

Habitat preference and breeding performance in four hole-nesting passerines at the northern limit of their range

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Habitat preference and its relation to breeding performance were studied with reference to two contrasting hypotheses: 1) birds at edge of their range select the optimal habitat, and 2) the birds are unselective as to habitat characteristics, because habitat-independent factors (e.g. weather) rule out any benefit from careful habitat selection. No preference for vegetational characteristics (dominant tree, field layer vegetation) was observed in the Siberian and Great Tits or the Redstart. This suggests that these species are less selective of those characteristics than in more southern regions. The Pied Flycatcher preferred birch forests at low altitudes, but pine forests at high altitudes. In two cases, however, other characteristics affected habitat selection: Redstarts preferred low altitude sites and Great Tits bred more often close to human settlement. Sites at the highest altitudes were avoided by the other species as well. Breeding success correlated positively with the habitat preference. As we analysed data from several years, this suggests that differences in habitat quality are fairly constant in spite of wide variation in weather conditions. The preferred habitats probably contain some food resources that are not completely governed by the weather conditions. Clutch size was affected by habitat only in the Siberian Tit, which suggests adjustment ability in this northern species.

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Introduction

The habitat preference of a species can be evaluated by measuring density variation along a habitat gradient. The interesting thing to study in habitat selection is its adaptive significance, i.e. whether or not the breeding performance varies in relation to the preference shown (e.g. Fretwell & Lucas 1970, Partridge 1978, Alatalo et al. 1985). At the edge of a species' range the optimal habitat may be selected to ensure high breeding success (e.g. Hildén 1965). In some situations, e.g. at the northern border of the range, birds may be unselective as to habitat characteristics, because variability in other factors or harshness of the environment (e.g. Krebs 1978, p. 46) may preclude any preference for a given habitat type. Habitat preference at the edge of the range may also differ from that in more central areas.

Here we will describe the habitat distribution of four hole-nesting species, the Redstart *Phoenicurus*

phoenicurus, the Pied Flycatcher *Ficedula hypoleuca*, the Great Tit *Parus major* and the Siberian Tit *Parus cinctus*, in northernmost Finland, Inari Lapland. The most important factor for the occurrence of these species is the presence of a hole or nest-box (e.g. von Haartman 1956, Hildén 1965), but other habitat characteristics may also play a role. First, we will examine how selective these species are in relation to forest type, field layer vegetation, altitude and distance from human settlement in a situation in which nest-boxes are available. Then we will analyse the variation of clutch size and breeding success in relation to the same variables, to find out whether the observed habitat distributions are connected with differences in reproduction. We expect no differences in breeding parameters if none of the habitats is preferred to others or if the effect of density on breeding success is large enough to make different habitats equally suitable (ideal free distribution of Fretwell & Lucas 1970 and Fretwell 1972, Partridge 1978). On

the other hand, we expect better success in a preferred habitat. A positive correlation between habitat preference and breeding success will indicate that habitat selection is of evolutionary importance. Further, it will support the ideal despotic habitat distribution model of Fretwell & Lucas 1970 (see also Fretwell 1972, Alatalo et al. 1985). Comparison of our observations with those from other areas will also shed light on the variation pattern of habitat selectivity within the geographical range of the four species.

Material and methods

In Inari Lapland, lying at the border of the boreal and subarctic vegetation zones, the growing season (daily average temperature above +5°C) is short, ca. 110–120 days (Kallio et al. 1969, in southern Finland ca. 175 days). Consequently, birds have little freedom in the timing of breeding. During the breeding period, temperature varies more between years (Järvinen 1983, 1989), and within the season and day (up to 30°C, Kallio et al. 1969) than in southern Finland.

About 1200 nest-boxes were put up in 1982–1986 (most of them in winter 1983). Some older nest-boxes adjacent to houses raises the total number to 1300. Most nest-boxes are situated in the Utsjoki valley and their density is highest near the Kevo subarctic research station (69°45'N, 27°01'E), 460 nest-boxes within a 4 km radius. The length of the study area in a north-south direction is about 90 km (69°52'N, 69°04'N) and it is traversed by the northern forest limit of Scotch pine, *Pinus sylvestris*, continuous pine forests being found only in its southern part. The northern part of the area lies in the zone of the mountain birch, *Betula pubescens* ssp. *tortuosa*, but scattered pines and pine woods are found in Utsjoki valley up to the northern edge of the study area. For the general characteristics of the area see Kallio et al. (1969).

