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Habitat selection by the Siberian Tit *Parus cinctus* in virgin and managed forests in northern Finland

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We studied the occurrence of the Siberian Tit *Parus cinctus* in relation to variation in the structure of forests and the size of homogeneous forest areas in northernmost Finland. Habitat structure was measured at sites where Siberian Tits were observed (mainly foraging, n = 100) in the summers of 1982–84 and at randomly selected sites (n = 91) in both virgin and managed forests. At each site 25 habitat variables were measured; these were combined in eight variables used to analyze the data. We used two-group discriminant analysis (observation vs. random sites) of the whole data set, separately for virgin and managed forests, and for comparing the nestling and fledgling periods.

The tits preferred habitats with dead trees, large coniferous trees and birches; they avoided very bushy areas. Canopy cover was the most important discriminating variable in virgin forests. In managed forests tits favoured a closed canopy with large coniferous trees and birches. During the fledgling period tits occurred in habitats with more birches than those used in the nestling period. The high proportion of correct classification of prior groups (89%) in the discriminant analysis of managed forests indicated that Siberian Tits selected these habitats non-randomly, contrary to the case in virgin forests: the proportion of correct classifications was relatively low (61%). The forest areas in which tits were observed were significantly larger than the randomly selected areas.

The preference of sedentary Siberian Tits for large trees and large forest areas is probably important for the foraging of this foliage-gleaning species. Dead and large coniferous trees, reduced in number in thinned forests, also provide both nesting and roosting sites for Siberian Tits. The effects of fragmentation of old virgin forests and loss of habitat heterogeneity in terms of heavy thinning affect the Siberian Tit adversely.

1. Introduction

The Siberian Tit *Parus cinctus* is a species of the northern coniferous forest biome, distributed from Fennoscandia in the west, through Northern Russia and Siberia, to the northwestern part of North America in the east (Vaurie 1959, Godfrey 1966, Harrison 1982). Both in Europe and in Siberia the Siberian Tit occurs mainly in coniferous forests up to the timber line in the north (Dementjev & Gladkov 1970).

Habitat selection is a mechanism which causes individuals to remain in a particular environment to which they are adapted. Consequently species usually occupy only a restricted part of the environments in their range. If a species has relatively specific habitat requirements, it is most likely to undergo a large population decline when certain parts of its habitats are altered (Rotenberry 1981). In Finland, the Siberian Tit prefers old, virgin forests (Virkkala 1987) and has declined during the last few decades as a consequence of silviculture (Järvinen & Väisänen 1979a). As a sedentary species, the Siberian Tit is not vulnerable to many stochastic factors affecting migrants (e.g. vagaries of the weather during migration). The effect of environmental changes (forest management) on the Siberian Tit can thus be more unambiguously interpreted than their effect on migratory birds.

In this paper we study habitat selection by the Siberian Tit in relation to variation in the structure of both virgin and managed forests in Finnish Lapland. Thinned, managed forests provide an example of the manipulation of habitat structure on bird species. Our objective is to quantify the habitat needs and preferences of the Siberian Tit in detail in order to produce more precise information about the occurrence of this decreased species in relation to changes in forest structure. This kind of approach has clear management implications. We measure environmental variables describing the structure of forest habitats, analyse these data using discriminant function analyses, and use silvicultural maps to estimate how the size of forest patches affects the occurrence of the Siberian Tit.

2. Material and methods

2.1. Study areas

Our study areas were located in northern Finnish Lapland, near the village of Vuotso, Sodankylä (68°N, 27°E). All the field work was done by R. V. in virgin forests in Sompio Nature Reserve and in managed forests in the Tankajoki-Mäkärärova area in the summers of 1982–1984. The forests of Sompio Nature Reserve in the main are over 200 years old and include both moist spruce-birch and dry pine forests. In managed forests pine-dominated, thinned or young (age about 50 years) stands are most common, and most of the dead trees and snags have been removed (see Virkkala 1987). Nest-boxes are available to the Siberian Tit in part of this area (350 in an area of approx. 5 km^2). The virgin forest area covers about 100 km^2 and the managed forest area about 30 km^2.

2.2. Measurement of habitat variables

Habitat variables were measured at 100 sites, where Siberian Tits were observed in June–July of 1982–84 (12 nest sites and 88 foraging sites, only one habitat measurement per observation) and at 91 randomly selected sites (Table 1). Below we call these plots (in size 0.06–0.08 ha) observation sites and random sites, respectively. The observation sites were divided into two groups by two criteria (Table 1): (1) virgin vs. managed forests, (2) nestling (June) vs. fledgling periods (mainly first half of July).

