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Reliability of local breeding records in estimating regional population fluctuations of *Parus* species

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Fluctuations in the breeding density of the great tit and the willow tit was studied in the Oulu area, northern Finland, in 1969–87. Comparison was made with the winter bird census data from Raahe, 60 km to the southwest. The aim was to investigate the effect of spatial scale on population patterns. Local great tit populations in two 50 ha plots fluctuated in synchrony (r=0.73), but winter predation in 4 winters in one of the areas weakened the correlation between the areas. It seems that spring migration does not fill vacancies left by winter predation. The agreement between the population fluctuations in the nest box areas and winter bird population indices obtained in late January censuses at Raahe was good. The annual variation of the breeding density in the two study plots was pronounced (CV=43%). This variation seems to mask the possible effects of stochastic variance and errors affected by small samples. Therefore, a 50 ha study plot seems to give reliable data in estimating population fluctuations, even on the regional scale for the great tit. The breeding density of the willow tit did not correlate significantly with winter bird census results at Raahe. The population of this species was less variable (CV=20%) compared with the great tit. I suggest that because the willow tit population studied lives in the most preferred habitats of the species, annual variation in the breeding density is dampened. In such a case, stochastic effects may efficiently contribute to the population size in a local plot.

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1. Introduction

A crucial problem in studying the dynamics of animal populations is how to apply local scale results to larger regions. Wiens (1981, 1983) claimed that what is valid in large regions is not necessarily so in local populations. Thus the scale of space and time on which ecological systems are viewed makes a difference in the patterns that are detected (Wiens et al. 1986a, b). Most of the bird population studies deal with local scale rather than with regional or geographic scale. This is understandable because of sampling problems, but interpretations of patterns emerging in such studies are constrained by scale problems.

Therefore, conclusions drawn from long-term studies in one community can be quite different from those reached in short-term studies of similar communities located over larger areas (Wiens et al. 1986b).

Results from work on Finnish bird communities suggest that bird populations on a local scale, e.g. in small forests reserves, have not dynamics of their own but the changes can only be understood with reference to regional habitat changes (Väisänen et al. 1986). Breeding populations of some bird species of old forests have declined more than the old forest areas themselves (Järvinen & Väisänen 1979). Thus changes at the scale of local communities may have no connection with habitat changes. Therefore, the changes that occur in a small area over a number of years may be to a great extent stochastic (Helle & Järvinen 1986).

The aim of this study is to compare the annual variation of the breeding density of the great tit *Parus major* in two nest-box plots of comparable size with reference to winter bird census results obtained in the same region about 60 km to the SW. The willow tit *Parus montanus* is used for comparison. The aim is to

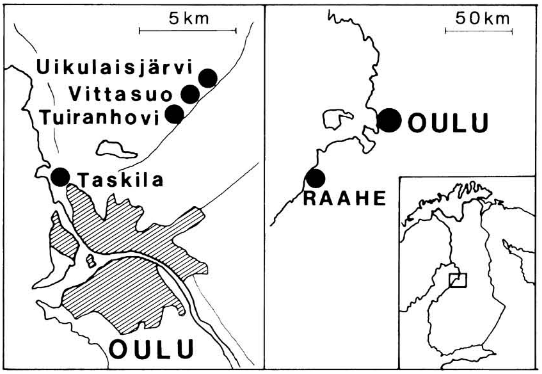

Fig. 1. Map of the study sites in the Oulu area.

assess the importance between the local and regional effects on population dynamics of these species. In particular, I investigated whether factors affecting the populations vary between different localities, or whether regional factors causing synchronized patterns among local populations dominate over the local populations.

