Ornis Fennica 76:115–122. 1999

Suitable habitat distribution for the Long-tailed Tit (*Aegithalos caudatus*) as indicated by the frequency of occurrence — a long-term study

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Received 11 January 1999, accepted 23 April 1999

Data from 22 seasons were used to analyse the occurrence of Long-tailed Tits (*Aegithalos caudatus*) in relation to the habitat distribution in 26 one km-squares on the island Aasla in the SW archipelago of Finland. The one km-squares most frequently used by Long-tailed Tits had considerably higher proportions of deciduous/mixed (all species) and alder forest, whereas the number of habitat patches in the km-squares were less correlated to bird occurrences. A threshold for the frequent presence of Long-tailed Tits showed at 15–20% deciduous/mixed forest in km-squares in a logistic regression model, which agrees with the level suggested from a study in a Swedish landscape where the total proportion of deciduous/mixed forest was much lower. Further, the occurrence pattern of Long-tailed Tits over time suggested a density dependent relationship. The six km-squares occupied in low density seasons had a mean proportion of deciduous/mixed forest twice as high and a mean proportion of alder forest three times as high as the 20 others. Long-tailed Tits were also present in these six km-squares in all seasons with higher population densities, as predicted by a density dependent habitat selection. The importance of long-term monitoring, scale considerations and the use of population densities for habitat or landscape assessments are discussed.

1. Introduction

Aspects of landscape ecology are now commonly introduced into Scandinavian forest management (Angelstam & Pettersson 1997). However, knowledge of species-habitat relationships on large geographical scales applicable in landscape management is scarce. This lack of general results may be due to, for example, different and complex patterns among species and for homogenous versus heterogeneous landscapes (Morris 1995), or unpredictable rates of patch colonisation in landscapes with partly isolated populations (Hanski et al. 1994, Edenhamn 1996). Further obstacles to the analyses of large study areas are the difficulty of determining relevant measures of habitat quality (Morrison et al. 1992, Wiens 1995) and that long-term studies and experiments covering large spatial scales are rare. The relationships between population density and habitat quality may also vary between, and within, species due to the scale of the study area, the season and geography (Wiens et al. 1993, Jokimäki & Huhta 1996).

In birds, long-term data are often available and are used for population surveillance, where changes in the relative density are analysed (Marchant et al. 1990, Koskimies & Väisänen 1991). However, these data are rarely used by managers because, for example, they are often not spatially explicit. It is also clear that the use of population density for assessment of habitat or landscape quality involves scientific pitfalls. Habitat selection by individuals is suggested to be density dependent (Svärdsson 1949, Fretwell & Lucas 1970). However, in territorial species with despotic distributions, population density may be inversely related to habitat quality or breeding success (Van Horne 1983, Pulliam 1988, Vickery et al. 1992). In general, studies of the dynamics of population density in relation to habitat quality show a great variation due to the species and scale under study (Whitham 1980, Holt 1985, O'Connor 1986, Maurer 1986, Pulliam 1988). In spite of the difficulties, the possible use of species occurrence frequency (if not density) for habitat assessments continues to interest ecologists (Furness & Greenwood 1993, Pollard & Yates 1993). For definition of habitat types plant species are often used (Bunce 1982, Hägglund & Lundmark 1984), but including animal species in such habitat evaluations as well would further improve their value (Morrison 1986, Angelstam 1997).

However, to obtain reliable data regarding the relationships between population densities or distributions and habitat characteristics, long-term studies are often a prerequisite. Also, the only tool to discriminate between good years and poor years and to define natural variations in population densities is long-term data on population trends (Koskimies & Väisänen 1991, Morrison et al. 1992, Beshkarev et al. 1994). Unfortunately, useful and/or comparable data on populations, spanning several seasons, are rare for most species and areas.

