

Changes in the breeding parameters of the Crested Tit *Parus cristatus*

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The Crested Tit was studied in 1975–1983 in the Oulu area (65°N, 25°30'E), northern Finland. The material comprised 30 nests. Additional data, collected between 1921–1948 from 24 nests, were obtained from the Merikallio Archives at the Zoological Museum of the University of Oulu.

In Sanginsuu, the breeding density varied annually between 2.3 and 3.8 pairs/km², in the other localities studied between 0 and 1.6 pairs/km². During 1975–1983 the median onset of laying was 28 April; in 1921–1948 it was significantly earlier, 20 April. The average clutch size in the present material was 4.5; in the earlier period it was about 0.5 eggs larger. The breeding success, calculated according to the method of Mayfield, was 55 % and the reproductive rate was 2.5 fledglings/pair/year. The losses were mainly due to predation and desertion.

The possible reasons for the decrease in the northern populations of this species are discussed in the context of the changes in the reproductive output.

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Introduction

The numbers of Crested Tit *Parus cristatus* have declined dramatically in northern Finland during recent decades (Järvinen & Väisänen 1978). The biology of this species has attracted little attention, however, possibly owing to its low breeding density and its tendency to prefer natural cavities to nest-boxes.

During our study of the breeding biology of hole-nesting species in the Oulu area (Ojanen 1983, Orell 1983a), we also collected data on the Crested Tit. The purpose of this paper is to describe the biology of a population of this species breeding in northern Finland and to compare the breeding biology of the tit species living in these northern latitudes.

Material and methods

The work on hole-nesting birds started in 1969 in the Oulu area (c. 65°N, 25°30'E, Ojanen et al. 1978). Two Crested Tit nests were found in natural holes during the early years, but systematic study of the Willow Tit *Parus montanus* and Crested Tit did not start until 1975. The breeding data and information on the densities of these birds originate from the following sites: Taskila, Kuivasjärvi, Sanginsuu, Isokangas (in Oulu), Tuiranhovi, Vittasuo and Uikulaisjärvi (in Haukipudas).

The areas are described in detail in our earlier papers (e.g. Orell & Ojanen 1983a). The bulk of the Crested Tit data originate from the Sanginsuu area, the species being very rare or absent at most of the other sites. As there were very few decaying trees at Sanginsuu suitable for the birds to make nest cavities in, stumps of decaying birches were collected elsewhere, transported to the selected sites and tied on to suitable tree trunks. Holes from previous years were also filled with decaying wood in order to induce females to re-excavate and to breed again in the same cavity. In addition, nest-boxes made from birch trunks were

filled with coarse sawdust or decaying wood and attached to trees. The Crested Tit also occasionally accepted normal nest-boxes.

The sites were visited about once a week from mid-April onwards to locate the nests. About half of the Crested Tit nests were found after the young had hatched and the rest mainly while the females were incubating.

The clutch and brood sizes were checked with a small mirror and torch. When the nestlings were seen for the first time their age was determined using information from selected Willow Tit nests in which the growth of the nestlings was followed daily (see Orell 1983). The growth rate of these two species seems to be the same, and therefore no corrections were applied.

The locations where the Crested Tits were seen were marked on a map during all visits to the study areas, and the number of breeding pairs was obtained from the information collected on the maps (see also Orell & Ojanen 1983c).

A laying frequency of one egg per day was used to determine the onset of laying for clutches found at the laying stage. For nests found at later stages (during incubation or at the nestling stage) the date of laying was counted back, taking into consideration the number of eggs/chicks present in the nest, the average incubation time (15 d, v. Haartman 1969) and the age of the nestlings on the day of discovery.

The clutch was identified as being completed if the number of eggs was the same during consecutive visits at an interval of at least 2 days and subsequently incubated, or if the eggs had evidently been incubated as judged from their dull colour (see Ojanen & Orell 1978, 1983a).

