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Breeding success and population dynamics in a northern great tit Parus major population

Markku Orell & Mikko Ojanen

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Data from 1219 broods examined during 1969–1980 in the Oulu area of northern Finland provide the basis for this study; 28 % of the broods failed to produce fledglings, while 78.8 % of the 976 pairs represented produced at least one fledgling. The reproductive rate was 6.09 young/ breeding pair. This, together with a female survival rate of 44.8–48.3 % resulted in a juvenile survival rate of 17.0–18.1 % to maintain a stable population.

Excluding human interference, the most important predator upon the great tit nests was the stoat, which plundered an average of 7.9 % of all clutches. The years following small rodent peaks were those of heaviest predation by the stoat.

The fledging success (percentage of eggs yielding fledglings) amounted to 54.8 % in the first broods, 45.6 % in the repeat broods and 65.7 % in the second broods. Starvation was the most important cause of nestling deaths. In first broods the nestling success decreased with increasing initial brood size. Nevertheless, the number of fledged young was highest in broods of largest initial size.

Second broods were laid in years when the success of the first broods was higher than average, and the females laying second broods had been more successful with their first broods than those which produced no second broods, suggesting that a second brood is profitable for the most competent females.

Among the repeat broods, those initiated after the first brood had been destroyed during the incubation stage were most successful.

The habitat differences in breeding success were small. Hatching success and nestling mortality among the first broods was not density-dependent, but the population size reduction during the non breeding season was relatively higher when the initial summer population was high.

Nestling success in the successful first breeding correlated positively with the average daily temperature during the period May-June. Shorter periods also showed positive relationships, but not significantly so. These results suggest that climatic factors contribute to a great part of the reproductive output in the Oulu area and are in this respect more important than density-dependent factors.

The number of fledglings was on average 2.0 young less than the number of eggs hatched in successful first broods. This result indicates the brood reduction strategy in the great tit in the Oulu area.

Markku Orell, Department of Zoology, University of Oulu, Kasarmintie 8, SF-90100 Oulu 10, Finland.
Mikko Ojanen, Department of Anatomy, Biological Section, University of Oulu, Kajaanintie 52A, SF-90220 Oulu 22, Finland.

1. Introduction

This work is part of a long term study on the ecology of hole-nesting birds carried out in the Oulu area, northern Finland. The northern location of this area provides good opportunities for studying adaptive strategies under varying environmental conditions in the great tit, a species adapted to southerly broad-leaved forests (see Perrins 1965, van Balen 1973).

Selection pressure may be different here than further south, causing different strategies. Many ecologically important traits are determined by the high proportion of heritable factors, e.g. clutch size, egg size, body size and time of breeding (Perrins & Jones 1974, Garnett 1976, Ojanen et al. 1979, van Noordwijk et al. 1980, 1981a, b) and selection may alter these traits over a short period (van Noordwijk et al. 1980, 1981a,b). Earlier results showed that there were marked differences in some important traits in the great tit between Oulu and more southerly areas (Ojanen et al. 1979). The size of the female was correlated only weakly with egg size, although the correlation was a closer one in Oxford (Jones 1973). Moreover, the smallest females apparently did not start breeding earliest here (Ojanen et al. 1979), in contrast to the situation in Oxford (Jones

1973). On the other hand, one ecologically important parameter, clutch size, does not deviate in the Oulu area from the figures further south (Orell & Ojanen 1983b).

The aim of this study is to investigate in the light of the above the selective adjustments in breeding in northern areas near the border of the great tit's range in an environment of climatic unpredictability (e.g. O. Järvinen 1979).

2. Material and methods

2.1 Study areas

Data on the breeding biology of the great tit were collected from 13 sites in the Oulu area (c. 65°N, 25°30′E) from 1969 onwards. Four small areas had to be abandoned after 1975 due to extensive forestry work. Wooden nest boxes with a bottom area of 121-156 cm^2 were available to the tits.

The study started in 1969 at 4 areas where most boxes had been available for some years, Taskila, Kuivasjärvi, Loppula and Isokangas, and also at Tuiranhovi, a site set up that year (Fig. 1, Table 1). The following year 8 new nest box sites were established at Kiviharju, Uikulaisjärvi, Lintumaansuo, Jokikylä, Onkamo and Räinänperä, and intensive study was also started at Sanginsuu. In the same year 5 boxes were also available at Vittasuo, although the area was not included in the study until 1971.

Except for Taskila, the sites were not close to inhabited areas. In the eastern part of Taskila the nest boxes were situated around an area of private houses and an abandoned field which became progressively overgrown by birch (*Betula pubescens*) and bushes of *Salix* spp. In the western part, which is larger than the eastern, the boxes were located in mixed forest.

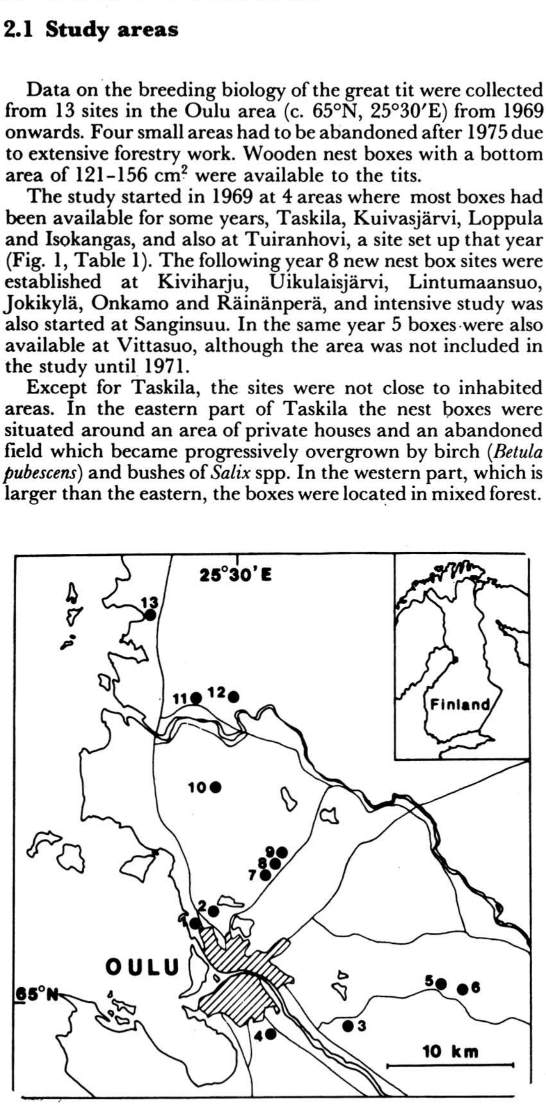

Fig. 1. Map of the surroundings of Oulu showing the locations of the sites studied: 1) Taskila, 2) Kuivasjärvi, 3) Sanginsuu, 4) Kiviharju, 5) Loppula, 6) Isokangas, 7) Tuiranhovi, 8) Vittasuo, 9) Uikulaisjärvi, 10) Lintumaansuo, 11) Jokikylä, 12) Onkamo, 13) Räinänperä.

The dominant trees in the eastern part are spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), while deciduous trees, birch, alder (*Alnus incana*) and aspen (*Populus tremula*), are abundant throughout. In the western part, where the soil is moist, the deciduous trees, especially birch, alder and *Salix* species are dominant in places. The individual stands of these trees are small, however, with small, intermittent spruce woods.

The lower vegetation in the drier eastern part is rich in dwarf shrubs (*Vaccinium myrtillus, V. vitis-idaea, V. uliginosum* and *Ledum palustre*), and there is only a little grass, mostly *Avenella flexuosa*. The same shrub species dominate in the western part, although grasses (*Calamagrostis spp.*), herbs (*Menyanthes trifoliata* and *Calla palustris*) and *Equisetum silvaticum* are found in most moist places.

Only the small part of the forest has been thinned during the years. Birch and *Salix* bushes have grown into thickets in places, especially in the western part, and these bushes have also encroached on many of the clearings which caused a pronounced edge effect at the beginning of the study.

At Kuivasjärvi, situated c. 2 km east of Taskila, 20 nest boxes were placed over an area of 100 ha in 1969, and 41 boxes have since been installed in an area of 41 ha. The forest is dominated by spruce, but Scots pine, birch and *Salix* species also grow in the area. Birch has become more abundant in later years, since the felling of some of the spruce. The same dwarf shrub species dominate in the undergrowth as in the eastern part of Taskila.

At Sanginsuu 15 boxes covered an area of 30 hectares in 1970, since when the area has been extended to 130 ha and the number of boxes has varied between 78 and 163. The dominant trees are spruce and Scots pine, with deciduous trees having only a minor influence on the habitat. The same dwarf shrub species form the lower vegetation as in the eastern part of Taskila.

The sites of Loppula, Tuiranhovi, Uikulaisjärvi, Jokikylä, Onkamo and Räinänperä are dominated by spruce forests. Scots pine, birch and aspen are less abundant. The same dwarf shrub species are dominant in the forest floor as at Taskila. Isokangas is dominated by Scots pine mixed with some spruce. The lower vegetation is mostly *Vaccinium myrtillus* and *V. vitis-idaea*. Part of the area is very dry pine forest with a field layer of *Calluna vulgaris* and *V. vitis-idaea* but this is not favoured by the tits.

Kiviharju, Vittasuo and Lintumaansuo are areas with a high incidence of deciduous trees, especially birch and *Salix* species, mixed with spruce. Kiviharju is an old drained bog with a field layer of *Ledum palustre, Vaccinium myrtillus* and *V. uliginosum*. Vittasuo has an abundance of grasses (*Calamagrostis* spp. and *Avenella flexuosa*) and herbs (*Convallaria majalis*) in the fields layer, and dwarf shrubs are also found. *Calamagrostis* species and *Avenella flexuosa* are the most common grasses at Lintumaansuo, and *Equisetum silvaticum* is also present in places.

2.2. Data collection

The nesting success data presented here were collected over the period 1969-1980. Each area was visited at least once a week during spring and summer to follow the progress of breeding. The first visits in May gave the number of great tit pairs attempting to breed at the sites. This information was important later in summer when estimating which of the late broods were repeat broods and which second ones. The number of eggs or young in the nest was recorded during each visit. When the nestlings were encountered for the first time their age was determined using experience regarding of the size of great tit nestlings attained by following the growth of selected broods. Weighing was sometimes also of help in age determination. The information on age was used when calculating the hatching date, which refers here to the date when the last chick hatched.

