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Breeding biology and population dynamics of the willow tit Parus montanus

Markku Orell & Mikko Ojanen

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The willow tit was studied in 1975–1981 in the Oulu area (65°N, 25°30′E), northern Finland. The data comprised 153 nests of 150 breeding pairs. The tits preferred to nest in areas of spruce bog in holes which they excavated in decaying birches or stumps tied onto tree trunks. Nests in wooden nest boxes filled with decaying wood or sawdust were rare, 6.5 % of the total.

The annual breeding density varied between 0.79 and 1.28 pairs/10 ha (average 1.07). The clutch contained 4–10 eggs (average 7.6). The clutch size decreased by 0.09 eggs per day when the start of laying was delayed. The incubation period varied between 11 and 19 days (average 14.1), and 79 % of the nests were successful. The main predator was the great spotted woodpecker, although the predation pressure was low. The hatching and nestling success was 84 % in all broods and in successful broods 96 % and 91 %, respectively. The nesting success was highest in the largest initial clutches. The breeding density did not contribute to the reproductive output, nor could the density-dependent mortality be verified outside the breeding season. Nestling mortality was high in spring when the May and June temperatures were low. The reproductive output of the population was 5.4 fledglings/breeding pair/season. The willow tit seems to employ the clutch adjustment strategy in the Oulu area in most years. It also invests a great deal of energy in survival as opposed to investment in the current reproductive effort, as can be seen in the fact that it has only one brood per season and the brood is often deserted when conditions deteriorate.

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1. Introduction

Although the genus *Parus* is one of the most extensively studied groups of birds, most of the work has concerned the species which prefer broad-leaved woodlands, the great tit, *Parus major,* and the blue tit, *P. caeruleus.* There are far fewer studies which concentrate on those living in coniferous woodlands.

The willow tit has a range extending over the northern parts of Eurasia (Hartert 1903–22, Snow 1953, 1954, Voous 1960). The North American black-capped chickadee, *P. atricapillus,* is now considered a separate species (Snow 1956, Vaurie 1959, Voous 1960), although this view is not fully accepted (Eck 1979). The many subspecies among the willow tits divide into three intra-specific sections: those living in Scandinavia and Finland belong to *P. m. borealis* (Snow 1956, Vaurie 1959) (*P. a. borealis* according to Eck 1979).

Data concerning the breeding biology of the willow tit and the black-capped chickadee are scanty and usually collected over only a couple of years (Odum 1941a, b, 1942, Foster & Godfrey 1950, Kluyver 1961, Inozemtsev 1962, Smith 1967, von Haartman 1969,Delmee et al. 1972, Ludescher 1973, von Brömssen & Jansson 1980).

This paper is a sequel to our earlier work (Orell & Ojanen 1983a) concerning the breeding time of this species. The emphasis here is on how the willow tit has adapted to living in unpredictable northern environments. A topic of special interest is a comparison between the strategies of this species and those of the great tit in northern areas, where the latter species lives close to the limit of its range.

2. Material and methods

The willow tit data were collected during a long-term study on hole-nesting birds started in the Oulu area (about 65°N, 25°30′E) in 1969 (see Ojanen et al. 1978, Orell & Ojanen 1980). Willow tit nests were frequently found in natural holes and sometimes in boxes when checking the nest boxes, but the

Table 1. Breeding densities of the willow tit in the Oulu area in 1975-1982 according to the mapping method and line transect censuses.

	Area studied (ha)	Number of breeding pairs	Density (pairs/10 ha)
1975	212.2	26	1.22
1976	196.8	18	0.92
1977	190.5	18	0.94
1978	203	16	0.79
1979	201	25	1.24
1980	201	23	1.14
1981	203	26	1.28
1982	207	22	1.06

intensive study did not start until 1975. The breeding data originate from 10 sites: Taskila, Kuivasjärvi, Sanginsuu, Isokangas (in Oulu), Tuiranhovi, Vittasuo, Uikulaisjärvi, Lintumaansuo, Jokikylä and Onkamo (in Haukipudas, north of Oulu). The last three areas were abandoned after 1975 because of the forestry work taking place there.

The areas are described in detail in our earlier papers (Orell & Ojanen 1983a, b). In Kuivasjärvi, Tuiranhovi, Vittasuo and Uikulaisjärvi, willow tit nests were also searched for outside the original nest box areas. All the study sites included moist forests and spruce and pine bogs, offering decaying trees for willow tits to excavate nest cavites in. In addition to natural holes and nest boxes, stumps of decaying trees (mostly birch) were tied onto tree trunks. Furthermore special willow tit boxes made from birch trunks and filled with decaying wood or sawdust were available from 1975 onwards in the old territories and in places where willow tits had been seen in the spring.

Each area was visited regularly from mid-April onwards at least once a week, but usually more often, in search of willow tit nests. Only about 10 % of the 153 layings were discovered after incubation had started. The clutch size was checked using a small mirror and a torch. The eggs in uncompleted nests were covered with hair by the female and therefore the number of eggs was sometimes difficult to record at this stage.

If a nest was destroyed, the area was visited repeatedly and the pair, if present was followed to find any repeat nest. The territory was similarly inspected for possible second nesting after successful breeding. The number of eggs or young was recorded at each visit to an active nest. When the nestlings were seen for the first time, their age was determined using experience from selected broods followed daily from when the first chick hatched. The incubation period, referring here to the period from the day of the laying of the last egg till the day of hatching of the last chick, was followed in 62 nests. Only those clutches for which both the laying date and the hatching date are precisely known are included.

Productivity estimates were available for 152 nests. It could not be decided whether one brood had been successful or not.

The calculations of hatching and nestling success include only clutches for which the fate of the eggs and young was known precisely, i.e. destroyed clutches were included if the number of eggs or nestlings was known before predation (see Orell & Ojanen 1983c).

The density of breeding pairs was estimated by line transect censuses (1975, main belt data) and the mapping method (1975-1982).

As the area where the willow tit nests were searched for varied slightly between the years, the number of nests was not used alone as the estimate of breeding density. The locations where willow tits were seen were marked on a map during all visits to Taskila, Kuivasjärvi, Tuiranhovi, Vittasuo and Uikulaisjärvi and at Sanginsuu from1976 onwards, and the numbers of breeding pairs were then obtained from the information collated on the maps. The known nest sites and the fact that many birds were colour-ringed helped in the estimation. The results of line transect censuses covering 6.1 km carried out at Tuiranhovi and Uikulaisjärvi in 1975 were also used.

3. Results

3.1. Density

The area censused, the estimated number of breeding pairs and the breeding density are given in Table 1. The average density over 8 years (including 1982) at Taskila, Kuivasjärvi, Tuiranhovi, Vittasuo and Uikulaisjärvi was 1.07 pairs/10 ha. The willow tit population was remarkably stable over these years, the coefficient of variation (CV) of the annual densities being only 16.4 %. The density at Sanginsuu (130 ha) during the period 1976-1981 was substantially lower, 0.77 pairs/10 ha, but fluctuated in parallel with that in the other areas.