Nest-boxes were set up 1–2 m above the ground in groups of four (distance between nest-boxes in a group about 25 m). The distance between the groups was 500 m. Near the Kevo station, 135 nest-boxes put up before 1984, were placed in a line at 50 m intervals. The nest-boxes were checked at least three times during each summer to record nesting, clutch size and breeding success. Most nest-boxes remained unoccupied every summer (83–95%, Table 1). Therefore, the birds could choose freely among available sites, irrespective of the natural availability of nest holes. In this paper we use data collected in 1983–

Table 1. Numbers of nest-boxes (n) and numbers of breeding females (at least one egg laid) in 1983–1988. Second and repeat clutches in brackets.

Year	n	<i>Ficedula hypoleuca</i>	<i>Parus major</i>	<i>Parus cinctus</i>	<i>Phoenicurus phoenicurus</i>
1983	750	30	3	4	2
1984	750	43	2 (1)	13	11
1985	750	56	11 (1)	23	7
1986	1150	122	16 (4)	22	15
1987	1300	134	33 (2)	26	27
1988	1300	95	11 (3)	13	34
Σ		480	76(11)	101	96

1988. Nest-boxes put up less than one year earlier were omitted from the analysis, because their occupancy may differ from that of older ones.

The forest around each nest-box was classified as pine, mixed or birch forest, using a vegetation map for northern Finland (Seppälä & Rastas 1986) and field checks. The distribution of forests around the nest-boxes deviated slightly from the general distribution of forests in Inari Lapland (Heikinheimo 1921) — relatively more boxes were located in pine and mixed forests than in birch forests. As another vegetation characteristic, we used the field layer around each nest-box employing the field layer types of Kalliola (1973). Arranged from the most barren to the most luxuriant types, these were: sELiT = subalpine Empetrum-Lichenes type, sELiPIT = subalpine Empetrum-Lichenes-Pleurozium type, sEMT = subalpine Empetrum-Myrtillus type.

The altitude of nest-boxes above sea level (a.s.l.) and the distance of each nest-box from the nearest house (hereafter referred to as winter feeder) were measured on topographic maps (scale 1:50000, accurate to the nearest 50 m). As a density measure of nest-boxes around each box we used their number in a 300 m square surrounding the nest-box concerned. The maximum density (3 nest-boxes/ha) occurred at low altitudes in the Utsjoki valley.

Because of covariation of the grouping factors, we used log-linear models to describe the habitat distribution of nests. Overcomplicated models were avoided by incorporating only five of six factors at a time (A = altitude, F = forest type, L = field layer, D = distance from winter feeder, N = density of nest-boxes, P = presence of nest in a nest-box; Sokal & Rohlf 1981). Three different initial models were fitted for the tits, and one for the migratory Pied Flycatcher

Table 2. Best-fit log-linear models, which explain the distribution of nests (P) in multiway frequency comparisons with three classes for forest (F), field layer (L), altitude (A), distance (D) and nest-box density (N) during 1983–1988 (limits of classes in text). Distance from winter feeders was excluded from the analyses of the Pied Flycatcher and Redstart. The trends found are portrayed in Fig. 1.

Species	Saturated model	Best-fit model	df	G	P
<i>Parus cinctus</i>	AFLNP	P,FLN,AFL	33	43.5	0.105
	AFDNP	FNP,FDN,AFD	29	40.0	0.085
	ALDNP	P,LND,ALD	32	37.5	0.231
<i>Parus major</i>	AFLNP	P,FLN,AFL	33	40.7	0.168
	AFDNP	DP,FDN,AFD	35	30.7	0.678
	ALDNP	DP,LND,ALD	30	22.9	0.820
<i>Ficedula hypoleuca</i>	AFLNP	AFP,ALP,FLP, NP,FLN,AFL	15	14.2	0.509
<i>Phoenicurus phoenicurus</i>	AFLNP	AP,FLN,AFL	31	38.4	0.168

and Redstart, in which distance from a winter feeder has no biological significance. The criterion in choosing an appropriate model was “parsimony” i.e. we attempted to find the model that contains the fewest number of terms and yields a non-significant ($P > 0.05$) test of fit (Benedetti & Brown 1978). BMDP4F was used to perform the analyses (Dixon & Brown 1985). We used three classes of altitude (80–140, 140–200, 200–300 m a.s.l.), distance (0–600, 600–1800, 1800–5800 m from winter feeder), forest type (pine, mixed, birch), field layer (sELiT, sELiPIT, sEMT) and nest-box density (1–4, 5–12, >12 nest-boxes inside a 300 m square). A small number of classes was used to minimize the number of empty cells in the contingency tables (see Vepsäläinen et al. 1988). Despite this, several cells had less than five counts and we therefore added a constant of 0.5 in each cell (see Sokal & Rohlf 1981).