Table 1. Numbers of nest boxes and sizes of the study areas (ha, in brackets) in 1969–1980. Note: the areas vary in size mainly due to partial clear fellings.

	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
Oulu												
1. Taskila	30	59	72	72	72	68	68	68	73	73	73	73
	(48)	(54)	(54)	(54)	(54)	(50)	(48)	(48)	(50)	(50)	(48)	(48)
2. Kuivasjärvi	20	41	41	41	41	41	39	39	41	41	41	41
	(100)	(41)	(41)	(41	(41)	(41)	(41)	(41)	(41)	(41)	(41)	(41)
3. Sanginsuu	-	15	78	163	163	163	155	121	121	119	119	119
		(30)	(130)	(130)	(130)	(130)	(130)	(130)	(130)	(130)	(130)	(130)
4. Kiviharju	-	10	10	17	20	20	18	18	21	23	24	24
	-	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)
5. Loppula	52	52	52	48	48	48	48	-	-	-	-	-
	(18)	(18)	(18)	(18)	(18)	(18)	(18)	-	-	-	-	-
6. Isokangas	50	50	50	20	17	23	23	23	39	39	39	39
	(16)	(16)	(16)	(16)	(16)	(16)	(16)	(16)	(16)	(16)	(16)	(16)
Haukipudas												
7. Tuiranhovi	16	66	41	28	28	28	11	11	11	14	14	14
	(20)	(33)	(24)	(16)	(16)	(16)	(5)	(5)	(5)	(5)	(5)	(5)
8. Vittasuo	-	-	38	48	57	63	60	59	51	51	51	51
	-	-	(26)	(26)	(26)	(26)	(26)	(26)	(20)	(20)	(20)	(20)
9. Uikulaisjärvi	-	34	34	34	34	34	50	38	38	38	37	37
	-	(22)	(22)	(22)	(22)	(22)	(26)	(22)	(22)	(22)	(22)	(22)
10. Lintumaansuo	-	12	12	12	21	21	20	-	-	-	-	-
	-	(22)	(22)	(22)	(22)	(22)	(22)	-	-	-	-	-
11. Jokikylä	-	5	5	5	5	5	5	-	-	-	-	-
	-	(7)	(7)	(7)	(7)	(7)	(7)	-	-	-	-	-
12. Onkamo	-	26	26	26	26	26	23	-	-	-	-	-
	-	(14)	(14)	(14)	(14)	(14)	(14)	-	-	-	-	-
Ii												
	-	10	10	15	20	10	-	-	-	-	-	-
13. Räinänperä	-	(10)	(10)	(10)	(10)	(10)	-	-	-	-	-	-

A number of clutches were visited daily before the expected date of hatching and during hatching to determine the hatching interval, i.e. the number of days required for all the eggs to hatch.

Before fledging the nestlings were marked with aluminium rings. At the same time the parents were captured and marked or they were identified by coloured rings.

Data for estimating the productivity were available for 1202 out of the 1219 great tit broods. The remaining 17 broods, about which it could not be decided whether they were successful or not, were 13 first broods in 1970, 2 in 1975 and 2 second broods in 1975.

According to our observations, the great tit removes dead nestlings from the box, a frequent event when the young are less than 9 days old. Beyond this age they were mostly found dumped in the nest material. In the majority of broods the number of nestlings was counted at an age of more than 13 days, and any deaths after that age were assessed by counting the carcasses in the box. There were 72 broods for which the number of fledged young was not known precisely, i.e. the number of nestlings was counted for the last time when the young were less than 9 days old, so that it was possible that some young had died after the visit and the parents had removed the carcass. In those cases the number of fledged young was estimated by assuming the average mortality rate typical of that year and applying it to the particular brood. These estimated values were only used when calculating the reproductive rate for the population.

Calculations of hatching and nestling success included only broods for which the fate of the eggs and young was known precisely. Clutches were included if the number of eggs was confirmed or the number of young hatched was known before predation.

In most of the nests which had been subject to predation it was easy to detect whether this had taken place during the laying or incubation stage, since the nests were checked frequently enough. Sometimes, however, an indirect method had to be used. The average number of eggs in a great tit clutch is nine or ten. If a nest contained five eggs of less at a visit and was found to have been attacked a week later, predation was estimated to have taken place before the completion of the clutch. In other cases predation was assumed to have occurred during incubation. Predation during the nestling stage was always easy to detect using the remains of chicks in the box as an indicator.

2.3. Determining the causes of nesting failures

The criteria for determining the cause for the most frequently existing types of failure are given below. The predator species was determined by direct observations or by special marks left in the nest. The marks of the stoat (*Mustela erminea*) were easy to interpret; faeces on the roof of the box, broken eggshells, usually with teeth marks, piled up in a corner of the box or broken wings and feathers of nestlings or the female, or headless carcasses in the box. Moreover, we have encountered the stoat in predating eggs or young in a nest-box at least ten times. Traces left by mischievoys boys in most cases comprised removal of the lid of the box and broken eggs or dead chicks nearby. Sometimes the box had been removed entirely.

In some cases the brood was apparently hit by some disease, the chicks dying after a few days and differing in appearance while still alive from those which had succumbed to undernourishment. Their skin was clearly dry, deep red or violet in colour and their behaviour was different, with no begging for food.

Nestling development was studied by repeated weighings of selected broods, and this procedure gave an idea of how starvation occurs among great tit nestlings. Hence all deaths which could not be attributed to predation, illness or short-term desertion were included under the heading of starvation.

If no marks of predation or other disturbances could be found in a clutch of unincubated eggs or a dead brood it was classified as having been deserted.

2.4. Terminology

First clutches refer here to cases when the female laid her first eggs in the season, repeat broods were those initiatied after the first nest had been destroyed, and second clutches were those laid after successful breeding. For details of the determination of these categories, see Orell & Ojanen (1983a). Nesting stages mean successive periods within nesting, i.e. laying, incubation and feeding.

3. Results

3.1. Nest losses

Altogether 30 % of the great tit nestings did not produce any fledglings (Table 2). The number of unsuccessful clutches was significantly different between layings (χ^2-test, $p<0.05$), 30 % of the first clutches being unsuccessful. The respective figure for repeat clutches was 38 % and that for second ones only 20 %. First clutches were destroyed at a similar rate at all nesting stages, but in the repeat and second layings there was a slight, although insignificant, tendency for greater losses during the nestling stage (Table 2).

Among the main four study areas, nest losses were clearly heavier at Taskila and Kuivasjärvi than at Vittasuo and Sanginsuu (Table 2, 2 x 2 contingency table, $p<0.001$). These relationships were not attributable to habitat differences, since areas with the smallest losses are different in nature. Vittasuo is a deciduous habitat and Sanginsuu mainly coniferous. Most of the variation was caused by human predation, which was heaviest at Taskila and Kuivasjärvi. The stoat preyed upon a higher proportion of nests in these two areas of heavier losses.

The stoat was the most important natural enemy of the great tit. Only in one year, 1980, were there no attacks upon tits' nests (Fig. 2). In 1971, when the predation pressure was the highest recorded so far, every third clutch and brood was plundered by the stoat. An average of 7.9 % of the great tit nests were affected by such predation during the period 1969–1980.

The predation by the stoat was apparently connected to some extent to the population cycles of the small rodents (the field vole *Microtus agrestis* and the bank vole *Clethrionomys glareolus*), which are among the main prey species of the stoat (Erlinge 1981). The peak years for the two species taken together in the Oulu area were 1969–1970, 1972–1973 and 1978 (Fig. 2). When the populations of small rodents crashed after the very high peak in the vicinity of Oulu in 1969–1970 (Heikura 1977) the stoats seriously turned to birds nesting in boxes in the season 1971. Two later peaks in populations of small rodents were similarly followed by increasing predation on great tits, but the incidence was delayed by some years and was not as heavy as after the first crash (Fig. 2).

3.2. Losses of eggs and nestlings

During the egg stage losses in clutches containing at least one egg were moderate in the first broods, heaviest in the repeat broods and

Table 2. Numbers and proportions of great tit nests destroyed at different nesting stages at 4 separate areas and all areas combined during 1969–1980.

	Clutches studied	Destroyed during							
		laying		incubation		feeding nestlings		total	
	n	n	%	n	%	n	%	n	%
First clutches									
Taskila	264	35	13	20	8	33	12	88	33
Kuivasjärvi	128	26	20	18	14	11	9	55	43
Vittasuo	68	3	4	6	9	6	9	15	22
Sanginsuu	193	21	11	17	9	15	8	53	28
All areas	942	104	11	87	9	88	9	279	30
Repeat clutches									
Taskila	59	9	15	5	8	9	15	23	39
Kuivasjärvi	31	5	16	6	19	6	19	17	55
Vittasuo	8	1	12	0	0	1	12	2	25
Sanginsuu	29	0	0	3	10	1	3	4	14
All areas	168	20	12	17	10	27	16	64	38
Second clutches									
Taskila	18	0	0	1	6	3	17	4	22
Kuivasjärvi	10	0	0	0	0	0	0	0	0
Vittasuo	9	1	11	0	0	1	11	2	22
Sanginsuu	31	2	6	1	3	2	6	5	16
All areas	92	4	4	4	4	10	11	18	20

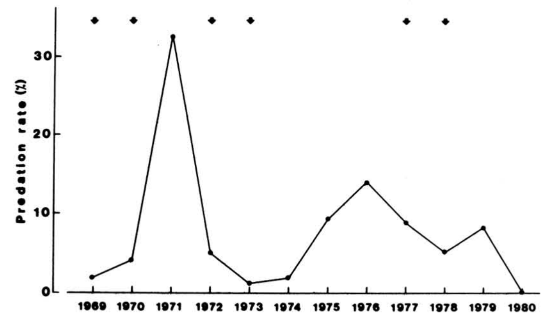

Fig. 2. Annual fluctuations in the percentage of great tit nests preyed upon by the stoat between 1969 and 1980. Arrows denote peak years for the small rodents, the bank vole and field vole. Small rodent data from Heikura & Lindgren 1979, Viro 1974, 1979, Kalevi Heikura, Seppo Sulkava and Pirkko Viro pers. comm.

lightest in the second broods (Table 3), the difference being significant (χ^2-test, $p<0.001$). The most important cause of failures in the first and repeat clutches was predation, whereas this accounted for a minor fraction of the second clutches. Man was the most severe predator in the case of the first clutches. This human interference also included disturbances caused by the nest checks. Stoats were the most common cause of predation in the repeat clutches. The red squirrel *Sciurus europaeus,* the cat *Felis domestica* and the great spotted woodpecker *Dendrocopos major* destroyed only 4 clutches altogether.