In addition to our material, data collected during 1921–1948 were available from the Merikallio Archives at the Zoological Museum of the University of Oulu. The nests totalled 24, including one from the 1920's, 14 from 1930 to 1934, two from the late 1930's, and seven from 1946 to 1948. Most of them were from Oulu and a few from the nearby communities of Haukipudas, Kempele and Kiiminki. The discovery dates had been given for the nests and the start of laying was estimated, using a rough but conservative method (i.e. we intentionally postdated the estimated laying for the first egg). The last egg was estimated to be laid on the day of discovery if the clutch contained "fresh" eggs or indications of incubation were lacking (N=6). Incuba-

tion was estimated to have lasted 5 days for clutches containing "slightly incubated" eggs ($N=2$) and 10 days for those containing "strongly incubated" eggs ($N=5$). If the age of the young was not given, "downy" young were recorded as 5 days old, "large chicks" as 10 days, chicks "near to fledging" as 15 days, chicks "just fledging" as 18 days and those "just fledged" as 22 days (one of each case). An early case where the age of the young was not given was recorded as just hatched and a late one as 10 days of age, i.e. about half-way to fledging. The clutches were regarded as completed if they contained "slightly" or "strongly" incubated eggs.

Results

Density. The average density at Sanginsuu was 2.9 pairs/ km^2 (Table 1). The mean for the other sites was only a fifth of that figure. No breeding Crested Tit pairs were observed in the subareas of Taskila, Kuivasjärvi and Vittasuo, while 1 to 3 pairs bred at Tuirahovi and Uikulaisjärvi in six of the nine years. Annually 3–5 pairs bred or occupied a territory at Sanginsuu.

Timing of breeding. The material from the years 1969–1983 contains 27 clutches for which the time of laying of the first egg could be estimated. The median onset of laying was on 28 April (Fig. 1). The data from the Merikallio Archives, on the other hand, point to a significantly earlier date in 1921–1948 (Mann-Whitney U, $P < 0.001$), 20 April on average.

In 1969–1983 the earliest clutch was started on 17 April and the two latest on 8 and 15 May. In the Merikallio Archives there were nine clutches which

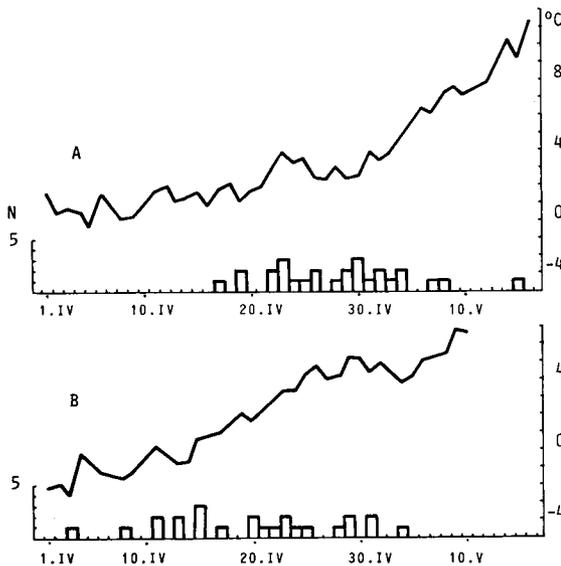


Fig. 1. Initial dates of Crested Tit clutches in the Oulu area in 1969, 1970 and 1975–1983 (A) and in the Merikallio Archives from the years 1921, 1930–34, 1936, 1939, 1946 and 1948 (B). The daily mean temperatures for 1975–83 (A) apply to Oulu airport and those for the years of the Merikallio Archives (B) to the town of Oulu.

Table 1. Numbers of breeding pairs of the Crested Tit (N) and the breeding density (pairs/ km^2 , mean \pm SD) in Sanginsuu and other sites in Oulu (subareas Taskila and Kuivasjärvi) and Haukipudas (subareas Tuirahovi, Vittasuo, Uikulaisjärvi).