2. Material and methods

2.1. Breeding data

The great tit study was performed during the years 1969–1987 at Oulu and Haukipudas, in northern Finland (65°N, 25°30'E, Fig. 1, see also Orell & Ojanen 1983a). The breeding data given here was collected in three study plots, Taskila (Oulu), Vittasuo and Uikulaisjärvi (Haukipudas). The site at Taskila was about 50 ha in area until in 1986 when it was enlarged up to 103 ha. Wooden nest-boxes numbering 30 in 1969 were increased up to about 75 in 1971 (Orell & Ojanen 1983a). After the enlargement of the study area in 1986, 150 nest-boxes were available (Orell 1988). The work at Uikulaisjärvi and Vittasuo, located about 8 km to the NE of Taskila (Fig. 1), started in 1970 and 1971, respectively. The former site is about 22 ha with 34–38 boxes during most of the study (Orell & Ojanen 1983a). In 1975 the area was enlarged up to 26 ha with 50 boxes but this part had to be abandoned due to forestry the year after. In Vittasuo changes were more frequent. During 1971–1977, about 26 ha was covered with up to 63 nest-boxes. After that year due to rearrangement of nest-boxes the area became somewhat smaller, about 22 ha with 51 boxes. It was enlarged again in 1983 up to 32 ha with 78 boxes. In all the areas, the whole of great tit population breeds in nest-boxes.

As the study plots of Uikulaisjärvi and Vittasuo are smaller than the Taskila area, their data have been pooled to form areas of comparable size. As the distance between these small plots is only about 600 m, the results describe the situation in the same locality and pooling is thus justified.

The nest-boxes of Taskila are located in mixed woods of birch *Betula pubescens*, alder *Alnus incana*, Scots pine *Pinus sylvestris* and Norwegian spruce *Picea abies* around typical Finnish suburban detached houses. The area is suitable for great tits to breed because of its deciduous nature. Due to small scale forestry and the building of new houses and roads, the location of boxes, especially in the eastern part, changed during the study. In 1986 the forest was thinned in about two-thirds of the area. Availability of food on feeding tables belonging to houses makes it possible for great tits to overwinter in the area. Part of the winter population takes advantage of roosting in nest-boxes.

Owing to lack of regular winter feeding at Uikulaisjärvi and Vittasuo, great tits are forced to move to inhabited areas for the winter. The distance from these study plots to the nearest houses is about 3 km. The Vittasuo area is a deciduous birch forest, but nest-boxes are also in small stands of Norwegian spruce. Uikulaisjärvi is dominated by spruce. In that area, as at Taskila, forestry has changed the environment to some extent. Owing to clearcuttings, the locations of boxes have been changed. The habitat at Vittasuo has undergone the fewest man-made changes, but in 1987 about 5 ha of the spruce-dominated stand was thinned.

Each spring the areas were visited at least once a week. The first visits in May gave the number of great tit pairs attempting to breed in the area. Late pairs, probably renesting birds of unknown origin, and pairs only holding a territory have been included when calculating the breeding density in the study plot. Every season practically all great tit fledglings have been ringed and most of the breeding adults individually marked with aluminium and coloured rings. Brood sizes were manipulated in 1986 and 1987 at Taskila and Vittasuo. Therefore, the reproductive values for those years are not comparable with the rest of the study period.

Breeding data on the willow tit has been gathered since 1975 in three study plots in Haukipudas: Tuiranhovi, Vittasuo and Uikulaisjärvi (Fig. 1, see also Orell & Ojanen 1983c). Because the study plots are located close to each other, the results are pooled. Compared with the habitat at Vittasuo and Uikulaisjärvi (see above), Tuiranhovi is more influenced by coniferous forests. The total area of these study plots is largely dominated by spruce swamps and moist spruce forests. These habitats account for about 55% of the environment. For a more detailed description of the study areas see Orell & Ojanen (1983c). Willow tits do not usually breed in nest-boxes in our study area (Orell & Ojanen 1983c), and a majority of the material here originates from nests in natural holes.

Despite intensive searching from mid-April onwards, nests of all the willow tit pairs holding a territory within the study sites were not found. During each visit locations of pairs observed were mapped and this information was used for estimating numbers of breeding pairs. The known nest sites and the many individually marked birds helped the estimation.

The area where the willow tit nests were searched for varied in size. At the beginning of the study the area fluctuated between 123 and 150 hectares. After 1980, it gradually increased up to 390 ha in 1985, but habitats were comparable over the whole area. In 1986 and 1987, the willow tit study concentrated only on Tuiranhovi-Vittasuo-Uikulaisjärvi, and the area where nests were searched for was increased up to 8 and 12 km^2, respectively. This area also includes habitats like open fens, clearfellings and young stands, which are unsuitable for willow tits to

Table 1. Mean dates of laying and size of first clutches, breeding density (pairs/10 ha) and the range in the number of breeding pairs of the great and the willow tit, and the range in size of the study areas.