In the present study we used data on Long-tailed Tit (*Aegithalos caudatus*) occurrences during 22 seasons in a landscape where suitable habitats were fairly well represented. The aim of the study was to define a suitable habitat distribution for Long-tailed Tits on a scale larger than single forest stands. We used the frequency of bird presence to reflect the quality of sample plots (one km-squares) and thereby determine measures of suitable habitat distributions.

The Long-tailed Tit is a resident species in Fennoscandia. Population densities are generally quite low but show great variations (Svensson 1996), where irruptive invasions and long-distance night flights occur (Lampolahti 1985). Pairs of the Long-tailed Tit defend territories only during the breeding season, approximately three months from early to mid-summer (Gaston 1973). Most of the year, however, they roam around in flocks searching for suitable habitat patches, with daily movements normally within 1 km^2 (Nakamura 1969, Gaston 1973, Bleckert 1991). The preferred habitat of the Long-tailed Tit is mature deciduous forests (> 30 years), often mixed with some conifers, where they feed on insects in the canopy (Gaston 1973, Rosenberg 1988, Harrap & Quinn 1996). Insects are most abundant on old deciduous trees of, for example, alder (*Alnus* spp.) and birch (*Betula* spp.) (Ehnström & Waldén 1986). These two genera are also known to be frequently used by foraging Long-tailed Tits (Bleckert 1991, L. Saari unpubl.). Long-tailed Tits are also shown to be sensitive to habitat isolation, as they are common only in areas with relatively dense aggregation of suitable habitats (Enoksson et al. 1995, Hinsley et al. 1995). Jansson and Angelstam (1999) presented a model, based on a five year study, for the occurrence of Long-tailed Tits prior to the breeding season (March–April) in habitat patches in a boreal landscape. Their model showed thresholds for the isolation of patches (< 300 m) and the proportion of suitable habitat (> 15% per km^2) for the reliable presence of Long-tailed Tits. We relate our results to their model.

2. Methods

2.1. Study area

The census was conducted on the island of Aasla (15.85 km^2) in the south-western archipelago of Finland (60°17´N, 21°55´E). The area is owned by private landowners and is characterised by a mosaic of coniferous and deciduous forest, agricultural fields and lakes. Forestry and agriculture are fine-grained and the distribution of forest habitats has not changed notably during our study period. The forest is dominated by scots pine (*Pinus sylvestris*) and norway spruce (*Picea abies*), and the most common deciduous species are birches (*Betula pendula* and *B. pubescens*), black alder (*Alnus glutinosa*) and aspen (*Populus tremula*) (Saari 1984). Deciduous trees occur both as pure or mixed stands and as single trees dispersed throughout most forest types. Deciduous and mixed habitats cover about 9% of the island.

Based on field determinations, the position and shape of all deciduous/mixed (deciduous–coniferous) and alder patches larger than approximately 0.25 ha were registered on a conventional topographical map (scale 1:20 000). These patches were not always delineated by clear borders from the surrounding habitats, but still, since they were relatively large, we treated them as separate patches. A grid of 26 one kilometre squares, which often included water (the Baltic Sea or lakes), covered all parts of the island. For each square we calculated the number of deciduous/mixed and alder patches, as well as the total proportion of the land area (%) covered by these habitats, and from that, also the proportions of deciduous/mixed forest except alders were calculated. The habitat proportions were measured from the map with a planimeter (Appendix).

2.2. Census

Long-tailed Tits were counted regularly on Aasla during 22 seasons, from 1975/76 to 1996/97. Data on the Long-tailed Tit occurrence were obtained by bird counts along a route that went through all the 26 one km-squares of the island, approximately twice a month all the year around. The route passed through all the habitat types present in each one km-square but because of, for example, the varying amounts of water the time spent in each km-square was not equal. To avoid the breeding period, when Long-tailed Tits are hard to detect, and to match the data used in Jansson and Angelstam's (1999) model, only data from October to March were used. All observations were recorded on the map and thereby attributed to a specific one km-square.