Year	Sanginsuu (130 ha)		Other areas		
	N	density	N	Area (ha)	density
1975	2	212	0.9
1976	4	3.1	1	197	0.5
1977	5	3.8	3	191	1.6
1978	3	2.3	1	203	0.5
1979	3	2.3	0	201	0.0
1980	4	3.1	1	201	0.5
1981	4	3.1	1	203	0.5
1982	3	2.8	2	207	1.0
1983	4	3.1	0	267	0.0
Average	3.8 \pm 0.7	2.9 \pm 0.1	1.2 \pm 1.0		0.6 \pm 0.5

were started earlier than the earliest in our material (Fig. 1). In four of these newly hatched young were noted in late April or during the first pentade of May. In two nests large young (15 and 18 days of age) were recorded in the middle of May, and there were two clutches with fresh and one with slightly incubated eggs. The error made in calculating the start of laying for these very early nests can be assumed to be slight. In our data the earliest hatchlings were noted during the first pentade of May (2 out of 24), the bulk of the broods hatching during the second pentade (16/24). Thus, the earliness of the laying in 1921–1948 is not due to misinterpretation of the old data.

The length of the laying season in 1969–1983 was 29 days. In 1921–1948 the laying season extended from 3 April to 4 May, a span of 32 days.

After predation or other nest failure no evidence was found of repeat nesting, in spite of searches carried out in the nearby areas. In a couple of cases the parents were seen for some days after the failure, the female begging for courtship feeding. Similarly, no attempts at second layings were detected.

An increase in the ambient temperature affected the start of laying. In the April clutches ($N=17$) an increase from ca. 1°C to ca. 3°C took place 3 to 8 days before the first egg was laid (Fig. 2). Laying in the first 5 days of May ($N=8$) was started at slightly colder temperatures than laying beginning in April (Fig. 2). In May laying starts very rapidly once the temperature has increased to around 3°C. The years 1976 and 1981, in particular, had warm periods in the middle of April, and a few Crested Tits started to lay at that time. A cold period then prevented the others from starting until the beginning of May. In 1977 and 1978 the April temperatures were quite low and none of the Crested Tits started to lay until May ($N=4$). During 1921–1948 laying started at slightly, although not significantly, lower mean temperatures than in 1975–1983. The mean temperatures for the first half of April in the early years were about 0.5–1.0°C lower than in recent years (Fig. 1). When single layings are considered, the same difference, about

Table 2. Clutch and brood sizes of the Crested Tit in the Oulu area.

Status	Clutch/brood size						Mean	SD	N	Years	Source
	2	3	4	5	6	7					
Completed clutches	1	6	9				4.50	0.63	16	1969–83	This study
			1	3	3		5.28	0.76	7	1930–39	Merikallio Archives
Brood size	1	2	8	2			4.77	1.01	13	1969–83	This study
		1	2	1	1		5.20	1.48	5	1921–48	Merikallio Archives

0.5°C, is noted in the mean temperatures prevailing 10 to 6 days before the egg was laid (Fig. 2, the same applies for even longer periods, 15 to 6 days before the start). However, large variation in the mean temperature between individual females and years indicates that other factors, such as food, also determine the onset of laying.

Clutch size. In 1969–1983 the mean size of the completed clutches in the Oulu area was 4.5 eggs, this being significantly ($P < 0.05$) smaller than in 1921–1948 (Mann-Whitney U-test, two-tailed) (Table 2). In the present data the range of the completed clutches was from 3 to 5 eggs. Amongst the broods two were found which contained 6 young and one in which there were only 2 (Table 2). The older material included a nest in which 6 newly hatched young were recorded and a clutch of 7 eggs (not mentioned as being completed).

In our material the proportion of clutches and broods which contained 6 or 7 eggs or young was 2/29 (7%); in the earlier material it was 6 out of 18 cases (33%, see also Table 2). The difference between these two data sets (>6 vs. ≤ 6) is significant (Fischer exact, $P = 0.041$).