	Parus major		*Parus montanus*
	Taskila	Vittasuo-Uikulaisjärvi	Haukipudas
Mean date of laying	17 May	20 May	15 May
Mean clutch size	9.4	10.4	7.8
Density	4.4	2.2	0.85
Number of pairs	11–45	4–17	6–33
Area, ha	48–103	42–54	123–390

breed because rotten stumps are lacking. When calculating density values for 1986 and 1987, only the part of the area (390 ha) which was also studied in 1985 was included.

2.2. Winter bird censuses

Regular winter bird censuses have been carried out in the Raahe area since 1975/76, about 60 km to the SW of Oulu (Karjalahti 1980, 1986). Seven routes, including urban and suburban areas, countryside, forests, bogs and seashore, measure 70 km altogether. Each winter the routes were censused once a month so that the first visit was in late October or early November and the sixth visit in late March or early April, using standard methods (see also Karjalahti 1980, 1986).

All the observers who have taken part in the censuses at Raahe are competent amateur ornithologists and the habitats and census routes have remained the same during the study. Thus the sources of error discussed by Sammalisto (1974) hardly have any significant contribution to the results.

3. Results

At Taskila, the great tit starts breeding earlier and its population is about twice that of Vittasuo-Uikulaisjärvi (Table 1). The willow tit is the earliest breeder of all. The size of the first clutches of the great tit, however, is larger in the Vittasuo-Uikulaisjärvi area. When the population was in its low phase, only 4 pairs bred in this area compared with 11 in the Taskila area. High density years have seen 17 and 45 pairs, respectively. Coefficient of variation in the breeding density has been about the same, 44%, for the great tit in both areas (Table 2) and 20% for the willow tit.

Table 2. Coefficients of variation for the great tit and willow tit population densities obtained using breeding records in the Oulu area and Southern Finland, from winter population indices at Raahe and in line-transect censuses of the whole of Finland. Figures in parenthesis denote the number of years.

	Coefficient of variation (%)		Source
	Parus major	*Parus montanus*	
Breeding population			
Haukipudas	– –	20.2 (13)	This study
Taskila	43.7 (19)	– –	—"—
Vittasuo-Uikulaisjärvi	43.5 (16)	– –	—"—
Häme	29.8 (17)	– –	Hildén 1985
Kirkkonummi	37.4 (18)	– –	Hildén 1985
SW-Finland	25.6 (10)	– –	Hildén & von Haartman 1987
Winter censuses			
Oct/Nov	32.5 (12)	33.4 (12)	This study
Nov/Dec	37.6 (12)	29.2 (12)	—"—
Dec/Jan	34.4 (12)	36.3 (12)	—"—
Jan/Feb	35.0 (12)	33.1 (12)	—"—
Feb/March	29.6 (12)	30.3 (12)	—"—
March/Apr	42.1 (12)	30.5 (12)	—"—
Line transects	19.2 (9)	26.8 (9)	Väisänen 1984 and unpublished

The breeding populations of the great tit at Taskila and Vittasuo-Uikulaisjärvi have in general fluctuated in a similar manner during 1972–87 (Fig. 2), r=0.735 (P<0.01). The year 1971 is excluded from the comparison because that was the first study year for Vittasuo and at that time the great tit population was hardly established there. Despite the overall parallelism, there were clearly deviating trends between the areas, especially at the beginning of the study. During 1971–1976, the population at Taskila showed pronounced fluctuations while the Vittasuo-Uikulaisjärvi population was stabilized at a high level compared with the year 1980. After 1976, the fluctuations were better synchronized, with the exception of 1982 and 1986 (Fig. 2).