3.2. Nest site and habitat

Decaying birch trees are the most favoured sites for willow tit nests in the Oulu area (Table 2), where half of the nests were situated in these trees. Alders were also used frequently, but other tree species much more rarely. After 1977, when the

Table 2. Sites of willow tit nests in the Oulu area in 1975-1981.

Site	1975	1976	1977	1978	1979	1980	1981	Total	%
Birch	21	8	7	5	6	14	14	75	49.0
Aspen	-	1	-	1	-	-	-	2	1.3
Alder	2	6	2	1	1	2	-	14	9.2
Great sallow	2	1	2	1	1	-	-	7	4.6
Spruce	-	1	-	-	-	-	-	1	0.6
Birch stump tied onto tree	1	1	1	7	8	14	12	44	28.8
Nest box	1	1	-	1	2	1	-	6	3.9
Willow tit nest box[1]	-	-	3	1	-	-	-	4	2.6
Total	27	19	15	17	18	31	26	153	100.0

[1]) Filled with rotten wood or sawdust.

Table 3. Distribution of willow tit nests in different habitats and the frequency of such habitats available at the sites studied (397 ha) in the Oulu area.

Habitat	Number of nests found	%	Availability of habitats %
Spruce bog	96	63.6	31
Spruce forest	14	9.3	17
Pine bog	14	9.3	8
Pine forest	5	3.3	18
Coniferous forest[1]	1	0.7	3
Deciduous forest	6	4.0	12
Field edge	12	7.9	4
Clearing	3	2.0	7
Total	151	100.1	100

[1]) Mixed spruce and pine.

number of birch stumps tied to tree trunks was increased, their frequency as nesting sites also increased, so that in later years about half of the nests were found in these. Willow tits did not seem to accept nest boxes willingly at these sites, neither when empty nor when filled with sawdust or decaying wood. Only 10 nests (6.5 %) were found in boxes in 1975-1981.

The habitat around the nest was determined in the case of 151 nests. Spruce bogs, pine bogs and field edges, being represented at higher frequencies than in the study area in general, were interpreted as being the favoured nesting habitats (Table 3). Spruce forests and pine forests were not represented as frequently as might be expected. Deciduous habitats were not favoured. Occasionally there were nests in clearings if decaying stumps were available. Field edge habitats were represented by nests situated at the borders of forests and the old fields of Syynimaat and Lauttasuo south of Kuivasjärvi, and the fields at Sanginsuu.

3.3. Clutch size

The clutch size varied between 4 and 10 eggs (average 7.6) in 138 completed layings during 1975-1981 (Table 4). The most common size was 8 eggs, and over 80% of nests contained 7-9 eggs. Of the three repeat clutches, two contained 6 eggs and one contained 4 eggs. The annual variation in the average clutch size was small, only 7.2-8.1, which resulted in a coefficient of variation of 5.5 %.

Table 4. Size distribution of first clutches of the willow tit in 1975-1981.

	Eggs 4	5	6	7	8	9	10	*n*	Mean	*SD*
1975	-	-	3	8	10	2	-	23	7.48	0.85
1976	-	1	3	6	7	1	-	18	7.22	1.00
1977	-	-	1	5	3	-	-	9	7.22	0.67
1978	-	-	1	3	7	5	1	17	8.12	0.99
1979	1	-	1	4	4	8	-	18	7.89	1.37
1980	-	-	1	8	10	7	2	28	8.04	1.00
1981	-	2	4	8	10	1	-	25	7.16	1.03
Total	1	3	14	42	51	24	3	138	7.62	1.07

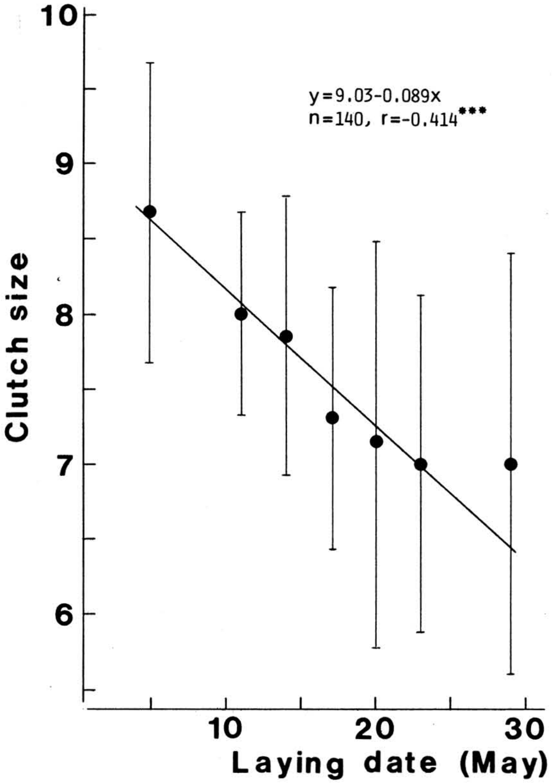

Fig. 1. Seasonal variation in the clutch size of the willow tit. Each dot represents the mean (±S.D.) for a 3-day period (longer at the beginning and end of the season). The regression equation is based on the total data, not the 3-day means.

The dependence of the clutch size (y) on the date of laying (x) was analysed by linear regression analysis. The decline in clutch size as a function of laying date is shown in Fig. 1, amounting to 0.09 eggs per day although the decrease seems to level off at the end of the season. The latter effect was attributable mostly to the exceptionally large clutches recorded in the late year of 1978. The analyses for separate years resulted in a decrease similar to that in Fig. 1, but this was significant in only 3 of the 7 years. Although the decrease was significant in the total material, the model explained only 17.1 % of the variation, which indicates a large unexplained variance in the numbers of eggs in the clutches initiated in a given day.

Table 5. Length of incubation period (days) in the willow tit in the Oulu area.

Days	11	12	13	14	15	16	17	18	19	*n*	Mean	*SD*
	1	6	15	20	12	3	3	-	2	62	14.11	1.56

Table 7. Causes of egg and nestling losses in 144 first and 3 repeat willow tit nests in the Oulu area.

	n	%		*n*	%
Egg stage			Nestling stage		
Eggs laid	1095	100.0	Hatched	923	84.3
Losses	172	15.7	Losses	149	13.6
Unhatched	37	3.4	Starvation	72	6.6
Desertion	61	5.6	Predation	17	1.6
Competition	28	2.6	Desertion	43	3.9
Predation	39	3.6	Other reason	17	1.6
Hard wind	7	0.6	Fledged	774	70.7

The average annual size of first clutches correlated negatively with the annual average start of laying, but not significantly ($r=-0.298$). The year 1978 with large clutches (Table 4) but late start of egg-laying (Orell & Ojanen 1983a) was exceptional among the years. If the 1978 data is excluded, the correlation is significant ($r=-0.902$, $p<0.05$), suggesting that in early years the clutch size is higher than in late years.