The variation of clutch size and breeding success (100 * numbers fledged/number of eggs laid) was examined with the analysis of covariance (GLM procedure of SAS, SAS Institute Inc., 1985). The continuous variables (altitude and distance) were entered in the model as covariates and the category variables as treatment factors. The annual variation of clutch size and breeding success was significant in the Pied Flycatcher and the Siberian Tit, and the variation of breeding success was significant in the Great Tit (Veistola 1989). As we were interested in habitat effects in general, we pooled the data of the whole study period and used standardized values (deviations from

annual means) in the analysis. The standardization should guarantee that habitat effects that are constant over the years are found, although the pooling of data could mask them (Lundberg et al. 1981). The clutch size distributions were usually close to normal and homoscedastic, but the breeding success distributions could not be normalized.

Results

Habitat preference

Model AFLNP was fitted for all four species studied (Table 2). This model includes all the factors except distance from a winter feeder. The best model for all the species had two terms of interaction between the habitat variables: FLN and AFL. As these two terms do not include the use of a nest box, the factor P, they do not explain habitat distribution, but only show that correlations between habitat variables exist. None of the habitat variables showed interaction with nest box use (variable P) in the *Parus* species. Thus, neither vegetation nor altitude affected the nest distribution of tits in our study area. Four interaction terms containing the variable P were found in the Pied Flycatcher: AFP,ALP,FLP and NP. The term NP is not interesting, because no habitat variables are included. Parameter estimates (λ) of the significant factors in the model show the trends of habitat distribution in the Pied Flycatcher: first (Fig. 1a), at low altitudes it prefers birch forests, but at higher altitudes

