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POPULATION FLUCTUATIONS OF THE GREAT TIT AND FEEDING CONDITIONS IN WINTER

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CONTENTS

1. INTRODUCTION

The annual fluctuations in tit numbers and the factors responsible for these fluctuations have interested ecologists for many years. As early as 1951, Kluyver presented data on the number of breeding pairs of the Great Tit *Parus major* in the area of Oranje Nassau's Oord near Wageningen (The Netherlands) over a period of 32 years, and distinguished between a long-term gradual increase and irregular annual fluctuations around the general trend. Among the factors causing fluctuations he mentioned: the number of young fledged per pair in the preceding breeding season, the amount of im- and emigration, and the severity of the winter. Other authors, especially Ulfstrand (1962) and Perrins (1966), have stressed the importance of beechmast as winter food, and have found correlations between the size of the beech crop and either the density of Great Tits in winter or the degree of increase or decrease of the breeding population. In a Finnish population studied by Von Haartman (1971, 1973), the winter temperature and the extent of additional feeding by humans appeared to affect the size of the breeding population. A short experiment reported by Dhondt (1971) also indicated that supplementary feeding in winter can increase the breeding density. On the other hand, Krebs (1971) found food supplementation in the winter to have no effect on the size of the breeding population. However, his results are not conclusive because his experiment lasted only one winter, wich happened to coincide with a good beechmast crop.

Moreover, several authors have found that fluctuations in breeding numbers can be attributed mainly to differences in the survival of yearling birds, from fledging to their first breeding attempt, and Dhondt (1971) has shown that the temperature in the period when these birds are still in the nest is strongly correlated with their survival after fledging, a relationship which is not found in the English data (*cf.* Webber 1975).

These considerations prompted us to study the breeding density and the annual survival rate of the Great Tit population of our study area in Hoge Veluwe, in relation to the feeding conditions in winter. This was done in two steps: the first step consisting of an analysis of the numerical relations between several parameters of the population and some environmental variables, for the period from 1960 to 1972. On the basis of the hypotheses derived from this analysis, observations were started on the foraging behaviour and the types of food consumed, on the whereabouts of the tits in the winter, both in and outside the study area, and on the importance of territorial behaviour for the survival of the individual tits. The relevant aspects of territorial behaviour and its implications for the survival in different feeding conditions will be dealt with in Drent's contribution to this Symposium.

2. FLUCTUATIONS IN NUMBERS AND THE UNDERLYING FACTORS IN THE PERIOD 1960—1972

The study was conducted in an area situated in the National Park De Hoge Veluwe, which has been described by Van Balen (1973). For this study the two subareas A and B were taken together. The whole area covered about 320 ha, including the parts unsuitable for Great Tits (farmland, young plantations, etc.), and contained between 215 and 280 nest-boxes. Regular inspections were carried out to determine the numbers of breeding pairs and the breeding parameters. The identity of most of the parent tits was assessed by catching and ringing when the nestlings were about 7 days old. In the winters of 1964/65 and 1965/66 seed food was provided on a small scale (at one site), but starting in the winter of 1966/67 the provision of seed food (sunflower and hemp seed) was extended over the whole area and was maintained from the beginning of September to the end of March.

The numbers of breeding pairs during the period under study are shown in Fig. 1, together with the breeding population of a control area with roughly the same size and vegetation and situated near Ede, about 7 km west of the Hoge Veluwe. Initially the two curves run parallel on about the same level, but since 1967 the Hoge Veluwe population has become considerably larger, and the increases and decreases no longer coincide. The curves for the two areas deviate from the start of the large-scale seed provision.

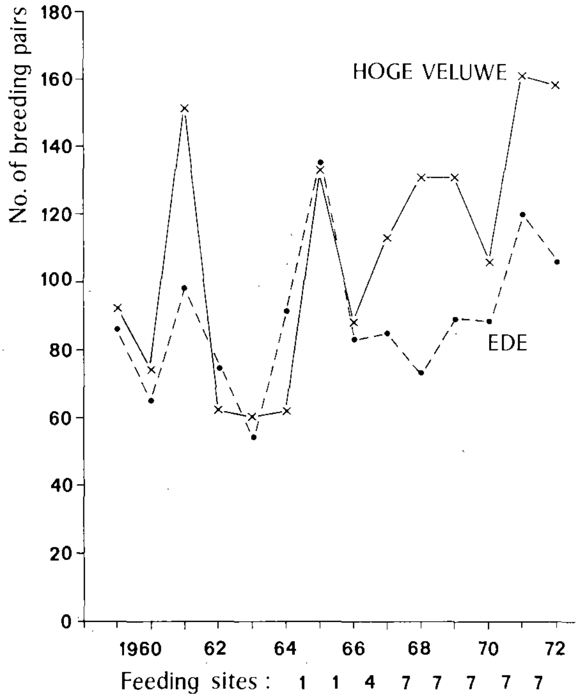


Fig. 1. Numbers of breeding pairs in two areas similar as to size and vegetation. Ede = Noord- and Zuid Ginkel, near Ede (see Stel 1959—1972). The numbers of food containers filled with hemp and sunflower seeds are given at the bottom.

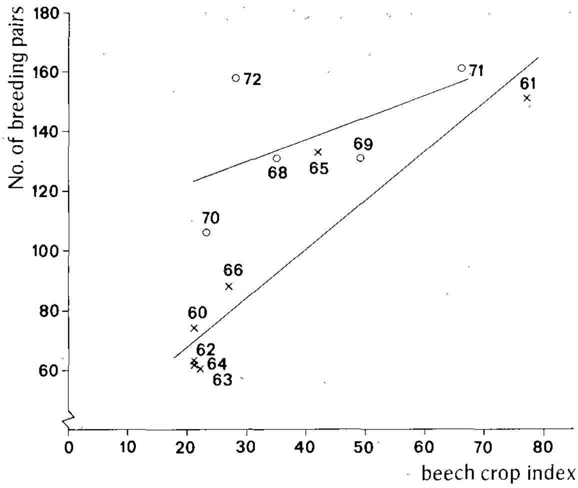


Fig. 2. Numbers of breeding pairs on the Hoge Veluwe in relation to the national beech-crop index in the preceding autumn (figures taken from La Bastide & Van Vredenburgh 1970, supplemented by Ludwig, State Forestry Service, *in litt.*), in years without (X) and with (O) extra seed provision. Numbers in the graph refer to year of breeding.

The role of the beechmast was studied first by comparing the national beech-crop index with the size of the next breeding population, separately for years with and without supplementary seed provision. Fig. 2 shows that there is a good correlation for the 1960—1966 period, and that the effect of the beech crop was much less pronounced in the years when extra seed was provided. The provision of seeds seems to have increased the breeding population, particularly after winters with a poor beech crop, such as 1969/70 and 1971/72, whereas in years with a rich crop the effect was small.

During the period under study the composition of the breeding population changed appreciably. As Fig. 3 shows the percentage of autochthonous older birds (birds that had previously nested in the study area) increased considerably, *i.e.* from 20—33 per cent in the early years to 38—52 per cent in the later years. The percentage of immigrants decreased, and the percentage of autochthonous yearlings (*i.e.* birds born in the study area in the preceding year) varied from year to year (between 12 and 42%) but did not show any

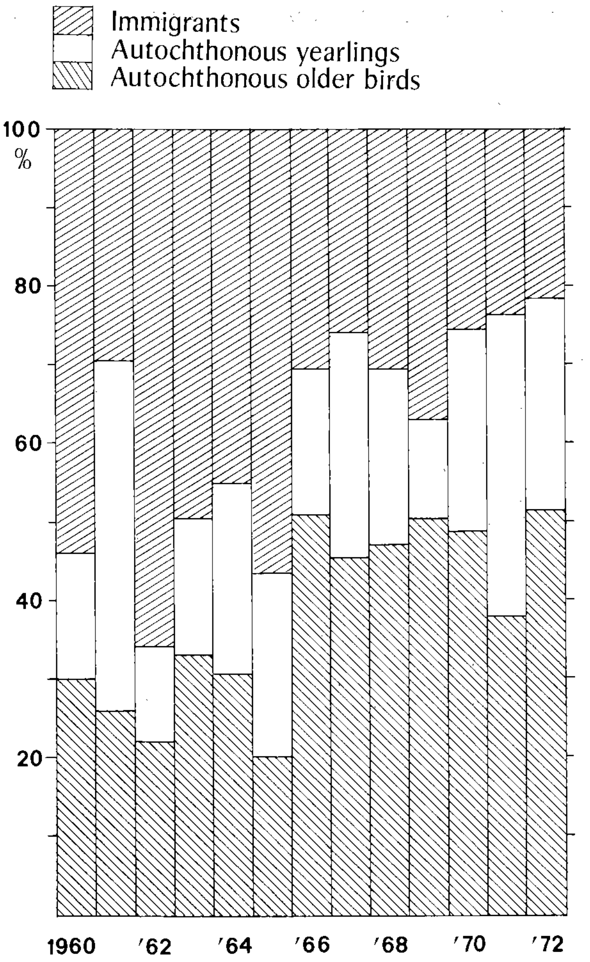


Fig. 3. Composition of the breeding population on the Hoge Veluwe in the 1960—1972 period according to age and place of origin. Autochthonous older birds = birds that have previously nested in the area. Autochthonous yearlings = birds hatched in the area in the preceding year. Immigrants = unringed birds that have entered the area since the preceding breeding season; these birds are mainly yearlings.

systematic change. This suggests that the older birds in particular profited from the extra food supply.