3.4. Incubation period

The length of the period from the day of laying of the last egg to that on which the last of the young hatched varied between 11 and 19 days (average 14.1 days, Table 5). There was a tendency for the incubation period to be shorter in years of late breeding than in years of early laying, but this was not significant.

3.5. Nesting failures

Of all the 152 willow tit nests with known success, 21 % failed to produce any fledglings (Table 6). There were no significant differences in failures between the different nesting stages (X^2-test), although losses seemed to be slightly smaller during the laying stage.

Altogether 84 % of the willow tit eggs laid were hatched (Table 7). Desertion for unknown reasons was the most frequent cause of egg failures, amounting to 35 % of all losses. Predation and unhatched eggs accounted for about 20 % of the losses each. The great spotted woodpecker *Dendrocopos major* was the most important predator on willow tits, being responsible for 62 % of all egg predation. The red squirrel *Sciurus vulgaris* destroyed only one clutch, corresponding to 15 %. The rest of the predation was by humans. Four clutches were lost when the wryneck *Jynx torquilla* or the pied flycatcher *Ficedula hypoleuca* took over the tits' hole, accounting for 16 % of the egg losses. One clutch was destroyed when the stump broke during a high wind.

Table 6. Numbers of willow tit nests destroyed at various nesting stages in the Oulu area.

Laying stage		Incubation stage		Nestling stage		Total		Number of nests studied
n	%	n	%	n	%	n	%	
8	5.3	13	8.6	11	7.2	32	21.0	152

Starvation was the most general cause of nestling failure, amounting to 48 % of all deaths. Predation led to 11 % of all deaths, in the form of 2 broods attacked by the great spotted woodpecker. Desertion was a more important cause of failure than predation. The heading 'other reason' (Table 7) includes cases in which some of the nestlings died because one of the parents had obviously died or abandoned the brood, one case where a brood was lost when the nesting stump broke during breeding, and one which was destroyed by forestry work.

Altogether 71 % of the willow tit eggs produced fledglings. Repeat breedings were comparatively unsuccessful. The hatching and fledging success in 3 repeat broods (included in Tables 6 and 7) were 56.2 % and 6.2 %, respectively. One clutch was destroyed by a red squirrel during incubation. In the two remaining clutches all except one of the eggs hatched. In one nest the male obviously abandoned the brood, and only one young fledged out of 6 hatched. In the other nest both parents were present, but feeding was very haphazard and all the young died within a few days after hatching. Both parents were later seen alive in the territory.

3.6. Nesting success related to clutch size

The hatching success in the completed clutches was 96 % (Table 8), featuring the same (95.7 %) also in the successful clutches. There was a slight tendency for the most common clutch sizes to have the highest success, but the difference was not significant (X^2-test).

Nestling mortality was proportionately higher in the small initial clutches than in the large ones

Table 8. Hatching and nestling success in the willow tit, by initial clutch size (three repeat nests included).

Clutch size	Hatched		Fledged		Number fledged per clutch	Number of clutches
	n	%	*n*	% of hatched		
4	5	62.5	1	20.0	0.50	2
5	14	93.3	14	100.0	4.67	3
6	63	95.4	53	84.1	4.82	11
7	254	98.1	197	77.6	5.32	37
8	356	96.7	317	89.0	6.89	46
9	198	95.6	168	84.8	7.30	23
10	25	83.8	24	96.0	8.00	3
Total	915	96.0	774	84.6	6.19	125

(Table 8; combining clutches 4–6 and 9–10, X^2-test $p<0.001$). Clutches of 4 and 7 eggs in particular showed low success. The repeat clutch of 4 was abandoned by the parents and in the first clutch of 4 in 1979 2 chicks hatched but only 1 fledged. Clutches of 7 eggs showed low success because of extensive abandonment during the poor years of 1976 and 1977. Considering only the successful broods, nestling success (average 91.0 %) did not deviate significantly between the broods of different initial size (X^2-test). The data in Table 8 reveal that the most productive clutches at the time of fledging were those with the largest numbers of eggs.

3.7. Seasonal and annual variation in nesting success

There were significant differences in the ratio of dead to fledged young between broods hatched at different times in the season (X^2-test, $p<0.001$). However no apparent trends attributable to the hatching time could be verified (Table 9). This, together with the fact that the early clutches were the largest, resulted in the brood size at fledging being the largest in clutches hatched at the beginning of the breeding season (Table 9).

The decrease in reproduction with the advancing season would be even more pronounced if the clutches deserted at the various stages were included. Broods deserted at the early stage, before June 10 represented 4 % of the total broods hatching within this period, and those deserted thereafter represented 10 % of the total (see also section 3.5.).

Table 9. Seasonal variation in nestling success in all willow tit broods in which at least one young fledged.

Hatching period	Number of hatched	% fledged	Number fledged per brood
May 26–30	42	92.8	7.80
May 31–June 4	264	95.8	7.20
June 5–9	348	86.8	6.29
June 10–14	141	94.2	6.65
June 15–24	56	85.7	6.86

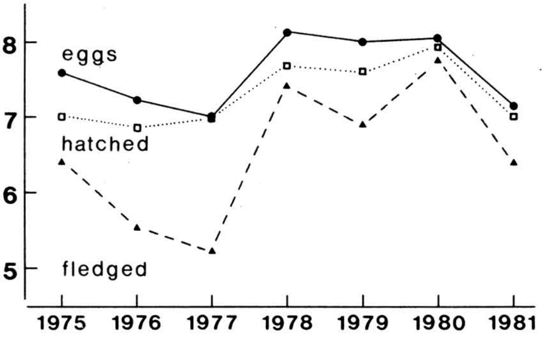

Fig. 2. Annual fluctuation in the average number of eggs, young hatched and fledglings in successful first nestings of the willow tit in the Oulu area.

The average clutch size in 115 successful broods varied annually between 7.00 and 8.13 (average of the annual means 7.60±0.47 (*SD*), Fig. 2). The corresponding average for all clutches was the same (see Table 4). Hence, there was no selective mortality attributable to clutch size. The number of unhatched eggs varied between 0 and 0.65 (average 0.31±0.23) and the number of dead young between 0.17 and 1.80 (average 0.78±0.58). The years with the largest broods at fledging were 1978 and 1980, while the most unsuccessful year was 1977 (Fig. 2). In 5 of the 7 years the nestling success in broods producing at least one fledgling was over 90 %.

3.8. Reproductive rate

The reproductive rate refers to the number of fledged young divided by the number of breeding pairs in a given year. If the pair lost its first nest and no repeat attempt was observed its productivity was estimated as zero.