Breeding success. The success was calculated according to the recommendations of Mayfield (1961), i.e. taking into consideration the number of nests found and the time for which each nest was under observation. The unit used is the nest-day, i.e. one nest observed on one day. The survival rate of the nests was

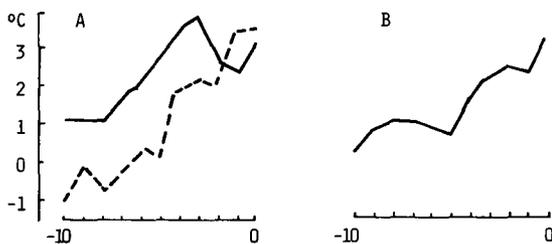


Fig. 2. Mean daily temperatures of the 10 days preceding the laying of the first egg (day zero). Each nest treated separately. A refers to the present data (1975 to 1983) in April (continuous line) and May (broken line) and B to the Merikallio Archives.

calculated for the different nesting stages and the survival of individual eggs and nestlings was calculated to include partial losses in otherwise successful nests. The final nesting success was calculated by combining the probabilities of success during the different nesting stages.

The analysis of breeding success by Mayfield's method, including data on 28 nests, gave a probability of nest survival during both the incubation and nesting stages of about 75% (Table 3). Partial losses of nestlings were especially low in the successful nests, these losses being only about 2–3% during the hatching and nestling periods. About 55% of the eggs laid produced fledglings.

The estimation of total losses assesses the fate of 29 nests, i.e. including one clutch which was judged to be deserted at the time of finding and which was not included in the material used for Mayfield's method. Of these 9 were lost (31%), 5 by desertion and 4 to various predators — most probably stoats, squirrels and woodpeckers.

Table 3. Nesting success of the Crested Tit (Mayfield method 1961). 28 clutches considered. (Incubation time 15 d and nestling time 20 d used in calculating the probability of survival.)

	Laying stage	Incubation stage	Nestling stage
Number of clutches	5	15	25
Total losses (no.)	0	3	5
Nest-days	19	170	356
Probability of nest survival	1.000	0.766	0.754
Nest mortality/nest-day	0	0.018	0.014
Egg-days during incubation		540	
Eggs lost during incubation		0	
Probability of survival		1.000	
No. of eggs in active nests at the start of hatching		46	
Unhatched eggs or nestlings lost		1	
Probability of survival		0.978	
Nestling days in successful nests			1474
Nestlings lost or dead after hatching stage			2
Probability of survival			0.973
Probability of survival:			
hatching — fledging			0.718
incubation — fledging			0.550
laying — fledging			0.550

Discussion

Densities and population fluctuations. The density of the Crested Tit has decreased in northern Finland from 1 to 2 pairs per km² in the 1940's to about 0.1 pairs per km² in the 1970's (Järvinen & Väisänen 1978). Väisänen & Rauhala (1983) reported a decrease of similar size in Simo, about 100 km north of the present study area, the density having decreased from 2.3 pairs per km² in 1959 to about 0–0.2 pairs per km² in 1977–1980.

In southern Finland the decrease has not been so dramatic as in the north (Järvinen & Väisänen 1978, Haila et al. 1979). The maximum densities were over 3 pairs per km² in the 1970's (Järvinen & Väisänen 1978), and in the Åland archipelago they were 2.9 pairs per km² (Haila et al. 1979). In Sanginsuu the density was the same as in the Åland archipelago and in the other study areas in Oulu it was greater than in Simo (0.6 vs. about 0.1 pairs per km²), but these results were obtained by different methods. Vilhunen (1984) has reported that areas with nest-boxes may induce the Willow Tits to breed in higher densities than in natural conditions, and the same may be true of the Crested Tit. Both of these species, however, were reluctant to select wooden nest-boxes in our study areas (Orell & Ojanen 1983c, this study). A density similar to that in Sanginsuu has been reported from a nest-box area in southern Sweden, near Gothenburg, where v. Brömssen & Jansson (1980) have noted 3–5 pairs per km². Densities may be very high in particular sites in Europe; in Switzerland, for example, densities as high as 4 pairs per 10 ha have been noted in coniferous forests, up to 3 pairs in mixed forests and up to 2 in deciduous forests (Glutz v. Blotzheim 1962).