At first glance, these irregularities could be attributed to the incomplete sampling of sparse populations (Wiens 1981). This is not the case, however. Great tits at Taskila stay in their breeding area also for winter and especially old birds roost during the winter nights in nest boxes (own unpublished data). In con-

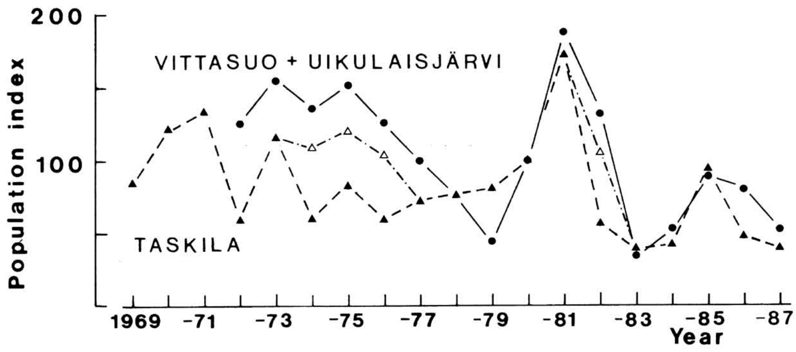

Fig. 2. Population fluctuation of the great tit in two sites in the Oulu area. The density in 1980 was given the index 100. At Taskila, estimated indices have also been shown for the four high predation years, adding the individuals which were roosting in boxes and predated during the winter to the actual breeding numbers (Δ, see also text).

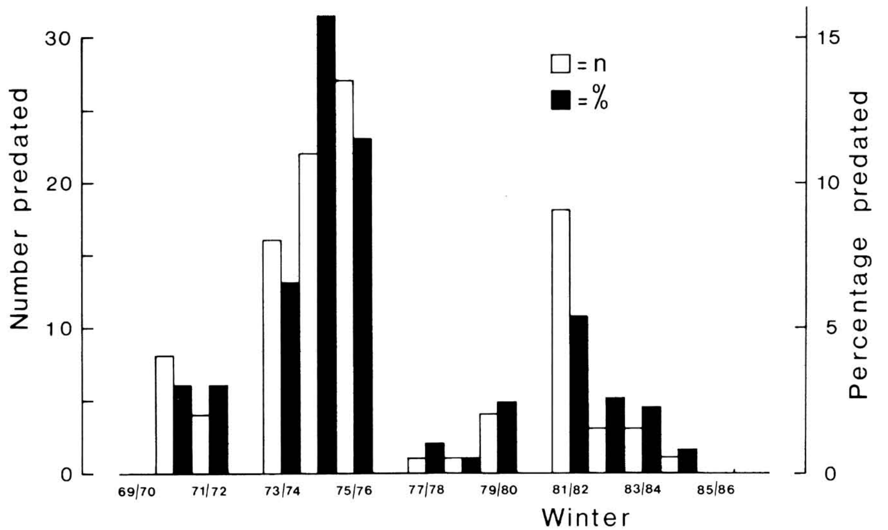

Fig. 3. Number of roosting great tits predated in nest-boxes during the winter and the predation values as a percentage of great tits present in the area after breeding in the preceding summer.

trast, great tits disappear from Vittasuo-Uikulaisjärvi in winter. In some winters, the great tit population roosting in nest-boxes at Taskila suffered heavy predation (Fig. 3), probably caused by the stoat *Mustela erminea* and occasionally the Pygmy Owl *Glaucidium passerinum* (see also Orell & Ojanen 1983a, Orell 1988).

In the winters 1973/74, 1974/75, 1975/76 and 1981/82 predation was especially heavy (Fig. 3). In those winters the number of great tit kills detected in boxes varied between 16 and 27. The population indices at Taskila were especially low in the following springs compared with the Vittasuo-Uikulaisjärvi area (see Fig. 2).

Similarity in the dynamics of the two study sites is also seen when comparing productivity of the great tit. In both study plots the variation in the annual number of young produced per area show a fairly good agreement (Fig. 4). This relationship holds although the areas differ in the frequency of second breedings. After successful first breeding, great tits more often make another attempt at Uikulaisjärvi and Vittasuo than at Taskila. This is probably attributable to higher density in the Taskila area (Orell & Ojanen 1983a). The most pronounced deviation from the linear relationship occurs in 1972 when the breeding population at Taskila was exceptionally low (see Fig. 2). There were a high number of fledglings per area in 1983 at Taskila due to frequent second breedings, while those were uncommon at Vittasuo-Uikulaisjärvi. The deep low in the breeding numbers in 1979 in the Vittasuo-Uikulaisjärvi area is also seen as a reproductive output lower than that expected from the overall trend.