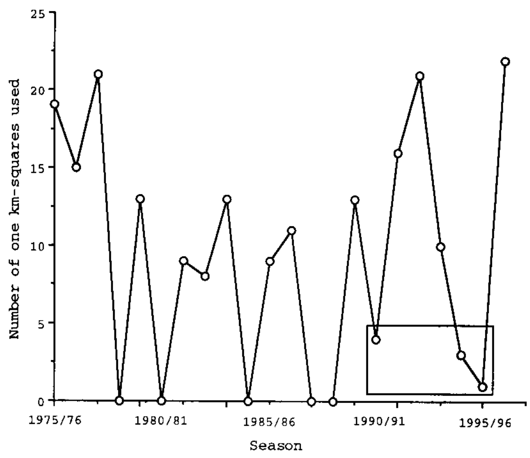

Fig. 1. The number of one km-squares at Aasla with Long-tailed Tit presence per season from 1975/76 to 1996/97. The rectangle frames the three seasons selected as low density seasons (see Discussion).

2.3. Analyses

Observations of Long-tailed Tits, flocks or individuals, were only used as presence/absence data per sample plot (one km-square) and season for the species-habitat analyses. Density was not used because flock size is often hard to determine and usually decreases during the season and may not be an accurate estimate of density. However, to what degree the frequency of observations reflected the number of individuals seen was tested.

The relationships between the number of seasons with Long-tailed Tits presence per one km-square and the measured habitat variables were analysed by simple and multiple regressions. A logistic regression was used to analyse the relationship between the most frequently used one km-squares and a significant habitat variable.

Further, the proportions of deciduous/mixed and alder forest in the one km-squares used by Long-tailed Tits in low density seasons (framed in Fig. 1) were compared to those of the other squares by the Mann-Whitney U test.

3. Results

The number of one km-squares with Long-tailed Tits presence per season over the study period are shown in Fig. 1. In five seasons (see Fig. 1) no

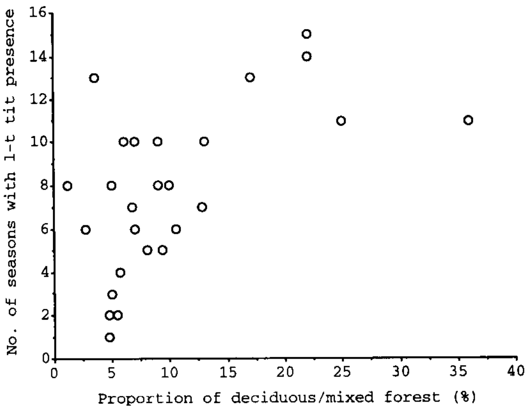

Fig. 2. The relationship between the number of seasons with Long-tailed Tit presence in one km-squares and the proportion (%) of deciduous/mixed forest in these squares (n = 26).

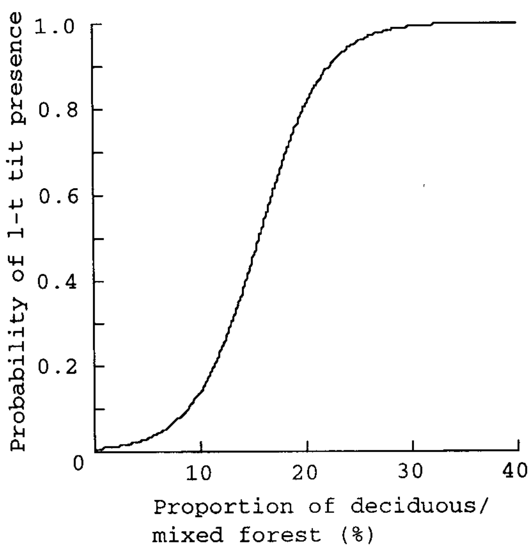

Fig. 3. The modelled probability of seasonal Long-tailed Tit occurrence in relation to the proportion (%) of deciduous/mixed forest in one km-squares at Aasla. The final equation used in the model was: y (= presence in > 10 seasons) = exp (– 5.04 + 0.32 x % mixed forest)/(1 + exp (– 5.04 + 0.32 x % mixed forest)).