The density of the Crested Tit is about the same as that of the Willow Tit in the Gothenburg area (v. Brömssen & Jansson 1980); in the Oulu area the Willow Tit density is 3-fold that of the Crested Tit in Sanginsuu, 18-fold in the other study areas and 6-fold

over the total area studied (data for the Willow Tit from Orell & Ojanen 1983c).

The population appears to be very stable in both Sanginsuu and Gothenburg, where the coefficients of variation (CV) in density were 19 and 15 %, respectively (Gothenburg data from Ekman 1979). In the less preferred areas of Oulu, however, the CV was 81 %, suggesting that these areas are only marginally accepted as nesting sites by the Crested Tit.

The reliability of the old data. Nest-card data collected by amateurs are often incomplete and the information on the cards is not easy to interpret (see e.g. v. Haartman 1969). In the present case one may question the reliability and accuracy of the data.

With the exception of one nest containing fresh eggs, the data on the Crested Tit in the Merikallio Archives were collected by experienced amateurs or professionals (Vainö Salonen, Aarne Hellemaa, Rauno Tenovuo), all known to have a keen eye for biological phenomena and to be accurate in recording them. Also, in the Merikallio Archives the bulk of the information on e.g. the Willow Tit and Great Tit *Parus major* nests is from late May and early June, and the possibility can thus be excluded that the Crested Tit data are biased towards early clutches.

Laying time. The laying of the Crested Tit begins in March in Holland (Lack 1950), Germany (Winkel 1980) and Sweden (Durango 1945), but the main period is in April in all the areas studied, including Oulu (Table 4). Very often the laying period extends into May, although repeat and second layings are found at this time in the southern populations (see Lack 1950, Delmée et al. 1972, Winkel 1980).

The Crested Tit lays 10 days later in Oulu than in Lingen, Federal Republic of Germany (52°27'N, data from Winkel 1980, incubation time taken as 15 d); the corresponding difference in the median dates for the Oulu and Gothenburg populations is 5 days (Gothenburg data from v. Brömssen & Jansson

Table 4. Median and mean times of laying in Crested Tit populations in different parts of Europe.

Population	Years studied	Laying date				Source
		Median	Mean	SD	N	
Finland						
Oulu area	1921–1948	20–21.IV.	20.IV.	8.08	24	Merikallio Archives
Oulu area	1969–1983	29.IV.	28.IV.	6.46	27	This study
S. Finland 60–62°	–1960's	c. 24–28.IV.			58	v. Haartman 1969
S. Finland 62–64°	–1960's	c. 24–28.IV.			12	v. Haartman 1969
Sweden						
Whole country	–1940's	c. 1–10.V.			111	Durango 1945 ¹
Gothenburg	1973–1979	24.IV ²			?	v. Brömssen & Jansson 1980
Fed. Rep. Germany	1974–1978		3.V.	7.3 ³		Winkel 1980

Notes: 1) finding dates of fresh or slightly incubated clutches — 2) mean of median dates for 1973–79 — 3) mean hatching date.

1980).

Thus the retardation of laying with advancing latitude was relatively small in this species, being only 0.8 days per degree of latitude between the populations of Lingen and Oulu and 0.7 days between those of Gothenburg and Oulu. The corresponding retardation in the Willow Tit was 0.5–1.5 days per degree of latitude, and in the Great Tit 1.6 days (Orell & Ojanen 1983a). These data thus suggest that the retardation in *Parus* species is smaller than the average of 2–3 days per degree of latitude given preliminary for 354 avian species by Baker (1938). It is indeed remarkably small in the Crested Tit, and more data are needed to confirm this.