Habitat variables of randomly selected sites were measured both in virgin and in managed forests (Table 1). Random sites were selected from the same areas where tits had been observed. These sites were sampled systematically by walking 4–6 km from a randomly selected starting point and making habitat descriptions at intervals of 500 m. A long distance between the random sites was necessary due to the large forest patches. All the random sites were located in forest habitats where forest passerines were in fact observed (open habitats, such as mires and clearcuts, were thus excluded).

Different habitat variables were measured on a grid as follows (Fig. 1, Table 2). The observer walked 20 m from a central point in each of the main compass directions (N, S, W, E). Four transect lines were thus established, each having a

Table 1. Habitat distribution of observation and random sites.

	Virgin forests	Managed forests
Observation sites (n = 100*)	74	26
Random sites (n = 91)	63	28

* Nestling period 34, fledgling period 66 observations.

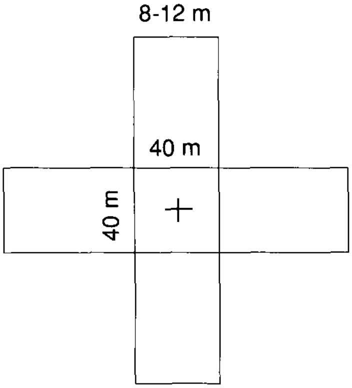

Fig. 1. The grid used in measuring habitat variables. The values of habitat variables in the middle of the grid were measured only once.

width of 8–12 metres (greater widths for less dense stands). Along the transect line all trunks over 3 cm in diameter at breast height (dbh) were measured for tree species and dbh classes using the following classification: 3.0–7.0 cm, 7.1–13.0 cm, 13.1–25.0 cm and over 25 cm. Dead trees were measured as a separate "tree species". In the analyses the number of trees at every site was standardized to a transect line width of 8 m (grid size 576 m^2). In the middle of every transect line stopping points were established at 4-metre intervals (making 20 stopping points per study site). Canopy cover (%, accuracy 10%) was estimated at these stopping points at a height of over 3 m using a cardboard tube with a diameter of 5 cm. The observer looked perpendicularly up-

Table 2. Original 25 variables measured in the plots, and their combined and transformed variables used in the analysis. Dbh = diameter at breast height, sqrt = square root, arcsin = arcus sin, ln = natural logarithm.

Original variables	Variable in the analysis	Transformations
Mean tree height (m)	Height	sqrt
Pine 3.1–7.0 cm dbh Pine 7.1–13.0 cm dbh Spruce 3.1–7.0 cm dbh Spruce 7.1–13.0 cm dbh	Small coniferous trees	sqrt
Pine 13.1–25.0 cm dbh Pine >25.0 cm dbh Spruce 13.1–25.0 cm dbh Spruce >25.0 cm dbh	Large coniferous trees	sqrt
Birch 3.1–7.0 cm dbh	Small deciduous trees	sqrt
Birch 7.1–13.0 cm dbh Birch 13.1–25.0 cm dbh Birch >25.0 cm dbh	Large deciduous trees	sqrt
Dead trees 3.1–7.0 cm dbh Dead trees 7.1–13.0 cm dbh Dead trees 13.1–25.0 cm dbh Dead trees >25.0 cm dbh	Dead trees	sqrt
Mean canopy cover (%)	Canopy cover	arcsin(sqrt)
Coniferous bushes Deciduous bushes	Bushes	sqrt
Wet moss (%) Dwarf shrub (%) Grass-sedge (%)	Moist vegetation	arcsin(sqrt)
Dry vegetation (%)	Not used	
Distance to the edge (m)	Distance	ln

wards through this tube at the stopping point. Coniferous and deciduous bushes were coded on both sides and in front of every stopping point. Trees and shrubs 1–3 m high and <3 cm dbh were interpreted as bushes. The proportions of different classes in the ground layer were estimated within the area of the whole site. In addition, the mean stand height and the distance to the nearest edge of an open area were estimated.

2.3. Analyses of habitat variables

We carried out the following analyses. We compared observation and random sites (1) for the data as a whole, (2) in virgin forests, and (3) in managed forests. We also compared the observations in the nestling and fledgling periods. In addition we carried out an analysis with four prior groups: observation and random sites in both virgin and managed forests. The original variables (Table 2) were highly intercorrelated and non-normally distributed, factors that bias multivariate analyses (Anderson 1981, Williams 1981). The ratio between sample size and number of variables measured should also be sufficient. In discriminant analysis Williams & Titus (1988) recommended that the number of samples per group should be at least three times the number of variables. Thus, we combined and transformed the original variables.