The fact that all young hatched in the study area are ringed each year and most of the parent tits identified enables us to study the annual survival of the breeding birds, classified into the three categories mentioned above. It should be kept in mind that here survival is understood as local survival, *i.e.* within the boundaries of the study area. Fig. 4A shows the annual survival of the breeding birds from one breeding season to the next in relation to the beechmast index. It is clear that the size of the beech crop had a strong effect on adult survival in the years without extra food provision, but scarcely any effect in the later years with supplementary food. In winters with a poor beech crop the survival of the adults increased about twofold, from 26 (9—33) per cent to 50 (39—58) per cent, due to the provision

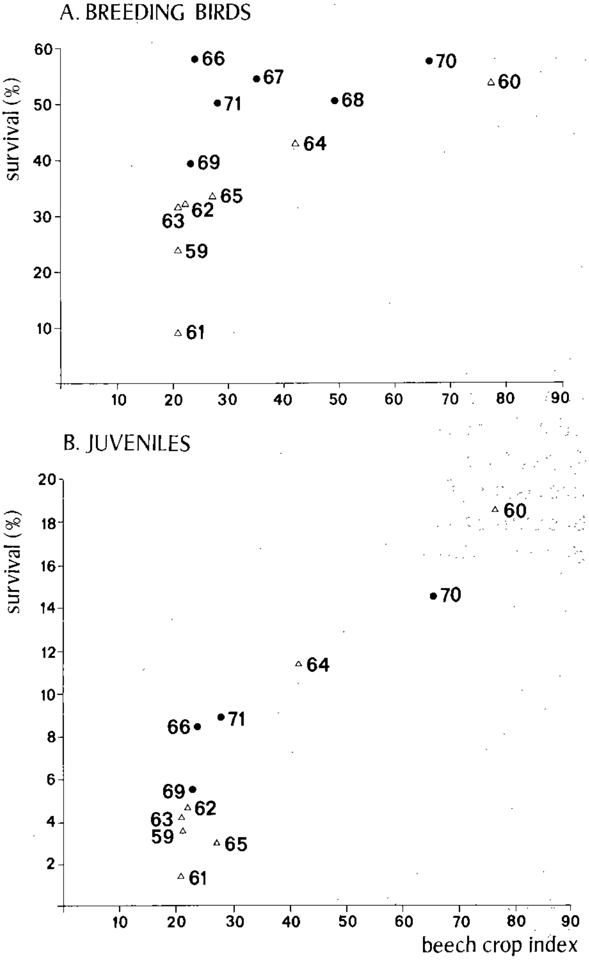


Fig. 4. A. Relationship between the annual survival percentages of the breeding birds and the beech-crop index in the intervening autumn. Numbers refer to the first of each couple of years.
Solid dots: years with, open triangles: years without, provision of extra food during the winter.
B. Relationship between the annual survival percentages of the juveniles (from fledging to first breeding) and the beech-crop index in the intervening autumn. Further as in A. 1967 and 1968 were omitted because of experiments (removal of large proportions of first-brood nestlings) which could have affected juvenile survival.

Table 1. Results of multiple regression calculations; Hoge Veluwe 1960—1972. In each cell the regression coefficient b and the corresponding value for t are given. Further explanation in text

Y	X_1	X_2	X_3	X_4	X_5
1. Numbers of breeding birds	- 0.066 0.251	- 0.021 0.267	+ 2.085* 3.138	+ 12.943* 3.192	+ 11.401 1.784
2. No. of autochthonous yearlings	- 0.312 2.297	+ 0.088 2.145	+ 1.352** 3.927	+ 5.412* 2.576	+ 2.655 0.802
3. No. of autochthonous older birds	+ 0.104 0.676	- 0.021 0.453	+ 0.262 0.674	+ 10.061** 4.245	+ 4.161 1.114
4. No. of immigrants	+ 0.142 0.767	- 0.088 1.572	+ 0.471 1.002	- 2.530 0.881	+ 4.585 1.013
5. Annual survival of autochthonous yearlings	- 0.035 2.068	+ 0.004 0.701	+ 0.197** 4.627	+ 0.478 1.840	+ 0.416 1.018
6. Annual survival of autochthonous older birds	- 0.118 2.100	- 0.003 0.192	+ 0.195 1.376	+ 3.895** 4.499	+ 2.163 1.585

*: $P < 0.05$ at d.f. = 7
**: $P < 0.01$ at d.f. = 7
$t(0.05) = 2.365$

of additional food. For the juveniles a different picture (Fig. 4B) emerges: apparently there is a favourable effect of the beech crop on annual survival, both with and without the extra supply of seed food. When additional food was provided in poor beech crop years the survival of the juveniles increased from 3.4 per cent (range 1.4—4.7%) to 7.6 per cent (5.5—8.5%). Although the provision of extra food enhances survival in poor beechmast years for both categories of tits, it evidently cannot compensate completely for a shortage of beechmast in the case of the juvenile tits, because in this age class the highest survival figures are found exclusively in years with a high beech-crop index.

In an attempt to obtain statistical support for these provisional conclusions a number of multiple regression calculations were performed of the following form:

$$Y = a + b_1 X_1 + b_2 X_2 + b_3 X_3 + b_4 X_4 + b_5 X_5$$

Among the independent variables three environmental variables were included (beech-crop index, amount of extra food provided, and an index of the winter weather) as well as two parameters concerning population size. The meaning of X_1-X_5 is as follows:

X_1 = the number of breeding birds in year n
X_2 = the number of young fledged in year n
X_3 = the national beech-crop index for the autumn of year n
X_4 = the number of food containers present from September (year n) to March (year n + 1)
X_5 = the average temperature at De Bilt (52°05′ N, 05°11′ E) over the period December 1st (year n) to March 1st (year n + 1)

As dependent variables use was made, in six different calculations, of:

Y_1 = the number of breeding birds in year n + 1
Y_2 = the number of autochthonous yearling breeding birds in year n + 1
Y_3 = the number of autochthonous older breeding birds in year n + 1
Y_4 = the number of immigrant breeding birds in year n + 1
Y_5 = the percentage survival of the autochthonous yearlings, from fledging (year n) to first breeding (year n + 1)
Y_6 = the percentage survival of the autochthonous older birds, from year n to year n + 1.

The results of the first set of calculations are given in Table 1, which shows some significant effects of the size of the beech crop and the supplementary food; the other three variables seem to have little influence. The beech-crop index was clearly correlated with the number of yearling breeding birds and their survival after fledging, but not with the annual survival of the older birds. On the other hand the amount of extra food provided is mainly correlated with adult numbers and survival, but only weakly with the number of yearling breeding birds. No relationship was found between the number of immigrant breeders and any of the variables under study.

Further calculations were made by replacing the average winter temperatures by the numbers

Table 2. Results of multiple regression calculations after stepwise elimination of insignificant X's. For each significant relation b and t are given (see Table 1). Further explanation in text

Y	X_1	X_2	X_3	X_4	X_5
1. Numbers of breeding birds	–	–	+2.588**	+11.950**	–
	–	–	4.561	3.801	–
2. No. of autochthonous yearlings	-0.310*	+0.099*	+1.479**	+ 5.266*	–
	2.338	2.660	4.954	2.574	–
3. No. of autochthonous older birds	–	–	–	+11.797***	-1.409* 1)
	–	–	–	8.157	2.419
5. Annual survival of autochthonous yearlings	–	–	+0.235***	–	–
	–	–	6.216	–	–
6. Annual survival of autochthonous older birds	-0.157**	–	–	+ 4.766***	-0.749* 1)
	4.447	–	–	6.540	2.954

*: $P < 0.05$,
**: $P < 0.01$,
***: $P < 0.001$
1) in both cases X_5 = the number of days with snow in the period 1 December—1 March.

of days with snow or with frost and snow. Calculations were also performed in which the most insignificant X's among the X_1—X_5 were eliminated stepwise. This procedure usually led to an increase of both the regression coefficients and the t-values of the remaining X's. The results are shown in Table 2, which gives the remaining regression coefficients and their t-values.

With respect to the beech crop (X_3), the results confirmed the above-mentioned conclusion that there is only a relationship with juvenile numbers and survival. This also holds for the relationship found between the extra supply of food on the one hand and adult numbers and survival on the other. A new feature is the significant relationship between adult numbers and survival (Y_3 and Y_6, respectively) and X_5, representing the numbers of days with snowfall in December, January, and February. When the average winter temperature or the number of days with frost and snow was taken for X_5, no significant correlations were found. Although the effect of the winter weather cannot be demonstrated convincingly, it is suggestive that the only relationships found concern the numbers and survival of the adult tits, the category that, as Drent's observations show (see Drent, this symposium), is the least inclined to leave the territory when weather conditions deteriorate.

The different effects of the beech crop and the food supplementation on the two age classes can be explained by differences in the spatial distribution of the two types of food, in combination with the tits' behaviour. Beechmast is distributed over a fairly wide area, tens of square metres for each tree, which permits many tits to forage simultaneously. Moreover, beeches occur both within and immediately outside the study area. The non-territorial part of the population, *i.e.* an appreciable part of the yearling class, benefits from both aspects. Non-territorial tits tend to roam over a fairly wide area and to concentrate on sites where food is abundant. Territorial tits are more or less restricted to a fairly small area. Many of the territories in our study area are not situated near beeches. Territory owners show little tendency to cover large distances to reach food sources outside their territory. The extra supply of seeds is distributed at a few discrete points where the locally dominant tits can easily dominate the others. This may explain why the extra food supply mainly benefits the territorial part of the population, in which the older birds form the majority.

From Table 2 it is apparent that the number of autochthonous yearlings in the breeding population (Y_2) is positively related to the number of fledglings in the preceding year (X_2) and negatively to the size of the parent population (X_1). The former relationship can be understood as a direct effect: the more young fledge, the more are recruited into the next breeding population. There is no indication of density-dependent survival of the yearlings: the regression coefficient of Y_5 on X_2 is nearly zero. The negative relationship between the number of yearling breeding birds (Y_2) and the size of the preceding breeding population (X_1) suggests that the yearlings' chances of settling in the natal area are related to the density of the settled population. On the other hand, the percentage local survival of the yearlings (Y_5) is not consistently related to the size of the preceding breeding population: in some calculations a regression coefficient with $P < 0.05$ was found, in others P amounted to > 0.05.

The number of older breeding birds (Y_3) is not related to their numbers in the preceding year, but the annual survival of this category (Y_6) definitely is. This implies that large breeding populations have a low, and small populations a high annual survival, a process which contributes to the numerical stability of the population. In this process both density-dependent mortality and emigration may play a role. Although birds that have been breeding in the study area usually do not leave that area permanently, an exception is formed by the category "immigrant breeding birds", *i.e.* birds which, in the absence of sufficient nest-sites, enter the area shortly before or during the breeding season, succeed in nesting within another bird's territory, and leave the area with their brood shortly after fledging (Drent 1978). These birds occur mainly in years with a high population density, and their disappearance after breeding has the appearance of density-dependent emigration.