What may be the reason for the significantly later breeding of the Crested Tit in the Oulu area now than in 1921–1948? According to the temperatures of the 10 days before the first eggs were laid, the laying tended to start at slightly lower temperatures in 1921–1948 than now (Fig. 2). The mean temperature for March was also lower in the earlier period, but not that for April:

	Mean temperature in 1921–1948	Long-term average 1975–1983	1931–1960
March	−5.8°C	−5.4°C	−7.0°C
April	0.9°C	0.7°C	−0.1°C

In addition, both the March and April temperatures were above those recorded for the period 1931–1960.

Slight differences in the local temperature may be decisive in the initiation of laying (e.g. O'Connor 1978), although a number of other factors are also important. In conclusion, it seems to us that the Crested Tits responded more quickly to the increase in temperature in the earlier years than nowadays, which caused an earlier onset of laying.

The Crested Tit laid its eggs a fortnight before the Willow Tit in Lingen, while in Gothenburg the difference was 12–13 days and in Oulu 19 days (Willow Tit data derived from Winkel 1980, v. Brömssen & Jansson 1980 and Orell & Ojanen 1983c). The Crested Tit thus lays relatively earlier in the Oulu area than in more southern populations.

During the eight years studied, the length of the breeding season of the Crested Tit population (from first egg laid to last chick fledged) was only 38 days; the corresponding time for the Willow Tit was 65 days (Orell & Ojanen 1983c).

Clutch size. The clutch size of the Crested Tit tends to be smaller in the northern populations than in those further south (Fig. 3, see also Perrins 1979). In the Oulu area the clutch is about 1.5 to 2 eggs smaller than in the populations in the Lithuanian SSR, Holland, the Federal Republic of Germany, Belgium and Sweden. The decrease in clutch size towards the north is about 0.12 egg per degree of latitude (Fig. 3). Similar decreases in clutch sizes towards the north have been reported in the Pied Flycatcher (Järvinen

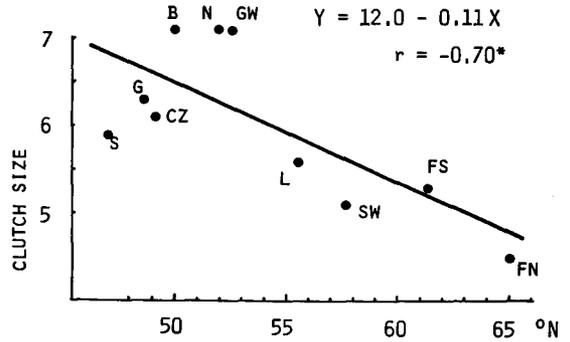


Fig. 3. Trend of the average clutch size of the Crested Tit in the following European populations: S = Switzerland, Glutz v. Blotzheim 1962; G = Fed. Rep. Germany, SW part, Löhr 1966; CZ = Czechoslovakia, Balat 1976; B = Belgium, Delmée et al. 1972; N = The Netherlands, Lack 1950; GW = Fed. Rep. Germany, Winkel 1980; L = Lithuanian SSR, after Winkel 1980; SW = Sweden, Gothenburg, v. Brömssen & Jansson 1980; FS = Southern Finland, v. Haartman 1969; FN = Northern Finland, this study.

& Lindén 1980) and Redstart (Pulliainen et al. 1982), and there is also a slight tendency for the clutch size of the Willow Tit to decline northwards from Central Europe (Orell & Ojanen 1983c).

