar to but less pronounced than the trends found in the populations in Wytham Wood (Gibb 1950, Lack et al. 1957, Perrins 1963b, 1965) and in Thetford Chase (Gibb & Betts 1963). In most of the years studied by Perrins the nestling weight decreased sharply with the date of hatching, whereas in the Dutch woods this decrease is much smaller. As mentioned in section 8.2., there is a similar difference in the seasonal trend in nestling survival. Once again, this suggests that feeding conditions deteriorate to a greater degree in British than in Dutch oakwoods.

On the other hand, Gibb & Betts (1963) obtained very low weights for early broods in Scots Pine and relatively heavy weights for the late broods (14.62 and 17.43 g). These results fitted in with the higher nestling survival in the late broods, and were related to the larger caterpillar stock available to these broods. As explained above, feeding conditions in Dutch pinewoods do not necessarily ameliorate during the breeding season, so it is not surprising to find only small differences in average weight between early and late broods.

The only other Great Tit populations for which extensive weight data are available are those studied by Dhondt (1970), who found no differences according to habitat. The overall averages varied from 15.3 to 15.8 g (computed by me from his Table 3–28), which is very low compared with the figures discussed above and the limited data given by Winkel (1970). This result is surprising, since the adults from Liesbosch and Gent do not differ in body size as measured by the wing length (van Balen 1967). Although an explanation for this discrepancy cannot be given, the seasonal trend in body weight in the population near Gent deserves some attention. Dhondt found that body weight fluctuated heavily during the season, usually with two peaks and a deep trough between. Some of the seasonal fluctuation in body weight was due to the effect of air temperature, periods of cold weather being associated with low body weights. The fact that the seasonal trend is different from the trends found in Dutch and British oak- and pinewoods suggests that the trend in food availability is also very different. Unfortunately, the food supply in these woods has not been investigated.

9.3.3. Annual and seasonal variations in fledging weight

The discussion in the preceding chapter led to the conclusion that feeding conditions for early oak broods are extremely reliable, resulting in a uni-

formly high survival of nestlings. Body weight in this category of broods shows annual variations with a range of 16.63 to 17.94 g. When the annual means for Oosterhout are compared with the timing of the breeding season in relation to the caterpillar peak, it appears that the body weight is lowest in years with an early caterpillar peak (1958 and 1960, see Table 5, column 9), and is maximal in years in which the caterpillar peak occurs 5 to 14 days after the mean hatching date. This suggests that the caterpillar abundance affects fledging weight, even at the high food level met by the early oak broods. The relation between breeding density and nestling weight was also examined, but we failed to find any depressing effect of high breeding densities. In fact, the highest mean weight occurred in the year with the highest density (1965).

Late broods in Oosterhout show fairly large annual variations in mean body weight (ranging from 15.63 to 17.73 g), but these are not related to the timing of the breeding season or to the breeding density.

Annual fluctuations were larger in both early and late pinewoods broods. The annual means for the Hoge Veluwe range from 15.17 to 18.37 g for the early broods and from 15.46 to 18.52 g for the late broods. Similarly, the overall variability as measured by the coefficient of variation *V* (see Table 25) is larger in pine- than in oakwoods and larger in late than in early oak broods.

From Chapter 3 we know that the breeding density fluctuates violently in pinewoods. These fluctuations had no effect on body weight at fledging. Similarly, it was found (8.3.) that the breeding density did not affect the survival of the nestlings.

Table 26. Seasonal trends in fledging weight

Period of hatching	Oosterhout		Liesbosch A		Hoge Veluwe A		Imbosch	
	sample size	mean weight (g)	sample size	mean weight (g)	sample size	mean weight (g)	sample size	mean weight (g)
30— 39	122	17.75	142	18.31	139	16.24	46	17.41
40— 49	429	17.79	379	18.15	289	16.71	105	18.09
50— 59	156	17.41	162	17.62	198	17.14	110	16.97
60— 69	46	15.91	30	17.51	87	18.05	36	17.93
70— 79	68	17.03	16	16.53	74	17.03	37	17.34
80— 89	47	17.58	58	16.47	191	17.02	69	18.17
90— 99	20	16.91	—	—	178	17.21	38	17.21
100—109	—	—	—	—	27	16.84		

Table 26 gives a detailed survey of the seasonal trends in fledging weight. The trends in the two pairs of woods do not correspond as well as the trends in nestling survival discussed above (see Table 20). In Liesbosch, body weight declined throughout the season, parallel to the decrease in nestling survival. In Oosterhout the decrease in weight is less apparent, mainly due

to an unexplained low weight in the middle period. The general picture for the Hoge Veluwe is one of a peak somewhere in the middle of the season, corresponding with the peak in survival. The earliest broods, which survived relatively well (see Table 20), have very low body weights. Although the reason for this discrepancy is obscure, its consequences are that the condition at fledging of the earliest young will be worse than that of the later fledglings.