An objection can be raised to the use of multiple regression analysis, since some of the dependent variables are interrelated, and the same holds for some of the independent variables. To overcome this objection another statistical technique, canonical correlation analysis, was used. The analysis results in the calculation of new variables instead of the original X's and Y's, in such a way that the canonical variables that replace the X's are not correlated with each other; the same applies to the canonical variables that replace the Y's. In other words: the within-set correlations are zero and the between-set correlations are maximized (see Pielou 1977, Chapter 22). The results are summarized in Table 3. The canonical variables are composed of the original variables in the numerical proportions indicated by the values in the table. Canonical variable 1 is mainly composed of the autochthonous older breeding birds, and is correlated with canonical variable 2, which consists mainly of X_4, the degree of extra food provision. This confirms the conclusion reached earlier, that especially the older birds benefit from the supply of extra food.

On the other hand, canonical variable 3 is composed mainly of the autochthonous yearlings, and the corresponding variable 4 consists almost exclusively of three factors: the size of last year's breeding population, the number of birds fledged, and the beech-crop index in the preceding autumn. These results confirm those derived from Tables 1 and 2, except that the small and barely significant effect of the number of food containers on Y_2 is not corroborated. The plus and minus signs attached to the independent variables in Table 3 correspond in all cases to those of the regression coefficients in Tables 1 and 2.

In sum, it is obvious that the size of the

Table 3. Results of canonical correlation analysis; $X_1 — X_5$ and $Y_2 — Y_4$ from Table 1 are used. The canonical variables are composed of the original variables in the proportions indicated by the figures

Canonical variable 1		Canonical variable 2	
Y_2 (Autochthonous yearlings)	3	$+\ 34\ X_1$	(Breeding birds preceding year)
Y_3 (Autochthonous older birds)	100	$-\ 38\ X_2$	(Fledglings preceding year)
Y_4 (Immigrant breeders)	26	$+\ 30\ X_3$	(Beech-crop index)
		$+100\ X_4$	(Number of food containers)
		$+\ 39\ X_5$	(Winter temperature)
Canonical variable 3		**Canonical variable 4**	
Y_2 (Autochthonous yearlings)	100	$-\ 100\ X_1$	(Breeding birds preceding year)
Y_3 (Autochthonous older birds)	62	$+\ 83\ X_2$	(Fledglings preceding year)
Y_4 (Immigrant breeders)	3	$+\ 86\ X_3$	(Beech-crop index)
		$+\ 4\ X_4$	(Number of food containers)
		$+\ 2\ X_5$	(Winter temperature)

breeding population is affected by the feeding conditions outside the breeding season, that the yearling tits profit from rich crops of beechmast by an increase in their local survival, that the older birds benefit especially from food sources like those provided in our experiment, that the influence of the severity of the winter has not yet been demonstrated convincingly by our data, and that density-dependent processes play a role in determining the population size. Moreover, the different responses of yearlings and older birds to the two types of food supply can be understood from the distribution of the food and the behaviour of the tits.

3. FLUCTUATIONS IN NUMBERS, FORAGING BEHAVIOUR AND DIET IN WINTER, USING DATA FOR 1973—1979

3.1. GENERAL REMARKS

The series of years discussed in section 2 was interrupted in the winter of 1972/73, when heavy storms uprooted many trees in the northern part of the study area, which forced us to change the area drastically. From 1973 onward the study area, which is an extension of the subarea Hoge Veluwe B (see Van Balen 1973), covered 165 ha and contained about 370 nestboxes. This area is a mosaic of plots of coniferous and deciduous forest with intervening open areas (fields, very young plantations, etc.). The main tree species are: *Pinus sylvestris, Larix* spec., *Pseudotsuga menziesii, Quercus robur, Quercus rubra, Betula* spec., and *Fagus sylvatica.* The beech trees are distributed unevenly in patches and rows (see Fig. 5). In the winters of 1973/74, 1974/75, and 1975/76 6 containers with seeds were present, after that time the provision of extra food was terminated. A possible source of "unnatural" food was around the only house in the area and neighbouring houses and farms.

Both feeding and weather conditions varied considerably in the second series of winters under study. Table 4 lists the numbers of breeding pairs, which show large increases and decreases, and the conditions in the intervening winters. According to the national beechmast index there was a poor to moderate crop in 1973, a fairly good crop in 1974, a poor one in 1975, and a very good crop in 1976. For the next two years no exact figures are available, but it is known that the crop failed in both years. Observations in the study area and its surroundings showed that virtually no beechmast was produced in these two years, whereas in 1976 about two-thirds of the trees carried nuts, albeit in widely varying amounts. The series of six years started with three mild winters, which were followed by two winters of average severity but differing in detail (see section 3.3), and the last winter was one of the most severe winters of the century.

Table 4. Population fluctuations and winter conditions in the 1973—1979 period

Year	Number of breeding pairs	Change in population size	Winter	Beech-crop index	Number of food containers	Average temperature (°C) Dec.—Febr.	Number of days with snow in Dec.—Febr.
1973	118						
		+ 5%	1973/74	38	6	3.9	13
1974	124						
		+ 36%	1974/75	62	6	5.3	6
1975	169						
		−21%	1975/76	27	6	3.1	14
1976	133						
		+ 51%	1976/77	75	0	2.3	26
1977	201						
		−46%	1977/78	low	0	2.4	30
1978	109						
		−24%	1978/79	low	0	−1.4	45
1979	83						

Notes: 1. No national beech-index figures have been published for 1977 and 1978, but the beech crop in the study area and its surroundings was virtually nil.

2. Weather data from Deelen (3 km NE of the study area); the (30-year) average winter temperature is 1.7°C and the average number of days with snow is 22.

As Table 4 shows, substantial population increases followed winters with beechmast and decreases occurred in winters without beechmast. The effect of the additional supply of seeds is not clear from these figures, and the influence of the weather only became clear from a detailed analysis of the last two winters, as will be discussed later.

In 1973 and 1974 no observations bearing on the subject were made, but starting in the winter of 1974/75 a special study was devoted to the fluctuations in the numbers of Great Tits present in the area during the non-breeding season as well as the foraging behaviour and diet in relation to feeding and weather conditions. In the southwestern part of the study area (part DF, see Fig. 5) most of the Great Tits were marked individually by means of coloured rings. Here, the identity of the territorial males and their partners was determined at regular intervals, which enabled us to follow settling attempts and changes of ownership in detail. The results of the behavioural part of the study, which proved to be particularly helpful for explanation of the numerical results, will be reported by Drent (this symposium).

3.2. METHODS

There are three sources of data on the presence of tits in the area: A. From January 1975 onwards, observations on the foraging sites of Great Tits were made once or twice a week along a standard route covering the southwestern part of the area (part DF, see Fig. 5); for each observed group (or individual) the number was noted on a map, as well as the species of tree in or under which foraging took place. This method made it possible to assess changes in foraging locations within and between years. Moreover, the total counts made on these routes can serve as a measure of the number of tits present by day, under the restriction that counts were made only in the morning hours, usually between 9.00 and 11.00 a.m. These

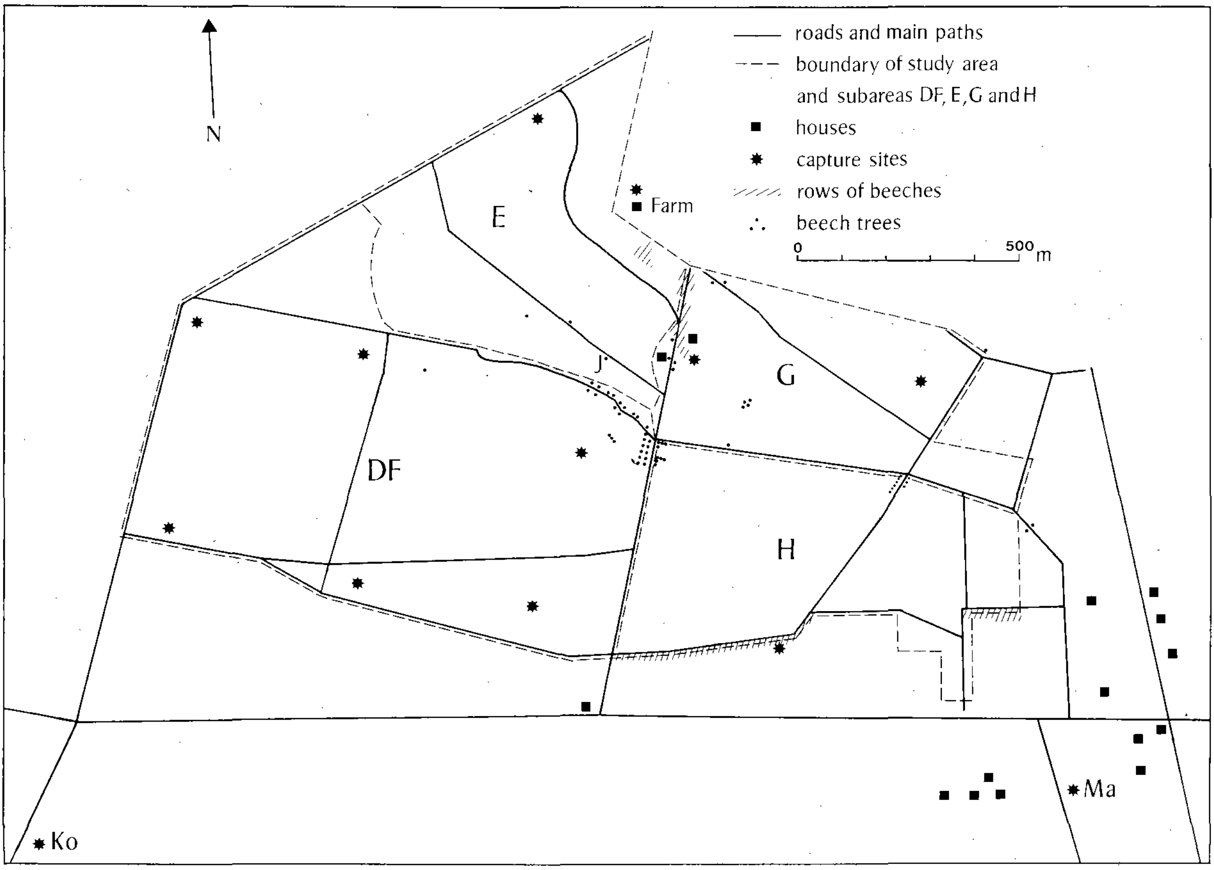


Fig. 5. Map of study area and surroundings.

data must be interpreted cautiously, because of the differences in the conspicuousness of the birds to the observer, due to changes in the vegetation (leaf fall) and in the birds' behaviour.