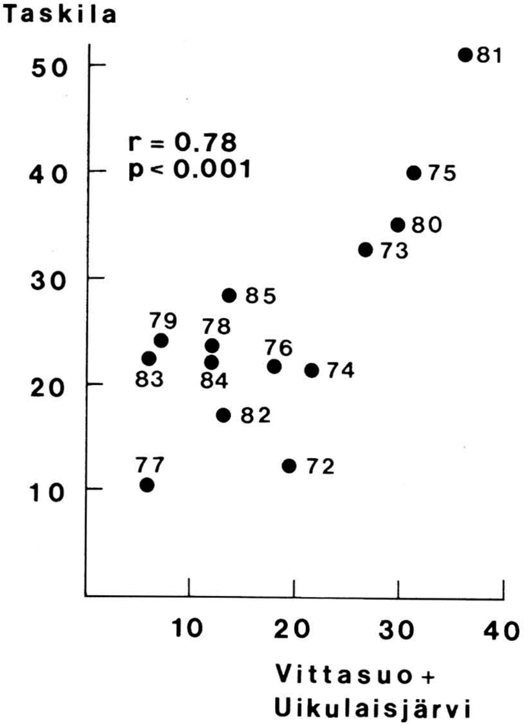

Fig. 4. The relationship between the young fledging/10 ha at Taskila and Vittasuo-Uikulaisjärvi.

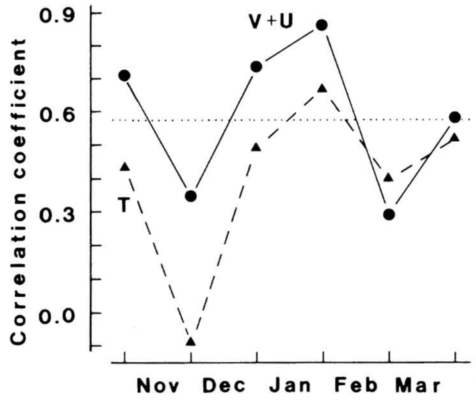

Fig. 5. Correlation coefficients between the winter (1975/76–1986/87) monthly indices of the great tit at Raahe and the breeding densities at Taskila (T) and Vittasuo-Uikulaisjärvi (V+U) in the following spring (n=12). The dotted line shows the level of significance P=0.05.

There were no adequate data available on the breeding time in the Oulu region for comparing whether the above results are applicable over a larger region. That is why the population densities were compared with winter bird censuses carried out at Raahe (Fig. 1). The comparison was made by calculating the correlation coefficients between the monthly results (birds/10 km) of winter censuses and the breeding density (pairs/10 ha) in the subsequent spring.

The results obtained in these analyses were rather similar for both nest-box areas. The data from Uikulaisjärvi-Vittasuo were a better fit with winter population indices than those of Taskila (Fig. 5). The results suggest the closest resemblance between the breeding density and the mid-winter population indices. When the correlation coefficient was the highest, the winter population index in the preceding January/February in the Raahe area showed about 74% common variation with the density recorded at Vittasuo-Uikulaisjärvi. It is worth mentioning that the correlations are linear and not affected by outliers. The correlations weakened as the spring advanced, especially concerning the population at Vittasuo-Uikulaisjärvi (Fig. 5).

3.2. Willow tit

The breeding density of the willow tit remained clearly below that of the great tit in both nest-box areas (Table 1). Both species featured low numbers in 1978 and 1979, but the overall patterns in the fluctuations of populations were dissimilar (cf. Fig. 2 and Fig. 6). The willow tit population proved to be less variable than the great tit (Table 2). When the breeding densities in the Oulu area were compared with the population indices obtained in the Raahe area, no significant relationships were found (Fig. 7). The closest correlation was with the data from late December, but the coefficient was not significant (r=0.53, P<0.1). However, the overall pattern, i.e. mid-winter indices showing the closest parallelism with the breeding density, was similar for both species. Furthermore, when comparison is made with the line-transect data from the whole of Finland, no agreement between the population trends can be found (Fig. 6). According to the breeding results the willow tit population density was less variable than suggested by line-transects. The relationship was just the opposite in the case of the great tit (Table 2).