9.3.4. The factors affecting fledging weight

In the preceding sections fledging weight was shown to vary according to habitat, year and part of the breeding season. These trends in body weight may be the effect of variations in several factors that affect body weight directly. Among these factors the food supply, as measured by the caterpillar frass fall, is important. The brood-size may also play a role, since it was shown (7.3.2.4.) that broods of different size differ in food requirements. Since Dhondt (1970) found that nesting success is correlated with both the breeding density and the air temperature, this was sufficient reason to examine the effect of these factors on body weight in our populations. A number of regression analyses were performed, which showed that an additional factor, viz. the percentage mortality in the brood, was significantly related to body weight. The regression equations were of the linear type

$$Y = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$$

in which

- Y = the average fledging weight (as defined in 9.3.1.) of the nestlings in a particular brood, in grams,
- X_1 = the mean weight of the caterpillar frass falling daily between the dates of hatching and weighing, in mg,
- X_2 = the number of young alive at the time of weighing,
- X_3 = the percentage mortality between hatching and weighing,
- X_4 = the mean air temperature during the period from hatching to weighing, measured by the K.N.M.I. at Deelen,
- X_5 = the breeding density, in pairs per 10 ha.

The regression coefficients are presented in Table 27. In order to exclude possible interactions between the five independent variables, the partial correlation coefficients were computed and their significance was tested. The results are shown in Table 28, in which r_1 means the coefficient of correlation between fledging weight and caterpillar frass fall, independent of the size of the other four variables. Comparison of Tables 27 and 28 shows complete agreement between the two, as far as the significance of the coefficients concerns.

Table 27. Regression coefficients (b) of the multiple linear regression of fledging weight on five variables (see text p. 80)
 * = $P < 0.05$, ** = $P < 0.01$

Area and season	Number of broods	b_0	b_1	b_2	b_3	b_4	b_5
Oosterhout, early	77	19.5389	+0.0005	-0.2151**	-0.0523**	+0.0343	-0.0189
late	22	18.0324	+0.0084	-0.6739**	-0.0446**	+0.3315	-0.0804
Hoge Veluwe, early	91	18.5534	+0.2785*	-0.3274**	-0.0337**	+0.0577	+0.1086
late	95	17.4585	+0.3155**	-0.1693	-0.0377**	-0.0014	+0.2008

Table 28. Partial correlation coefficients (r) of the correlation between fledging weight and five variables (see text p. 80)

Area and season	r_1	r_2	r_3	r_4	r_5
Oosterhout, early	+0.0997	-0.3638**	-0.3363**	+0.0553	-0.0791
Oosterhout, late	+0.1875	-0.7307**	-0.6085**	+0.3820	-0.4237
Hoge Veluwe, early	+0.2255*	-0.2747**	-0.2921**	+0.0382	+0.0593
Hoge Veluwe, late	+0.4431**	-0.1512	-0.3327**	-0.0018	+0.1379

The correlation between fledging weight and caterpillar abundance is only significant in the pinewood Hoge Veluwe. This is not very surprising, since in oakwoods the caterpillar abundance is so large, at least for the early broods, that body weight is not limited by it at all. The indication obtained earlier (9.3.3.), suggesting that body weight is highest in years with a favourable timing of the caterpillar peak, is not confirmed by the regression analysis.

It was shown above that the effect of caterpillar abundance on the growth rate of the nestlings was stronger the lower the mean caterpillar abundance (Table 23). In a similar way, the size of the regression coefficient of body weight (b_1) is largest for the pinewood, where food is in short supply, and is larger in late than in early oak broods, in accordance with the mean amount of caterpillar frass (Table 27).

In three out of four groups, body weight was significantly correlated with X_2 , the number of young present at weighing. This suggests that the parents find it difficult to rear large broods up to the maximum weight. According to the calculations presented above large broods need considerably more food than small broods, in spite of the heat conserving properties of large broods (see p. 71). This is reflected in the smaller fledging weights of large broods. Similar results were obtained by Perrins (1965) and Winkel (1970).

All four categories of broods were found to show a negative correlation between percentage mortality and fledging weight. This implies that high

nestling mortality is associated with low body weight, irrespective of the level of food abundance and the size of the brood. The relationship between body weight and percentage mortality is unlikely to be a causal one in the sense suggested by the regression equations. Most probably, both are affected by a common factor. It is conceivable that broods differ in the quality of the nestlings, which may influence their growth and survival. Likewise, parents may differ in ability to rear nestlings, resulting in differences in growth and survival. A third possibility is that these differences are due to local variations in food abundance or food quality, which undoubtedly occur, but which were not accounted for in the present calculations. No choice between these possibilities can be made at the present stage.