Group size was usually recorded as 1, 2, 3—5, 6—10, 11—15, etc. The total number per count is expressed as a minimum and maximum value. The monthly averages represent the averages of the minimum and maximum counts. For the calculation of percentages of foraging birds at different food sources, the mean of the minimum and maximum counts was used.

In the winters of 1977/78 and 1978/79 similar observations were made in the northern part of the study area. In 1977/78 we recorded not only the tree species but also the positions of the foraging tits, classified as: ground, trunks, main branches, smaller branches, twigs, leaves, and buds. The height of foraging in relation to tree height was also noted as well as the position in the horizontal plane (central or peripheral part of the crown). In 1978/79 only the tree species and a rough measure of foraging height were recorded.

B. The second source of data is formed by the nocturnal inspection of nestboxes. Twice a month, all boxes in part DF were inspected for roosting tits, and the rest of the area was inspected less frequently, in the later winters once a month. When these data are considered it must be kept in mind that tits roosting within the area may have foraged outside it. Occurrence of the reverse is very unlikely, because of the large number of boxes available in the area (compared with the few boxes placed locally outside the area) and because of the general shortage of natural holes in the whole region. Moreover, it must be taken into account that not all of the birds present during the day roost in the nestboxes at night. There is competition for these roosting sites, and the occupation of a box for roosting has something to do with the territorial status of the male. A large proportion (in our area about 80 per cent) of the territorial males and their partners roost in boxes, whereas only a smal proportion (about 20 per cent) of the non-territorial males and their partners succeed in occupying a box for roosting (Drent, pers. comm.). This means that the number of roosting birds is a rough measure of the territorial part of the population. Further, in male tits the tendency to roost in holes gradually decreases in the course of the winter. This is not the case for the females, which results in a change in the sex ratio found in the spring in the population of roosting birds.

C. Additional data were obtained by the regular capture of tits at the feeding sites shown in Fig. 5. In the later winters, when seeds were no longer provided, we increased the number of netting sites to 10, and attracted the birds to these sites by providing water and by placing a captive Great Tit as a decoy near the nets. The number of tits captured per day gives a general indication of the level of abundance.

In the last two winters two feeding stations were installed outside the area (Ko and Ma in Fig. 5). Here, regular observations on the presence of colour-ringed tits were made, and once a week large numbers of tits were captured. This enabled us to assess the presence of tits belonging to the population of the study area.

In September 1976 we started to measure the supply of beechmast available under the trees at regular intervals throughout the winter. This was done in two ways, one (frequent sampling at the same spot) giving a picture of the fall of the nuts and the other (sampling at longer intervals and each time at a different spot) providing data on the amount available throughout the winter. With the first method samples of 25 x 25 cm were taken under 10 trees and for the second method 32 trees were sampled; in both cases three samples were taken per tree. In sorting the samples a distinction was made between healthy, empty, damaged, and decaying nuts, and both the numbers of nuts and the fresh weight of the kernels were determined. In the next two winters a single sample was taken in October to determine the amount under the 32 trees sampled in 1976/77. The virtual absence of nuts made further sampling unnecessary.

In February and March 1978, some samples of stomach contents were collected by the use of an emetic. For a discussion of this technique, see Radke & Frydendall (1974). Trials with captive tits had shown that tincture of digitalis was suitable for this purpose, because almost all birds regurgitated most of the food consumed and no harmful effects were observed. Birds were captured in the wood or taken from their roosting boxes in the late afternoon, treated with the emetic (0.1 cc was brought into the esophagus and proventriculus by injection through a soft plastic tube), and kept in a dark box for about 30 minutes. The regurgitated food was collected, and stored in 70 per cent alcohol until examination. The food samples were divided into an animal and a vegetable component, on the basis of volume. Where possible, the animal material was identified according to systematic groups, but these results will not be reported here.

In the winter of 1978/79 food samples were collected regularly in the study area during routine catching operations from late September to March. In midwinter samples were also taken from roosting birds, shortly after they entered the roosting box. The latter birds did not regurgitate as regularly as the birds treated during the day. These results will be discussed separately.

3.3. RESULTS

Winter 1974/75. This winter was unusually mild, and there was a fairly good crop of beechmast. The observations on foraging locations, which were not started until January, revealed that a minority of the tits in the subarea DF, where the route was situated, foraged at the food containers and under the beeches. Although the food containers seemed to be the most important food source for the groups in March, the overall importance of this source was much smaller, because most of the tits were then moving about individually or in pairs.

Nocturnal nestbox inspections were performed 12 times in part DF, but only twice in the remaining area. Fig. 6 shows that the numbers of roosting tits followed a bimodal curve. A peak early in the winter, often in December, has been found by many authors, but a second peak in February is rather unusual (*cf.* Mayer 1962). Most of the increase in numbers in February can be attributed to the category of yearling females. The observations on territorial settlement

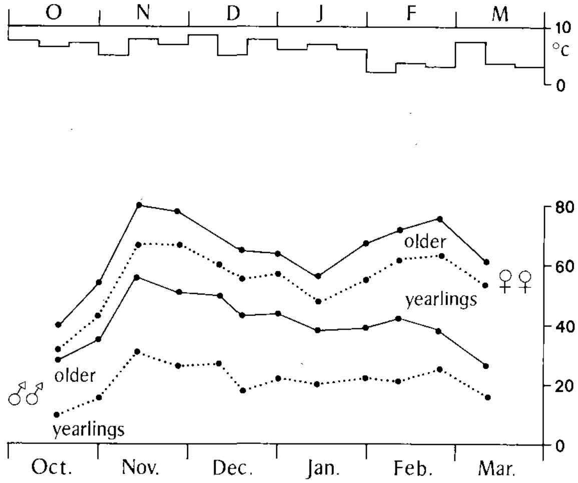


Fig. 6. Numbers of Great Tits roosting in subarea DF in the course of the winter of 1974/75. Upper graph: average temperatures during 10-days periods, recorded at De Bilt.

showed that in this period many new females entered the area, after a period with a shortage of females in midwinter (Drent, pers. comm.). This was confirmed by the results of the netting operations, which revealed an increase in the number of yearling immigrants in February after a two-month period with very little immigration.

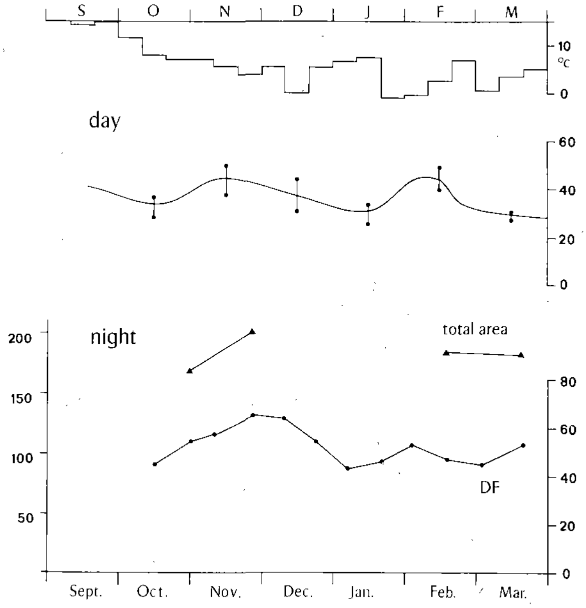


Fig. 7. Numbers of Great Tits counted on a standard route (vertical bars) and numbers roosting in the study area (triangles and lefthand axis) and in subarea DF (dots and righthand axis), in the winter of 1975/76. Upper graph: see Fig. 6.

Winter 1975/76. This was also a mild winter with very little snow, and with a poor beech crop. The only substantial period with frost lasted from January 26th to February 6th.

The daytime counts along the route showed (see Fig. 7) a somewhat fluctuating trend, with a peak in February, possibly associated with a change in behaviour after the frost period. In February, and also in March, a large proportion of the birds occurred singly or in pairs. The revival of territorial activity increases their conspicuousness, which may lead to larger counts. The figures for September/October were possible underestimated, because the trees still carry leaves in that period.

Nocturnal nestbox inspections in the whole area were held only four times, but in the intensively studied part DF we made 12 inspections which gave the following picture: a peak in November-December, then a decline, followed by a small peak during the frost period in February and a final increase in March. The February peak was caused by an increase in the number of roosting young males, not only birds which after having roosted earlier had abandoned this habit temporarily and returned, probably as a response to the cold weather, but also birds which had belonged to the non-territorial part of the population for some time, became territorial during the winter, and subsequently occupied a box for roosting (Drent, pers, comm.).

The daytime catching operations at the food containers resulted in high catches throughout the winter, as is usual in winters without beechmast. The number of captures per day increased from 38.9 in October to 90.4 in December, and then decreased to 62.7 in February. Many immigrants entered the study area in the autumn, in numbers which decreased from September to November. After a fairly stable period in midwinter, a second wave of immigrants occurred from about February 20th to the end of March.

With respect to the foraging locations, it may be remarked that in October-November most tits foraged in oaks, birches, and conifers, whereas in December-March the food containers were

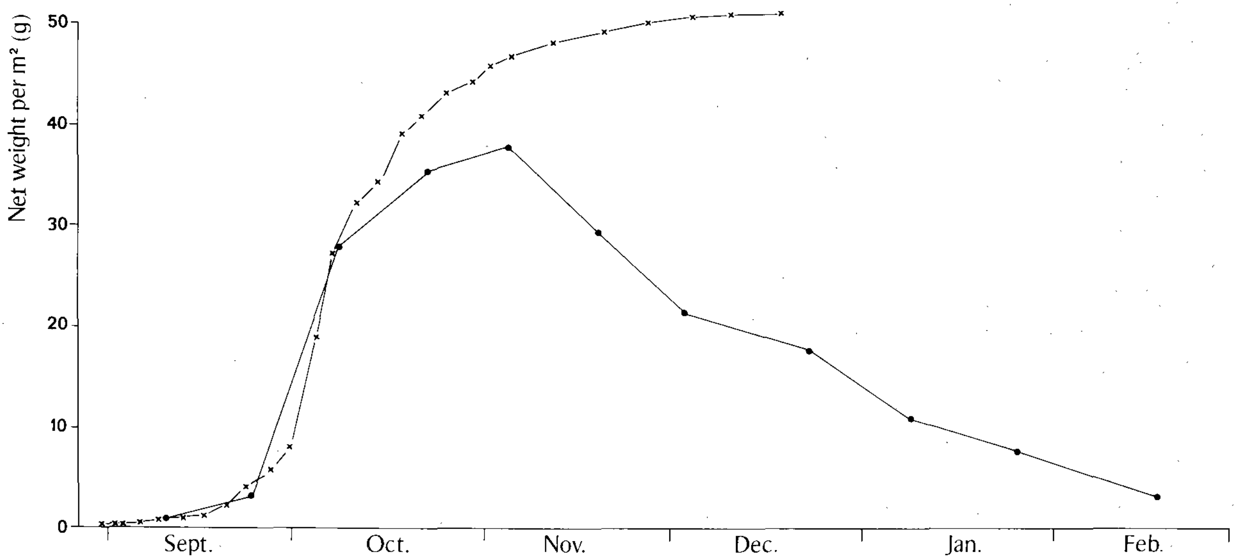


Fig. 8. Cumulative fall (crosses) of beech nuts, in gram net weight per m², and subsequent decline of beech nut supply (dots) on the forest floor in the winter of 1976/77.

visited frequently and foraging in the abovementioned tree species decreased in importance. Beeches were seldom visited during this winter.