The two smallest and two largest size-classes of both pine (Scots Pine *Pinus sylvestris*) and spruce (Norwegian Spruce *Picea abies*) were combined (Table 2). Pines and spruces could not be considered separately, because most of the coniferous forests in this area are either pine or spruce forests, and, in consequence, the original variables were highly skewed due to the mode in the zero class. Birches (mainly Mountain Birch *Betula pubescens*) larger than 7 cm in dbh were combined into a single variable. Small and large birches were highly positively intercorrelated ($r = 0.6$–0.9), and we combined small and large birches for the discriminant analysis. All the dead trees were combined into a single variable, as were coniferous and deciduous bushes. Moist and dry vegetation in the ground layer measure the same characteristic (high negative correlation, $r = -0.99$), and we omitted the other variable (dry vegetation). Mean tree height was also positively correlated with many variables, such as the number of both deciduous and coniferous trees, and thus this variable was omitted from the multivariate analysis. The combination and deletion of variables reduced the number of variables to ten for univariate and eight for multivariate analyses.

After the combination and transformation (see Table 2) of variables no highly intercorrelated variables remained in the data sets ($|r| < 0.5$; see Noon 1981).

We considered preassumptions of the discriminant function analysis, such as equal variances of variables between different groups and normality of variables, in relation to our data (see Williams 1981, 1983). We tested the normality of each variable in different data sets (Table 3), but only a few variables proved to be significantly ($P < 0.01$) non-normally distributed. We compared variances of variables between groups in the different data sets (F-test). In our four analyses, each with eight variables, only one variable differed significantly ($P < 0.05$): the variance of the number of birches in managed forests was

Table 3. Variables that differed significantly ($P < 0.01$) from normality in the different data sets (O = observation site, R = random site). Testing was based on either the Kolmogorov ($n > 50$) test or Shapiro-Wilk's test ($n < 50$). Abbreviations: DEAD = dead trees, SCON = small coniferous trees, DEC = deciduous trees, BUSH = bushes.

Whole data		Virgin forests		Managed forests		Period	
O	R	O	R	O	R	nestling	fledgling
DEAD	DEAD	–	–	SCON DEAD DEC	DEAD DEC	BUSH DEAD DEC	–

much greater in observation than in random sites ($P < 0.001$).

In our data sets we applied different discriminant analyses as a multivariate technique. We used the stepwise discriminant analysis (PROC STEPDISC in SAS, SAS Institute Inc., 1985a, 1985b), in which variables are selected stepwise to produce a discrimination model. In stepwise analysis variables are either entered or removed at each step depending on the discriminatory power of the model, which is measured by Wilks' lambda.

We applied the predictive discriminant analysis (PROC DISCRIM) in order to discover the separation of different groups. This analysis is based on linear combinations of the variables measured, and it develops a classification criterion using a measure of generalized squared distance based on the pooled covariance matrix.

We used the descriptive discriminant analysis (canonical analysis, PROC CANDISC) to identify the features by which our four groups are best separated. The analysis derives a linear combination of the variables that has the highest possible multiple correlation with the groups.

2.4. Forest patch size

The effect of forest tract size on habitat selection by Siberian Tits was studied using silvicultural maps, which show homogeneous units of forest. The sizes of homogeneous forests in which tits were observed were compared with those of randomly selected ones. This procedure was carried out only in the virgin forest area. Selection criteria for random forests included: (1) the productivity of forest patches should be equal to that of tit forests, and (2) forests had to have a mean stand volume of at least 20 cubic metres/ha (to eliminate open patches and very sparse forests).

3. Results

3.1. Univariate analyses

Siberian Tits seem to prefer habitats with large birches and dead trees (Table 4). In virgin forests canopy cover was the only variable that differed significantly between observation and random sites. During the fledgling period tits occurred in areas with more birches than those used during the nestling period. The habitats of observation and random sites differed most markedly from each other in managed forests; seven out of ten variables differed significantly (Table 4).

The quality of the ground layer (moist vegetation), which is also reflected as different dominant coniferous tree species in the forests, did not appear to be important as regards habitat selection by the Siberian Tit: no statistically signifi-

Table 4. Mean values of the variables in observation (O) and random sites (R) in different analyses. The number of trees is standardized in a grid size of 576 m^2. Statistical significance (P) based on t-tests (two-tailed); * = $P < 0.05$, ** = $P < 0.01$.