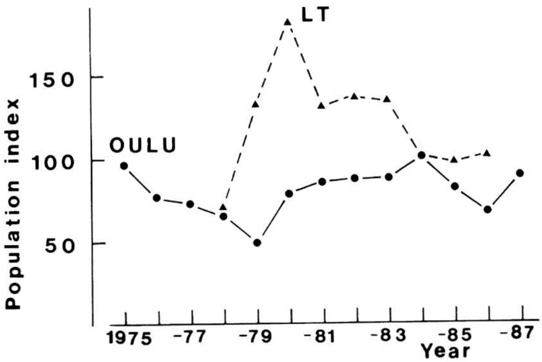

Fig. 6. Population fluctuation of the willow tit in the study plot near Oulu and according to the line-transect (LT) censuses (Väisänen 1984 and unpublished) in the whole Finland (100 = 1984).

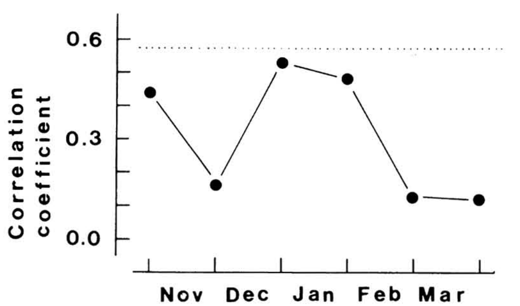

Fig. 7. Correlation coefficients between the winter monthly indices of the willow tit at Raahe and the breeding densities of the following spring near Oulu (n=12). The dotted line shows the level of significance P=0.05.

4. Discussion

4.1. Factors affecting breeding numbers

The aim of this study was to test the reliability of local breeding records when estimating the population fluctuation on a regional scale. The breeding density values of the great tit here are based on nest-box areas. There are many factors contributing to the actual numbers of pairs attempting to breed in the area: the density of the birds in the region, availability of nesting holes (e.g. Stephan 1961), migration (mostly juveniles: Koskimies 1948, Källander 1983) from the south, site tenacity and winter mortality of resident adult birds, predation (Nilsson 1984), weather in late winter and spring, winter feeding intensity (Hansson 1986), the nature of the habitat and competition (Enemar & Sjöstrand 1972, Löhrl 1978, Dhondt & Eyckerman 1980, van Balen et al. 1982). Thus many factors can possibly cause variation in the density in local populations even so that the variation on the regional level can be masked.

Interspecific competition for nest-boxes is not an important factor contributing to the annual variation of the breeding density of the great tit in the Oulu area, because the pied flycatcher *Ficedula hypoleuca*, the other species occupying boxes there, does not start breeding until 2 weeks later.

The nest-box areas have met changes which have affected the habitat. However, in all cases the new areas resembled the original habitat as much as possible. The area covered with boxes varied in every study site, but converting the number of pairs into density values gives comparable data between successive years. Furthermore, the number of nest-boxes available in plots has varied to some extent but this hardly had any influence on the breeding density because every summer, when the pairs established their territories, a surplus of boxes was left vacant.

Great tits are faithful to their breeding places (e.g. Kluyver 1951, Hildén 1979). However, after unsuccessful breeding, great tits can change their nesting area (e.g. Kluyver 1951) and this behaviour perhaps can partly explain the low breeding density at Taskila in 1972. Here, the breeding season a year before was carnage for great tits and pied flycatchers (Orell & Ojanen 1983b and unpublished). Over 30% of great tit clutches or broods were plundered by stoats, and at least 27% of the great tit females were taken by the predator. The local survival rate of females alive after breeding was low (11%) between the seasons 1971 and 1972, the long-term average being 41% (Orell 1988). Thus part of the females may have bred elsewhere in 1972.

Recently Hansson (1986) showed in Sweden that great tits breed in higher numbers in the vicinity of winter feeding places than they do farther from these places. The case is exactly the same at Taskila (winter feeding) compared with Uikulaisjärvi and Vittasuo (no feeding). There are no data available to assess the intensity of winter feeding at Taskila, but the intensity has certainly not varied sufficiently to have any important influence on the size of the subsequent breeding population.