Long-tailed Tits were observed, which is why these are excluded from our analyses. Both the number of individuals and flocks observed per season were correlated to the number of one km-squares with Long-tailed Tits presence per season ($R^2 = 0.661$ and 0.671, $P < 0.0001$ for both, n = 22), suggesting that the mean flock sizes do not vary over time.

Simple regressions showed that four of the six habitat distribution variables were positively correlated to the number of seasons with Long-tailed Tits presence per one km-square, while two variables, specifically the number of alder patches, showed poor relationships (Table 1). The relationship between the number of seasons with Long-tailed Tits presence and the proportion of deciduous/mixed forest per one km-square is shown in Fig. 2 (simple regression: P = 0.002, polynomial regression: P = 0.006). The probability of the frequent presence of Long-tailed Tits in one km-squares on Aasla, here more than 10 seasons (of the 22 seasons possible), was modelled by a logistic regression (Fig. 3). The model suggested a steep threshold for the frequent presence of Long-tailed Tits of 15–20% deciduous/mixed forest in the one km-squares. The level for the dependent variable (y = > 10 seasons) was arbitrarily selected to represent suitable areas; therefore, it was put well above the mean number of seasons with Long-tailed Tits presence for all the one km-squares (mean = 8, range = 1–15 seasons).

Table 1. Data from simple regressions on the number of seasons with Long-tailed Tit presence per one km-square (n = 26) in relation to the habitat distribution variables.

Variable	R^2	p
Decid./mixed forest (tot.)		
Proportion (%)	0.328	0.002
No. of patches	0.153	0.048
Alder		
Proportion	0.356	0.001
No. of patches	0.027	0.424
Decid./mixed forest excl. alder		
Proportion	0.153	0.048
No. of patches	0.093	0.129

The multiple regression included four variables; the proportion and number of patches of deciduous/mixed forest (total) and alder forest, and explained significantly the number of seasons with Long-tailed Tits presence per one km-square ($R^2 = 0.538$, P = 0.002). The result was similar ($R^2 = 0.476$, P = 0.0024) when the number of alder patches, which alone showed no relation to the bird occurrences (Table 1), was excluded. (The variables regarding deciduous/mixed forest except alder were not used since they only constituted proportions of the other variables.)

The one km-squares (n = 6) used by Long-tailed Tits in low density seasons (Fig. 2) showed considerably higher means regarding the proportion of deciduous/mixed forest (17.6% vs. 8.1%) and the proportion of alder forest (9.0% vs. 3.2%) compared to the 20 other squares, but only the latter difference was statistically significant (Mann-Whitney, $P = 0.019$).

4. Discussion

In our long-term data set from Aasla we found the occurrences of Long-tailed Tits to be strongly related to the distribution of suitable habitats in respective one km-squares. In general, the proportion of suitable habitats showed stronger relationships to Long-tailed Tits occurrences than did the number of habitat patches. The strongest correlation emerged for the proportion of alder forest, while the number of alder patches did not show any tendency in relation to Long-tailed Tits occurrences. This was because the proportion of alder and the number of alder patches in one km-squares were not correlated ($R^2 = 0.15$), one km-squares often contained several very small patches or a few large ones (see Appendix). The result suggests that the amount of alder was more important in deciding the attractiveness of km-squares for Long-tailed Tits on Aasla, than was the travelling distances between separate patches. Further, since the total amount of deciduous/mixed forest in the squares also included some aspen, which is only rarely used by Long-tailed Tits (Bleckert 1991), a lower correlation to that variable was expected. However, stand quality, e.g. tree species composition, may be more important than landscape composition for the patch selection of individuals when suitable habitat is relatively abundant, i.e. easy to find, as on Aasla.