	Whole data		Virgin forests		Managed forests		Period	
Variable	O	R	O	R	O	R	nestling	fledgling
Small conif. trees	3.28	3.33	2.84	3.08	4.56	3.90	3.24	3.31
Large conif. trees	2.90	2.71	2.98	2.98	2.67*	2.10	2.87	2.92
Small decid. trees	2.89	2.63	3.28	3.54	1.77*	0.59	2.29*	3.20
Large decid. trees	2.61*	2.06	2.96	2.73	1.60*	0.56	2.17*	2.84
Canopy cover	0.46	0.47	0.48**	0.55	0.40*	0.32	0.44	0.47
Moist vegetation	0.43	0.42	0.41	0.36	0.49	0.54	0.41	0.44
Distance	2.14	2.22	2.23	2.27	1.86*	2.11	2.10	2.16
Dead trees	1.10*	0.83	1.26	1.09	0.64*	0.23	1.03	1.14
Bushes	1.34	1.61	1.42	1.58	1.11*	1.67	1.19	1.42
Height	3.75	3.84	3.91	3.99	3.32	3.50	3.80	3.73

cant differences were found in any of the analyses. Densities of the Siberian Tit were similar in virgin, dry pine forests and virgin, moist spruce-birch forests. Based on line transect censuses (see Virkkala 1987), the density of the species was 4.0 pairs/km^2 (29.8 km of transects, $n = 6$) in dry pine forests and 4.4 pairs/km^2 (45.5 km of transects, $n = 10$) in moist spruce-birch forests (difference: ns, df = 1, χ^2-test) in 1982–84 (for this test, see Virkkala 1987). Thus the pooling of pine and spruce numbers to give coniferous tree numbers for the purpose of the analysis can be considered valid. The mean stand height did not differ between observation and random sites in the different analyses, and exclusion of this variable due to high intercorrelation with other variables (see methods) did not affect the results of the multivariate analyses.

3.2. Multivariate analyses

The two-group stepwise discriminant analyses are all statistically significant (Table 5). Siberian Tits preferred habitats with dead trees, large coniferous trees and birches, but avoided very bushy and closed canopy areas. However, closed canopy was avoided only in virgin forests, probably due to the preference for very old forests: the latter are not so closed as younger virgin forests. In managed forests, tits selected areas of more closed canopy with many coniferous and deciduous trees. Thinned, more open forests avoided by tits were usually also very bushy, which was reflected in negative correlations between bushes and trees, e.g., bushes/small coniferous trees ($r = -0.270$, df = 52, $P < 0.05$), bushes/large coniferous trees ($r = -0.164$, ns). Birch was the most important variable discriminating between nestling and fledgling periods.

The percentages of correct classifications of prior groups in the different discriminant analyses are presented in Table 6 and the frequency distributions of discriminant scores in Fig. 2. The high proportion of correct classifications in managed forests (89%) indicates that Siberian Tits clearly selected these forest habitats according to habitat characteristics. Such clear patterns were neither observed in virgin forests (see also Fig. 2), nor in a comparison of the nestling and fledgling periods — the percentage of correctly classified sites in these analyses was considerably lower (about 60%) than in managed forests.

Table 5. Results of two-group stepwise discriminant analyses, when the significance level for each variable to enter the analysis was 0.15. Obs+ = greater values of variable at observation sites, obs– = greater values at random sites. When different periods were compared, fle+ = greater value of variable in the fledgling period. The values of Wilks' lambda at each step and their statistical significance are presented.

Analysis	Variable entered	Wilks' lambda	P
Whole data	1. Dead trees (obs+)	0.972	0.021
	2. Bushes (obs–)	0.954	0.012
	3. Distance (obs–)	0.933	0.005
	4. Deciduous trees (obs+)	0.910	0.002
	5. Canopy cover (obs–)	0.889	<0.001
	6. Large coniferous trees (obs+)	0.864	<0.001
Virgin forests	1. Canopy cover (obs–)	0.933	0.002
Managed forests	1. Deciduous trees (obs+)	0.877	0.009
	2. Bushes (obs–)	0.736	<0.001
	3. Distance (obs–)	0.618	<0.001
	4. Small coniferous trees (obs+)	0.521	<0.001
	5. Large coniferous trees (obs+)	0.492	<0.001
Period	1. Deciduous trees (fle+)	0.950	0.025

Table 6. Percent of correctly classified observation and random sites in different discriminant analyses, which are based on variables obtained in stepwise discriminant analyses (see Table 5). Values in parentheses show the percentages of correct classifications, when all eight variables were taken into account.