In the Crested Tit populations the maximum number of eggs is reached in Western and Central Europe, where 9 eggs have often been recorded, and sometimes even more (Lack 1950, Löhr 1964). Löhr (1964) suggests that the largest clutches, 9 to 12 eggs, may result from situations where a female has lost her nest during laying and lays additional eggs in the nest of another Crested Tit. A female may also take over a Coal Tit *Parus ater* nest, for example, and lay a full clutch there. The size of the mixed clutch will then exceed that laid in normal situations, and if the eggs of the two species are indistinguishable, such cases may pass unnoticed. Winkel (1980) also reports cases where two Crested Tit females had probably laid in the same nest, the resultant clutches being exceptionally large.

The maximum number of eggs for the Crested Tit in the Oulu area is evidently six (see section Clutch size under Results in this study). In the Merikallio material there are two records where a clutch size of 7 eggs is suggested. In southern Finland the maximum is 8 eggs (v. Haartman 1969); one of these nests was found surprisingly late, on 9 July, and was suggested by Suomalainen (1927) to be a second laying.

Breeding success. The Crested Tit generally had a very high breeding success in the populations studied (Table 5). Total losses may be higher in the Oulu area (31 %) than further south in Europe, but more

Table 5. Breeding success of the Crested Tit in different parts of Europe.

Population	Total losses		Partial losses			Source
	Initial no. of clutches	Loss %	Initial no. of clutches	eggs	Loss %	
Finland	29	31	9	41	5	This study
Sweden Gothenburg	—	—	?	?	13	v. Brömssen & Jansson 1980
Fed. Rep. Germany						
Lahr	29	7	27	171	11	Löhr 1966
Lingen	50	6	47	?	17 ¹	Winkel 1980
Holland	—	—	?	6869	14	Lack 1950
Belgium	—	—	18	122	10	Delmée et al. 1972
Czechoslovakia	6	67	—	—	—	Balat 1976

Note: 1) difference between mean clutch size and mean size of fledged broods.

data are needed to confirm this. In two German populations the total losses averaged about 6–7 % (Winkel 1980, Löhr 1966). In most of the populations studied (Table 5), partial losses amounted to about 10–17 %, while in the Oulu area they accounted for only about 5 % of the eggs laid.

In the Oulu area, the total success of the Crested Tit was the same as that of the Great Tit. When account is taken of total and partial losses, the Great Tit raised 55 % of the eggs to fledglings (Orell & Ojanen 1983b), while the corresponding figure for the Willow Tit was 71 % (Orell & Ojanen 1983c). The reproductive rate (number of fledglings per pair per year) was 6.09 in the Great Tit (Orell & Ojanen 1983b), 5.37 in the Willow Tit (Orell & Ojanen 1983c) and 3.14 in the Crested Tit (91 fledglings, 29 pairs started breeding, Table 5). This figure for the Crested Tit is probably too high, as Mayfield's method gives an estimate of 2.5. No estimates of total success or the reproductive rate have been given for the other European populations of the Crested Tit.

Reasons for the decline in Crested Tit populations. According to Järvinen & Väisänen (1978), between the 1940–50's and the 1970's the Crested Tit populations have decreased drastically in northern Finland, by up to 95 %. The reason they suggest is the impact of forestry; clear-cutting of large areas in the north has decreased the proportion of old forests (Järvinen et al. 1978).

The present observations regarding the breeding parameters — delay in the start of laying, smaller clutch size, heavy losses — may be considered to support the hypothesis of Järvinen & Väisänen (1978). Clearly, all the facts point to a low breeding effort in this species.

The scarcity of suitable nesting holes most probably prevents some pairs from breeding annually, thus lowering the production. The small number of rotten trees, in which the nests are located, may make them

more easily detected by predators than earlier, thus causing extra losses. The structure of modern forests, with large clear-cut areas and a scarcity of old trees, may make it more difficult for the females to find the extra food needed for producing eggs, causing delayed laying and a smaller clutch size.

Microevolutional shifts must also be considered when populations are living in unpredictable areas. Wiens (1977) remarked that selection can be very intense when populations experience "ecological crunches". Studies on the morphological traits of Darwin's Finches on the Galapagos islands have shown that under harsh conditions populations were subjected to stabilizing, directive or disruptive selection (Boag & Grant 1981, Grant & Grant 1983, see also Dhondt et al. 1979). During the crash of the Crested Tit population selection may have been intense.