The average reproductive rate of the 149 willow tit pairs with known breeding success in the present areas in 1975–1981 was 5.4 fledglings (Table 10). Unsuccessful pairs amounted to 20 %. The outcome in 1977 was exceptionally low because large numbers of nests were abandoned during the egg or nestling stage. The years 1978 and 1980 featured the highest success. The *CV* of the reproductive rate was 30.9 %.

The prevailing breeding density of willow tits did not contribute to the reproductive rate, as the correlation coefficient between these variables was weak ($r=-0.142$).

Table 10. Annual variation in the reproductive rate of the willow tit (young/breeding pair) in the Oulu area in 1975-1981.

		1975	1976	1977	1978	1979	1980	1981	Total
Pairs		26	19	14	17	18	29	26	149
Pairs failing to reproduce	*n*	4	4	8	2	2	5	4	29
	%	15.4	21.0	57.1	11.8	11.0	17.2	15.4	19.5
Reproductive rate		5.42	4.47	1.93	6.53	6.11	6.41	5.38	5.37

3.9. Weather conditions and nestling mortality

The impact of weather conditions 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. The analysis was performed by plotting the nestling mortality (log (young hatched/young fledged)) against these two factors. For the analysis see Orell & Ojanen (1983c).

Temperatures in May and June showed a significant negative correlation with the nestling mortality (Fig. 3). Temperatures during May and June alone also correlated negatively with the nestling mortality but the relationship was not significant. Increased rainfall was associated with lower mortality to a slight but insignificant extent. It should be especially mentioned that the year 1981 did not involve the highest mortality even though the summer was exceptionally rainy; 101.5 mm in June compared with an average of only 36.0 mm in 1975-1980.

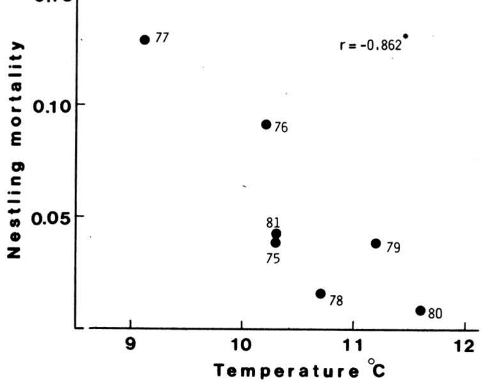

Fig. 3. Relationship between nestling mortality (log (young hatched/young fledged)) in successful first broods of the willow tit and the ambient temperature during May-June.

3.10. Density-dependent mortality in the willow tit population

Using the method of Varley & Gradwell (1960, 1970; see also Blank et al. 1967, Krebs 1970b, Watson 1971, Southwood 1978) it is possible to analyse population data in order to identify the particular mortality rates which contribute most to the annual fluctuations in numbers (key factor analysis). Mortality (*k* value) is expressed as the logarithm of the ratio between the population before and after a particular period:

k_i=log (initial population size/final population size). Mortality rates calculated for each stage in the annual cycle may be summed to obtaine the total annual mortality ($k_1+k_2+k_3$ etc. $=K$). The mortality factor which most closely parallels the fluctuations in *K* is then the main factor causing the annual fluctuation in numbers, the key factor.

Density-dependence is tested by plotting the annual *k* values against the logarithm of the initial population size (n_t). A significant positive slope indicates density-dependence. However, these correlations are not fully conclusive since *k* and n_t are not independent. Any relationship suggesting density-dependence should therefore be verified by plotting the log survivors (n_{t+1}) against the initial population, log n_t, and log n_t on log n_{t+1}. The latter relationship, of course has no biological meaning and is only used in a statistical test that a density-dependent relationship exists (e.g. Benson 1973, Southwood 1978). In these regressions the null hypothesis is $b=1$, i.e. there is no density-dependent mortality. If the regression coefficients in these plots lie on the same side and differ significantly from the unity the density-dependence can be considered real.

The following mortality factors were analysed in this study:

1. Mortality operating before the eggs are laid, i.e. variation from the maximum potential number of eggs. In these calculations the maximum potential clutch size was set at 8.2 eggs, a constant which does not affect the calculations.

k_1=log ((potential max. clutch +2) density/(observed clutch +2) density).

The addition of 2 is necessary because the

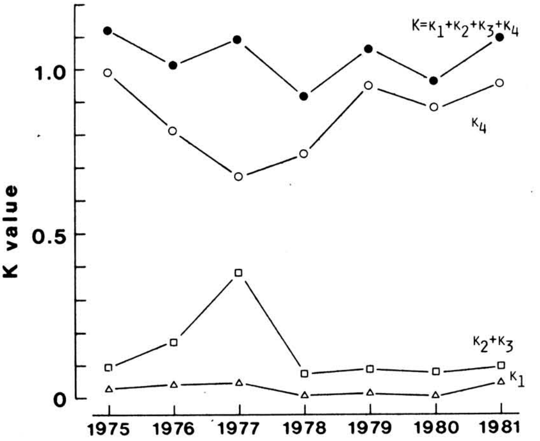

Fig. 4. Key factor analysis of the population data on the willow tit in the Oulu area. k_1 = clutch size reduction, k_2 = hatching failure, k_3 = nestling mortality, k_4 = mortality during non-breeding season.

adults must also be considered. The annual density values (pairs/10 ha) are taken from Table 1.

2. Mortality operating during incubation (=hatching failure): k_2=log ((clutch +2) density/(hatched +2) density).

3. Mortality during the nestling stage: k_3=((hatched +2) density/(fledged +2) density).

4. Mortality during the non-breeding season: k_4=log ((fledged +2) density/(next year's breeding density)).

The k values for the willow tit population in the Oulu area are plotted against each year in Fig. 4, in which it is seen that the factor k_4 (mortality outside the breeding season) parallels to K most closely, and is therefore the key factor. Factors k_1–k_3 generally contributed to K only to a slight extent, the only exception being the year 1977.

The tests for density dependence showed no contribution of density to losses during the laying, incubation or nestling stages (Fig. 5). The significant negative slope during the nestling time is caused by the 1977 data, with a low breeding density but high mortality. There was a significant positive correlation between mortality outside the breeding season and the initial summer population, suggesting a density-dependent reduction in the non-breeding population. The plot of log survivors (n_{t+1}) on log summer population (n_t) resulted in a slope b=0.322±0.158 (SD) which was significantly