The wryneck, *Jynx torquilla,* the pied flycatcher, *Ficedula hypoleuca,* and the starling, *Sturnus vulgaris,* competed with the great tits over boxes, especially at the beginning of the breeding season. When laying by the great tit was delayed due to the cold spring, competition with the pied flycatcher caused most of the losses observed (see also Slagsvold 1976).

Table 3. Losses of eggs and nestlings during 1960–1980 in first, repeat and second clutches of the great tit

	First		Repeat		Second	
	n	%	*n*	%	*n*	%
Egg stage						
Eggs laid	7995	100	1128	100	499	100
Losses						
disappeared	5	0.1	-	-	-	-
unhatched	390	4.9	71	6.3	53	10.6
deserted	220	2.8	37	3.3	26	5.2
competition	133	1.7	7	0.6	-	-
predation	1086	13.6	205	18.2	13	2.6
Total	1838	23.0	320	28.4	92	18.4
Nestling stage						
Young hatched	6157	77.0	808	71.6	407	81.6
Losses						
starvation	985	12.3	172	15.2	51	10.2
predation	402	5,0	82	7.3	6	1.2
deserted	111	1.4	-	-	13	2.6
other reasons	279	3.5	40	3.5	9	1.8
Total	1777	22.2	294	26.1	79	15.8
Number fledged	4380	54.8	514	45.6	328	65.7
Number of nests	857		133		68	

Of the nest desertions, some were apparently caused after the death of the female and others after disturbance of the nest by a predator, for example. In four extraordinary cases a box with an uncompleted clutch was taken over by a bumblebee, *Bombus* spp., forcing the tits to move to another box.

Unhatched eggs made up 5 % of the egg failures in the first clutches, 6 % in the repeat clutches and 11 % in the second clutches. These figures are slightly too small, since they include material where some of the eggs were destroyed and their hatchability was not tested. Exclusion of the eggs lost through desertion, disappearance and predation gave an unbiased proportion for unhatched eggs of 5.9 % in the first clutches, 8.2 % in the repeat clutches and 11.5 % in the second clutches. Hence both of these calculations resulted in an increasing number of unhatched eggs the later the clutch is laid.

Egg disappearance during incubation was negligible in all three groups of clutches.

The hatching success calculated by taking all egg losses into account was higher in the first and second clutches than in the repeat ones (Table 3, χ^2-test, $p<0.001$).

Starvation accounted for over half of the total nestling mortality in all the broods (Table 3), but seemed to be more important in the first and repeat broods than in the second ones.

Predation was not as heavy during the nestling stage as during the egg stage (Table 3). This is attributable mostly to predation by man, which decreased as the season advanced (9 % during the egg stage and 2 % during the nestling stage in the first broods). Correspondingly, the figure for stoat predation stayed the same, 3 %. The viper, *Vipera berus,* apparently caused the death of all the nestlings in one brood (Ojanen & Orell 1980).

Desertions were rare (1.4 % of all broods), and were probably caused mostly by the death of the parents, or disturbances, e.g. by man at the time when the chicks were young (c. 0–5 days old).

The heading 'other reasons' included cases in which the nestlings had obviously died of some illness, deaths caused by temporary abandonment and deaths following the disappearance of one parent where the other could not feed all the nestlings.

71.1 % of young which hatched in first broods were alive at fledging, 63.6 % of those in repeat broods and 80.6 % in second broods. 54.8 % of all eggs laid in the first clutches produced fledglings, 45.6 % in the repeat clutches and 65.7 % in the second clutches. Deletion of human predation resulted in hatching and fledging success rates of 85.3 and 61.9 % in the first broods, 77.3 and 50.2 % in the repeat broods and 82.6 and 67.4 % in the second broods.

3.3. Density-dependent failures during nesting

Mortality is expressed here in terms of the log ratio of the population before and after the particular mortality inspected: mortality = log (initial population/final population). The density refers to the number of breeding pairs per 10 hectares at a given site. The density for all the sites is the number of pairs in a year breeding in the area of all sites together. Density-dependence was tested by plotting the mortality values against the population density. The following parameters were calculated:

a) mortality operating between eggs laid and hatched:

hatching failure = log (eggs laid/young hatched),

b) mortality during the nestling stage:

nestling mortality = log (young hatched/young fledged).

All those first clutches for which the fate of the eggs and young were known exactly were included in these analyses. Repeat and second broods were excluded since they deviated from the first ones in many respects, occurring later in time and involving females having at least one breeding attempt behind them that season and a density of birds in the area which had increased once the young from the first broods had fledged.

Separate analyses were also made for Taskila and Sanginsuu, where the data were sufficient for this.

There was no significant density-dependent mortality during the egg stage at Taskila, Sanginsuu (Fig. 3) or in the combined data of all areas and years (r=0.253, n=12).

Similar results, with no indication of density dependence, were obtained regarding the nestling stage at Taskila, Sanginsuu (Fig. 3) and in the total material (r=0.600, n=12). Data from 1971 deviated clearly from the other years at Taskila due to the high incidence of clutches plundered by the stoat, but no correspondingly heavy predation was evident at Sanginsuu (Fig. 3).

In neither of these analyses was the density dependence masked by human predation, the results obtained when all the clutches and broods with human interference were excluded being similar to the above.

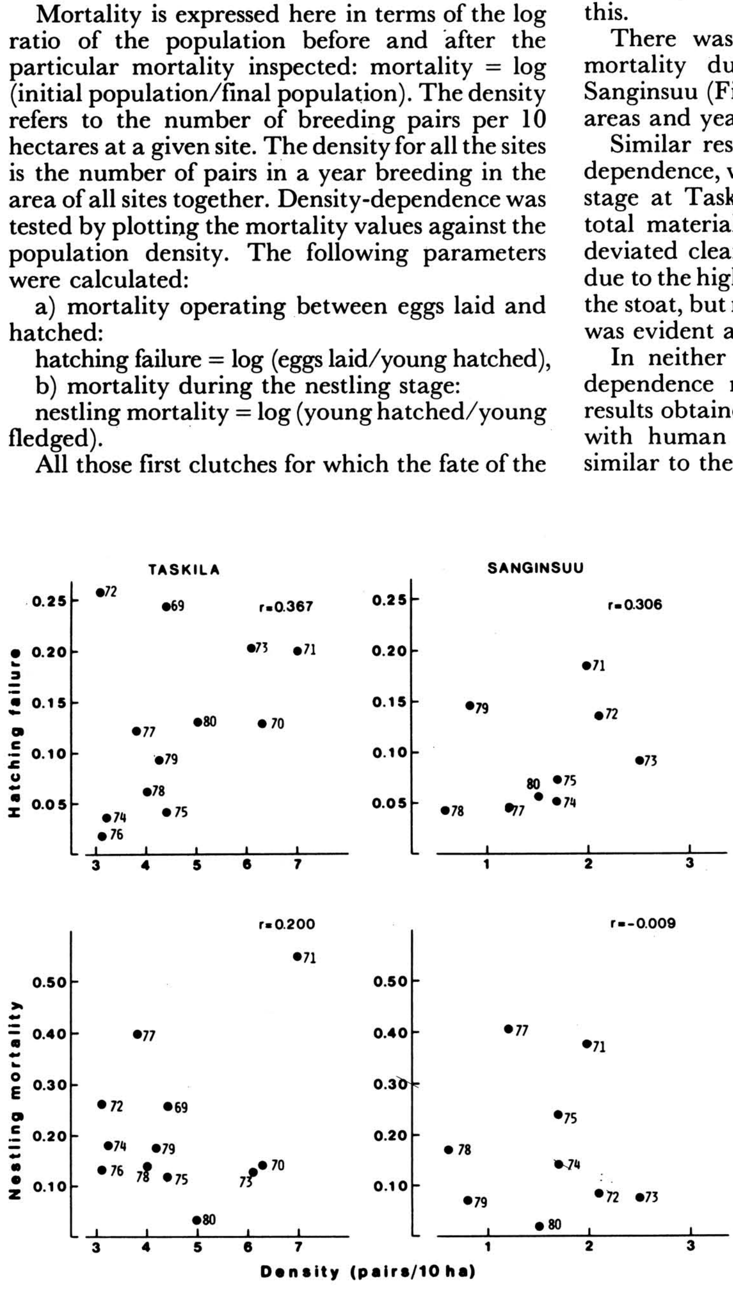

Fig. 3. Relationships between hatching failure, nestling mortality in first clutches and prevailing breeding density in the great tit at Taskila and Sanginsuu. Only clutches for which the fate of eggs and nestlings was known exactly are included. Data from 1976 were limited and are thus omitted from Sanginsuu.

3.4. Weather and nestling mortality

The impact of the weather on nestling success was studied using the ambient temperature (°C) and precipitation (mm) as indicators. The climatic data, which were obtained from the monthly reports of the Meteorological Institute of Finland, comprised readings taken at Oulu airport. Only the first broods were included in the analysis. To avoid the erratic incidence of predation and other disturbances, broods which failed totally were excluded. The analysis was performed by plotting the nestling mortality, log (young hatched/young fledged), against these two weather factors separately.

Weather data for periods of different lengths in late spring and early summer were used. The periods were as follows: May, June, May-June and the nestling period. The latter period comprised the 20 days from the day before the last young hatched until they were 18 days old, the average age at fledging in the Oulu area (Orell & Ojanen 1983a). The temperature during the period in question was expressed as the average of the daily means, the exception being the nestling period, for which it was calculated as follows. The average of the daily means during the 20-day period was computed for each successful brood and these were summed and averaged to obtain the annual mean. The amount of rainfall refers to the sum of the daily precipitation during the period in question. The daily figures for the nestling period were summed over the 20 days and then the average of these sums was computed to obtain the annual mean.