It seems, however, that the causes of the decrease may be more complex than those presented here, and that further research is needed to clarify the situation.

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Selostus: Töyhtötaian pesimätuloksen muutoksista viime vuosikymmeninä

Pönttölintututkimuksemme yhteydessä olemme seuranneet töyhtötaian pesimistä systemaattisesti vuosina 1975–1983. Aikaisemmin löydetty kaksi pesää huomioiden aineistoa on yhteensä 30 pesinnästä vuosilta 1969–1983. Vertailuaineistoa koottiin Oulun yliopiston Eläinmuseon Merikallion arkistosta 24 pesästä vuosilta 1921–1948.

Vuosittain on tutkimusalueille saatu 1–2 töyhtötaiaa pesimään ripustamalla lahonneita koivupötkkelöitä puunrunkoihin ja vuolaismalla tuohien aloitusreikä. Myös muutama luonnonkoloon rakennettu pesä on tavattu vuosittain, sensijaan pönttöihin laji pesii vain harvoin. Töyhtötaian pesimätiheys vaihteli Sanginsuussa vuosina 1976–1983 2.3–3.8 paria/km². Muilla tutkimusalueilla tiheys oli alhaisem-

pi, 0–1.6 paria/km² (taul. 1). Ehkä pesimäpaikkojen tarjonnasta johtuen tiheys Oulun seudulla oli suurempi kuin Simossa (1977–1983 vain 0–0.2 paria/km²).

Vuosina 1969–1983 muninnan alkamisen mediaanipäivä oli 28.IV, varhaisimmillaan 17.IV ja myöhäisimmillään 15.V. Vuosina 1921–1948 pesintä oli merkitsevästi aikaisempi (alkamisen mediaanipäivä 20.IV). Tuolloin muninnan alku vaihteli rajoissa 3.IV–4.V. Molempina jaksoina muninnan alku oli yhteydessä lämpötilan nousuun 3–8 päivää aikaisemmin (kuva 2). Aineisto viittaa lisäksi siihen, että vuosina 1921–1948 muninta alkoi hiukan alhaisemmissa lämpötiloissa kuin nykyisin. Pesän tuhouduttua uusintapesimistä ei todettu, ei myöskään toisia pesintöitä. Pesyekoko oli keskimäärin vain 4.5, mikä on merkitsevästi alhaisempi kuin vuosina 1921–1948. Varmistettujen pesyiden koko oli 3–5, lisäksi todettiin kahdesti 6 poikasta (taul. 2); aikaisempien vuosien maksimi on 7. Päinvastoin kuin monilla muilla lintulajeilla työttöisä pesyekoko laskee Euroopassa etelästä pohjoiseen (kuva 3). Mayfieldin menetelmällä laskettu pesimätulos oli alhainen: 55 % munituista munista tuotti poikasen (taul. 3). Hylkäämisistä ja predaatiosta johtuneet kokonaistappiot olivat suhteellisen suuret, 31 %, sensijaan onnistuneiden pesintöjen osittaitappiot jäivät alhaisiksi (taul. 5). Työttöisä poikastuotto vaikuttaa alhaisemmalta Oulun seudulla kuin muualla Euroopassa.

Pohjois-Suomessa on työttöisä pesivä kanta romahtanut viime vuosikymmeninä, mikä saattanee liittyä toteamiimme muutoksiin pesinnän ajoittumisessa ja poikastuotannosta. Yleensä myöhäinen pesintä merkitsee normaalia alempaa poikastuotantoa. Pesinnän myöhäistyminen saattaisi siten selittää kannan romahdusta. Nykyinen lehtipuita syrjivä metsänhoitotapa on ehkä perussyynä todettuihin muutoksiin työttöisä pesimisbiologiassa.

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