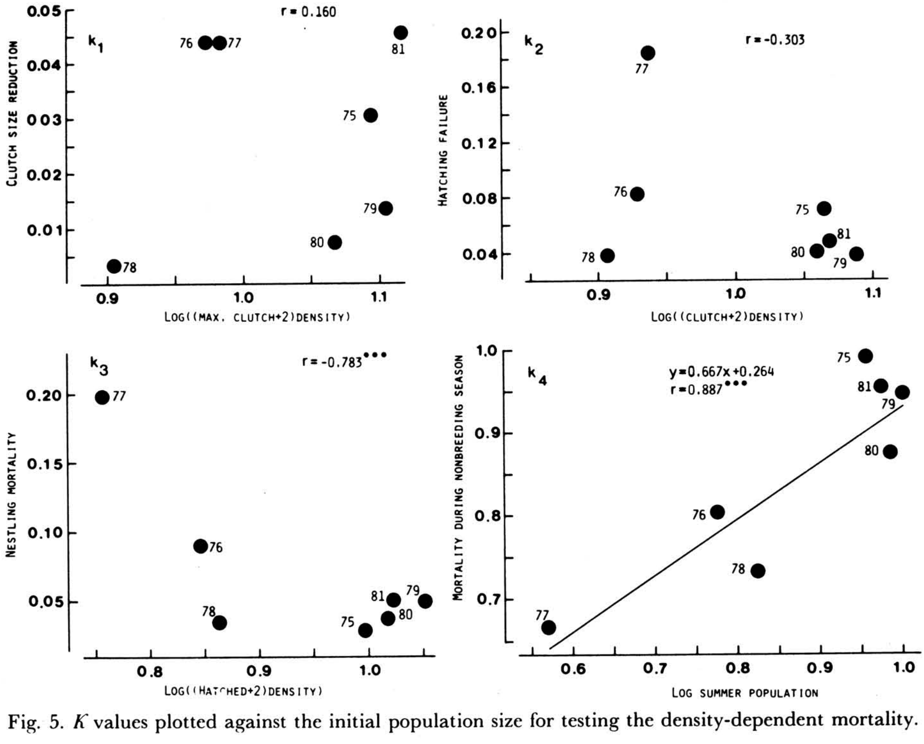

Fig. 5. K values plotted against the initial population size for testing the density-dependent mortality.

different from unity (*t*-test, $p<0.01$). Another plot of log n_t on log n_{t+1} revealed a slope $b=1.410\pm0.690$, which did not differ from $b=1$ (*t*-test). Hence, the density-dependent relationship could not be verified but we may suspect that it exists.

4. Discussion

4.1. Habitat and nest site

According to Snow (1953, 1954), the willow tit is the most euryoecious tit in the taiga belt of the north-eastern Palaearctic region. It breeds in dark, mainly damp, coniferous forests with spruce predominating, but also in mountain and subalpine forests and in the northern birch zone (Snow 1953, 1954, Voous 1960, Glutz 1962, Thönen 1962). Further south it becomes more stenoecious. In western and central Europe it breeds in mixed swamp forests, willow thickets beside rivers, wet alder woodlands and deciduous woods (Snow 1953, 1954, Voous 1960, Ludescher 1973, Perrins 1979).

The willow tit is one of the most versatile birds in Finland breeding most frequently in spruce-birch forests, but also in pure coniferous forests and pure deciduous woods (Palmgren 1930, Merikallio 1958, von Haartman et al. 1963-72). In the Finnish Forest Lapland it breeds in more luxuriant forests than the Siberian tit *Parus cinctus* (Järvinen 1982b).

In the Oulu area the willow tit seems to prefer places with damp forests, especially with spruce predominating, although nests were also found in variety of other habitats. The highest densities were nevertheless reached in spruce-dominated areas. The availability of decaying stumps seems important in the selection of the nesting habitat. This was seen in the fact that the tits willingly adopted stumps tied to tree trunks as their nest site. There is certainly a lack of suitable stumps in modern forests, and therefore even pairs with their territory in an optimum habitat may not succeed in finding a suitable nest-site. The willow tit prefers to breed in holes it has excavated in birch and alder, but does not avoid other tree species (Putkonen 1942, von Haartman 1969, this study).

In central and western Europe willow tits may breed in nest boxes (e.g. Berndt 1936, van den Brink 1938), but prefer holes they have excavated (Ludescher 1973). Löhrl (1982) filled boxes with a damp mixture of flour and sawdust. After drying, the mixture hardened and willow tits excavated nesting cavities in the boxes. In southern Sweden the willow tit also seemed to be willing to adopt nest boxes, and 70 % of the nests were found in boxes filled with coarse sawdust (von Brömssen & Jansson 1980). In the Oulu area the situation seems to be the reverse, as only 6.5 % of nests were built in boxes.

It seems that the willow tits adopt boxes or old holes in areas where there is lack of decaying stumps. If these are present in the habitat the tits prefer them to boxes (see also Kluyver 1961). The willow tit's companion species, the crested tit, *Parus cristatus,* apparently selects nest boxes for its nest site more often, e.g. 6 of the 24 cases in the Oulu area (own observations, see also von Brömssen & Jansson 1980).

4.2. Breeding density

The Finnish population of the willow tit has decreased since the 1940s, especially in the northern parts of the country, as have the other tit species inhabiting coniferous woods. This decrease is assumed to have been most pronounced during the late 1940s and early 1950s (Järvinen et al. 1977, Järvinen & Väisänen 1977). The total density of the foliage-gleaning guild of over-wintering species, the willow tit, crested tit, coal tit *Parus ater,* Siberian tit and Siberian jay *Perisoreus infaustus,* decreased by 80 % from 1945 to 1975 in the northern part of the country. The reason for this crash has obviously been the cutting of old forests, which are important winter resources for these species (Järvinen et al. 1977).

Merikallio (1958) reports willow tit densitites of 5.1 pairs/km^2 in Ostrobothnia and 4.6 pairs/km^2 in the Tornio-Kainuu region. More recent line transect censuses in the Kemi-Tornio area, approx. 100 km north of Oulu, have revealed a decrease in the breeding density to 3.2 pairs/km^2 (Rauhala 1980). Our results suggest higher densities than these (10.7 pairs/km^2), the differences not being wholly attributable to the census methods used.

The study areas near Oulu were optimum for willow tits in that they comprised a varied landscape rich in forest edges and spruce and pine bogs containing or provided with a rich supply of decaying stumps. Further, the sites included only small clear-felled areas, which are not used by willow tits.

The breeding densities in the Oulu area were somewhat lower than those recorded at Lammi, southern Finland (15.3 pairs/km^2, Solonen 1981), but higher than near Gothenburg, southern Sweden (3.6-4.8 pairs/km^2, von Brömssen & Jansson 1980).

The population fluctuation in the Oulu area during the 7-year period was small, with a coefficient of variation of 16 %. The population near Gothenburg was similarly quite stable over 4

Table 11. Mean breeding density (pairs/10 ha) and the coefficient of variation (*CV* %) in annual breeding densities in some willow tit and great tit populations. If the size of the area is not given, the calculation of the *CV* is based on the number of breeding pairs.