Although the relationship between the tits and the total proportion of deciduous/mixed forest was only the second strongest, that variable was selected for graphs because it is the most convenient one for possible use in forest management for at least two reasons. First, alder patches are rarely acknowledged in forestry manuals and, secondly, unlike several of the other deciduous tree species the occurrence of alder stands can rarely be planned for, since the site requirements of alders are relatively narrow (wet and/or steep sites).

The one km-squares with the most frequent presence of Long-tailed Tits showed proportions of deciduous/mixed forest, here 15–20%, very similar to the level suggested by Jansson and Angelstam (1999) for the reliable presence of the bird in south-central Sweden. The steepness of the curve (Fig. 3) suggests a threshold regarding the proportion of suitable habitat, as also shown in their model. Jansson and Angelstam's (1999) study was performed in a landscape with a very low total proportion of deciduous/mixed forest (< 5%), while on Aasla several one km-squares held more than 10% suitable habitat and some even 20–30%. Nevertheless, almost identical levels of suitable habitat per square-kilometres showed as a threshold for the frequent presence of Long-tailed Tits, suggesting a reliable result. This level (> 15%), for the proportion of suitable habitat in landscapes, most likely also applies to the patch occurrence of the Blue Tit (*Parus caeruleus*), the Marsh Tit (*P. palustris*) and the Lesser-spotted Woodpecker (*Dendrocopos minor*) (Jansson 1998). However, in Jansson and Angelstam's (1999) model the distance between suitable patches was the best predictor of bird occurrences. Unfortunately, this was not a proper variable to test in our data, because on Aasla much of the deciduous forest was more or less connected along fields or shores, while totally isolated suitable patches were rare.

Although we used only presence/absence data, our study suggests a density dependent pattern of Long-tailed Tit occurrences in relation to the proportion of suitable habitats in the one km-squares. Three seasons with few, but some, bird observations were arbitrarily selected as low density seasons (1990/91, 1994/95 and 1995/96, framed in Fig. 1). The one km-squares used by Long-tailed Tits in these seasons were all, but one, top ranked regarding the total number of seasons with bird presences (Appendix). Furthermore, these one km-squares used at low densities, i.e. the best ones according to the general hypothesis concerning density dependent habitat selection (Fretwell & Lucas 1970), had much higher proportions of deciduous/mixed and alder forest than the other squares. Without knowledge of the reproductive success of individuals in the later breeding season, we could not say if the occurrence pattern of Long-tailed Tits on Aasla came out of an ideal free or a despotic distribution of individuals (Fretwell & Lucas 1970). The pattern could even follow both distribution types at different spatial scales (Huhta et al. 1998). However, in general, it followed the predictions from a density dependent behaviour of the species.

Although we present data at only one scale (one km^2), we address the importance of choosing a relevant scale in ecological field studies related to the species under study and the general composition of the study area. We learned more about the preferrences of Long-tailed Tits regarding the distribution of habitats than would have been the case if we studied single stands or used the whole island as one sample. Species have different needs at different spatial and time scales (Kareiva 1990, Wiens et al. 1993, Morris 1995, Jokimäki & Huhta 1996), and the general habitat composition, range of variation in the study area, the length of study period, among other things, may dramatically influence the outcome of ecological field studies. Therefore, to examine relationships at several scales, and when possible, to define measurements of those useful for land managers, are urgent research tasks for ecologists (Li & Reynolds 1994, With & Crist 1995, Doncaster et al. 1996, Jokimäki & Huhta 1996). Such measures, for example on documented threshold levels, would be applicable indicators for use in landscape management (Jansson & Angelstam 1999).

In order to reach the knowledge suggested above, long-term data are invaluable. For example, if data from only one season on Aasla had been available, one could have drawn contradicting conclusions regarding the suitability of the island for Long-tailed Tits depending on whether they were collected at a peak, middle or low density year of the species. Moreover, long-term data appear to be necessary when relating varying population densities to habitat qualities and possible habitat changes (Van Horne 1986, Morris 1995, Fuller et al. 1997). Of course, occurrence data alone have the limitation that non-occurrences give no information on possible reasons for the absence. For many studies and monitoring counts, however, that may not always be the question asked. Instead, the possible influence of coincidence on species occurrences is mitigated when long-term data are used. Therefore, if the occurrence frequency of species should be used to study habitat and/or landscape quality, it must be assessed using data from long-term monitoring and probably with special attention paid to the situation at low population densities.