Analysis	Observation sites	Random sites	Total
Whole data	67.0 (68.0)	61.5 (61.5)	64.4 (64.9)
Virgin forests	59.5 (60.8)	61.9 (61.9)	60.6 (61.4)
Managed for.	84.6 (80.8)	92.9 (92.9)	88.9 (87.0)

Nestling period: 55.9 (67.7)
Fledgling period: 60.6 (59.1)
Total: 59.0 (62.0)

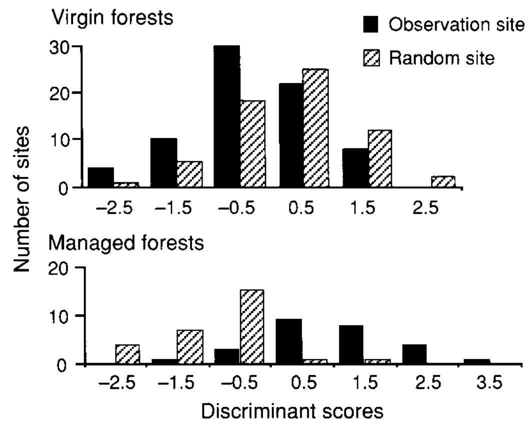

Fig. 2. Frequency distribution of discriminant scores between observation and random sites in virgin and managed forests.

The canonical discriminant analysis showed the distribution of observation and random sites in both virgin and managed forests (Fig. 3). The first canonical function (abscissa) discriminated between virgin and managed forests and the second between observation and random sites. Virgin forests had more deciduous, large coniferous and dead trees, whereas small coniferous trees and bushes were more numerous in managed forests. As a result of forest management the amount of deciduous saplings and bushes generally increases. However, virgin forests in Fig. 3 comprise both spruce-birch and pine forests, but managed forests comprise only pine-dominated

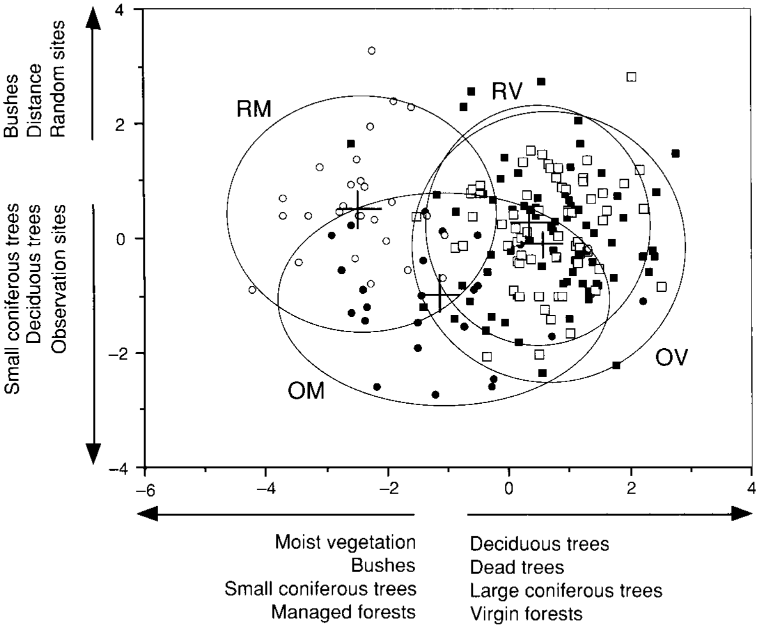

Fig. 3. The result of the four-group canonical discriminant analysis. Black squares = observation sites in virgin forests, open squares = random sites in virgin forests, black circles = observation sites in managed forests, open circles = random sites in managed forests. Mean values with 95% confidence circles of groups (OV = observation sites, RV = random sites in virgin forests, and OM = observation sites, RM = random sites in managed forests) and the most important discriminating variables and their increasing values on the first and the second canonical function are presented.

stands, which do not contain as many deciduous trees as spruce-dominated forests. In places in managed forests the ground surface has been ploughed, which has probably increased the amount of moist vegetation and bushes (see Virkkala 1987). The first canonical function explains 80.8% of the variation observed and the second one adds 13.4% to the variance explained.

3.3. Forest patch size

The mean size of the forests in which Siberian Tits were observed in virgin forest areas was 117 ha, whereas the mean size of randomly selected forests was 57 ha. The difference is statistically significant ($t = 4.16$, $df = 126$, $P < 0.001$). In the nestling period tits occurred in larger forests (mean = 161 ha) than those they inhabited in the fledgling period (mean = 100 ha, $t = 2.56$, $df = 62$, $P < 0.02$).