Brood-size (X_2) and percentage mortality (X_3) are strongly negatively correlated. The partial correlation coefficients between the two amount to -0.4920 , -0.8351 , -0.8318 and -0.8333 (from Oosterhout early to Hoge Veluwe late), and are very significant ($P < 0.01$). This implies that the effects of both factors on fledging weight counteract each other, for both are negatively correlated with fledging weight.

The results of the regression analyses do not support Dhondt's findings, i.e. that the air temperature affects the survival of the fledglings, presumably via an effect on the condition at fledging. Positive correlations between air temperature and body weight were indeed established, but they were non-significant in all cases. The evidence for an influence of breeding density on body weight is even more scanty. The regression coefficients differed in sign in both woods, and were all non-significant.

10. DISCUSSION

In the introduction the question was raised as to whether the preference of the Great Tit for breeding in deciduous habitats is ultimately determined by differential feeding conditions for the rearing of young. It is conceivable that the tits settle in rich and poor habitats in a ratio such that the resulting breeding densities are proportional to the respective food supplies. If this ideal breeding distribution is achieved, the food supply per pair should be the same in both habitats, and no differences in nestling mortality and/or fledging weight would be found. This means that the absence of differences in breeding success and related phenomena between a rich and a poor habitat does not support the view that feeding conditions had not been ultimately operative. On the other hand, if differences in breeding success and nestling condition are found between populations in habitats with different feeding conditions, this is strong evidence for the view that the feeding conditions have operated through natural selection to evolve the observed habitat preference.

The preceding chapters have made it clear that the choice of breeding habitat has profound effects on many aspects of the breeding cycle. At the base of most of the differences found there is an overwhelming difference in food supply (4.3). During the early part of the breeding season, when the first broods (i.e. the broods that contribute most offspring to the next generation) are reared, feeding conditions in oakwoods are far better than those in pinewoods. The situation later in the season was not clarified to the same extent by the present study, especially because the non-preferred types of food were not sampled.

In view of the distinct seasonal trends in food supply, it is for a tit of utmost importance to start the breeding cycle at the appropriate time. In oakwoods this can be achieved approximately for the first broods. From Fig. 1 it is obvious that the peak in caterpillar abundance lasts for only 2 to 3 weeks. Moreover, indications were obtained for the existence of several critical periods, together lasting for at least five weeks (5.2). In fact, the peak in caterpillar abundance usually occurs between the two critical periods and coincides roughly with the growth period of the nestlings.

Repeat and second broods are reared when the caterpillar density in the oak canopy has decreased to a relatively low level. Presumably, alternative sources of food are available, the density of which is still unknown.

As shown in 4.3, the seasonal trends in caterpillar abundance differ considerably in the two types of habitat. The start of the breeding cycle coincides in both (5.3), resulting in an inadequate timing of the first broods in pinewoods. In most years repeat and second broods in pinewoods are reared under relatively favourable feeding conditions. However, the timing of these broods is not connected with the food supply, but is mainly determined by the date on which the preceding brood fledged or was disturbed. The course of the breeding events in pinewoods depends solely on the starting date of the first clutches, which is in turn proximately determined by the temperature in spring and, possibly, by the availability of food in the laying season.

The fact that the average laying dates in the two habitats do not differ, suggests that the mechanism which determines the onset of laying proximately is the same in both populations. To this proximate mechanism belong stimuli that enhance the development of the ovaries, and limiting factors that must reach a certain level to insure the production of eggs. The availability of food is often supposed to be one of these factors, but the coincidence of laying in oakwoods and pinewoods contradicts this view. Judged from the better condition of oakwood tits in late winter (van Balen 1967) and from the high caterpillar abundance during late April and May, feeding conditions during the spring are probably much better in oakwoods than in pinewoods. Nevertheless, the average laying dates coincide.

We have mentioned (p. 18) that the laying dates did not differ in localities with early- and late-developing oakleaves (and consequently equally dis-

similar feeding conditions). This also supports the view that the onset of laying is not proximately affected to any great extent by the feeding conditions in the spring. In the present state of knowledge it is not clear which factors, besides daylength and air temperature, play a part in the mechanism mentioned above.

Whatever these factors are, it is obvious that the timing mechanism is well suited to breeding in oakwoods, and that it fails to enable the tits to breed at the appropriate time in pinewoods.

The overall clutch-size of first clutches does not differ between the two habitats, but when a correction for the effect of breeding density is applied, the clutches in pinewoods prove to be considerably smaller than those in oakwoods (6.6). Although the ultimate significance of this adaptation is obvious, its proximate mechanism is yet unsolved. The availability of food for egg production has been put forward as a factor determining the *start* of laying (Perrins 1965, 1970), but in Perrins's view the spring food is unlikely to affect the *size* of the clutch, if clutches within a habitat are compared. Earlier (p. 38) we tentatively reached the same conclusion regarding the annual variation in clutch-size in our oakwoods. When comparing clutches in oakwoods and pinewoods we cannot dismiss the possibility that the food supply affects clutch-size in a general way, since the oakwood clutches are laid during a period of rapidly increasing insect biomass and this is probably not the case in pinewood.