Winter 1976/77. Once again there was a fairly mild winter with only short periods of frost, which occurred particularly during the last four days of December. The size of the beechmast crop was determined by regular sampling (see 3.2) of part of the approximately 200 beeches in the study area. As can be seen in Fig. 8, nut fall occurred mainly in October. From about mid-October onward, the curve of the beech nut supply on the forest floor deviated from the cumulative curve. The supply gradually declined during the winter months, and in February only about 10 per cent was left. This marked decline was due to predation by birds, mammals, and insects, and in addition many nuts lost weight by decay. The caloric content of the nuts reached a peak (about 6.3 Kcal per gram dry weight) in October and then declined. In January the caloric content of decaying nuts amounted to only 5.5 Kcal per gram dry weight.

Most of the early consumption of beech nuts by birds was accounted for by Chaffinches (*Fringilla coelebs*) and Bramblings (*F. montifringilla*), but from about mid-November Great Tits, Blue Tits (*Parus caeruleus*), Marsh Tits (*P. palustris*), and Nuthatches (*Sitta europaea*) were also observed feeding under the beeches. This feeding was, however, very irregular, and one could wait for many hours near a nut-bearing beech tree without observing any foraging tits. It became evident that the tits mainly fed on beechmast on cold days. Fig. 9 shows the results of counts made at a site with a particularly rich supply of beechmast (beech J); here counts were done either over a period of 3 hours or throughout the day, and tits were only observed in appreciable numbers on days when the average temperature was below zero. In particular this was the case during a four-day period in late December, when snow covered the forest floor and tits from a large part of the area congregated near this tree.

The impression gained from observations at selected beech trees was roughly confirmed by the records of foraging locations along the fixed route, where hardly any tits were found foraging in or under beeches in October and November, and appreciable numbers were present in December-February. The percentage of all Great Tits observed foraging under beeches along the route amounted to 26 in December, 44 in January, and 14 in February. Foraging on beechmast was most common in early January, shortly after the already-mentioned cold spell. It

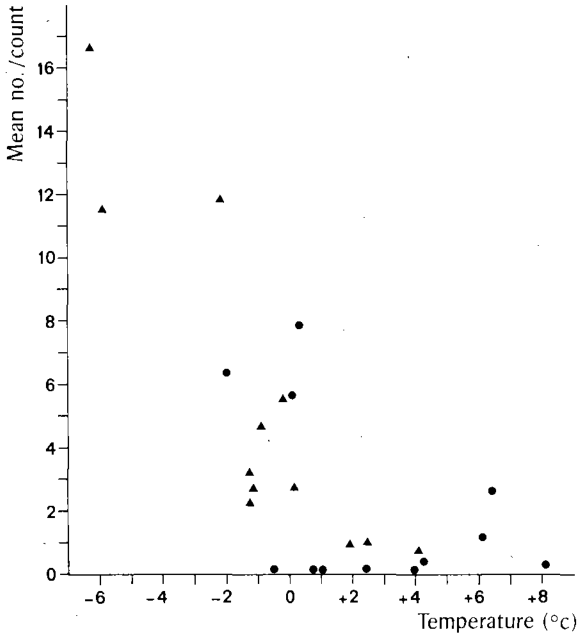


Fig. 9. Mean number of foraging Great Tits present at beech J in relation to the average temperature recorded at Deelen. Values are averages of counts made at 5-minute intervals during observation periods lasting for 3 hours (dots) or throughout the day (triangles).

is therefore clear that, in spite of its abundance from October onwards, beechmast did not function as staple food during the winter of 1976/77, but was used mainly as emergency food in periods with frost and snow.

The counts of foraging tits along the fixed route in subarea DF revealed (Fig. 10) that here numbers were fairly low in the early winter, at least during the morning hours when these counts were made. However, part of the population may have foraged outside its usual feeding range, *e.g.* at beech J (see Fig. 5), which was frequented by large numbers of tits in December and January, and at beeches along the road bordering the south side of the area.

The nestbox inspections showed that very high numbers were present at night, both in subarea DF and in the whole area (Fig. 10). These high numbers of roosting birds continued throughout the winter, in contrast to the pattern found in most winters. Numbers even increased from December to February. This was due to the fact that only very small numbers of birds disappeared after roosting in November/December, and that appreciable numbers of new birds came to roost. The latter were either birds that were territorial in the area during the autumn, or birds that had established a territory in the course of the winter (Drent, pers. comm.). The good feeding conditions resulted in many non-territorial birds being present in and around the area, ready to take over any vacant ground.

Due to the absence of food containers, netting operations were less successful than in the preceding winters. The numbers of tits caught per day decrased from 34.4 in September to 11.1 in January, but increased to 15.8 in February, when immigrant tits, mostly yearlings, entered the area.

In sum it may be said that in the winter of 1976/77 large numbers of tits were present in and just outside the study area, and that feeding on beechmast occurred when conditions deteriorated.

Winter 1977/78. Weather conditions were on average slightly better than normal, except for a cold spell with some snow which lasted for two weeks in February. The daytime counts on the

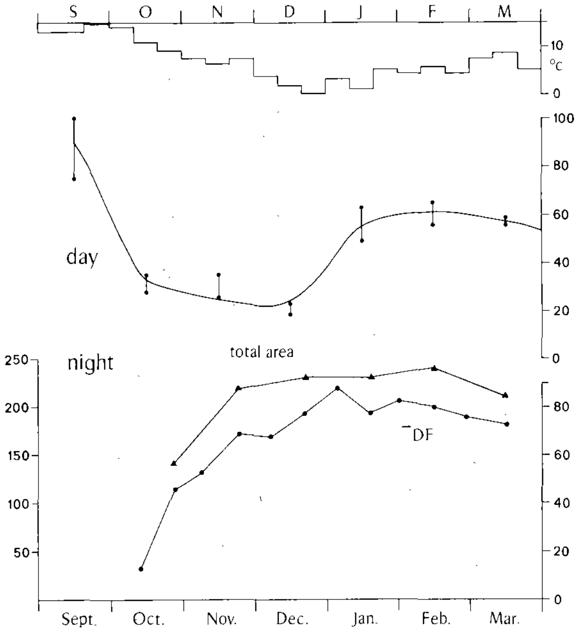


Fig. 10. Numbers of Great Tits counted on a standard route (vertical bars) and numbers roosting in the study area (triangles and lefthand axis) and in subarea DF (dots and righthand axis), in the winter of 1976/77. Upper graph: see Fig. 6.

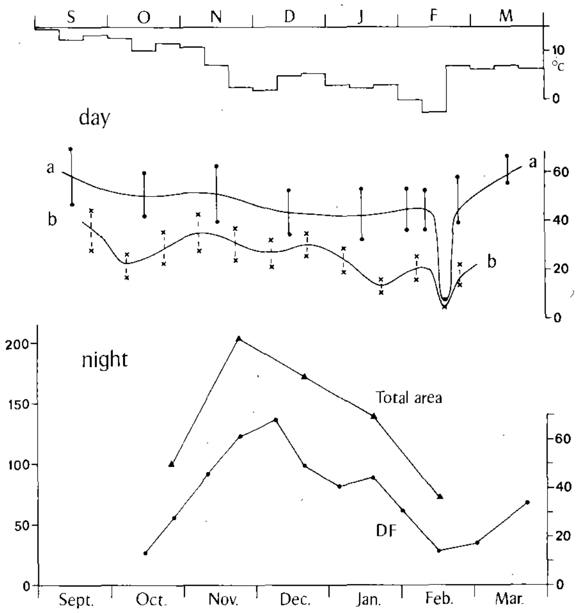


Fig. 11. Numbers of Great Tits counted on standard routes in subarea DF (curve a) and subarea EG (curve b), and numbers roosting in the study area (triangles) and in subarea DF (dots), in the winter of 1977/78. Upper graph: see Fig. 6.

standard route (see Fig. 11, curve a) showed a slight decrease up to December, and no change in January. February could be divided into 4 periods of one week each with different weather conditions; from February 1st to 7th the temperatures were slightly above zero and a layer of a few centimeters of snow was present, during the second week the average temperature fluctuated between -1° and -6° and little snow was present, on the 14th conditions were very unfavourable: continuous snowfall for several hours. After that the cold weather continued for about a week; and from the 22nd onward warmer spring weather prevailed. The counts in February gave very striking results (Fig. 11, curve a). During the first two weeks the numbers were similar to those in December and January, but in the third week only a very few tits were present by day: on average about 9, as compared with 38—55 individuals a week earlier. Two days after the thaw set in, the numbers increased about 5-fold, and this increase continued in March. Frequent counts on a standard route in the northern part of the study area (E and G in Fig. 5) also showed a sharp drop in numbers in mid-February, followed by an increase in the last week of the month (Fig. 11, curve b).

Observations on colour-ringed tits in part DF showed that in the course of the winter about 80 per cent of the males present there in December disappeared. This holds for both territorial and non-territorial males. Moreover, 70 per cent of the disappearances occurred in the first half of February, mainly around the 15th. Of the birds that disappeared in November and in the first half of December, a small proportion returned to the area in the spring (called „winter emigrants"), but none of those which disappeared in the critical period in February returned. Presumably these birds had died. Apart from the category of winter emigrants, the influx of birds in late February was due to yearling birds that had left the area as early as late summer and to a large proportion to real newcomers, unringed birds that had never been caught in the area (Drent, pers. comm).