There were negative correlations between mortality and temperature at Taskila and Sanginsuu and in the data for all areas (Table 4), but only the long period (May-June) produced a significant relationship, indicating that the nestlings from the first broods managed well when it was warm during late spring and early summer (Fig. 4). The nestling mortality correlated negatively with the amount of rainfall, but none of the periods gave significant coefficients (Table 4). This result would mean that mortality among the nestlings was lower when there was a lot of rain. Since these climatic variables showed over 10 % common variation in many cases, partial correlation coefficients were calculated to study the influence of one factor when the other was kept constant. As can be seen in Table 4, temperature still remained the most important factor explaining the annual variation in mortality. The partial correlation coefficients for rainfall appeared to be positive, but usually not significantly so. Hence no significant relationship can be said to exist here between mortality and rainfall.

Furthermore 1977, a year with a high number of nestling deaths, was selected for detailed analysis of the impact of the precipitation on nestling mortality. No dependence between mortality and rainfall was found, however.

3.5. Mortality and age of the nestlings

In order to avoid the erratic incidence of predation, only successful broods were selected for this analysis. The data were obtained from Taskila and Kuivasjärvi, where a number of broods were followed daily, or at least frequently enough to permit such an analysis.

Table 4. Correlation coefficients between ambient temperature (°C), rainfall (mm) and nestling mortality in successful first broods of the great tit.

Period	Number of years	Linear correlation (r)		Partial correlation (r_p)	
		Average temp.	Rainfall	Average temp.	Rainfall
Taskila					
May-June	12	-0.705*	-0.095	-0.717*	0.207
June	12	-0.474	-0.243	-0.446	-0.166
nestling period[1]	12	-0.411	-0.087	-0.403	0.019
Sanginsuu[2]					
May-June	9	-0.907***	-0.054	-0.970***	0.819*
June	9	-0.668*	-0.271	-0.636	-0.065
nestling period	9	-0.579	0.127	-0.570	-0.003
Combined area					
May-June	12	-0.763**	-0.194	-0.755**	0.096
June	12	-0.571	-0.350	-0.543	-0.287
nestling period	12	-0.380	-0.019	-0.380	0.002

Note: 1) The average temperature and amount of rainfall were calculated for each brood during the nestling period (from one day before the last young hatched until the day the young were 18 days old = 20 day period) and then averaged over all broods in the year.

2) The year 1976 was excluded because of the small number of broods for which the exact number of young hatched and fledged was known.

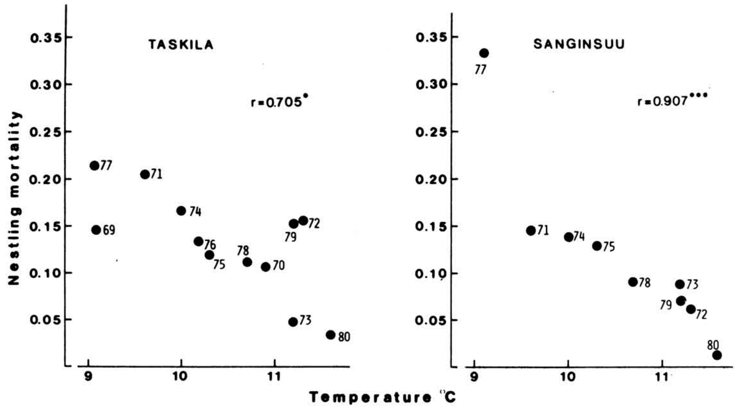

Fig. 4. Relationship between nestling mortality in successful first broods and ambient temperature during the period May-June (see section 3.4.). Other explanations as in Fig. 3.

More deaths among the first broods occurred at the beginning of the nestling period (χ^2-test, $p<0.05$) than later on (Table 5). Some deaths just after hatching were obviously not caused by starvation but by some other factors. According to our experience however, most of the young dying in the first few days after hatching were late hatchers and were thus unable to compete with their older siblings under poor feeding conditions and succumbed in a few days. The deaths recorded after the age of approx. 4 days were obviously all caused by starvation, many occurring just at the time of rapid growth, i.e. from 4 to 9 days of age, when energy requirements are heaviest (van Balen 1973). A high frequency of deaths was also found at ages of 10-15 days, suggesting that starvation likewise played a role near the fledging date.

In the repeat and second broods deaths occurred with the same frequency among the young and old nestlings, indicating that starvation was similarly the cause in late broods at all of the nestling stages.

Table 5. Mortality and age of great tit nestlings at Taskila and Kuivasjärvi.

Age (days)	Deaths *n*	%	Deaths per 100 hatched
First clutches			
0-4	48	37	8.8
5-9	28	22	5.1
10-14	24	18	4.4
15-19	30	23	5.5
Total			23.9
Repeat and second clutches			
0-9	10	48	12.3
10-19	11	52	12.8
Total			25.1

3.6. Seasonal variation in nestling success

There was a significant heterogeneity in the nestling success according to the hatching periods in the first and second broods (Table 6, χ^2-test, $p<0.001$) but it was not found in the second broods. In the first broods this was caused by high success in broods hatched during the period May 31 — June 9 and low success in broods hatched 20 days later. In the repeat broods the heterogeneity was caused by high success in the earliest broods.

The overall nestling success was high in the first broods, lower in the repeat broods and high again in the second broods (Table 7), although the last-mentioned feature was partly the outcome of the fact that second clutches are laid only in favourable seasons (Orell & Ojanen 1983a), so that the young in these broods experience better conditions on average than those in the first and repeat broods.

Calculation of the nestling success separately for those years with second breedings altered this picture (Table 7). Then the success of the first broods was higher on average (83.6 %) than in the years with no second breedings (72.5 %, Table 7), although even in such cases the nestling success of

Table 6. Seasonal trends in nestling success in first, repeat and second broods in which at least one young fledged.

Hatching period	First broods Hatched	First broods Percent fledged	Repeat broods Hatched	Repeat broods Percent fledged	Second broods Hatched	Second broods Percent fledged
May 21-30	51	72.5	-	-	-	-
May 31-June 9	2035	82.6	-	-	-	-
June 10-19	3185	79.1	134	91.8	-	-
June 20-30	216	63.4	247	74.5	-	-
July 1-10	16	75.0	195	72.3	8	(87.5)
July 11-20	-	-	88	65.9	197	87.3
July 21-30	-	-	9	(88.9)	168	85.1
July 31-Aug. 9	-	-	-	-	6	(100.0)

Note: Figures in parenthesis are based on less than 10 nestlings.

the females which produced only one brood was significantly lower than that of the females producing a second brood (χ^2-test, $p<0.05$). The females with two successful broods in the same season managed equally well with both breeding attempts.

It is also worth considering whether a female or pair rearing two broods a season had a smaller number of young in the first brood than did those with only one brood altogether, thus being in better condition for a second breeding. This was not so, however, for the former group even tended to rear more young than the latter one (Table 7). These findings are the opposite of those of Kluyver (1963) for Dutch great tits, among which second breeding was more common when the pair reared a small number of fledglings during first breeding.

In those years in which second breedings occurred, the overall size of the first broods at fledging was larger (mean 7.95 young) than in years when they were not found (6.05 young). This also suggests that the years with second breedings were more favourable on average.

Partitioning of the successful repeat breedings into three categories according to the stage at which the corresponding first brood failed produced some interesting results. Success was low when the first breeding failed at either the laying or the nestling stage (72.3 %, 23 broods, 64.9 %, 5 broods respectively) but clearly higher after failure at the incubation stage (83.0 %, 19 broods). These results are in accordance with the energy requirements of the female at the various nesting stages. Laying and feeding are very costly periods compared with incubation (Ricklefs 1974, Ettinger & King 1980), which can be accomplished close to the level of adult resting metabolism (Mertens 1977, Gessman & Findell 1979). Thus when the female loses her clutch during the laying or feeding stage she is unable to muster her body resources to the level required to support adequately the new breeding attempt. But when desertion occurs at the incubation stage she can apparently recover sufficiently to make a successful new attempt.

Table 7. Nestling success and average brood size in successful first, repeat and second broods.

	Broods	Eggs hatched	Percent fledged	Brood size at fledging	
				mean	*SD*
First broods					
All years	595	5503	79.7	7.37	2.33
Years[1] with successful second breedings	349	3317	83.6	7.95	2.36
— females having first brood only	282	2690	82.9	7.91	2.36
— females with successful second 3brood[2]	57[3]	524	87.2	8.02	2.23
Years with no second breedings	85	709	72.5	6.05	1.98
Second broods	55[3]	379	86.8	5.96	1.86
Repeat broods					
All years	80	673	76.4	6.42	2.39
Years with successful second breedings	50	498	68.1	6.78	2.60

Note: 1) 1971–1973, 1975, 1979–1980. Data for the years 1970 and 1974 are excluded because the exact number of eggs or fledglings in second nestings was not ascertained.

2) 10 females failing with their second breeding attempt are not included.

3) The numbers of broods differ from each other because there were 2 successful second broods for which the exact number of fledglings was not know.

3.7. Habitat and nestling success

The success among first broods was the same at Vittasuo, Kuivasjärvi and Sansinguu, exceeding 80 %, but was significantly lower at Taskila (Table 8, χ^2-test, $p<0.05$). Despite the small differences between the areas, the predictability of the environment is not good in any of them, as is seen when inspecting the annual variations in nestling success. The lowest annual success rate was recorded at Taskila (61.2 %) and the highest at Sanginsuu (96.7 %). The coefficient of variation, calculated from the annual percentages, was rather high at all the sites, 12.8 % at Taskila, 13.5 % at Vittasuo, 17.9 % at Sanginsuu, but exceptionally high at Kuivasjärvi, 34.8 %. This, however, is due to two years with small number of nests and a very low survival rate for the nestlings. Hence habitat quality is perhaps only of minor importance for nestling success, and all habitats at the latitude of Oulu are quite unpredictable for great tits. The same picture of habitat unpredictability appeared from the figures for repeat and second broods. The minor differences were not significant, even though the survival rate in second broods was somewhat higher than for first or repeat broods.

3.8. Brood size and nestling success

There was a significant heterogeneity in the nestling success according to the initial brood size in the first and repeat broods (Table 9, χ^2-test, $p<0.001$), but not in the second broods. The decrease in the success when the initial brood size increased is apparent in first broods. The regression analysis showed a decrease in the success by 1.8 %-units ($p<0.01$) when the initial size increased by one chick. In the repeat broods the heterogeneity was caused by high success in broods of 2–6 and low success in broods of 9. The regression analysis yielded a decrease in the

Table 8. Nestling success at four sites in the Oulu area. Only successful broods are included.