It was found in an earlier study (van Balen 1967) that Great Tits in oakwoods are considerably heavier during the winter and carry more fat than pinewood tits. This might suggest that the energy reserves of the oakwood birds are greater, which might be helpful in producing a larger clutch. One objection to this view is that the fat reserves left over from the winter are probably less important than the availability of insect food (rich in protein) during the spring. Moreover, the onset of laying, which could be similarly affected by the energy reserves in the spring, coincides in the two types of habitat. Hence, I suggest that the condition during winter and early spring is at most of minor importance for egg production (cf. Jones 1972).

Whatever the factors are that determine clutch-size, they lead the tits to produce a well-adapted clutch in oakwoods, and to produce an unsuitably large clutch, from which often many nestlings die, in pinewoods.

Regarding both the clutch-size and the timing of the breeding season the Great Tit appears to be well adapted to breed in oakwoods, and probably in other deciduous habitats with a similar food supply. The planting of pine plantations throughout Western Europe has created vast areas of marginal habitat. The introduction of nestboxes into these areas induces part of the Great Tit population to settle there, the consequences of which were discussed in this study.

The consequences for the rearing of nestlings of the choice of oakwood or pinewood as a breeding habitat became evident in Chapters 7–9. Food consumption, body weight, and survival are affected to such an extent that a pair of Great Tits in an oakwood succeeds in rearing on average 9.0 well-grown young up to fledging, whereas in pinewoods the mean number of fledglings amounts to only 6.5 (both in early broods), and the condition at fledging is inferior.

The difference in the number of fledglings in rich and poor habitats should also have consequences for the period after fledging, when mortality and dispersal reduce the number of juvenile tits in the breeding area considerably. Dispersal leads to the exchange of individuals between areas of high and low production. It has indeed been found (van Balen, unpubl.) that where habitats of high and low production are adjacent, the proportion of the breeding population in the poor habitat (Hoge Veluwe A) reared in the richer habitat (Hoge Veluwe B) is significantly larger than the proportion of the population in the rich habitat reared in the poor habitat. In this way, populations in poor habitats will be regularly replenished which, however, does not imply that these populations are dependent of regular replenishment for their continued existence.

11. SUMMARY

In this report the breeding ecology of the Great Tit, *Parus major*, is compared in two types of habitat, oakwood and pinewood. The study is based on the striking difference in breeding density in two habitats, and is aimed at describing the feeding conditions and their effect on reproduction (especially the rearing of nestlings), in other words, at checking whether the observed breeding distribution has adaptive significance.

Breeding data were obtained by regular nestbox inspections, carried out over periods of 6 to 16 years in four areas, two pinewoods on sandy soil (Hoge Veluwe, Imbosch), and two oakwoods on more fertile soil (Oosterhout, Liesbosch). These areas ranged in size from 11.4 to 320 ha.

As indicated in the literature, the breeding density in poorly developed pinewoods amounts to 1–4 pairs per 10 ha and in mature oakwoods on fertile soil varies from 10 to 23 pairs per 10 ha. The density figures for our study areas (Table 1) are in good agreement with these results.

The feeding conditions were studied by sampling the caterpillars feeding in the canopy, which form the main type of prey fed to the nestlings. Sampling was performed by collecting, sorting, counting, and weighing the faecal pellets (frass) which drop from the canopy. Only those species and stages that were accepted as food, were sampled.

Differences in feeding conditions between oakwoods and pinewoods were divided into differences in the level of caterpillar abundance and differences in the period of maximum abundance. The level of abundance is much higher in oakwoods than in pinewoods. This holds especially for the peak densities (Table 2), and to a lesser extent for the periods before and after the annual peak.

The annual peak in caterpillar abundance in oakwoods usually occurs in the second half of May. In the pinewoods the time of the annual peak varies between 10 June and 15 July.

The timing of the breeding season was studied by analyzing the relationship between the period of maximal food requirements and the periods of maximal food availability. The timing mechanism has both proximate and ultimate aspects. The proximate aspect concerns the factors that directly determine the onset of laying and the development of the caterpillar populations.

In oakwoods the onset of laying is affected primarily by the air temperature during the period from 1 March to 20 April, and the date of the caterpillar peak partly by temperatures during a much later period. This means that the hatching of the young tits can only be adjusted approximately to the period of optimal feeding conditions. The young hatch on average 7 days before the caterpillar peak, but this interval is rather variable (Tables 5 and 7).