The influx of immigrants in early spring was also found in the tits captured with nets in the daytime. During a three-month period (November—January) the number of birds caught per day gradually decreased, and the catch consisted mainly of old birds, born before 1977. In February catching results were very low, but the number of birds increased again in March. Almost all of the latter captures concerned yearlings, both autochthonous and immigrant birds.

The numbers of roosting birds also varied considerably throughout the winter (see Fig. 11). After a peak in November/December the numbers decreased, reaching a minimum in February, and increased in March. This trend differed from the fairly constant numbers of birds seen by day in October—January. The early increase in the number of roosting birds is explained by an increasing tendency to roost in boxes. The decrease in December-early February is less easily explained. It could possibly mean that some of the territorial birds disappeared from the area, while the total population remained more or less constant.

Observations on the tree species frequented during foraging showed that during the whole winter foraging took place mainly in oaks, followed by birch and Scots Pine in that order.

Beech was visited locally during October—November. Distinct changes in foraging locations occurred in the sense that from October to January foraging shifted more and more from the crowns to the tree trunks and to the forest floor.

In this winter we also started to investigate the food consumed by Great Tits by using an emetic (see 3.2). Samples of 8 and 4 tits, captured in February and March, respectively, contained 90—95 per cent animal food, whereas for 7 birds caught near a house in the study area the percentage of animal food was lower, on the average 63. This method was also used extensively in the last winter.

Winter 1978/79. The final winter of the series was the most severe one in many years. Two short cold periods occurred in November-December and a prolonged period with frost and deep snow lasted from December 30th, with minor interruptions, until the end of February. Neither beechmast nor extra seed food were available.

The counts of foraging tits clearly showed that at first the numbers present in subarea DF decreased rather sharply in the autumn, and later also in December (Fig. 12). From the end of December tot the end of February, hardly any tits frequented this area by day. Similar counts in the northern half of the study area showed a less pronounced decrease (curve b). Here, the average numbers in January/February ranged from 11 to 21 individuals, representing a decrease of about 65 per cent as compared with the numbers found in the second half of October. It will be seen below that the roosting population too did not decrease evenly over the whole area.

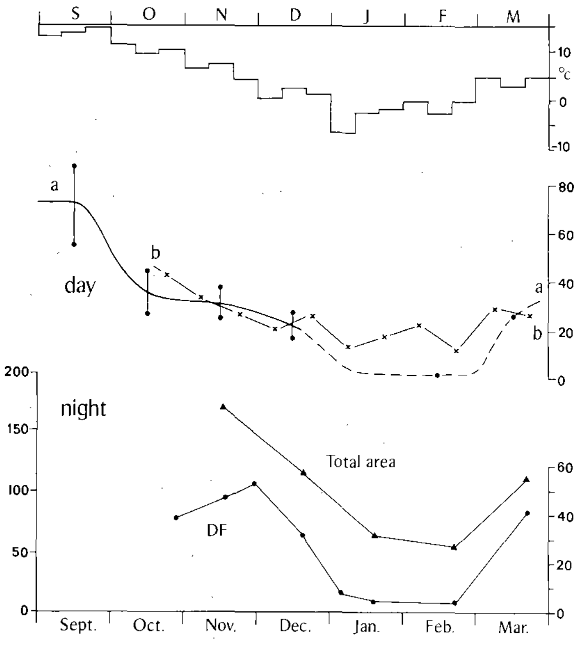


Fig. 12. Numbers of Great Tits counted on standard routes in subarea DF (curve a) and subarea EG (curve b), and numbers roosting in the study area (triangles) and in subarea DF (dots), in the winter of 1978/79. Upper graph: see Fig. 6.

The numbers of tits caught during routine catching operations throughout the area also decreased strongly during the autumn and winter. This applies particularly to the yearlings, both autochthonous birds and immigrants, whereas the numbers of autochthonous older birds remained on the same level from October to December and only declined sharply in the period of severe winter weather.

From all sources of data it was evident that starting in early March the area was repopulated, partly by birds which had left the area temporarily (see later), and partly by newcomers.

The curve of the number of roosting birds is very similar to that of the foraging birds, apart from the usual build-up in the autumn (Fig. 12). The decrease in the numbers of roosting birds did not show the same pattern in all parts of the study area, and also differed for yearlings as compared with older birds. In part DF, where the proportion of yearlings among the roosting birds was very high in November, the number of yearlings decreased sharply until December and also afterwards, whereas the number of older birds mainly declined from December to January, *i.e.* when the cold period started. In the remaining part of the study area yearlings and older birds were equal in number in November, and both declined in number at similar rates during the winter. These findings suggest that some of the older birds had already left subarea DF before November. This was confirmed by diurnal observations on the presence of the territory owners (Drent, pers. comm.).

In midwinter, when hardly any tits were observed or caught in the area during the day, an appreciable number of roosting birds were still

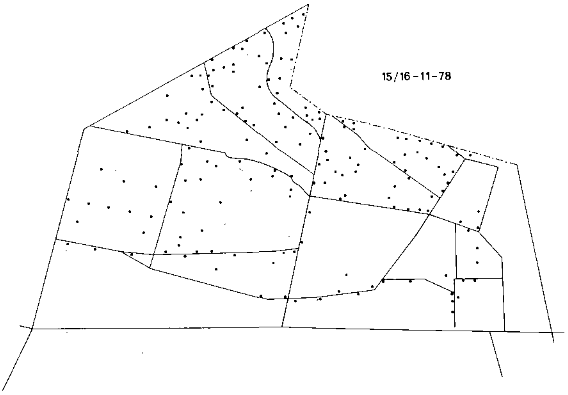


Fig. 13. Distribution of nestboxes occupied by roosting Great Tits on November 15th and 16th in 1978.

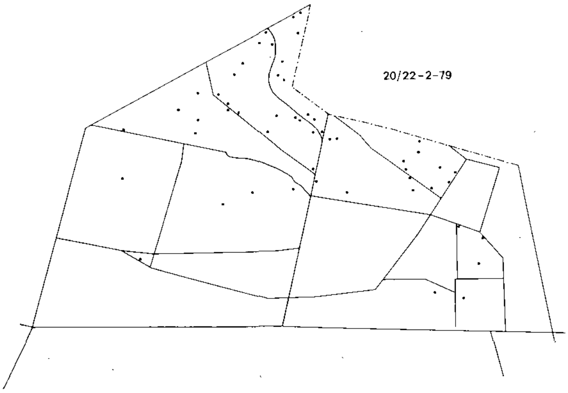


Fig. 14. Distribution of nestboxes occupied by roosting Great Tits on February 19th, 20th, and 21st in 1979.

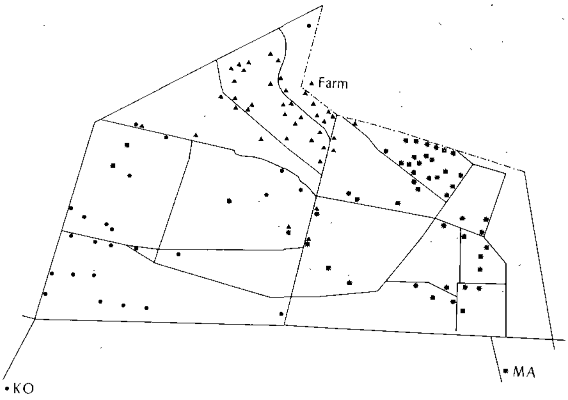
present. This suggests that most of the roosting birds foraged outside the area. The distribution of the roosting birds supports this assumption. In November, when numbers were still high, the birds were fairly evenly distributed over the area, with the highest density in the northern half (Fig. 13). In December the total number decreased but the distribution remained as before, whereas in January and February (Fig. 14) almost all of the birds were concentrated on the north and east sides of the area. This does not necessarily mean that changes in roosting sites occurred within the area. The individuals missing from the evacuated part of the area no longer roosted in the area; some of them were caught by day at feeding sites outside the area. Presumably, they also roosted outside the study area.

There are several possibilities for feeding near houses in the immediate surroundings (Fig. 5). To the north there is a farm where suitable food was available in the form of maize, and a similar store of maize was available 1 km north of that. Along the eastern border there are several houses where presumably food was provided, as well as some houses on the southeast side and also some 800 metres southwest of the study area. At the latter two sites food containers, filled with seeds, were present in this winter (Ma and Ko, respectively, see Fig. 5).

At several of these sites we observed and captured tits that belonged to the population of the study area. At the farm about 40 individuals were observed on two dates in January; most of them had roosted in the part of the study area nearest to the farm, an area with a radius of about 500 m (Fig. 15).

At the northern site 28 individuals were caught in January: among them there were two breeding birds from the study area, but no birds that had been present earlier in the winter.

No observations could be made near the houses around the area, but the presence of tits at our two feeding sites (Ko and Ma) was recorded on many occasions by catching and ringing, and by observing colour-ringed individuals. Fig. 15 shows the area from which these individuals came. Each dot represents a nestbox used for roosting in the period November—February by an individual that was caught or observed at one of the three feeding sites. It is clear that feeding site Ma attracts birds from a large



15. Distribution in the period November 1978 — February 1979 of roosting boxes occupied by individual Great Tits caught or observed during the day at the three feeding sites outside the study area: Farm, KO and MA.

Table 5. Results of analysis of food samples collected in the winter of 1978/79 by means of an emetic. Frequency of occurrence of plant material is expressed as a percentage of the sample volume

a. Samples collected by day in the study area

Month	No. of samples	Percentage plant material								Percentage of samples with less than 50% plant material
		< 1%	1—5%	5—10%	10—20%	20—50%	50—80%	80—90%	> 90%	
September	9	9	0	0	0	0	0	0	0	100
October	41	21	6	3	0	1	4	0	0	90
November	33	20	2	1	2	3	2	1	2	85
December	16	6	3	0	0	1	4	2	0	63
February	1	1	0	0	0	0	0	0	0	—
March	29	24	1	0	0	1	3	0	0	90

b. Samples collected from birds roosting in the study area

Month	No. of samples	< 1%	1—5%	5—10%	10—20%	20—50%	50—80%	80—90%	> 90%	Percentage of samples with less than 50% plant material
December	8	3	0	1	0	1	0	0	3	63
January/ February	5	1	0	0	0	0	0	0	4	20

part of the study area, *i.e.* the whole eastern half, whereas site Ko attracts tits only from the southwestern corner. In the central part of the area there is some overlap. On several occasions individuals were caught at the feeding sites during the day and again while roosting in the study area on the same night. For most birds, however, the observations made inside and outside the area refer to different dates. Since it is known that virtually no birds were present in the area during the day in January—February, it is certain that many of the dots on the map refer to individuals which travelled daily between roosting sites in the area and feeding sites outside it, over distances of 100 to 1200 metres.