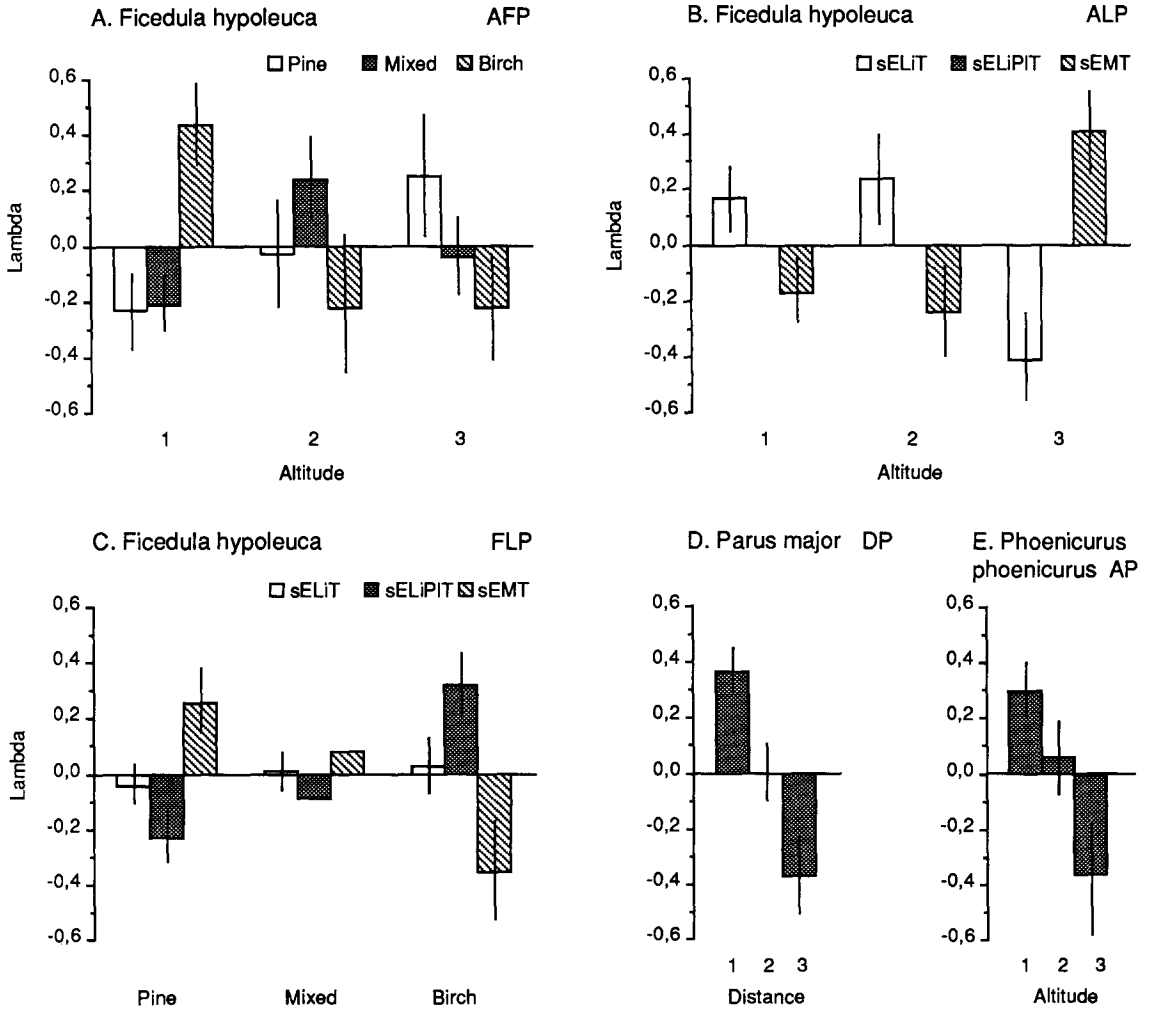


Fig. 1. Parameter estimates (lambda) of habitat occupancy in the best-fit log-linear models found (see Table 2). Positive estimates indicate preference for that habitat type. a: effect of altitude and forest type on nest distribution of the Pied Flycatcher, b: effect of altitude and field layer on nest distribution of the Pied Flycatcher, c: effect of forest type and field layer type on nest distribution of the Pied Flycatcher, d: effect of distance from winter feeder on nest distribution of the Great Tit, e: effect of altitude on nest distribution of the Redstart.

pine forests; second (Fig. 1b), it seems to require a more luxuriant field layer at higher elevations; and, third (Fig. 1c), a more luxuriant field layer is required in pine forests. Altitude was the only habitat variable that affected the nest distribution of the Redstart: in our study area it favours low altitude habitats (Fig. 1e).

The second model, AFDNP (for the tits only), includes distance from the winter feeder instead of the field layer. The best models for both species had the

terms FDN and AFD in common (Table 2). We will not consider these terms, because they do not include P, presence of nest. The model for the Siberian Tit included the term FNP: the effect of nest-box density to presence of nests is different in different forest types. This does not mean, however, that Siberian Tits breed more densely in a certain forest type. In our study area the density of nest-boxes increases with the occurrence of pine forest. This led to the negative effect of nest-box density on the proportion of occu-

Table 3. General linear models (GLM) of clutch size in the species studied. Distance from the nearest winter feeder was included as a covariate in the models for *Parus* species only. Completed clutches whose incubation was started were included in the analysis.

	<i>Par cin</i>		<i>Par maj</i>		<i>Fic hyp</i>		<i>Pho pho</i>	
	F	P	F	P	F	P	F	P
<i>Main effects</i>								
Fo(rest)	3.64	0.035	0.30	0.744	0.51	0.601	0.61	0.546
Fi(eld)	2.05	0.141	0.19	0.826	0.69	0.503	1.38	0.261
<i>Covariates</i>								
Alt(itude)	0.65	0.424	0.29	0.593	2.46	0.118	0.22	0.641
Dis(tance)	0.54	0.466	0.11	0.742
<i>Interactions</i>								
Fo*Fi	3.80	0.017	0.25	0.779	1.60	0.175	1.32	0.278
Fo*Alt	2.34	0.109	0.75	0.484	0.49	0.610	0.82	0.448
Fi*Alt	0.01	0.920	0.98	0.332	0.48	0.617	0.18	0.677
Alt*Dis	0.80	0.375	0.07	0.797
Model	1.64	0.108	0.63	0.804	1.16	0.310	0.87	0.573
n		55		36		411		56

pied nest-boxes, most probably because the territories of Siberian Tits are large (e.g. Haftorn 1973). Distance from a winter feeder explained the nest distribution of the Great Tit in this model (Table 2): in our study area, Great Tits breed near winter feeders (Fig. 1d).