Evidence was obtained showing that the food requirements of the young are maximal shortly before and after fledging. On the other hand, it was concluded from the amount of weight lost by the female parents that they go through a critical period at the transition from the incubation to the nestling period. The breeding season is timed such that the caterpillar peak usually falls between these two critical periods.

The onset of laying in pinewoods is affected by the air temperature in the same way as in oakwoods. The average laying dates of the first clutches in both habitats do not differ significantly. The average laying date in pinewoods (and consequently the average hatching date) is not correlated with the date of the caterpillar peak, which is primarily influenced by the air temperature during May and June. The caterpillar peak falls on average 41.5 days after the hatching of the first broods, but the dates vary widely from year to year. In many years repeat broods profit the most from the annual peak in caterpillar abundance.

The size of first clutches in different habitats was compared, allowing for the effect of other factors on clutch-size.

To a small extent clutch-size is affected by the age of the female, yearling females having slightly smaller clutches than older females.

The effect of breeding density, laying date, and food supply was studied by multiple regression analysis. Clutch-size is inversely related to breeding density in all four areas, but the regression coefficient was significant only for Oosterhout. The effect of breeding density is greatest in the most sparsely populated habitats.

In agreement with reports in the literature, the clutch-size in pinewoods and mixed woods is largest at the start of the season. In the oakwoods the clutch-size remains constant throughout April (Oosterhout) or shows a peak near the end of April (Liesbosch). The seasonal trend in clutch-size is related to the breeding density. High density causes a reduction in the size of the earliest clutches.

Only slight indications were obtained for the existence of any proximate or ultimate effect of the food supply on clutch-size.

At the densities occurring normally, the average clutch-size is similar in all habitats, but at equal density the clutch-size in oakwoods is considerably larger than in mixed or pinewoods (Fig. 7).

The food brought to the nestlings was studied by observing the feeding process at close range, i.e. in a glass-backed nestbox. During each observation period the weight of each prey was estimated; the feeding frequency was recorded automatically during longer periods in a large number of broods.

Caterpillars form the main type of prey in both habitats. In oakwoods, where *Tortrix viridana* and *Operophtera brumata* are extremely abundant during the first half of the breeding season, the relation found between caterpillar abundance and food composition indicates that the level of abundance is far in excess of the food requirements during the annual peak as well as during part of the decline in caterpillar abundance. In pinewoods, where *Panolis flammea* is predominant at the time of the annual peak, the frequency of its occurrence in the food can reach very high values. Its percentage in the food increase with increasing *Panolis* density. Other types of prey are mainly fed when the above-mentioned preferred species are not available.

The daily food consumption was computed from the observed prey weight and the recorded feeding frequency, these quantities being inversely related. The food consumption increases sharply during the first week of life, and thereafter remains constant.

Early oakwood broods receive the largest amount of food; in late oakwood and all pinewood broods the level of food provision is much lower, which probably is the cause of the mortality observed in these broods. At equal brood-size the food consumption is only slightly higher in oakwood than in pinewood.

Tits in pinewoods have longer feeding days than those in oakwoods, mainly due to extended feeding in the evening, but in spite of this they are unable to satisfy their young completely.

Days with a low food consumption are usually followed by mortality, which brings the number of nestlings into balance with the feeding capacities of the parents.

Nestling survival is very high in early oakwood broods, and decreases in later broods (Tables 19 and 20). In pinewoods survival is on average much lower, with slight increases at the start and in the middle of the season. The annual variation in nestling survival is also very low in early oakwood broods, and increases in late oakwood broods and in all pinewood broods, indicating that feeding conditions are less reliable for the latter. In late oakwood broods and early and late pinewood broods nestling survival is positively correlated with the feeding conditions. Starvation plays a major role in most of the cases in which nestling mortality occurs.

Nestling survival is not related to brood-size. In all areas the largest broods are the most productive (Tables 22 and 23). This was an unexpected finding, since feeding conditions should be worse for large than for small broods. The reasons for this discrepancy are discussed.

The growth curve for well-fed nestlings is sigmoid in form (Fig. 24), with the highest growth rate between day 2 and day 9. The growth rate in this period is higher in oakwood than in pinewood. The effect of several factors on growth rate was investigated by multiple regression analysis. The caterpillar abundance has a significant effect in both habitats, whereas brood-size is only operative in the oakwood. The effect of caterpillar abundance is increasingly apparent the more the feeding conditions deteriorate (Table 24).

Many broods were weighed between the 15th and the 18th day of life, these weights being considered to represent the body weight at fledging. Fledging weights are highest in early oakwood broods, but the differences between the categories are small and often not significant. The annual variations in weight also suggest that feeding conditions are most reliable for the early oak broods, and much more variable in the other categories of broods. The seasonal trends in fledging weight generally correspond with the trends in feeding conditions, but several unexplained deviations occurred.