Among the tits caught at the two feeding sites and originating from the study area, the yearlings predominated initially. They were present from the second half of November, and their proportion in the captures increased until the second half of December. Later, in de second half of January and in February, many older birds, *i.e.* breeding birds from the study area, were present, but the birds of this category obviously stayed in the breeding area much longer than the yearlings did.

As already mentioned, the method of collecting the stomach contents by the use of an emetic was applied rather extensively during this winter. Starting in late September we treated tits caught during routine catching operations in the area, and succeeded in getting good samples up to the end of December. After that, only a very few samples could be taken. Table 5a gives the results, expressed as the frequency of the percentage of plant material found in the samples. In the autumn almost all samples contained purely animal material, and then a gradual change occurred. The percentage of birds with less than 50 per cent plant material in the stomach decreased from 100 in September to 63 in December. Although in December quite a few samples contained considerable plant material, there was an overall tendency for the birds caught by day within the area to have consumed mainly animal food.

Supplementary samples were collected from birds shortly after they had gone to roost (section 3.2). The few results obtained are given in Table 5b. The evening samples from December tend to contain some very high percentages of plant material, not found in the corresponding daytimes samples. The few data from January-February suggest that these birds mainly consumed plant food. This was especially the case for the birds known to visit one of the feeding stations outside the area.

To summarize we may say that: 1. in November and December part of the population (especially yearlings) left the area and foraged to a large extent at feeding stations outside the area; 2. the birds remaining in the area consumed predominantly animal food; 3. during the period with frost and snow in January and February almost all tits foraged outside the area, but some of them roosted inside it, and consumed plant food; and 4. from early March onward the area was rapidly repopulated.

4. CONCLUDING REMARKS AND DISCUSSION

A review of the last five winters shows that the population trends during the winter reflect the feeding conditions. For instance, from the numbers of roosting birds in part DF (Fig. 16), it is evident that the numbers in January/February were largest in the two winters with a good beechmast crop, intermediate in the winter with only the extra seed supply, and smallest in the two winters without an abundant seed supply. The effect of a severe winter is apparent from a comparison of the last two winters.

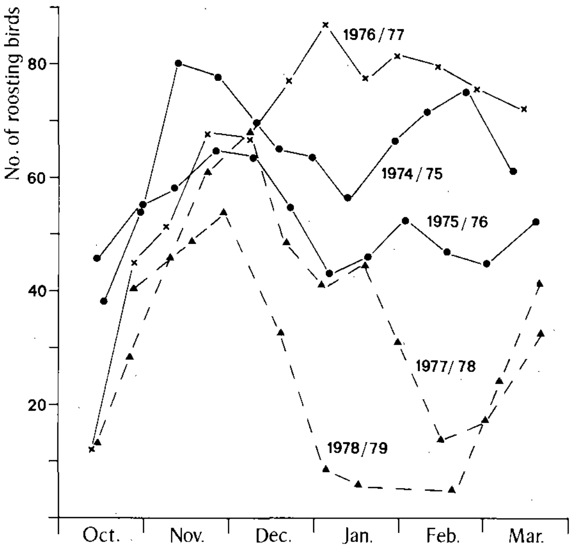


Fig. 16. Seasonal trends of the numbers of roosting birds in different years. Data for subarea DF in 1974—1979.

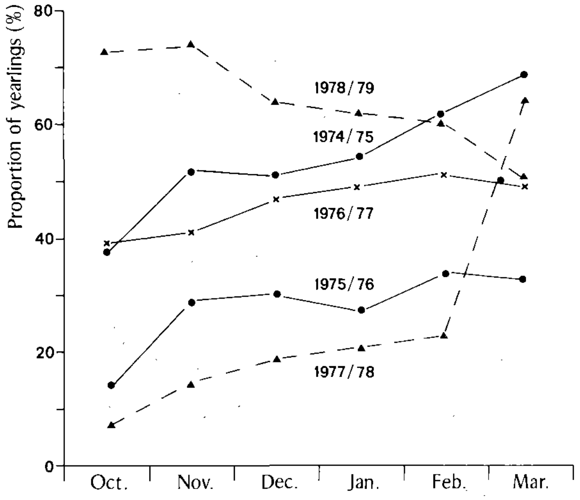


Fig. 17. Seasonal trends of the percentage of yearlings among roosting birds in different years. Data for subarea DF in 1974—1979.

Not only the size but also the composition of the roosting population often showed considerable changes in the course of the winter. In most winters there were few yearling birds among the earliest roosters in October, and their percentage increased strongly up to November and gradually after that (Fig. 17). This pattern is the result of two processes: in the first place yearlings tend to start using the nestboxes for roosting at a later time than the older birds, and in the second place territorial birds disappear at various moments in winter and their territories are taken over by yearlings. An especially strong increase in the percentage of yearlings occurred in March 1978, when a high number of these birds entered the area after the fatal cold spell in February.

The winter of 1978/79 led to a picture differing completely from that in the foregoing winters. As mentioned earlier, the percentage of yearlings in the autumn was very high. The decrease in this percentage in November/December was probably related to the appearance of predominantly yearling birds at the feeding stations outside the area. The percentage of yearlings also decreased in the spring, when the area became repopulated after the severe winter. This means that the birds entering the area in March included rather many old birds which probably had left it at the start of the cold period or even earlier.

It was found (see Fig. 18), that the percentage of yearlings in the autumn and also the number of yearlings roosting in November are negatively related to the size of the previous breeding population: high breeding populations are followed by low numbers of roosting yearlings in November and vice versa. This relationship was maintained throughout the winters under study except the last disastrous winter. Since the habit of roosting in nestboxes is a result of territorial ownership, this relationship implies that territorial settlement

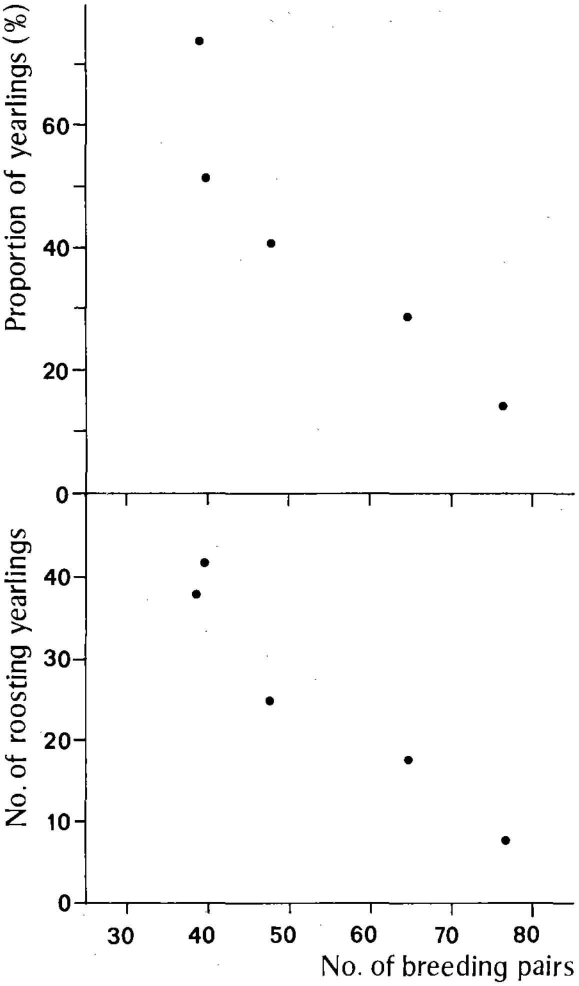


Fig. 18. Relationship between the size of the breeding population and: (a) the percentage of yearlings among roosting tits in the following November and (b) the number of roosting yearlings in that month. Data for subarea DF in 1974—1978.

by yearlings is negatively related to the size of the preceding breeding population. As shown above, the number of yearling birds in the breeding population was negatively correlated with the size of last year's breeding population. Here we see that a similar relationship is already apparent in November, when the first period of territorial settling is over. Hence, it is evident that part of the disappearance of yearling tits (due to either death or emigration) takes place before November.

When we look at the numbers of roosting birds in different winter months in relation to the size of the *next* breeding population, it is clear that generally there is a strong positive correlation. The numbers of roosting birds in January and February in particular permit reliable prediction of the next breeding population (Fig. 19). On the other hand, it is obvious from the results presented so far — *e.g.* the relationships between weather conditions, winter food supply, and local survival — that processes which determine the size of the future breeding population play a role *throughout* the winter.

The role of winter cold. It is striking that the severe winter of 1978/79 was followed by a small (24%) decline in breeding numbers, compared with the marked (46%) decline in the preceding winter. The findings for the cold spell of February 1978 show that a relatively short unfavourable period can have serious consequences for the survival of individuals and for the size and the age composition of the breeding population. Presumably, the impact of unfavourable conditions is stronger the later they occur in the winter, because the energy reserves (as measured by body weight) decrease from midwinter to February/March (Van Balen 1967, Haftorn 1976).

Usually, the winters in western Europe are not sufficiently severe to have a distinct effect on

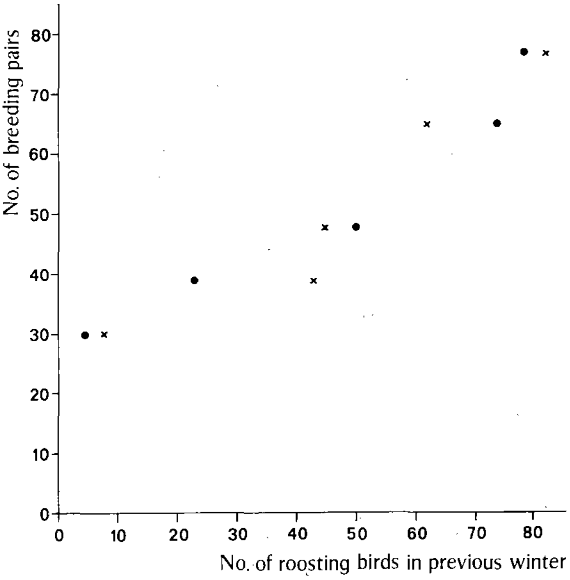


Fig. 19. Relationship between the numbers of roosting birds in the winter (crosses: January, dots: February) and the size of the next breeding population, in subarea DF. Data for 1975—1979.