Population	Mean density	*SD*	*CV*	Source
Willow tit				
Finland				
Oulu area	1.1	0.2	16.4	This study
Sweden				
Gothenburg	-	-	16	Ekman 1979
Great tit				
Finland				
Vittasuo	3.1	0.9	31.4	Own unpubl. data
Taskila	4.6	1.3	35.9	—"—
Kuivasjärvi	2.8	0.8	31.5	—"—
Sanginsuu	1.6	0.6	39.8	—"—
Lammi	2.0	0.7	34.6	Solonen 1981
Lemsjöholm	-	-	37.2	von Haartman 1969
Sweden				
Linnebjer	19.3	6.4	33.2	Källander in litt.
Germany				
Anhalt	-	-	37.2	Berndt & Henss 1967
SE Lower Saxony (Hattorfer Wald)	-	-	44.4	—"—
SE Lower Saxony (Near Braunschweig)	-	-	25.5	—"—
Holland				
Oranje Nassau Oord	4.3	1.8	41.7	Kluyver 1951
Hoenderloo	1.3	0.4	30.2	—"—
Belgium				
COO	10.9	2.7	24.8	Dhondt in litt.
Maaltepark	13.8	3.3	24.2	—"—
Zewergem	18.1	4.3	23.8	—"—
England				
Marley Wood	13.5	6.8	49.9	Lack 1966

years, with a resulting coefficient of variation of 16 % (Ekman 1979). Both of these figures are very much lower than those obtained for the great tit in different parts of Europe (Table 11). Some of the latter high coefficients were obviously caused by the fact that great tit populations have gradually increased, e.g. the Oranje Nassau Oord population in Holland, but this does not hold true for all populations, and the *CV* was markedly high in all the Fennoscandian populations.

In contrast, winter bird censuses showed only moderate fluctuations in both these species, *CV*=18 % for the willow tit and 16 % for the great tit (Sammalisto 1974). A permanent study area is nevertheless perhaps better than winter bird censuses for following population fluctuations. We should therefore conclude that northern populations of the willow tit fluctuate less than those of the great tit, irrespective of these decreases in population size caused by man via alterations to the natural environment of the species.

Correlations between winter temperature and population size in the following spring have revealed decreases in the number of breeding great tit pairs in southern Finland after a hard winter (von Haartman 1971, 1973). The small fluctuations in willow tit populations suggest that this species is not as susceptible as its counterpart to adverse weather conditions in winter (see also Berndt & Frantzen 1964).

4.3. Clutch size

According to the available data the clutch size of the willow tit varies between 4 and 11 eggs (Table 12), although Siivonen (1936) reported a clutch of 12 from Pieksämäki, southern Finland. It is difficult to compare the clutch size of the species between different parts of its range since the relevant studies are few in number and are usually based on only a small sample. Outside Fennoscandia the average clutch size usually seems to exceed 8 eggs (Table 12). On the other hand, records of the most southerly populations, in southern Belgium, southwestern Germany and Switzerland, show that the clutch size was the same or even smaller than in the northern populations. For these reasons one is tempted to suggest that clutch size in the willow tit decreases from western and central Europe to Scandinavia and Finland, an idea already proposed by Lack

Table 12. The clutch size of the willow tit in some populations in Europe.

Population	Mean	Range	Number of clutches	Source
Finland				
Oulu area				
Whole country	7.62	4-10	138	This study
	7.74	5-11	101	von Haartman 1969
Sweden				
Gothenburg				
Whole country	8.21	-	97	Ekman 1983
	7.73	5-11	94	Durango 1944
Soviet Union				
Near Moscow	8.00	6-11	26	Inozemtsev 1962
Germany				
Near Lingen				
Lower Saxony	8.33	-	12	Winkel 1975
Southwest	8.21	7-10	19	Greve 1962
Oberlausitz	6.8	-	34	Ludescher 1973
Whole country	7.58	6-9	12	Melde 1978
	8.27	5-11	33	Diesselhorst 1956
Holland				
Whole country	8.24	-	346	Lack 1950
Belgium				
South	7.75	5-11	16	Delmee et al. 1972
England				
Whole country	8.36	-	37	Foster & Godfrey 1950
China				
Changbai Shang Mts.	-	6-10	5	Song 1980

(1950). This is supported by the results from Gothenburg and Oulu. The average clutch size of the willow tit was higher in Gothenburg than in the Oulu area in each of the years 1975–1980, varying between 7.50 and 9.00 (Ekman 1983). The nest card data from Finland (von Haartman 1969) show no differences between different parts of the country in this respect, however. Thus more data are needed in order to resolve whether clutch size in the willow tit decreases towards the north in Fennoscandia.

The clutch size of the willow tit decreased as a function of the laying date in Oulu, thus supporting the results of von Haartman(1969) and those of Kluyver (1961) for the black-capped chickadee. The variation was also similar to that noted in the great tit in Oulu and in other populations (see Orell & Ojanen 1983b). In view of the considerable variation in size within clutches laid on the same day, the regression model still explained only about 17 % of the variation, as was the case in the great tit (14–36 %, Orell & Ojanen 1983b).

The annual variations in clutch size seemed to be explained to a great extent by the calendar, although 1978 was a clear exception. The reason for this might be that few fledglings were produced in 1977 (Table 10), and there were therefore obviously more old breeders than usual in 1978. Since it is known that old tits lay larger clutches than yearlings (Kluyver 1951, van Balen 1973, Perrins & Moss 1974, Hildén 1981), this may have led to a high average clutch size — higher than would be expected from the calendar.

4.4. Incubation period

The average length of the incubation period of the willow tit recorded in the Oulu area (14.1 days) was the same as that given by the Finnish nest card data, 14.2 days (n=6, von Haartman 1969). The incubation period of the great tit in Oulu was only slightly longer, averaging 14.5 days (n=263, first clutches, own unpublished data). The Siberian tit in Finnish Lapland tends to incubate longer than the willow tit in the Oulu area, the average being 16.3 days (n=8, Pulliainen 1977, Järvinen 1982b). Järvinen (1982b) explains that incubation in the Siberian tit is longer in Finnish Lapland than in southern Norway because the period spent resting in the nest at night is shorter in the former area, reducing the incubation efficiency of the female.

This is not the whole truth, however, since the incubation period is also affected by the time-lag between the laying of the last egg and the start of efficient incubation, which may amount to several days in the willow and great tits (own observations). The incubation period is also short at times of high ambient temperature, becoming correspondingly longer with decreasing ambient temperature (von Haartman 1956). This may result from the fact that the night temperature of the willow tit eggs, for example, was about 0.3°C lower for every decrease of 5°C in the air temperature, with mean values in the range 4–14°C (Haftorn 1979).