The effect of several factors on fledging weight was examined by multiple regression analysis. The effect of caterpillar abundance is only significant in pinewoods, and increases the more the feeding conditions deteriorate (Table 27). In three out of four categories of broods, body weight was negatively correlated with brood-size. Furthermore, high nestling mortality is associated with low fledging weight, irrespective of the size of the brood and the level of food abundance. Several explanations for the latter relationship are suggested. No effect of air temperature or breeding density on fledging weight was found.

In the discussion the difference in feeding conditions between oakwoods and pinewoods, and its consequences for the timing of the breeding season, are treated. The Great Tit is evidently adapted for reproduction in deciduous habitats; the pinewood populations have not adapted their breeding season to local feeding conditions, but start breeding at the time appropriate for breeding in oakwoods. The consequences of this inadequate timing are evident throughout this report.

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14. SAMENVATTING

In dit artikel wordt een vergelijkende studie gemaakt over de oecologie van de Koolmees in eikenbos en dennenbos, speciaal tijdens het broedseizoen. Het onderzoek ging uit van de reeds vroeger geconstateerde verschillen in populatiedichtheid in deze twee biotopen, en van de door Kluyver & Tinbergen (1953) gevonden voorkeur voor gemengd bos boven zuiver dennenbos. Door het analyseren van de voedseltoestand en van de relaties van deze met de reproductie en met het grootbrengen van de jongen kon worden nagegaan in hoeverre de waargenomen biotoopkeuze zinvol te noemen is.

In hoofdstuk 2 worden de proefterreinen beschreven, waarin gedurende een reeks van jaren broedgegevens verzameld werden, op grond van regelmatige controles van nestkasten. Twee terreinen (Hoge Veluwe en Imbosch, resp. 320 en 75 ha) zijn gelegen op de zandgronden van de Veluwe, en bestaan voornamelijk uit dennenbos. De twee andere terreinen (Oosterhout bij Nijmegen en Liesbosch bij Breda, resp. 11.4 en 18 ha) zijn op vruchtbare grond gelegen, en bestaan uit rijk ontwikkelde eikenbossen.

De dichtheidscijfers uit deze terreinen (Tabel 1) illustreren opnieuw het grote verschil in dichtheid tussen populaties uit eiken- en dennenbos. De resultaten komen goed overeen met opgaven in de literatuur uit vergelijkbare biotopen. In bossen zonder nestkasten is de dichtheid echter veel lager, vooral in dennenbos. Dit biotoop wordt door het ophangen van nestkasten bewoonbaar voor Koolmezen gemaakt.

De voedselsituatie werd beoordeeld door het bemonsteren van de rupsensoorten die het belangrijkste voer voor de jongen vormen. Hiertoe werden de rupsenfaeces, die uit de boomkruinen vallen, opgevangen, gesorteerd en gewogen. Het gewicht aan rupsenfaeces, dat per dag op een bepaald oppervlak valt, wordt als maat gebruikt voor de rupsdichtheid (Fig. 1).

Het dichtheidsniveau bleek in de eikenbossen veel hoger te liggen dan in de dennenbossen. Tijdens de jaarlijkse top is de hoeveelheid rupsenfaeces in het eikenbos het honderdvoudige van de hoeveelheid in het dennenbos (Tabel 2). De op grond hiervan geschatte rupsdichtheid komt goed overeen met gegevens in de literatuur.

De jaarlijkse top van de rupsenpopulatie valt in het eikenbos gewoonlijk in de tweede helft van mei, en in het dennenbos omstreeks eind juni (Tabel 4).

De ligging van het broedseizoen in relatie tot de periode van het grootste voedselaanbod werd in beide biotopen vergeleken. De beschikbaarheid van voedsel voor de jongen wordt gewoonlijk beschouwd als de "ultimate" factor, die in de loop van de evolutie ervoor heeft gezorgd, dat de jongen gemiddeld in de gunstigste periode geboren worden. Ieder jaar opnieuw wordt echter het tijdstip van geboorte - via de legdatum van de eieren - beïnvloed door "proximate" factoren, zoals de daglengte, de luchttemperatuur en het voedsel kort vóór en in de legtijd.

In het eikenbos wordt het begin van de leg vooral beïnvloed door de temperatuur in de periode 1 maart - 20 april, terwijl de periode waarin de rupsen het talrijkst zijn (rupsentop) mede afhankelijk is van temperaturen in april en mei. Dit heeft tot gevolg dat de periode waarin de jonge mezen opgroeien niet ieder jaar precies samenvalt met de rupsentop.