Area	Years	Hatched *n*	Fledged *n*	Success %	Number fledged per brood
First broods					
Vittasuo	1971-80	456	374	82.0	8.13
Taskila	1969-80	1459	1115	76.4	6.56
Kuivasjärvi	1969-80	558	487	87.3	7.85
Sanginsuu	1971-80	1207	965	80.0	7.60
Repeat broods					
Vittasuo	1971-80	51	34	66.7	5.67
Taskila	1969-80	224	173	77.2	5.96
Kuivasjärvi	1969-80	93	69	74.2	6.90
Sanginsuu	1971-80	161	125	77.6	6.58
Second broods					
Vittasuo	1971-80	46	38	82.6	6.33
Taskila	1969-80	53	42	79.2	5.25
Kuivasjärvi	1969-80	42	39	92.8	5.57
Sanginsuu	1971-80	144	126	87.5	6.00

success when the initial brood size increased, but the relationship was not significant.

Although the mortality was proportionately greater in larger first broods, these still produced more fledglings than the smaller ones (Table 9).

Table 9. Nestling survival and initial brood size in successful broods.

	Initial brood size	Young hatched	Percent fledged	Number fledged per brood	Number of broods
First broods					
	2-4	48	97.9	3.53	14
	5	75	85.3	4.27	15
	6	126	84.1	5.05	21
	7	329	90.0	6.30	47
	8	624	81.2	6.50	78
	9	1206	79.4	7.14	134
	10	1310	78.8	7.88	131
	11	1023	77.7	8.55	93
	12	540	75.4	9.04	45
	13-14	222	78.8	10.29	17
Repeat broods					
	2-5	25	92.0	3.28	7
	6	42	83.3	5.00	7
	7	42	76.2	5.33	6
	8	112	77.7	6.21	14
	9	171	69.0	6.21	19
	10	170	79.4	7.94	17
	11-12	111	75.7	8.40	10
Second broods					
	2-5	42	85.7	3.60	10
	6	72	90.3	5.42	12
	7	77	80.5	5.64	11
	8	80	92.5	7.40	10
	9	108	84.2	7.58	12

3.9. Annual variation in nesting success

The annual average number of eggs in successful first broods in all the study areas combined varied between 8.77 and 10.81 (Fig. 5, average of the annual means 9.81±0.72 (*SD*)). The corresponding average for all the completed first clutches was 9.82 (Orell & Ojanen 1983b). These results show that there was no selective mortality among first clutches. The average number of unhatched eggs varied between 0.21 and 1.06 (Fig. 5, average 0.72±0.25). The average number of dead young showed a somewhat larger range, between 0.47 and 3.57 (average 2.0±0.78).

The years with the largest broods at fledging were 1973, 1975 and 1980, while the most unsuccessful were 1971 and 1977 (Fig. 5). In 1980, the year with the highest success, 94.9 % of eggs hatched producing fledglings; this was the only year in which the number of young roughly corresponded to the number of eggs laid. Similarly, in 1973 and 1975, when broods were large, the nestling success remained below 90 %, at 86 and 81 %, respectively. Also the years 1978 and 1979 saw success rates of over 80 %, being 83 and 80 %, respectively. The same picture appeared when the areas were studied separately.

3.10. Reproductive rate

The number of young fledged from all broods in a year was divided by the number of breeding pairs to obtain the productivity. When a pair lost

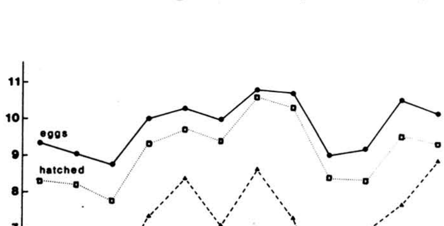

Fig. 5. Annual fluctuation in the average number of eggs, young hatched and fledglings in successful first clutches at all the sites in the Oulu area during 1969-1980.

Table 10. Annual variation in reproductive rate (young/breeding pair) in the great tit in the Oulu area during 1969–1980. Productivity was not known for 13 pairs in 1970 and 2 pairs in 1975.

		1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	Total
Reproductive rate		5.42	5.38	2.75	5.78	7.53	6.50	7.08	5.90	3.14	5.74	6.88	10.26	6.09
Number of pairs		41	83	129	101	128	99	93	72	58	50	48	74	976
Pairs failed to	*n*	5	11	66	22	19	11	19	12	21	8	7	5	206
reproduce	%	12.2	13.2	51.2	21.8	14.8	11.1	20.4	16.7	36.2	16.0	14.6	6.8	21.1

its first or repeat brood and was no longer seen in the area its productivity was estimated as zero, even though there is a small possibility that some of these birds reared successfully outside the study area.

Altogether 991 great tit pairs were noted in the present areas during the 12 years, 34 of which had made their first breeding attempt outside (see Orell & Ojanen 1983a). These immigrants amounted to 3.4 % of all pairs.

The average reproductive rate of the 976 pairs with a known outcome of breeding was 6.1 fledglings (Table 10). Unsuccessful cases amounted to 20 % of all pairs breeding. The result in 1971 was exceptionally poor, caused by heavy predation by the stoat. In a number of cases the female was also lost, which in turn lowered the population available for repeat breeding. The most pronounced productivity was seen in 1980, when it exceeded 10 young per pair. This was partly caused by the high frequency of second breedings. The pronounced annual variation in the reproductive rate was caused together with the success of first and repeat breedings by the proportion of second breedings, since none were recorded in 3 of the 12 years.

In order to analyse the contribution of population size to the reproductive rate, the number of fledged young was plotted against the breeding density. Separate analyses were run for Taskila, Sanginsuu and all areas combined.

The correlation coefficients between reproductive rate and breeding density were negative for Taskila and positive for Sanginsuu, but none of these were significant. The correlation coefficient for all areas combined was zero. Hence breeding density scarcely contributed at all to the number of fledged young in the population in the Oulu area.

3.11. Mortality during the non-breeding season and population density

The same procedure as above (section 3.3.) was used to test whether the mortality noted between one summer population and the subsequent breeding population was density-dependent. The initial population consisted of the number of fledged young and the number of adults in the area. The final population was the number attempting to breed the next year (see also Lack 1966, Krebs 1970, Fretwell 1972). The model presupposes that the decrease in population size is attributable to deaths and emigration of individual birds born inside the area. On the other hand, immigration of birds born outside the area tends to balance out the emigration. Hence the mortality outside the breeding season was:

log (summer population/next breeding population).

The density-dependence was analysed by plotting the mortality against the summer population. The corresponding figures for the combined area were the number of individuals per 10 hectares, since the total area studied varied from one year to the next.

For both Taskila and Sanginsuu (Fig. 6) and for the combined area there was a significant positive correlation between mortality and population size during the preceding summer (r=0.599, n=12, p<0.001). At Taskila 1970 and 1980, with a high density in summer but low subsequent mortality (Fig. 6), deviated from the other years. A high breeding density was also a feature of 1970, but 1980 showed only a moderate one (6.3 and 5.0 pairs/10 ha, respectively, see Fig. 3), while the following years, 1971 and 1981, had the highest number of breeding pairs at Taskila so far (7.0 and 9.0 pairs/10 ha, respectively).

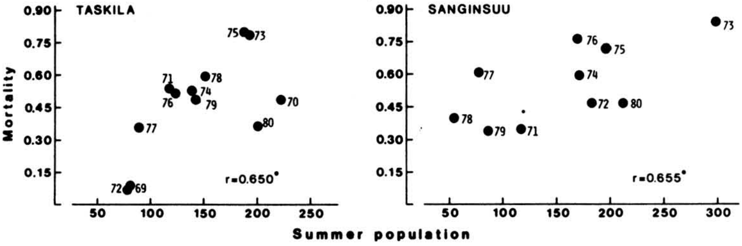

Fig. 6. Relationship between mortality during the non-breeding season and the initial summer population at Taskila and Sanginsuu (see section 3.9). The numerals refer to the first of each pair of years.

4. Discussion

4.1. Nest failures

The number of unsuccessful great tit broods in the Oulu area was roughly the same as observed in investigations from further south (Table 11). Only reports from central Sweden give a somewhat exceptional picture (Johansson 1972, 1974). Presenting no data, he stated that desertion and nest losses in the great tit were quite small in the long term study.

According to the literature causes for failures are variable. Human disturbance has been reported as a cause by many researchers (Gibb 1950, Lack 1950, 1966, Kluyver 1951, Krebs 1970, Larsen 1974, Balat 1976, Kondelka 1978), but no exact figures are given. The nest checks themselves are also involved in nesting failures, especially since capturing the female may cause desertion (Pinowski et al. 1972, Berndt 1974, Larsen 1974, own observations). Great tit parents have been captured in most of the long-term studies: Holland (Kluyver 1951, van Balen 1973), England (Perrins 1965, Lack 1966, Perrins & Moss 1974), West Germany (Winkel 1975), southwestern Finland (von Haartman 1969) and Belgium (Dhondt & Eyckerman 1980) and this may have caused desertion, as was the case in the Oulu area.

The material of which the box is made, the size of the entrance and any special constructions to prevent predators from entering the box will naturally influence the rate of predation (Delmee et al. 1972, Perrins 1979). After human beings, the mustelids are the most important predators on great tits during breeding. Kluyver (1951) attributed losses to plundering by the weasel (*Mustela nivalis*), and also the pine marten (*Martes martes*). Delmee et al. (1972) named the weasel as one of the predators on tits, but the main mammalian predator in southern Belgium was the pine marten. In southern Moravia the most frequent losses were caused by this species too, the weasel being rare and unimportant as a predator (Balat 1976). On the other hand, in the district of Karviná the stoat and the weasel caused most losses (Kondelka 1978). In a Kentish oakwood the weasel preyed upon great tit and blue tit (*P. caeruleus*) nests in only 2 out of 10 years (Flegg & Cox 1975). Larsen (1974) assumed that 6.4 % of the nests of the great tit had been plundered by the weasel in Mid-Funen, Denmark, a rate somewhat lower than that recorded in the Oulu area. He also gave similar figures for the blue tit and the coal tit (*P. ater*), but the marsh tit (*P. palustris*) suffered less, only 3.2 % of its nests being attacked.