4.5. Nesting success and reproductive rate

The frequency of unsuccessful nests in the willow tit in the Oulu area (approx. 20 %) was less than that for the great tit (30 % in the same area, Orell & Ojanen 1983c). Predation on willow tit nests near Gothenburg averaged 21 % over 7 years (Ekman 1983). In the case of the willow tit and the great tit in Oulu the difference in nest failure rate is attributable to human disturbance, which was conspicuous in the latter species, but practically negligible in the former. Similarly the other predators caused fewer failures to the willow tit than to the great tit. In southwestern Germany, willow tits suffered from high nesting failures, as 61 % of the nests were destroyed by the great spotted woodpecker during a 4-year study (Ludescher 1973). The same species was the most important predator on the willow tit in the Oulu area. Some of the losses in Germany were possible attributable to the jay *Garrulus glandarius* (Ludescher 1973). The stoat *Mustela erminea*, which has been a severe predator on the great tit in the Oulu area in some years, has not been observed to destroy willow tit nests here. Perhaps this is because great tit nest-boxes, situated close together, are more easily detectable than the widely dispersed willow tit nests built in camouflaged stumps. Hence, the searching image for great tit nests is much easier to develop than that for willow tit nests.

The reason for the abandonment of clutches or broods cannot be ascertained with certainty, but some hypotheses can be suggested. One possibility is that one or both of the parents have died, or else it may be attributed to food shortage. Abandoned nests were exceptionally numerous in 1977 (33 % of all nests) and the nestling survival rate in broods which produced at least one fledgling was also low, only 74.3 % of those hatched fledged (see Fig. 2). Similar results were also noted in the great tit (Orell & Ojanen 1983c). Hence, the tits clearly suffered a food shortage that year. This is also suggested by the retarded development of the nestlings of both the great and willow tits (own observations). When conditions deteriorate the adults adapt to an investment in survival and future reproduction rather than attempting to rear young, which would put their own lives at risk under meagre feeding conditions (see also Ricklefs 1969). The strategy of deserting a nesting attempt — investing in future young — appears to be more common in the willow tit than in the great tit, since the former species deserted 9.5 % of the eggs laid (Table 7), but the latter only 4.2 % (Orell & Ojanen 1983c; Table 3).

The nestling success, concerning total losses of nests and partial losses of eggs or nestlings, was better in the willow tit than in the great tit in the Oulu area (Orell & Ojanen 1983c). The hatching and nestling success rates among the first broods were 77.0 % and 71.1 % respectively in the latter species and 84.2 % and 84.3 % in the former (Table 3, calculated from all eggs laid and young hatched). The exclusion of total losses did not alter the picture, success then being 93.4 % and 79.9 % for the great tit and 95.7 % and 91.6 % for the willow tit respectively. The hatching success did not vary much between these species, but the nestling success was again higher in the willow tit. The main cause of nestling loss was starvation, and was much more pronounced in the great tit.

Although the nestling success of the willow tit was better than in the great tit among the first broods, the success in repeat broods was much poorer. The three repeat clutches observed in 1975-1981 produced only one fledgling, while 46 % of the eggs of the great tit produced fledglings (Orell & Ojanen 1983c).

The difference in success between the willow and great tits is partly explained by the fact that large first broods in the latter species suffer from proportionately heavier nestling mortality (Orell & Ojanen 1983c). In the willow tit the success in successful broods was about the same in all initial brood sizes.

The average brood size of the willow tit was 6.7 young in the Oulu area (including one repeat brood), being about the same as in some other populations studied; 6.46 near Moscow (Inozemtsev 1962), 7.0 in southern Belgium (Delmee et al. 1972) and 6.3 near Gothenburg (von Brömssen & Jansson 1980). In terms of nestlings raised per first brood, the productivity of 5.96 fledglings observed near Gothenburg (Ekman 1983) was somewhat higher than that in the Oulu area (5.36 young).

According to the 47 completed clutches, the average number of eggs in the clutch of the black-capped chickadee (5.98, Kuyver 1961, Smith 1967) appears to be somewhat smaller than that of the willow tit. According to those studies the hatching success varied between 51% and 84 % and the nestling success between 88 % and 94 %.

According to this study the willow tit also seems to manage better than its norther counterpart, the Siberian tit, in Finnish Lapland, as the hatching and nestling success rates in unharmed nests were 85.7 % and 44.4 %, respectively, at Värriö (Pulliainen 1977) and 80 % and 81 % at Kilpisjärvi (Järvinen 1982b).

The annual fluctuation in the reproductive rate of the willow tit was slightly less (*CV* 31 %) than that in the great tit in Oulu (*CV* 35 %, Orell & Ojanen 1983c). The data is insufficient to be able to calculate the annual mortality rate for the adult willow tits in Oulu, but in southern Sweden this amounted to 41.9 % (Ekman 1979). Assuming the same for the Oulu area, together with an average reproductive rate of 5.37 young/breeding pair/season (Table 10), one obtains a juvenile survival rate of 15.6 % for a balanced population (calculated from the formula of Henny et al. 1970). Ekman (1979) obtained an estimate of 14.6 % for the juvenile survival rate in the Gothenburg population, a figure close to our value. Both of these are slightly smaller than the values estimated for the great tit in the Oulu area, about 17-18 % (Orell & Ojanen 1983c).

4.6. Weather conditions and nestling success

The density-independent factor, the ambient temperature during breeding, was the most important factor affecting the nestling success of the willow tit, as was also the case in the great tit in the Oulu area (Orell & Ojanen 1983c). In both species the long-term temperature for the period May-June produced the closest correlation with the survival rate. This relationship is perhaps attributable to the condition of the parents, which, perhaps being better after a warm rather than a cool May, helps them to resist any unfavourable periods encountered during the nestling time. In May the high ambient temperature raises the activity of insects, but during cool periods they are inactive. Later in summer the variation in the temperature does not contribute so pronouncedly to insect activity (Blomberg et al. 1976, 1978). Hence it seems that, especially in spring the temperature is important in affecting the condition of feeding parents by affecting the availability of insect food.

The ambient temperature in June may have more direct effects. During cold weather the parents and young must use more energy for survival and less is left for gathering food and growth respectively.

In both the willow tit and the great tit the warm summer of 1980 led to the lowest nestling mortality. The summer was exceptionally favourable for hole nesters even in the far north of Finnish Lapland (Järvinen 1982a).

It is worth noting that the amount of rainfall did not explain the nestling mortality in either the willow tit or the great tit (Orell & Ojanen 1983c). The exceptionally rainy summer of 1981 did not result in the lowest success for either of these species (willow tit, this study; great tit, own unpubl. data), as has been observed for many bird species, including the great tit, in many parts of Finland (Hildén et al. 1982). Large differences between great tit populations are reported in this respect, however. The fact that the Oulu area was among those with the most severe failures is supported by data from Kemi and Liminka given by Hildén et al. (1982), who also point out that the discrepancies were attributable to differences in the weather and also in the condition of the boxes. Unsatisfactory boxes allowed the rain to run in and the young perished.

4.7. Density-dependent factors affecting the willow tit population

Our results suggest that density-dependent factors did not influence the reproductive output parameters in the willow tit. This is roughly the same result as in the great tit, although there were indications of the clutch size becoming smaller with increasing breeding density (Orell & Ojanen 1983b). In many other studies from further south, increased density has been observed to reduce the reproductive output in the great tit (Kluyver 1951, Perrins 1965, Lack 1966, Krebs 1970b, Dhondt 1977, Dhondt & Eyckerman 1980, O'Connor 1980) and willow tit (Jansson et al. 1981), although Flegg & Cox (1975) did not find any relationship in the great tit.