The third model fitted (for *Parus* species) was ALDNP, now including the type of field layer instead of forest type. None of the habitat variables influenced the distribution of the Siberian Tit (Table 2). In this model also, distance from a winter feeder was the only factor that influenced the distribution of the Great Tit.

As we used a rather coarse classification for altitude, its effect may be underestimated in the models. In all species, the distributions of nest frequency by altitude suggest an inverse relationship. The Redstart and the Siberian Tit did not breed above 220 m, or the Great Tit above 250 m a.s.l., although hundreds of nest-boxes were available at these altitudes.

Clutch size

The clutch size of the Great Tit, the Pied Flycatcher and the Redstart was independent of the habitat characteristics studied (Table 3). In the Great Tit and the Redstart our analysis may not be efficient due to the small number of data. The proportion of variance accounted for (R^2) in the model for the Pied Flycatcher was very low (Table 3). As the data base for this

species is large, we are confident that there are no important habitat effects on clutch size in this species.

The clutch size of the Siberian Tit varied among forest types (Table 3). The picture was complicated by significant interaction between forest type and field layer type. In pine forests, the greatest clutch size was observed when the field layer was luxuriant, but in birch and mixed forests when it was less luxuriant (Fig. 2a). However, since the number of clutches in four cells was only one, the result should be regarded as merely tentative. None of the factors that affected habitat distribution in the other three species (Table 2, Fig. 1) affected their clutch size (Table 3).

Breeding success

Breeding success did not vary among habitats in the Siberian Tit (Table 4). In the Great Tit, distance from a winter feeder affected breeding success statistically significantly. The closer to winter feeders Great Tits bred, the higher was their breeding success. This factor also explained the habitat distribution of the Great Tit.

In the Pied Flycatcher, breeding success depended on forest type, but in addition there was interaction between forest type and altitude (Table 4). At lower altitudes, breeding success was better in birch than in pine forests, but at higher altitudes the reverse was true (Fig. 2b). Thus, Pied Flycatchers nested more successfully in their preferred habitat (cf. Figs 1a and

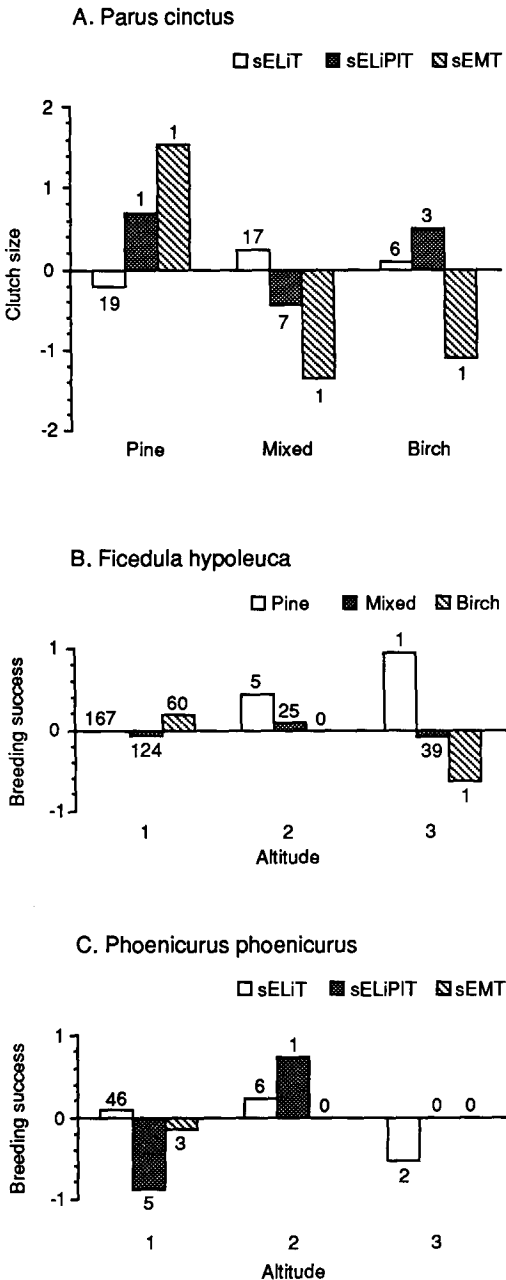


Fig. 2. The significant effects of habitat factors found in GLM's on clutch size in the Siberian Tit (a: forest type and field layer type), and on nesting success in the Pied Flycatcher (b: altitude and forest type) and the Redstart (c: altitude and field layer type). The values presented are standardised deviations from annual means. Numbers of clutches in each habitat type are given at the bars. See Tables 3 and 4 for the GLM's. Note that altitude was used as a linear covariate in the GLM's, but is presented here in the same way as in log-linear models.