In Wytham Wood, near Oxford, the most important cause of losses has been the weasel (Lack 1955, 1958, 1966, Perrins 1965, 1979, Dunn 1977), and these losses accounted for much higher figures than in Mid-Funen or Oulu, an average of 23.3 % of the great tit nests being subject of predation in 1947–1975 (Dunn 1977). The other tit species also suffered from high predation pressure in this forest (Dunn 1977). The yearly figures for the great tit varied from 0 to 50 % of all nests. Although the stoat is also found in Wytham Wood, it has been seen entering a box only once, and the species is recorded as an unimportant predator on tits (Dunn 1977). The prevailing rodent density was relevant in Wytham Wood in the sense that at low densities the tits suffered from increased predation. An increase in tit density also promoted predation by the weasel.

Table 11. Percentage of nest failures during incubation, nestling and all nesting stages in some populations of the great tit.

Population	Incubation stage	Nestling stage	All stages	Source
Fihland				
Oulu	9.0	10.4	30.0	This study
Lemsjöholm	-	-	27	von Haartman 1969
Denmark				
Funen	6.6	19.6	-	Larsen 1974
Holland				
Oranje Nassau Oord	-	-	26.3	Kluyver 1951
Czechoslovakia				
Karviná	11.7	11.9	-	Kondelka 1978
England				
Northward Hill	-	-	36	Flegg & Cox 1975

Although the pygmy weasel (*Mustela rixosa*) and the stoat are common mustelids over whole of Finland (Siivonen 1977), there is no evidence that the former could be responsible for nesting failures in Oulu. Hence stoat consumes birds in nest boxes as a supplementary source of food in the years when small rodent densities are low, in the same way as the weasel in Wytham Wood.

Ricklefs (1969) suggests that predation pressure becomes lower the farther north one moves, and the results of Järvinen (1980) from Kilpisjärvi support this. The rates of predation by the weasel in Denmark and northern Finland are clearly lower than in southern England, and one might regard this as supporting evidence for Ricklefs' hypothesis, but we believe that it is only a question of an extraordinary situation in Oxford, where weasels attacked so many tits' nests (see also Dunn 1977). Perrins (1979) himself points out that predation by the weasel on the Continent is not as strong as it is in Wytham Wood, and the low rate of weasel predation on Northward Hill (Flegg & Cox 1975) also suggests an extraordinary situation in Wytham Wood.

The sparrowhawk (*Accipiter nisus*) appears to be an important predator on adult great tits and blue tits during breeding. After its return to Wytham Wood in 1973 it caused large nest losses (Geer

1978, Perrins & Geer 1980). The sparrowhawk nests near Taskila and in 1976 and 1977 even inside the nestbox area, but no increase in the numbers of abandoned or totally destroyed great tit broods was found in the part of Taskila where the hawks' nest was situated. A check on the remains of prey species found in 1977 near the hawks' nest revealed that its diet included many passerine birds and also waders, but no remains of the great tit were found. Hence it seems that the species is not as important predator upon great tits in the Oulu area as it is in Wytham Wood, where it may take 20-25 % of the population during the breeding season (Geer 1978).

Other animals are also known to cause nesting failures in tits, but these are of minor importance (Perrins 1979).

4.2. Hatching success

The following values are reported for the hatchability of the eggs of the great tit in different parts of its range: 76.6 % (Mayer 1961), 87.1 % (Larsen 1974), 77.4 % (Balat 1976), 66.8 % (Flegg & Cox 1975) and 79.6 % (Kondelka 1978). Perrins & Moss (1974) observed 87.7 % of eggs in successful first clutches to hatch in Wytham Wood, and the corresponding figure for southern Sweden was 94.0 % (Johansson 1972, 1974, 1977). The results from the Oulu area fit well within these limits: 76.6 % for all clutches and 94.0 % for successful first clutches. The hatching success of other hole-nesting passerines breeding north of Oulu, in Finnish Lapland, is reported to be 89.1 % (Pulliainen 1977) and 81.2 % (Järvinen 1978) in the redstart (*Phoenicurus phoenicurus*), 84.2 % (Pulliainen 1977) and 80.9 % (Järvinen 1978) in the pied flycatcher (*Ficedula hypoleuca*) and 85.7 % (Pulliainen 1977) and 73.9 % (Järvinen 1982b) in the Siberian tit (*P. cinctus*). These figures do not include clutches which suffered human distur bance. The hatchability rate of 85 % without human interference recorded for the great tit in the Oulu area is in good agreement with these figures.

Proportions of addled or infertile eggs or eggs with dead embryos for all clutches amounted to c. 5 % (Lack 1966), 7 % (Bumerl 1970), 4.7 % (Dyck et al. 1972), 5.4 % (Larsen 1974, recalculated from his Table 6), 10.7 % (Balat 1976) and 9.1 % (Kondelka 1978, recalculated from his Table 3). The corresponding figure in the Oulu area was 6.5 %, which is in good agreement with those obtained further south.

Thus, there is hardly any distinguishable trend in the hatchability of eggs in different parts of the range of the great tit. In this respect great tits are well adapted to a northern environment.

4.3. Nestling success

Adaptation in the time of breeding

Although breeding success in second broods was higher than in first and repeat ones in the Oulu area (Table 3), it is advantageous to breed early. Breeding late is possible only in years with a warm summer, and in 3 of the 12 years no second breedings were observed. The parents breeding twice in a season were those who bred earliest in the spring (Orell & Ojanen 1983a) and reared their first brood with somewhat better success than those which did not breed twice. The latter followed from the fact that the first broods, hatched between May 31 and June 9 suffered less than the late broods from nestling mortality (Table 6). The fact that repeat breeding is the least profitable of the different breeding types also supports this interpretation, although admittedly the parents are in any case already under stress (see e.g. Williams 1966) due to their unsuccessful first breeding attempt.

In northern areas, where the season for breeding is short, early breeding is especially advantageous. If the early attempt fails parents still have time for repeat breeding. Since the postnuptial and postjuvenile moults are costly phases in the life cycle, it is also advantageous to undergo these at a suitable season. These phases limit the time for late breeders, although great tits in the Oulu area are able to overlap breeding and moulting to some extent (Orell & Ojanen 1980), a pattern not known further south (e.g. Dhondt 1981). The postnuptial moult in the great tit population in Oulu is over by the first days of October (Orell & Ojanen 1980). Juveniles fledged from late broods may have difficulties in moulting before the winter. When capturing tits in autumn we have recorded juveniles which were still moulting in mid-October, during the time of the first snow. If these did not finish their moult before the winter they would not survive. Hence, late breeding represents a risk for the parents, and especially for their descendants, and that is why such breeding attempts are seen only rarely in the most favourable seasons at the latitude of Oulu.

Although it is important to breed early in northern areas, it is disadvantageous to breed too early, since sudden cold spells may cause heavy losses (e.g. Pulliainen 1978, Ojanen 1979).

Clutch adjustment and brood reduction strategies

Lack (1947-48) developed the theory that the clutch size is adapted to the highest number of young the parents can successfully raise. O'Connor (1978) extended this hypothesis to three different breeding strategies in birds based on the predictability and stability of food resources for nestlings. He argued that the availability of food for the nestlings may or may not be predictable at the time of egg-laying, and may or may not fluctuate during the nestling period. When both of these are predictable and stable prior clutch size adjustment is appropriate. When they are unpredictable during egg laying but stable during the nestling stage, brood reduction is appropriate; i.e. starvation of the smallest nestlings, the last to hatch, proceeds until the size of the brood matches the ability of the parents to feed them. The third strategy, resource storage, is not available to tits.

According to O'Connor (1978) the typical representative of the clutch adjustment strategy is the blue tit, with negligible mortality among its young and low variation in egg size within the clutch (*CV* = 6.8 %). The house sparrow *Passer domesticus* with a high rate of starvation is a typical brood reduction strategist (O'Connor 1978). In this case a hierarchy is achieved between the siblings by marked hatching asynchrony.

O'Connor (1978), following Lack (1966), stated that early broods of the great tit are hatched from adjusted clutches while late broods encounter declining food resources and therefore show brood reduction.

Clutch adjustment seems to be the rule for great tits living in oak woods as the nestling success in all of these populations exceeded 90 %, i.e. the number of eggs laid is practically equal to the number of young fledged (Table 12). For late broods, brood reduction is the strategy, and the rate of nestling starvation is rather high (Table 12, see also Gibb 1950, Lack 1955, 1958, 1966, Lack et al. 1957, Perrins 1965, van Balen 1973). The only exceptions among the late broods are those described in an oak wood at Tärnsjö, Sweden, where nestling mortality was negligible (Table 12). In the other habitats nestling mortality appeared to be much higher even in the first broods (Table 12), supporting the brood reduction strategy rather than clutch adjustment. The brood reduction strategy is perhaps valid for Norwegian great tits because of a high asynchrony in hatching, attained by asynchronous incubation (Haftorn 1981).

The annual differences in nestling success proved to be large in Oulu, the coefficient of variation being in the range 13-20 % at Taskila, Sanginsuu and Vittasuo, and as high as 35 % at Kuivasjärvi. The corresponding figure in Dutch oak woods was c. 2.5 % and that in pinewoods, with a lower success rate, 8.7-17.8 % (van Balen 1973). Hence the environment in Oulu may be said to be more unpredictable for great tits than the best habitats further south.

Royama (1966), confirmed by van Balen (1973), showed that food requirements increased from small to large clutches, although the food consumption per chick in broods under natural temperature conditions varied inversely with the number of young in the brood (Royama 1966, Mertens 1969, van Balen 1973). O'Connor (1975) showed that the parental feeding rate increases rapidly with brood size when the young are small. Accordingly the newly hatched young of large broods are fed more intensively than they would otherwise be. Gibb (1950) and Kluyver (1950), however, showed that the parents are unable to increase the rate of feeding over the whole nestling stage in proportion to the increase in the number of chicks. From these facts one is tempted to predict increased nestling mortality due to starvation or a decrease in nestling weight with increasing numbers of young in the brood.

In English habitats nestling survival did not vary according to clutch size (Lack 1950), apart from one exceptional year (1961) in which high breeding density probably caused a local food shortage in Marley Wood (Perrins 1965). A large number of nestlings in the nest was only reflected in a lower fledging weight of young than with small broods (Lack et al. 1957, Perrins 1965, Lack 1966).