Gemiddeld valt de rupsentop in de periode dat de jongen 7 dagen oud zijn (Tabellen 5 en 8). De voedselbehoefte van de jongen is vermoedelijk het grootst kort vóór en in de eerste weken na het uitvliegen. Aan de andere kant wordt door gegevens over

het gewichtsverlies van de ♀♀ (Tabel 10) gesuggereerd dat deze een kritieke periode doormaken omstreeks het uitkomen van de eieren. De ligging van het broedseizoen is zodanig dat de rupsentop gewoonlijk tussen de twee kritieke perioden in valt.

Het begin van de leg is in eiken- en dennenbos op dezelfde manier afhankelijk van de temperatuur. De gemiddelde legdata van het eerste ei in de beide bostypen verschillen dan ook niet significant. Hetzelfde is het geval voor de uitkomstdata van de eieren. De ligging van de rupsentop in het dennenbos wordt vooral beïnvloed door temperaturen in mei en juni, en is niet gecorreleerd met de gemiddelde geboortedatum van de jongen. Gemiddeld valt de rupsentop in de periode dat de jongen 6 weken oud zijn. In sommige jaren valt hij samen met de kritieke periode van de jongen, in andere jaren valt hij veel later en zullen de vervolgbroedsels nog het meeste profijt hebben van de tijdelijke verbetering in de voedselsituatie.

Bij het vergelijken van de grootte van de eerste legsels in beide biotopen werd zoveel mogelijk rekening gehouden met de storende invloed van andere factoren op de legselgrootte.

De legselgrootte is in zoverre afhankelijk van de leeftijd van het vrouwtje, dat eerstejaars minder eieren leggen dan overjarige vrouwtjes (Tabel 12).

De invloed van de populatiedichtheid, de legdatum en het voedsel werd geanalyseerd door een multiële regressie analyse. De legselgrootte neemt af met toenemende populatiedichtheid, maar deze relatie was slechts voor de gegevens van Oosterhout significant (Tabel 13). De grootte van dit effect neemt toe naarmate de gemiddelde dichtheid in een terrein kleiner is.

De relatie tussen de legdatum en de legselgrootte is niet in alle bossen dezelfde. In dennenbos en in gemengd bos zijn de legsels het grootst aan het begin van het seizoen, in eikenbos blijft de legselgrootte eerst enige weken constant (Oosterhout) of neemt toe tot eind april (Liesbosch, zie Figuren 8 en 9). De verschillen in verloop tussen de bossen hebben te maken met de gemiddelde populatiedichtheid. In zeer dicht bevolkte bossen zijn de vroegste legsels kleiner dan op grond van het algemene dalende verloop verwacht kan worden.

Er zijn slechts zwakke aanwijzingen voor een eventuele invloed van het voedsel op de legselgrootte, wanneer de gegevens binnen een terrein bekeken worden. Ook blijkt het gemiddelde aantal eieren van de eerste legsels in verschillende biotopen nauwelijks te verschillen, maar na een correctie voor het effect van de bevolkingsdichtheid treden duidelijke verschillen aan het licht (Fig. 7). Dan zijn de legsels in de eikenbossen bij gelijke dichtheid aanzienlijk groter dan die uit het dennenbos (Tabel 15).

Het voedsel van de jongen werd bestudeerd door waarnemingen bij observatienestkasten met aangebouwde schuilhutten. Het gewicht van de prooien werd geschat en de voederfrequentie werd automatisch geregistreerd.

In beide biotopen vormen rupsen het voornaamste type prooi (Tabel 16). In het eikenbos is het aandeel van de rupsen (vooral *Tortrix viridana* en *Operophtera brumata*) zeer hoog tijdens de jaarlijkse top van de rupsenpopulaties, maar ook daarna is het nog zeer aanzienlijk. Bij een relatief lage dichtheid van de rupsen zijn de percentages in het voedsel al hoog (Fig. 12). Gewoonlijk zijn de rupsenpopulaties veel groter dan voor de voedselbehoefte van de mezen nodig is. Het relatief lage gewicht van deze rupsensoorten wordt gecompenseerd door zeer hoge voederfrequenties, tot 1535 bezoeken per dag. Later in het seizoen verandert deze situatie en worden veel andere prooien gegeten (vooral vlinders, vliegen en muggen).

Ook in het dennenbos werden vooral rupsen gevoerd (Tabel 16b), en hier was sprake van een duidelijke opeenvolging van soorten in de loop van het seizoen. Tijdens de jaarlijkse rupsentop, die overwegend uit rupsen van *Panolis flammea* bestaat, is het aandeel van deze soort in het voedsel maximaal (als voorbeeld Fig. 13). Het aandeel in het voedsel neemt toe naarmate de dichtheid in het bos stijgt (Fig. 14). Andere prooitypen overwegen vooral in het begin van het seizoen. Dan worden vaak ook eikenrupsen gevoerd bij die broedsels die in de nabijheid van eiken leven.