It seems that the mortality caused by predators in winter was not compensated by influx of birds outside Taskila in spring. Krebs (1971) experimentally removed great tits in the Wytham Wood just prior to breeding, and vacant territories were immediately filled by intruders from the less preferred hedgerow areas. Ekman et al. (1981) noted that willow tit groups removed in winter were quickly replaced by new groups from territories bordering the experimental area, but the size of the total population decreased.

At Taskila some tits obviously can hold territories throughout the year. They feed in gardens and feeding tables and sleep during the night in boxes within their territory. Great tits occupy their roosting holes in late autumn in the Oulu area. During night checks at Taskila in November, old birds, local juveniles and immigrants were found sleeping in nest-boxes (own observations). Great tits keep roosting in the same hole throughout the winter if not disturbed (Schmidt & Drengwitz-Nees 1984). A majority of the roosting birds still breed at Taskila (own unpubl. data). Therefore, predation on the roosting part of the overwintering population affects the potential breeders next spring.

The fact that all of the vacancies left at Taskila after the predation were not filled during spring migration suggests that tradition can be important when great tits occupy breeding territories. It is also possible that although the great tit populations were abundant in the mid-1970s, individuals occupying territories in poor habitats, i.e. potential settlers in Taskila, were not present in greater numbers. Willow tits removed experimentally during egg laying were not replaced by immigrants, suggesting that territorial behaviour in this species does not limit breeding numbers in a given area (Cederholm & Ekman 1976). However, the predators removed Taskila great tits long before laying time. Thus the same interpretation is not necessarily valid here.

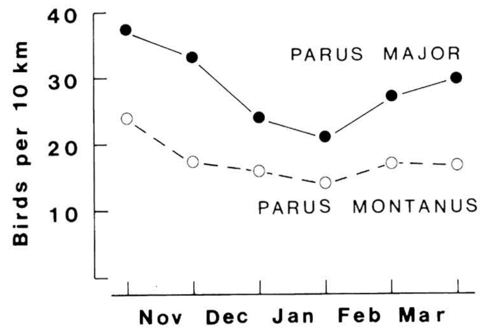

Fig. 8. Changes in the number of great and willow tits (birds/10 km) during the winter shown in the censuses at Raahe. Mean values for 12-year data.

4.2. Regional effects

The significant correlation in the breeding density of the great tit between the areas of Taskila and Vittasuo-Uikulaisjärvi suggests that the same factors contributing to the breeding numbers operate on a larger scale than in a local study plot. This occurs despite predation that could temporarily change the overall trend (stoats at Taskila). Moreover, the good agreement of the breeding densities with the results of winter bird censuses in Raahe, located at a distance of 60 km, suggests that the great tit population fluctuates synchronously, perhaps over a large region.

It is interesting that the breeding densities showed the closest resemblance to the mid-winter censuses, the highest correlation coefficient resulting from late January data (Fig. 4). As was stated earlier, in northern latitudes great tits overwinter in inhabited areas. According to Järvinen (1980) the great tits come to towns in the order: juvenile birds, old females, and old males. Some of the birds migrate a long distance southwards (e.g. Källander 1983) and the winter population will not be established until possibly December. As far as the availability of food is concerned, the winter is hardest for tits during late winter (e.g. Haftorn 1976). Thus it is obvious that during that time most of the great tits can be found around houses and feeding tables. Therefore, carrying out censuses then in and near inhabited areas seems to give the most reliable estimate with respect to the subsequent breeding density.

Low correlation for February/March can be accounted for by spring movements starting at that time. The increased population indices in spring (Fig. 8) suggests that there is a bias in the observability (Ekman 1981) in both tit species (but see Hogstad 1984). When the spring advances and days become longer, great tits spend more and more time moving in forests and come for shorter periods to feeding tables (own observations). The song activity of male birds increases and the birds start to occupy territories (e.g. Hinde 1952). It is probable that the onset of spring largely determines when this behaviour takes place. So, as far as the spring counts are concerned, these changes in behaviour can heavily mask the real fluctuations because the springs are not alike. That is why counts in late spring cannot give reliable estimates for the size of the subsequent breeding population. This is supported by the fact that the population index in March/April showed the highest level of variation (CV=43%) in the whole data set (Table 2).