Kluyver (1951) found that nestling mortality in Oranje Nassau Oord was not dependent on clutch size, except for a slightly higher mortality in larger broods. Later van Balen (1973) found no contribution of initial brood size to subsequent nestling mortality in early or late broods in oak or coniferous habitats in Holland. This was true in spite of the fact that the overall nestling mortality was high in coniferous habitats and late broods in oak woods, as summarized in Table 12. In pinewoods near Bzenec in Czechoslovakia, where nestling survival was almost as high as in oak woods (Table 12), survival did not vary according to clutch size (as calculated by the present authors from Balat 1976). In fruit gardens in Czechoslovakia (Kondelka 1978) and in the Oulu area (this study), with a nestling mortality of 20-25 %, survival decreased with increasing initial brood size. Hence starvation was most pronounced in broods with many chicks.

In habitats where nestling mortality is high due to starvation, deaths also occur in high numbers among the older nestlings (c. 10-19 days). This concerns early and late broods in coniferous woods and late broods in oak woods in Holland (van Balen 1973) and populations in fruit gardens in Czechoslovakia (Kondelka 1978) and in Oulu (this study). In localities with low nestling mortality deaths are concentrated among the younger nestlings (c. 0-10 days, van Balen 1973,

Table 12. Nestling success, number of fledged young as a percentage of hatched, for the great tit in some localities in Europe. All except Funen and Möggingen-Radolfzell denote successful broods only.

Locality	Habitat	Broods			Source
		First	Second	All	
Finland					
Vittasuo	mixed decid.[1]	82.0	86.8[5]	80.6	This study
Kuivasjärvi	spruce	87.3		85.8	—"—
Taskila	mixed[2]	76.4		76.6	—"—
Sanginsuu	coniferous	80.0		80.4	—"—
Lemsjöholm	mixed decid.	-	-	80.6	von Haartman 1969
Sweden					
Tärnsjö	oak	98.6	92.1	-	Johansson 1972, 1974, 1977
Denmark					
Funen	mixed decid.	-	-	83.9	Larsen 1974
Holland					
Hoge Veluwe A	pine	70.9[3]	73.2[4]	-	van Balen 1973
Hoenderloo	pine	75	80	-	Kluyver 1951
Oranje Nassau Oord	mixed	79	82	-	—"—
—"—	pine	74	74	-	—"—
Oosterhout	oak	97.9[3]	79.3[4]	-	van Balen 1973
Liesbosh	oak	96.0[3]	80.3[4]	-	—"—
Imbosh	pine	78.5[3]	71.3[4]	-	—"—
Federal Republic of Germany					
Near Lingen[6]	coniferous	68.1	84.3	-	Winkel 1975
Möggingen-Radolfzell[6]	-	-	-	68.5	Zink 1959
Czechoslovakia					
Near Bzenec	pine	-	-	88.6	Balat 1976
Karviná	fruit garden	-	-	77.6	Kondelka 1978
Austria					
Near Linz	deciduous	-	-	87.9	Mayer 1961
England					
Southern part	oak+Marley wood	95	59	-	Lack 1958, 1966
Breckland	Scots pine	62	87	-	—"—
—"—	Corsican pine	60	78	-	—"—
Oxford	gardens	54	-	-	Perrins 1965

1) Mixed deciduous habitat refers to an environment with several deciduous tree species dominant.
2) Mixed habitat contains coniferous trees in large numbers alongside deciduous trees.
3) Early broods.
4) Late broods
5) All sites in the Oulu area
6) Data from one year.
Success exceeding 90 % underlined.

Larsen 1974, Balat 1976).

Daily food consumption increases sharply during the first week of the nestling's life, and remains high from an age of about 8 days until fledging (see van Balen 1973). Hence, not all deaths which take place before this age are necessarily due to starvation, but may arise for some other reason, since the parents are able to respond to the needs of the young chicks (van Balen 1973). It is possible that the parents may adjust their brood size to the prevailing food conditions during hatching. This may be attained by active reduction (Löhrl 1968, Bumerl 1970, Neub 1979), as is supported by the rapid disappearance of young chicks from their nests in Oulu.

There is a clear hatching asynchrony in the great tit in the Oulu area, i.e. the time interval between the hatching of first and last egg in the clutch varied from 1 to 5 days (average 2.1 days, *n*=93). Similar or even more pronounced asynchrony in hatching has been reported, e.g. 1.8 days in Norway (Haftorn 1981), 3.0 days in England (Gibb 1950) and 2.9 days in Western Germany (Neub 1979). According to these data it seems that hatching is more synchronous in northern populations of the great tit, but more studies are needed to verify this statement.

Asynchronous hatching being pronounced especially in late broods, in which incubation starts before the clutch is completed (Gibb 1950, Kluyver 1950, Zink 1959, Winkel 1970, Neub 1979, Haftorn 1981), results in size variation between the newly hatched chicks. Under poor feeding conditions the size differences rapidly increase and the runts die (e.g. Löhrl 1968, Neub 1979). Even in early broods a slight size variation is sufficient to produce runts, and mortality rapidly increases among the last to hatch because of competition for food (Neub 1979). Deaths at an early age may therefore also be caused by starvation, but it is difficult to determine what proportion of all deaths among young chicks this accounts for.

Starvation is the main reason for deaths among the older chicks. Sometimes runts will survive up to fledging time, but die when the parents no longer feed them. Feeding conditions may worsen temporarily during the nestling time (own observations) and size variations may again increase rapidly, causing mortality. A great deal of energy is therefore wasted in rearing chicks for many days before they succumb. This effect is especially pronounced in the large clutches studied in Oulu. The risk of high chick losses is evidently large in unpredictable environments, but large clutches are sometimes profitable since even the runts may survive if feeding conditions improve (Löhrl 1968, Neub 1979, own observation). When there is plenty of food, the last chicks to hatch rapidly achieve the same weight as their older siblings and they may even attain a greater weight than the older ones by the time of fledging (Löhrl 1968, Neub 1979). Thus the last of the young to hatch are not always doomed to death; asynchronous hatching is an efficient mechanism for reducing the brood size to one which can be raised by the parents in conditions of food shortage.

In broods where the runts die, asynchronous hatching results in a shortened breeding period, which has also been implicated as an adaptation to predation or the probability of encountering a period of bad weather (Neub 1979). For open nesters the former explanation may be valid, since such nests are more vulnerable than concealed nests to predators (e.g. Nice 1957). Clark & Wilson (1981) suggested that asynchronous hatching cannot be an adaptation to food shortage and explained it to be a means of avoiding preation. This explanation is too simple, however, since the late broods of tits are no more vulnerable to predation than early ones (Dunn 1977, this study), but it may provide an extra advantage in addition to the benefits gained by the brood reduction mechanisms. Moreover, asynchronous hatching in birds of prey (Newton 1979) cannot be attributed to the avoidance of predation.

Chicks hatching from large eggs are known to grow more rapidly than those from small eggs (Schifferli 1973), so that hatching from large eggs would be advantageous under conditions of unpredictable food resources. Gibb (1950) showed an increasing trend in the egg size within the clutch in English great tits, and Winkel (1970), studying German great tits, suggested that the last-laid egg is larger than the others. No such trends have been found in the Oulu area, and the *CV* for egg size is only 7.6 % (Ojanen et al. 1981). The high nestling mortality in the great tit in the Oulu area is therefore more suggestive of the brood reduction strategy, which is enhanced by hatching asynchrony, but this strategy is not reflected in increased intraclutch variation in egg size.

4.4. Reproductive rate

Geographical variation

In Europe north of the Mediterranean region, the clutch size (first clutches) varies between 8.45 and 11.82 eggs, according to long-term studies at 27 sites (summarized in Orell & Ojanen 1983b). No significant trends are found according to latitude or longitude, however. One important population parameter is productivity, the factor which, together with the annual mortality rate, determines the stability of the population in question. The average brood size in different populations in Europe varied between 5.91 and 11.06 for first nestings and between 4.48 and 7.75 for second nestings (Table 13). The lowest values are not found in the northern areas, but in Belgium. If that study area, Maaltepark, is deleted because it is a park and obviously not very suitable for great tits, the situation remains the same, and what is more important, the values obtained in the Oulu area, although low, do not differ markedly from the others.

The reproductive rate recorded in the Oulu area during 1969–1980 (6.09 fledglings) was the lowest, alongside that in Maaltepark, but still lower values were recorded at different sites in Oulu (Table 13). In the Harz Mountains Zang (1980) found the reproductive rate to be on average 6.71 young in successful pairs at 15 sites combined. In all areas (Table 13) except Moscow, the reproductive rate remained below 10 fledglings. In the Oulu area the low proportion of second broods, and their absence in some years, lowered the total number of fledglings produced. The same effect is more pronounced in Wytham Wood, where second breeding is very unusual (e.g. Perrins 1965, Lack 1966), although the productivity of the first broods there was much higher than in Oulu resulting in a higher reproductive rate.

The coefficients of variation calculated from the annual reproductive rates in the various populations of the great tit studied were as follows:

	CV	Scource
Finland		
Oulu	32.5	This study
Holland		
Hoenderloo	21.2	Kluyver 1951
Oranje Nassau Oord	30.9	—"—
Belgium		
COO	29.2	Dhondt in litt.
Maaltepark	33.5	—"—
Zewergem	27.0	—"—
England		
Marley Wood	25.5	Lack 1966

Table 13. Brood size and reproductive rate in the great tit in some localities in Europe.

Locality	Broods			Reproductive rate	Source
	First	Second	All		
Finland					
Vittasuo	8.13	5.96[1]		6.80	This study
Kuivasjärvi	7.53			4.91	—"—
Taskila	6.56			5.01	—"—
Sanginsuu	7.60			6.99	—"—
Lemsjöholm	-	-	7.67	-	von Haartman 1969
Kirkkonummi	-	-	6.96	6.59	Hildén et al. 1982
Sweden					
Tärnsjö	8.16	6.31[4]	-	9.78[4]	Johansson 1972, 1974, 1977
Denmark					
Funen	7.5	5.9	-	7.6	Larsen 1974
Soviet Union					
Near Moscow	11.06	7.70	-	11.57	Likhachev 1953
Near Rjasan	-	-	9.96	-	Stephan 1961
Holland					
Imbosh	7.29[2]	5.64[3]	-	-	Van Balen 1973
Hoge Veluwe A	6.50[2]	5.64[3]	-	-	—"—
Hoenderloo	-	-	-	9.2	Kluyver 1951
Oranje Nassau Oord	6.98	6.32	-	7.6	—"—
Oosterhout	9.02[2]	5.95[3]	-	-	van Balen 1973
Liesbosh	8.90[2]	6.04[3]	-	-	—"—
Belgium					
Coo	6.42	4.90	5.97	7.49	Dhondt & Eyckerman 1980
Maaltepark	5.91	4.48	5.49	6.27	Dhondt in litt.
Zevergem	7.24	4.78	6.62	7.51	—"—
l 'Entre-Sambre-et-Meuse	-	-	8.2	-	Delmee et al. 1972
Federal Republic of Germany					
Near Lingen	6.48	7.75	-	7.71[5]	Winkel 1975
Czechoslovakia					
Near Bzenec	-	-	7.02	8.02	Balat 1976
Karviná	-	-	6.41	-	Kondelka 1978
Austria					
Near Linz	-	-	8.01	6.9	Mayer 1961, Donner & Mayer 1964
Hungary					
Pilis Mt.	9.56	6.05	-	-	Sasvári in litt.
England					
Northward Hill	-	-	7.8	-	Flegg & Cox 1975
Wytham Wood	8.26	-	-	6.24	Perrins 1965, Lack 1966
Oxford gardens	-	-	7.56	-	Perrins 1965

Note: 1) All areas in Oulu. 2) Early broods.
3) Late broods. 4) Refers to 3 of the 18 years when the productivity for second broods was known.
5) Estimated value.