De dagelijkse voedselaanvoer werd berekend door het waargenomen gemiddeld prooigewicht te vermenigvuldigen met de geregistreeerde voederfrequentie. Deze twee grootheden zijn negatief gecorreleerd (Fig. 16). De voedselaanvoer neemt sterk toe gedurende de eerste 8 dagen en blijft daarna ongeveer constant. (Tabel 17). Vroege broedsels in het eikenbos krijgen de grootste hoeveelheid voer, late eikenbroedsels en alle dennen-

broedsels aanzienlijk minder (Fig. 17). Dit hangt nauw samen met de broedselgrootte, die in de laatstgenoemde categorieën door sterfte afneemt. Bij gelijke broedselgrootte verschilt het voedselverbruik in eiken- en dennenbos nauwelijks (Fig. 18).

Koolmezen in dennenbossen besteden een groter gedeelte van de dag aan het voeren van de jongen dan hun soortgenoten in het eikenbos. Dit komt vooral doordat zij 's avonds later het voeren beëindigen, wat suggereert dat zij moeite hebben hun jongen geheel te verzadigen (Fig. 19).

Na dagen, waarop weinig voedsel wordt aangevoerd, sterven vaak een of meer jongen (Tabel 18). Hierdoor blijft het aantal jongen min of meer afgestemd op de voercapaciteiten van de ouders.

Het voedselverbruik per jong is bij zeer kleine broedsels (2-3 jongen, zie Fig. 20A) duidelijk groter dan bij de andere broedsels. Nadat het effect van de luchttemperatuur was uitgeschakeld, bleek dat het voedselverbruik per jong geleidelijk toeneemt van grote naar kleine broedsels (Fig. 20B), wat meer in overeenstemming is met de literatuur. Dit verschijnsel berust op de slechte thermoregulatie van kleine broedsels.

De sterfte onder de jongen (vóór het uitvliegen) is zeer gering bij de vroege broedsels in het eikenbos, en neemt toe in de loop van het seizoen (Tabel 19 en 20). In het dennenbos overleven de jongen gemiddeld veel slechter dan in het eikenbos. In het begin en in het midden van het seizoen treedt een kleine verbetering in de situatie op. De jaarlijkse variatie in de jongensterfte is bij de vroege eikenbroedsels zeer gering, en is veel groter bij de late eiken- en alle dennenbroedsels. Dit wijst erop dat de voedselsituatie in het laatste geval minder betrouwbaar is.

De sterfte onder de jongen hangt in beide bossen samen met de voedselsituatie, gemeten aan de faecesafval van de rupsen (Fig. 22 en 23). In het dennenbos is de voedselsituatie doorlopend slecht, gewoonlijk ook tijdens de jaarlijkse rupsentop.

De procentuele sterfte in kleine en grote broedsels is niet verschillend. In beide bos-typen produceren de grootste broedsels gemiddeld het grootste aantal vliegvlugge jongen (Tabel 22 en 23). De oorzaak van dit onverwachte resultaat werd besproken.

De groei van goed gevoede jongen verloopt volgens een S-vormige kromme (Fig. 24). De groeisnelheid is het hoogst van de 2e tot de 9e levensdag, en is dan hoger in eiken- dan in dennenbos, resp. 1.49 en 1.36 gram/dag. De groeisnelheid is afhankelijk van de voedselvoorraad in het bos, en van de broedselgrootte. Het effect van de voedseltoestand op de groei is des te groter naarmate de voedseltoestand slechter wordt (Tabel 24).

Vele jongen werden kort voor het uitvliegen gewogen. Jongen uit vroege broedsels in het eikenbos zijn gemiddeld het zwaarst, maar de verschillen met de andere broedsels zijn gering (Tabel 25). Uit de geringe variabiliteit bij de vroege eikenbroedsels blijkt opnieuw, dat voor deze categorie de omstandigheden het meest constant zijn. Het seizoensverloop van het gewicht (Tabel 26) vertoont overeenkomst met dat van de voedselvoorraad, maar wijkt op ondergeschikte punten af. In het algemeen komt een slechte voedselsituatie meer tot uiting in extra sterfte dan in een laag gewicht bij het uitvliegen.

Door regressie-analyse werd het effect van verschillende factoren op het lichaamsgewicht onderzocht (Tabel 27).

Het lichaamsgewicht neemt toe naarmate er meer rupsen in de boomkruinen zijn en naarmate de broedsels kleiner zijn. Bovendien gaat een grote sterfte onder de jongen samen met een laag gewicht. De luchttemperatuur heeft geen invloed op het lichaamsgewicht.

De Koolmees vertoont in zijn broedseizoen en zijn legselgrootte een aantal aanpassingen die hem geschikt maken voor het broeden in eikenbossen en biotopen met een soortgelijke voedselsituatie. Populaties in dennenbossen kunnen hun broedseizoen niet aanpassen aan de lokale omstandigheden, met de hierboven omschreven consequenties.

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