Wiens (1981) introduced the concept of scale effect into the discussion on stability of communities. Accordingly patterns valid for continental or regional scales may not be apparent for local scales. In his critical review Wiens (1981) concluded that any pattern emerging when comparing different communities may be artifacts of inappropriate or incomplete sampling (see Wiens & Rotenberry 1981a). However, what is true of some communities is not necessarily true of others, as suggested by this study.

The breeding density of the great tit in the Oulu area, as well as the winter population around Raahe, show a pronounced interannual variation (Table 2). It seems that variation in the regional source population exceeds the variation at the local scale. Thus one can conclude that for the great tit, nest-box areas about 50 ha in size give a fairly good estimate for the annual variation in the population size even on a regional scale.

The great tit populations studied in the southern part of Finland are somewhat less variable than in my study populations in northern Finland (Table 2), but different populations fluctuate in synchrony (Häme vs. Kirkkonummi: r=0.87, n=17, data from Fig. 2, Hildén 1985; and Kirkkonummi vs. SW Finland: r=0.87, n=10, data from Fig. 2, Hildén & von Haartman 1987). Thus nest-box studies of the great tit seem to give reliable material in assessing population fluctuation even on a regional scale (see also Perrins 1965, Lack 1966, Karlsson et al. 1987).

The results for the willow tit seem more complicated. The population trends in the Oulu and Raahe areas are not similar, yet the variability of the population size differs, being clearly smaller in the former area. The breeding density variation resembles those reported by Svensson (1981), Wiens & Rotenberry (1981b) and Wiens et al. (1986a) for stable species.

The overwintering habits of the willow tit may be responsible for the deviating patterns. These birds form social groups in winter which use adjacent, non-overlapping territories (Ekman 1979a). Those individuals unable to enter these groups are known to live as floaters in unpreferred habitats. The winter bird census routes in the Raahe area include a variety of habitats covering areas marginal for overwintering and for breeding territories. Conceivably not only those birds which have a permanent winter territory but also a number of floaters are included in the census data. As the proportion of willow tits excluded from the winter territories may vary annually (Ekman 1979b), this is likely to increase the year-to-year variation in the winter census data around Raahe.

When occupying the territory it is decisive for the willow tits to find decaying stumps for excavating nesting holes. In the study sites of the Oulu area these stumps have been available either naturally or transported there by the researchers. For this reason and because the habitats favoured by the species, i.e. spruce swamps and spruce forests, dominate the study sites (Orell & Ojanen 1983c), the breeding data refer to a population living in the most preferred environment of this species, featuring low interannual variation in breeding density. Therefore, it is possible that if also less preferred areas, the buffer habitats, had been included in the study, the annual fluctuation in the breeding density would have increased (e.g. Kluyver & Tinbergen 1953, Brown 1969; sink and source populations in Wiens & Rotenberry 1981b).

There is one data set which throws some light to this question. At Räkäsuo in Ylikiiminki, about 30 km east of Oulu, line-transect censuses have been conducted during spring and summer since 1978 along a permanent route measuring 16.5 km (Lähdesmäki & Rautiokoski 1980, Lähdesmäki & Arvela 1986). The annual variation of the number of willow tits recorded in spring (March/April) and in the breeding season amounted to CV=39% and 33%, respectively. The census route consists mainly of bog areas which include less preferred habitats for willow tits. Spruce swamps cover only 8% of the area (Lähdesmäki & Arvela 1986). Thus the habitats along Räkäsuo census route can be regarded as buffer habitats for the species. The results are in agreement with the suggestion that willow tit populations are more stable in the most preferred habitats than in the marginal ones. Thus it seems that in order to obtain adequate data for studying the population fluctuation of the willow tit, the study area should be at least hundreds of hectares wide. It is important that a variety of representative habitats are included within the study plot.

Data on the breeding strategies of these two *Parus* spp. support the hypothesis that willow tit populations are less variable than those of the great tit. The willow tit lays smaller clutches, nearly exclusively has only one brood per year, and the breeding success is better than for the great tit (Orell & Ojanen 1983c). Thus along the r-K-continuum, the willow tit is more of a K-strategist (Orell 1983), which are expected to have less variable populations than the more r-strategic species.

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