The annual variation was most striking in the Oulu area, and also high in the Belgian park. In the other populations, especially at Hoenderloo and Marley Wood, the variation was clearly less. This result also supports the idea of environmental unpredictability for the great tit in the Oulu area.

Impact of breeding density

A decrease in fecundity and reproductive rate in the great tit as a function of breeding density has been recorded for some populations from further south (e.g. Kluyver 1951, Lack 1966, Dhondt & Eyckerman 1980). Although most of this variation is explainable by the decrease in clutch size and proportion of second broods as the population density increases, Kluyver (1951) found that the correlation between density and reproductive rate disappeared at densities lower than 4 pairs per 10 ha in Holland.

Dhondt (1977) and Dhondt & Eyckerman (1980) found that the effect of intraspecific and interspecific competition on reproductive output was lower in the great tit than in the blue tit at high densitites of both species. Since the reproductive rate showed a positive correlation with food conditions, they argued that food conditions were affected by intraspecific and interspecific competition, this being most striking in suitable habitats, i.e. in areas with many breeders.

The values obtained near Oulu, implying no impact of breeding density on the reproductive rate, confirm the findings of Kluyver (1951) and Dhondt & Eyckerman (1980) that the effect of density is low or may even vanish when densities become very low. The breeding densities in the Oulu area were usually below 4 pairs/10 ha.

In practice it is only at Taskila that great tit densities higher than this are recorded. Thus, although one might think that the lower limit should be lower in northern areas, where the natural habitats are very different, this does not seem to be so.

Krebs (1970) found that egg mortality increased with increasing breeding density in the Marley population, but nestling mortality remained unaffected. The increase in egg mortality was attributable to increased weasel predation (see also Dunn 1977). On the other hand, O'Connor (1980) did not find any relationship between hatching success and breeding density, but instead the number of young reared decreased as a result of a reduction in clutch size in the great tit recorded in different parts of England.

The only year when there was obviously a connection between the high population density of the great tit and predation by the stoat in Oulu was 1971, as seen previously. On average no connection between population level and breeding success could be found. We therefore conclude that the breeding densitites prevailing in Oulu are too low to contribute much, if anything, to the reproductive output of the great tit.

Impact of weather

Kluyver (1951) found that nestling survival showed a positive correlation with the prevailing ambient temperature during the time when the young were in the nest. Longer periods did not produce significant relationships. He also obtained a positive correlation between mortality and rainfall.

In Denmark, Larsen (1974) obtained a positive correlation between nestling survival and temperature during hatching, but not during other periods, and not with precipitation.

Although we failed to prove it, rainy periods during nestling time evidently increase mortality among young (Heynen according to van Noordwijk et al. 1981b, Hildén et al. 1982). Rain during the daytime is especially important in this respect, because then the parents cannot forage as effectively as they would otherwise be able.

The relationship was different in the Oulu area, where the temperature during May did not predict much of the nestling success of the first broods, nor did that during the nestling time itself, but the combined effect of both of these did do so quite well. The effect of this long-term temperature upon mortality was seen to be especially clear in some exceptional years. June temperatures in 1975 and 1976 were the lowest recorded during the period 1969–1980, and while nestling mortality for the great tit was not related to these temperatures, it did reach only average values. Obviously food was not in short supply during the nestling time, and parents were in good condition to meet the demands of the cool nestling time as a result of the warm weather in May. On the other hand, May featured only moderate temperatures in 1980, but June was exceptionally favourable, resulting in the highest breeding success recorded so far in the Oulu area (see also Järvinen 1982a). The reason why even the temperature during May seems to play an important role in nestling mortality is perhaps partly based on the fact that after a favourable May, parents are in better condition and are therefore able to feed more efficiently.

From the tits' point of view, this kind of situation is unpredictable and the low predictability of the environment is confirmed by the occasional occurrence of cold spells with snow in northern Finland, causing heavy losses (see Pulliainen 1978, Ojanen 1979).

As the success of the first broods contributed much of the total production in the great tit population and as second breeding is most frequent in warm summers (Orell & Ojanen 1983a), the prevailing weather condition is an important factor determining the reproductive output of the populations in northern areas (see also Järvinen 1980). The effect of climatic factors is still more pronounced due to the fact that the density-dependent mortality of eggs and nestlings was low or negligible.

4.5. Population reduction during the non-breeding season

Many researchers have suggested that the population size of the great tit is regulated by density-dependent factors. Kluyver (1966, 1971) showed that the reduction of the numbers of eggs and young in Vlieland, Holland, was compensated for by a higher survival rate among the adults. Thereafter van Balen & Eck (according to Klomp 1980) improved the adult and juvenile survival rates in the same population by removing some of the breeding adults. For English great tits, O'Connor (1980) showed that female survival decreased at a high density, the males being essentially unaffected by the population level.

Another way of regulating population size is the emigration of inferior birds, which are juveniles (e.g. Kluyver 1951, Perrins 1963, 1965, Dhondt & Hublé 1968, Dhondt 1971, 1979, Greenwood et al. 1978, van Balen 1980). Kluyver (1971) showed that high densities induce a higher proportion of young tits to either emigrate or die, and emigration was pronounced at high densities in England (O'Connor 1980).

On the other hand, Krebs (1970), analysing the Marley population, was cautious as to whether even a weak density-dependent mortality existed, and he argued that density-dependent clutch size and hatching success are sufficient for population regulation, a theory supported by Perrins (1971). Fretwell (1972) nevertheless concluded that there was a sigmoidal relationship between prevailing density and mortality during the non-breeding season in the Marley population, in which there would be no apparent density-dependent effect at low and high densities but such an effect would be seen clearly at intermediate densities.

The results obtained in Oulu support the idea of density-dependent regulation, and it is important that the relationship seems to exist even at densities much lower than those recorded in populations further south.

Changes in the numbers of breeding great tits have been shown to be closely correlated with the juvenile recruitment rate, but not significantly with the adult survival rate (Slagsvold 1975, Dhondt & Eyckerman 1980). On the other hand, the juvenile recruitment rate was mainly influenced by the juvenile survival rate and less by the reproductive rate (Slagsvold 1975, Dhondt & Eyckerman 1980). Hence the most important factor regulating the level of the population in the next breeding season is the survival of the young tits (Klomp 1980), a fact already pointed out by Perrins (1965), Lack (1966) and Krebs (1970).

The critical period in the life of a young tit consists of the months after fledging, which is when most of the deaths occur (e.g. Perrins 1963, 1965, Lack 1966, Dhondt 1971, 1979, Kluyver 1971, Frederiksen & Larsen 1980), although winter mortality and spring territorial behaviour also play a role in population regulation (Kluyver 1951, Berndt & Frantzen 1964, Hildén & Koskimies 1969, Dhondt 1971, von Haartman 1971, 1973, Krebs 1971, Perrins 1971, Slagsvold 1975, van Balen 1980, Klomp 1980). Hildén (1978) proposed that three factors are involved in the regulation of population size in the great tit in northern Europe: autumn and spring migrations, winter mortality and territorial behaviour in spring.

We have no data to prove when juvenile mortality is heaviest in Oulu, but in southern Sweden, post-fledging mortality accounted for 88 % of the young during the 11 weeks after fledging (Dhondt 1979). In Funen 78.9 % of the fledged young had died during the first six months (Frederiksen & Larsen 1980). The mortality at Oulu must obviously take place during the same period as in these two populations.

Applying the model of Henny et al. (1970), it is possible to calculate the juvenile survival rate for a stable population from fledging to the next breeding season when the adult survival rate and reproductive rate are known. The equation is as follows: $\bar{m}= (1\text{-}s) / s_0$, where $\bar{m}$ is the production of female fledglings per adult female, s is the adult survival rate and s_0 is that for juveniles. The mortality rates for adult great tit females in the Oulu area calculated by the methods of Lack (1951) and Haldane (1955) were 51.7 and 55.2 % respectively (Orell & Ojanen 1979). Using these values and a reproductive rate of 6.09 young ($=2\bar{m}$) the resulting juvenile survival rates are 17.0 and 18.1 %. Assuming a constant adult mortality rate in the different study areas, the juvenile survival rate is found to vary in the range 20–22 % at Taskila and Kuivasjärvi, but 15–16 % at Sanginsuu and Vittasuo. Most of these values are somewhat lower than that reported earlier (21.9 %, Orell & Ojanen 1979), but this value was evidently a little too high, since it was based on ringed juveniles only, overlooking those escaping from the boxes without being ringed.

Dhondt (1979) estimated the juvenile survival rate in southern Sweden at c. 15 % and Frederiksen & Larsen (1980) calculated the corresponding value for Danish great tits to be 14.3 %. The results indicate that juvenile survival may be somewhat higher in the Oulu area than in southern Scandinavia, or in Holland, where it was 13.2 % (Kluyver 1951). This idea is also supported by the statement of Hildén (1978) that juvenile survival may be higher in Kirkkonummi, southern Finland, than in Oxford, where it was 20–22 % (Bulmer & Perrins 1973). The results are obviously affected by the fact that density-dependent mortality has a more pronounced effect upon higher density populations further south than upon the less dense populations of the north. The high survival rate in Oxford speaks agains this, however, but it may be that great tits in Britain have partly different strategies in this respect, as they do with respect to many other variables.

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