4. Discussion

4.1. Habitat preferences of the Siberian Tit

Habitat selection by birds can be characterised as a two-stage process: firstly, individuals estimate the general features of the landscape and terrain and then respond to more specific habitat features, such as food availability and structural characteristics (Hildén 1965). According to the "niche-gestalt" model of habitat selection (see James 1971, James et al. 1984), individuals respond to structural features of habitats in general independently of other species, because habitat features are correlated with species-specific nesting and feeding sites (Holmes & Robinson 1981). In a study on the Ovenbird *Seiurus aurocapillus*, Smith & Shugart (1987) observed that birds selected habitats by using structural habitat cues as a proximate factor for prey abundance. This structural cue hypothesis implies that habitat structure reflects habitat quality. A similar hypothesis can be advanced for habitat selection by the Siberian Tit.

In the fledgling period tits preferred areas having more birches compared to the areas they inhabited during the nestling period. During the fledgling period (July), the density of invertebrates on birch is higher than in the nestling period (June) owing to the fact that in northern Lapland birches burst into leaf in late June (Hågvar 1976), and tits also make a shift towards foraging on birch in the fledgling period (Virkkala 1988). In managed forests a sufficient tree density seems to be important because tits avoided open and very thin forests. These preferences were probably due to the food resources available to the foliage-gleaning Siberian Tit (Virkkala 1988). More generally, Cody (1978, 1981) has suggested that vegetation density may be positively correlated with insect density or food supply. In virgin forests the abundance of dead and large coniferous trees is essential to the Siberian Tit for foraging and nesting cavities. Thus, it seems probable that the tits use the structure of forests as a cue for habitat quality (food, nesting sites) in their habitat selection.

Virgin forests comprise much denser stands than managed forests (see random sites in Table 4). As the Siberian Tit avoided closed canopy in virgin forests, yet preferred this in managed forests, it is possible that Siberian Tits need a forest of moderate closeness: very sparse and dense stands are avoided.

Habitat selection can also be considered as a hierarchical process with ranking order (Johnson 1980, Ruggiero et al. 1988). First-order selection comprises the selection of the geographical range of a species, second-order selection defines the home range of an individual, third-order selection is connected with the usage of various habitat components within the home range, and fourth-order selection is correlated with the usage of food items at feeding sites.

In the present study of the Siberian Tit, the size of the forest area is connected with second-order selection, and preferences or avoidances of habitat variables with third-order selection. However, the concept of habitat preference or avoidance can be complicated, because a habitat component vital to the species can be so abundant that the species requires it only in small amounts. Therefore, in studying habitat preferences, a species can even avoid its vital habitat component (Johnson 1980). In the Siberian Tit no clear preferences of habitat variables were observed in virgin forests, in contrast to managed forests.

This may be the result of the abundance of habitat components important to the Siberian Tit. Tits may have selected virgin forests owing to, e. g. the high numbers of large coniferous trees and dead trees (second-order selection), even though these trees may not be preferred within the home range (third order) as a consequence of their general abundance in virgin forests (see Fig. 3).

Population density of the Siberian Tit was 3–4 pairs/km^2 in virgin forests and about 0.5 pairs/km^2 in managed forests with no nest-boxes (see Virkkala 1987). In the heavily managed forest area where nest-boxes were available population density was still only about 1.5 pairs/km^2 (Virkkala, unpubl.). Thus, the offering of nest-sites did not increase the density of the Siberian Tit to the same level as in virgin forests, when the structural features, and possibly also the prey abundance, of heavily thinned forests were adverse.

Wiens (1985) and Wiens et al. (1986) have stressed the effect of time lags on the habitat selection patterns of birds. When habitat structure is drastically altered birds may still be present in the habitat due to site tenacity. Managed forests in our study were cut in the late 1950s and early 1960s and thus the time lag effect is no longer relevant.

Interspecific competition can affect habitat selection of a particular species (see Sherry & Holmes 1988 and references therein). Competitive interactions usually occur between similar-sized species, and in our study area only a few species — the Willow Tit *Parus montanus* and the Pied Flycatcher *Ficedula hypoleuca* — resemble the Siberian Tit in size and ecology. Both of these species are scarce, with forest densities of below 0.5 pairs/km^2 (Virkkala 1987). The occurrence of the Willow Tit is related to species-specific habitat requirements in winter and summer (Virkkala 1988). Competition for nest sites between the Siberian Tit and the Pied Flycatcher has been documented at Kilpisjärvi, northwestern Lapland (Järvinen 1982). The Pied Flycatcher prefers areas where nest-boxes are available. In managed forests with nest-boxes suitable for hole-nesters, only about 10–20% were occupied annually by the Pied Flycatcher, while most of the boxes remained empty. Thus, we consider interspecific interactions to be a minor factor affecting habitat selection by the Siberian Tit and stress, instead, the role of species-specific habitat requirements (see James et al. 1984).