Great Tit populations. Such effects only occur under certain combinations of frost and snow cover.

In the past, several winters of exceptional severity, such as those of 1916/17, 1928/29, 1939/40, 1941/42, 1946/47, and 1962/63, have been followed by strong decreases in the breeding populations of hole-nesting passerines in western Europe (see *e.g.* Kluyver 1951, Berndt & Frantzen 1964). Kluyver's data show clearly that winter cold affected the Great Tit population of Oranje Nassau's Oord significantly in winters after a large breeding population had been reached, and not in winters after a small breeding population. This could imply that competition for food plays a role in determining survival during the winter. Berndt & Frantzen reported a large decrease (32%, as calculated by me from their Table 2) in breeding numbers for the Great Tit in 1962/63 in areas without food supplementation whereas in areas with the provision of extra food the decrease was negligible. In the other severe winters the losses were even higher. Data published by Von Haartman (1971) for an area in southern Finland revealed a consistently negative relationship between breeding numbers and average winter temperature, over a wide range of temperatures. A similar phenomenon was found for the Blackbird *Turdus merula* in southern Sweden by Karlsson & Källander (1977) and for the Goldcrest *Regulus regulus* in Finland by Siivonen (1956), but other species seem to be more strongly affected by the depth and duration of the snow cover (Siivonen 1963). Because the Great Tit finds an appreciable proportion of its food on the forest floor, especially in midwinter, the amount of snow cover should be at least as important as low temperature *per se*, but since these two aspects of the winter weather usually fluctuate in parallel, it is not clear which of the two affects the winter survival most.

The influence of the winter weather on the numbers and the distribution of the Great Tit is also apparent from Haftorn's (1957) findings about the extension of the northern limit of the breeding range in Norway during the last decades. This author connects the range extension with the amelioration of the winter climate.

Hildén & Koskimies (1969) have pointed out that in the winter of 1965/66, which was very cold and snowy in Finland, the numbers of several species did not decrease as strongly as expected. These species, *e.g.* Great Tit, House Sparrow (*Passer domesticus*), and several fringillids and corvids, are "entirely dependent on food supply from human inhabitations for their winter survival, primarily on direct feeding, and in natural conditions they would have hardly any chances of survival in Finland". Extreme as this view seems to inhabitants of countries with milder winters, it certainly suggests that in the northernmost parts of its range the Great Tit depends predominantly on food found near human habitations in the winter. This would apply especially to the regions north of the range of the beech, where at least some of the populations seem to be resident.

In his study on the winter ecology of tits in pine plantations in East Anglia, Gibb (1960) showed that not only the stock of invertebrates in the pine foliage but also the winter survival of the Coal Tit (*Parus ater*) were positively related to the mean air temperature in winter. His suggestion that tit survival is directly related to the food supply and only indirectly to the winter temperature, is consistent with the view expressed here, *i.e.* that in general the effect of severe winter weather on bird populations acts via the availability or accessibility of their food.

The role of beechmast. Although several authors have establised correlations between population parameters of the Great Tit and the size of the beechmast crop in the preceding autumn, opinions as to the causal mechanism differ widely. A short review of the relevant literature will be given, and the results compared with the situation in the Hoge Veluwe study area.

In Marley Wood, near Oxford, Gibb (1954) found that hazelnuts and beechmast, which were unusually abundant in the autumn of 1950, were a staple food of Great Tits from September 1950 to March 1951. Most of the beechmast fell in November and December, which is definitely later than is the case in The Netherlands. From September to March/April an increasing percentage of the tits fed on the ground, and the success in finding beechmast decreased considerably after December. From Gibb's observations it is not clear, however, whether foraging in the trees in the autumn concerned beechmast or animal food.

Betts (1955) observed that in the oak plantations of the Forest of Dean the majority of the gizzard samples of Great Tits contained more than 50 per cent beechmast tissue in the winter of 1950/51; in other winters, when the beech crop was poor, acorns and sweet chestnuts were taken. Beechmast seemed to be preferred to the other two species.

Ulfstrand (1962) determined differences in foraging behaviour in winters with and without a good beechmast crop in a beechwood in Skåne, and described how the tits foraged on beechmast hanging in the trees from September to February. Beechmast appeared to be the staple food of the Great Tit in winters with a good crop, and animal food in other winters. Moreover, the numbers of tits present in midwinter were positively correlated with the presence of beechmast. This applied to the study areas in Skåne, as well as to large regions of southern and central Sweden. He postulated that the extent of migratory movements in autumn, started as a response to increased population density, is strongly influenced by the presence of beechmast. In conclusion, although it is not clear whether the availability of beechmast directly promotes survival during the winter, its overwhelming effect on foraging behaviour and dispersive or migratory movements is beyond any doubt.

Perrins (1965, 1966) observed that beechmast formed an important source of winter food for the Great Tits in Wytham, and stated that exploitation started in late November. He found a good correlation between the size of the crop (in The Netherlands) and population changes (in The Netherlands and England). However, he doubted that the correlation is causal, because the size of tit populations tends to fluctuate in parallel over wide areas, including some without beech trees. He further suggested that the beech crop indicates the general level of food abundance late in the summer, when the critical mortality of the juveniles is supposed to occur.

Webber (1975) found that the juvenile survival up to November/December and the immigration rate in the first autumn were related to the size of the beech crop. He postulated that part of the regulation of the Great Tit population in Wytham occurs in autumn as the result of dominance or territorial behaviour in relation to a variable food supply in the form of the autumn seed crop. These seeds, which originate from several tree or shrub species, would then be correlated in abundance with the beech crop, and would be available in August-October.

Finally, Nilsson (1979) observed that the distribution of several species, including the Great Tit, in a beech wood in southern Sweden was correlated with beech-seed density in one winter but not in another winter when beechmast was also abundant. In the second winter, when bird predators were present, the distribution of the tits was positively correlated with the amount of low cover in the wood. Yet very little food apart from beech seeds was consumed. Utilization, in terms of bird days per month, was highest in December-January.

On the basis of present knowledge it appears that in southern Scandinavia the presence of a good beech crop is a decisive factor in the feeding ecology during a large part of the nonbreeding season, probably promoted by the occurrence of large pure beech forests. In the milder climate of southern England the consumption of beechmast seems to vary, as far as known, between areas or years, and other evidence indicates that beechmast does not affect juvenile survival in a proximate way. The situation in The Netherlands, as judged from our findings on the Hoge Veluwe can be tentatively summarized as follows: the size of the beech crop influences the local survival of the juveniles by affecting both their dispersal and their survival. As shown by Drent (this symposium), local survival is lower in autumns with little beechmast than in autumns with an abundant supply of seeds (beechmast or seeds provided by man). This is largely due to a difference in dispersal caused by birds leaving the area, temporarily or permanently, from October onwards. Later, in December-February, beechmast serves as a supply of emergency food which is used whenever weather conditions force the birds to change from a presumably evenly dispersed (animal) food source to a more patchily distributed source, enabling them to satisfy the increased food requirements within the short period of daylight. Presumably, the reduced accessibility of the invertebrate food stocks under certain weather conditions also plays a role here.

The uneven distribution of the beech trees over the area is responsible for differences in the accessibility of the beech crop to different categories of Great Tits. Non-territorial birds (part of the category of juveniles) and birds with territories close to nut-bearing beeches profit most from the beech crop.

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6. SUMMARY

The fluctuations in breeding numbers of the Great Tit population in the 1960-1972 period on a 320 ha study area on De Hoge Veluwe were analysed. This was done by an analysis of the numerical relations between parameters of the population and some environmental variables. During part of this period extra seed food was provided in the winter.

A preliminary analysis showed that the size of the beech crop has a large effect on juvenile survival, and hence on population size; the provision of extra seed food by the observers enhanced the survival of the older age classes in particular. Further analysis by multiple regression and canonical correlation techniques gave following results:

— The number of autochthonous yearlings in the breeding population (*i.e.* young born in the study area in the preceding year) is positively correlated with the number fledged the year before and with the size of the beech crop; moreover, it is negatively related to the number of breeding birds in the preceding year, which indicates that the yearlings' chances of settling depend on the amount of space left vacant by the older birds. The beech crop influences juvenile survival between fledging and first breeding.

— The number of older breeding birds is affected by the provision of extra seed food, which enhances the survival of this category. Furthermore, there are indications that density-dependent losses (due to mortality and/or emigration) occur, and that the severity of the winter plays a role.

— The different responses of yearlings and older birds to the two types of seed food can be understood from the distribution of the food sources, the degree of site-attachment, and the dominance relations of different categories of birds.

The fluctuations in numbers, foraging behaviour, and diet in winter are discussed next, on the basis of observations carried out in 1973-1979. In these years the number of breeding pairs fluctuated considerably, which was in accordance with the prevailing feeding conditions and the severity of the winters.

In the winter of 1976/77 there was a very good crop of beechmast. Although beechmast was already available in September/October, large-scale feeding on these nuts only occurred in December-January, and especially on days with frost and snow cover. This suggests that beechmast functions as an emergency food source. The impact of a short spell of unfavourable weather was very distinct in February of 1978, when the number of tits present suddenly decreased by about 80 per cent after a period of snow on the 14th. The absence of a seed food supply and unfavourable winter weather resulted in the largest decrease in breeding numbers (46%) found in this study.

A similar situation occurred in the winter of 1978/79, but now the unfavourable period started earlier and lasted much longer. During this period a large part of the study area was evacuated by day, and to a lesser extent by night. A large part of the population then foraged at feeding stations outside the area. The area was repopulated in March, and the overall decrease in breeding numbers only amounted to 24 per cent. The tits that foraged in the area from September to December, and also in March, consumed mainly animal food. This too indicates that animal food is preferred, and that seeds serve as emergency food.

It is shown that part of the disappearance of the yearlings already occurs befor November; on the other hand, processes that determine the size of the breeding population act throughout the winter.

There are regional differences in the extent to which beechmast is consumed in the autumn and winter. In southern Scandinavia the Great Tit seems to be much more dependent on beechmast than is the case in The Netherlands and (possibly) in England. The impact of severe winter weather on Great Tit populations differs considerably between countries in relation to the general climate and the feeding conditions.

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