Acknowledgements. We thank H. Andrén, J. Jokimäki and two anonymous reviewers for comments that improved the manuscript. The study was supported by the Swedish Environmental Protection Agency, the Foundation for strategic environmental research (MISTRA) and the private foundations "Stiftelsen Oscar och Lili Lamms Minne" and "Olle och Signhild Enqkvists Stiftelser" (Jansson) and by the University of Helsinki and the Cooperative Board for Nordic Forest Research (Saari).

Sammanfattning: **Gynnsam biotopfördelning för Stjärtmesen (*Aegithalos caudatus*) indikerad genom besöksfrekvens — en långtidsstudie**

Data från 22 säsongers (1975/76–1996/97) fågelinventeringar användes för analys av stjärtmesens (*Aegithalos caudatus*) förekomst i provrutor (1 km^2) i relation till biotopfördelningen. Studien utfördes på ön Aasla i Finlands sydvästra skärgård, ett för stjärtmesen överlag lämpligt landskap, dvs. med jämförelsevis hög total andel lämpliga biotoper. De km^2-rutor som under studieperioden användes flitigast av stjärtmes innehöll avsevärt högre andelar lövblandskog och al, medans däremot antalet bestånd av dessa skogstyper endast visade svaga samband. Ett tröskelvärde att överskrida för erhållande av pålitlig förekomst av stjärtmes sågs kring 15–20 % lövblandskog i provrutorna. Denna nivå på andelen lämplig biotop stämmer väl överens med en studie av stjärtmesförekomsten i ett Svenskt skogslandskap, där mängden lövblandskog totalt var mycket låg. Förekomsten av stjärtmes över studieperioden pekade även på täthetsberoende samband. De sex provrutor som användes vid låga populationstätheter innehöll > dubblad medelandel lövblandskog och >tre gånger högre andel al än de 20 övriga provrutorna. Stjärtmesen förekom i dessa sex rutor också under alla år med högre populationstätheter, vilket även förutsägs av den generella teorin angående täthetsberoende biotopval. Fördelarna med

långtidsstudier, överväganden avseende användandet av populationstäthet vid bedömning av områdens kvalitét samt avseende skalberoendet vid ekologiska studier diskuteras.

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Appendix. Habitat data on the 26 one km-squares at Aasla, ordered according to the number of seasons with Long-tailed Tit presence. Bold type denotes the six one km-squares used by Long-tailed Tits in low density seasons (Fig. 1). Data on the proportion and number of patches of "Deciduous/mixed forest except alder" (as used in Table 1), were calculated from the habitat data presented here.

No. of seasons used	% deciduous/mixed forest of land area	No. of patches	% black alder of land area	No. of patches
15	22.0	10	19.0	7
14	22.0	6	10.0	6
13	17.0	11	7.0	4
13	3.5	7	2.4	3
11	36.0	3	12.5	3
11	25.0	7	5.0	5
10	13.0	8	8.0	6
10	9.0	5	3.0	3
10	7.0	3	3.6	3
10	6.0	10	1.3	5
8	10.0	9	3.1	5
8	9.0	3	5.0	2
8	5.0	7	3.0	4
8	1.2	5	0.4	1
7	12.8	6	4.5	6
7	6.7	8	2.2	2
6	10.5	7	4.4	6
6	7.0	3	2.0	2
6	2.7	7	2.8	7
5	9.4	6	1.1	6
5	8.1	4	5.4	3
4	5.7	5	1.7	4
3	5.0	4	1.8	2
2	5.5	6	5.0	6
2	4.7	7	2.0	5
1	4.7	4	1.4	2