Conflicts between territorial pairs in spring may be more frequent in high-density populations, reducing the female's feeding time and the food available for egg formation (see e.g. Krebs 1970b, van Balen 1973). Courtship feeding, an important source of food for the female (Royama 1966, Krebs 1970a, Smith 1980) may also be less efficient if there are many territorial conflicts. Experiments with supplementary food have given conflicting results, however (Yom-Tov 1974, von Brömssen & Jansson 1980, Drent & Daan 1980, Högstedt 1981, Newton & Marquiss 1981). Other factors may also be involved in high-density populations, but their effect on the clutch size variation is probably quite small (see Krebs 1970b).

Predation by the weasel *Mustela nivalis* on tits in Wytham Wood, England, where egg losses were density-dependent (Krebs 1970b), proved to be much higher than that occasioned by the stoat predation in the Oulu area (see Perrins 1965, Dunn 1977, King 1980, Orell & Ojanen 1983c).

In the case of the willow tit in Oulu the breeding densities are perhaps too low to contribute anything to the clutch size, and predation pressure on the nests has also been low and quite stable, so that again no connection could be found between this and tit population density (see also Orell & Ojanen 1983b, c).

The fact that the weather, a density-independent factor, has a greater effect than the density-dependent factors on the reproductive output in northern areas confirms the suggestion of Krebs (1972), which was also supported by data on the pied flycatcher in Kilpisjärvi (Järvinen 1980).

The results from the Oulu area suggest that there may be a weak density-dependent mortality during the non-breeding season in the willow tit population. The result is similar to that found in the great tit in the same area (Orell & Ojanen 1983c) and further south (see Kluyver 1966, 1971, Dhondt 1971, 1979, Klomp 1980, O'Connor 1980, but see Krebs 1970b, Perrins 1971). Ekman (1979) found a positive relationships between losses during and after breeding, up to October, and the initial population size in the willow tit in southern Sweden. The losses contributed most to annual variation in the population size. The correlation was of no causal significance, however, since the low breeding densities coincided with years of spruce flovering. Nevertheless, Ekman did not deny that numbers could have been affected by density-dependent processes during that period. Most of the losses were first-year birds, which either died, emigrated or were prevented from establishing a winter territory (Ekman 1979), and it was suggested that prewinter numbers are adjusted behaviourally in accordance with the available winter food. Experiments have shown that winter losses among willow tits are also density-dependent (Ekman et al. 1981), again with mortality higher among juveniles. This is probably caused by competition, through interference from adults (Ekman et al. 1981). The provision of extra food during winter has been shown to increase the population level of tits in some studies (Krebs 1971, von Haartman 1973, van Balen 1980, Källander 1981). Jansson et al. (1981) showed that winter feeding improved the survival of the willow and crested tit at least partly by decreasing the risk of predation.

Studies in southern Sweden (Jansson et al. 1981) also showed that a high population level caused by extra feeding during the winter was only weakly compensated for by density-dependent spring losses, which would then be an effect of territorial behaviour (see also Smith 1967). It thus seems that spring territorial behaviour has only a weak influence on breeding population (Krebs 1971, Cederholm & Ekman 1976, Jansson et al. 1981) although Dhondt et al. (1982) suggest that in the case of the blue tit this may limit the population in high-density areas but not in low-density areas. Studies from Sweden have revealed that regulation of the willow tit population is maintained by autumn territorial behaviour and winter mortality, in both of which the density-dependent factor is important (Ekman 1979, Jansson et al. 1981).

The willow tit population in the Oulu area may be regulated in a similar way to that in southern Sweden. The reduction during the non-breeding season is obviously affected by the prevailing density, although this may be masked by marked density-independent factors.

4.8. Breeding strategies of the willow tit

It is important to breed early in northern areas, since the season is short, but not too early, because sudden cold spells may cause heavy losses (e.g. Pulliainen 1978, Ojanen 1979). Willow tits lay slightly earlier in the spring than the great tits, i.e. their response to the warmer weather is more rapid (Orell & Ojanen 1983a). In the Oulu area and other coniferous habitats the great tit is not able to adjust its clutch size to render nestling mortality negligible (ignoring predation). Instead serious starvation of the nestlings usually occurs (Ojanen et al. 1981, Orell & Ojanen 1983c). This is called brood reduction strategy (O'Connor 1978). In broad-leaved woods the great tits have the clutch adjustment strategy, i.e. the clutch size is adjusted to the conditions prevailing during the nestling period so that mortality is negligible.

In five of the seven years, nestling survival among the willow tits of the Oulu area exceeded 90 %, showing the clutch adjustment strategy.

Nestling mortality also seems to be small elsewhere, 3.4 % near Moscow (Inozemtsev 1962) and 9.7 % in southern Belgium (deduced from Delmee et al. 1972). The environmental unpredictability around Oulu is so great, however, that the clutch adjustment strategy does not succeed every year, resulting in major nestling starvation.

The breeding strategy of the willow tit involves a strong tendency to discontinue its present investment in offspring when conditions deteriorate, thus relying on future reproduction. No other cases of this strategy have been recorded in such small birds as far as we know.

The breeding period of the willow tit in Oulu is shorter than that of the great tit (Orell & Ojanen 1983a). It rarely lays replacement clutches and hardly ever second clutches, although it may breed twice under extremely favourable feeding conditions further south (von Brömssen & Jansson 1980). The great tit frequently produces second broods in Oulu, especially during favourable seasons (Orell & Ojanen 1983a). The great tit is therefore more opportunistic, judging from its larger clutch size and the higher frequency of second broods. In terms of the *r-K* continuum, the willow tit can be regarded as more of a *K* strategist, investing more energy in survival.

The adult willow tits can start moulting in summer while still caring for their nestlings if conditions are favourable. The great tit may also do this, but not as frequently (Orell & Ojanen 1980). This habit is not found in more southerly populations of the great tit (e.g. Dhondt 1981). It is also important for the willow tit to start storing food early, since this habit is an important part of its adaptation to winter survival (Haftorn 1956). The great tit does not do this (Haftorn 1954), and its important winter food source in broad leaved habitats is beechmast, a shortage of which may cause increased winter mortality (e.g. Ulfstrand 1962, Perrins 1965, Lack 1966, van Balen 1980). In northern areas the great tit is dependent on man during the winter (e.g. Snow 1953, Haftorn 1957, von Haartman 1973). The willow tit has an additional important adaptation mechanism for saving energy during winter — hypothermia at night (Haftorn 1972).

These predictions suggest that the population fluctuations in the willow tit will not be as pronounced as those in the great tit, as was confirmed by the data available.

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