4.2. The effects of forest management and forest size on the Siberian Tit

Based on the multivariate analysis of habitat variables, in many studies variations in the structure of forests have been observed to influence habitat selection patterns of forest birds (e.g., James 1971, Anderson & Shugart 1974, Sabo 1980, James & Wamer 1982, Conner et al. 1983). Habitat manipulation can provide an important framework for studying the effects of habitat structure on the occurrence of birds (see Wiens et al. 1986). In our study area the structure of managed forests differed markedly from that of virgin forests (Fig. 3).

Nowadays, forest management is a major factor affecting the structure of both temperate and boreal forests. Thus particular attention in the study of bird-habitat relationships has been paid to the effects of silviculture (e.g., in North America: Titterington et al. 1979, Crawford et al. 1981, Mannan & Meslow 1984, Chadwick et al. 1986; in North Europe: Nilsson 1979, Helle & Järvinen 1986, Järvinen & Väisänen 1979b, Järvinen et al. 1977, Väisänen et al. 1986). Modern forestry removes dead trees and snags from forests, and the importance of these trees for cavity-nesting birds, also observed in the present study, has often been emphasized (Haapanen 1965, Conner et al. 1975, Zarnowitz & Manuval 1985, Chadwick et al. 1986). Crawford et al. (1981) observed that variation in canopy cover was the most important habitat variable separating bird groups in managed Central Appalachian hardwood forests. Variation in canopy cover also seems to be an important factor in the habitat selection of the Siberian Tit. Because a high proportion of prior groups was correctly classified in managed forests (Table 6, Fig. 2), Siberian Tits obviously select these habitats non-randomly. In virgin forests tits seem to occur randomly in relation to the availability of measured habitat variables. As a result the Siberian Tit occurs patchily in managed forests due to fragmented distribution of its preferred habitat, whereas in uniform, virgin forests the Siberian Tit is distributed more evenly.

The Siberian Tit declined drastically from the 1940s to the 1970s due to large-scale clearcuttings, which started in northern Finland in the 1950s (Järvinen & Väisänen 1979a, Väisänen et al. 1986). The Siberian Tit has, however, declined even more than the area of old-growth forests, and thus Järvinen et al. (1977) and Helle & Järvinen (1986) postulated that the Siberian Tit requires large forest areas and is susceptible to the fragmentation of old forests. The present study shows that Siberian Tits do prefer large areas in virgin forests, especially during the nesting period. During the fledgling period, birds move to smaller forest areas, in which there are also more birches. The sensitivity to forest fragmentation has often been related to the territory size and minimum area requirements of a species (see Whitcomb et al. 1981).

Minimum area requirements of the Siberian Tit seem to restrict the occurrence of this species in small woods. As a tit species, the Siberian Tit has a very large breeding territory, at least 15–20 ha but as much as 50–100 ha in the marginal habitat of the species (Haftorn 1973, Järvinen 1982, Virkkala, unpubl). Haila (1983) studied the colonization of birds in the archipelago of Lake Inari (69°N, 28°E) in northernmost Finland on the basis of census data from forest islands with a size range of 0.5–885 ha. In his data the smallest island inhabited by the Siberian Tit was 17 ha, and the species was regularly found only on islands of over 200 ha in size. The smallest isolated forest patch in which the Siberian Tit was observed in virgin forests of our study area during the nesting period, was 15 ha. Thus, as a consequence of its large area requirements, the Siberian Tit is susceptible to forest fragmentation caused by silviculture.

Of course, observations on habitat selection of the Siberian Tit in the present local population cannot be generalized to a large geographical area (see Collins 1983, James et al. 1984). For instance, in Alaska the Siberian Tit (Alaska Chickadee) has been reported to prefer lush forests along riversides and forest edges (Murie 1928), thus resembling the Willow Tit in its habitat selection in northern Finland (see Virkkala 1988).

4.3. Adaptive consequences

The Siberian Tit is a sedentary species living in harsh conditions; for instance, the sun does not rise for a month in winter. Overnighting Siberian Tits are able to fall into hypothermia in order to save energy in winter (Haftorn 1972). In addition, Siberian Tits hoard food in the autumn for the winter (Haftorn 1953). What are the adaptive consequences of the patterns observed in our study?

Siberian Tits prefer large forest areas. This may be a consequence of saving energy during cold, short winter days, because in uniform forests tits do not need to move as much as in fragmented forest areas (see Virkkala 1987, and for optimal foraging of birds in trees, Norberg 1983). Adult birds occur year-round in their territory (Virkkala, unpubl.). We have observed that tits prefer dead trees and large coniferous trees. Besides nesting sites, trees with cavities also provide roosting sites in winter. Siberian Tits seem to avoid heavily thinned, open managed forests, perhaps due to their scanty food resources. In managed forests Siberian Tits probably suffer from the loss of habitat heterogeneity in terms of reduced numbers of large coniferous and dead trees. Heavily thinned forests are also clearly suboptimal habitats for the Siberian Tit, because the number of fledglings produced is significantly lower and nesting success poorer in these forests compared to only moderately managed forests (Virkkala, unpubl.). Protecting structurally heterogeneous, large virgin forests is important for the survival of the Siberian Tit.

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Selostus: **Lapintiaisen elinympäristön valinta Pohjois-Suomen luonnontilaisissa ja hakatuissa metsissä**

Lapintiaisen esiintymistä suhteessa metsien rakenteen ja koon vaihteluun tutkittiin Vuotson ympäristössä, Sodankylän pohjoisosissa (68°N, 27°E) kesinä 1982–84. Metsän rakenne mitattiin paikoista, joissa lapintiainen havaittiin (yleensä ruokailemassa, n = 100) sekä satunnaispisteistä (n = 91) sekä luonnontilaisissa että hakatuissa metsissä. Kussakin paikassa mitattiin 25 ympäristömuuttujaa, jotka yhdistettiin kahdeksaksi muuttujaksi erotteluanalyysiä varten. Tutkimuksessa verrattiin lapintiais- ja satunnaispisteitä kuvaavia ympäristömuuttujia koko aineistossa sekä erikseen luonnontilaisissa ja hakatuissa metsissä; lisäksi verrattiin lapintiaisen pesäpoikasajan (kesäkuu) ja lentopoikasajan (heinäkuu) havaintopisteitä kuvaavia ympäristömuuttujia. Metsäkuvioita, joissa lapintiainen havaittiin verrattiin satunnaisesti valittuihin kuvioihin.

Lapintiaiset suosivat ympäristöjä, joissa oli satunnaista enemmän kuolleita puita, kookkaita havupuita ja koivuja; ne välttivät pensaikkoisia alueita. Hakatuissa talousmetsissä tiaiset suosivat sulkeutunutta metsää, jossa oli runsaasti suuria havupuita ja koivuja. Lentopoikasaikana lapintiaiset esiintyivät paikoissa, joissa oli enemmän koivuja kuin pesäpoikasajan havaintopaikoissa. Koivun lehdet kehittyvät kesäkuun lopulla, jonka jälkeen koivuissa on huomattavasti enemmän hyönteisiä, joita lapintiaiset syövät. Ennalta valittujen *a priori* -ryhmien (lapintiais- ja satunnaispisteet) ympäristömuuttujien päällekkäisyys oli pieni hakatuissa talousmetsissä, sillä 89% *a priori* -ryhmien havainnoista säilyi erotteluanalyysissä alkuperäisissä ryhmissään, kun taas päällekkäisyys oli varsin suuri luonnontilaisissa metsissä: vain 61% havainnoista säilyi alkuperäisissä ryhmissään. Näin ollen lapintiaiset valikoivat selvästi elinympäristönsä hakatuissa metsissä ja esiintyivät laikuttain. Sen sijaan luonnontilaisissa metsissä tiaiset esiintyivät varsin tasaisesti suhteessa mitattuihin ympäristömuuttujiin. Metsäkuviot, joissa lapintiainen havaittiin, olivat merkitsevästi laajempia kuin satunnaiset metsäkuviot.

Lapintiaisten suurten puiden ja laajojen metsäalueiden suosinta on todennäköisesti tärkeää lajin ravinnon hankinnan kannalta. Kuolleet puut ja suuret havupuut, joita on hakatuissa talousmetsissä huomattavasti vähemmän kuin luonnonmetsissä, ovat myös tärkeitä pesintä- ja yöpymispaikkoja. Vanhojen havumetsien pirstoutuminen hakkuiden seurauksena sekä harvennushakkuiden aiheuttama metsän rakenteellisen monimuotoisuuden väheneminen ovat epäedullisia lapintiaiselle.

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