2b). The interaction is probably due to the fact that at higher elevations pine forests grow on more luxuriant and climatically favourable sites than birch forests, while at lower altitudes pine forests are usually barren (see Table 2, term AFL).

In the Redstart, breeding success depended on field layer type, but there was interaction between this factor and altitude (Table 4). The interaction is non-linear (2c) and, in fact, may be due to the small numbers at higher altitudes. It may also be noted that the risk level for forest type was close to 0.05. If real, the situation is similar to that in the Pied Flycatcher, although it emerges through a different set of factors.

Discussion

Habitat-specific breeding success decreased with decreasing preference in the Great Tit, Pied Flycatcher and Redstart. In the Siberian Tit, clutch size varied similarly to habitat preference. In addition, high altitude sites were avoided by all four species (see Zang, 1980, for the situation in Central Europe). This may be due to less favourable microclimates and/or food conditions. In our study area, altitude gradually increases from north to south and so does the distance from the sea. This means that microclimatic differences, especially in the beginning of the breeding period, may be larger and more important than the rather small variation in altitude would suggest.

The data used in the present analysis were collected in a large nest-box area (length c. 90 km), where the density of available boxes was at most moderate (0.4–3 boxes/ha). Yet more than four out of five boxes remained unoccupied every year. When breeding density is so low it is unlikely to have a direct intraspecific effect on breeding performance.

The Siberian Tit preferred pine forests, as it does in more southern areas (von Haartman et al. 1967–72, Virkkala 1985). It also bred in birch forests (see also Järvinen 1982), where the average clutch size was lower than in pine forests, but the breeding success was the same. This variation pattern, i.e. that the clutch size, but not the breeding success, correlates with habitat preference, may indicate an ability to adjust the clutch size in relation to the expected breeding success. The distribution of nests, clutch size and breeding success in the Siberian Tit were not affected by distance from winter feeders. In this respect the species differed from the Great Tit. Both the lack of influence of winter feeding and the ability to adjust clutch size in relation to habitat type indicate a high

Table 4. GLM of nesting success (100 * fledglings/eggs laid) in the species studied. All nests in which egg laying was started were included. Distance from the nearest winter feeder was included as a covariate in the models for *Parus* species.

	<i>Par cin</i>		<i>Par maj</i>		<i>Fic hyp</i>		<i>Pho pho</i>	
	F	P	F	P	F	P	F	P
<i>Main effects</i>								
Fo(rest)	1.33	0.275	0.03	0.968	3.56	0.029	2.60	0.084
Fi(eld)	0.31	0.733	1.80	0.184	0.60	0.550	4.73	0.013
<i>Covariates</i>								
Alt(itude)	0.00	0.999	0.06	0.809	0.04	0.846	2.29	0.137
Dis(tance)	0.00	0.958	4.49	0.043
<i>Interactions</i>								
Fo*Fi	1.14	0.345	0.25	0.778	0.70	0.591	1.84	0.152
Fo*Alt	2.15	0.128	0.08	0.922	4.25	0.015	1.35	0.268
Fi*Alt	0.07	0.798	3.03	0.092	0.25	0.778	3.88	0.027
Alt*Dis	0.06	0.806	4.10	0.052
Model	1.15	0.344	1.41	0.214	1.70	0.057	1.46	0.172
n		58		42		430		62

degree of adaptedness to northern conditions in the Siberian Tit. The means by which this tit has adapted to the local conditions are food hoarding and the use of feeding sites and food items that are less likely to be affected by adverse weather (Eeva 1989).

The Great Tits settled close to winter feeders and did better there than elsewhere. This result is similar to those of Hansson (1986) from Central Sweden (60°N) and Orell (1989) from the Oulu district (65°N), who reported that Great Tits breed near winter feeding stations more often than far from them. We were able to demonstrate better breeding success close to winter feeders. At present we do not know the mechanism underlying the better breeding success. There are at least the following possibilities: 1) higher quality birds may conquer the territories close to winter resources, 2) the proximity of human settlement may be directly beneficial during the nestling period, e.g. during cold spells, which are not infrequent in our study area, 3) the distance from human settlement correlates with some environmental variable which was not included in our analysis.

We did not observe any habitat preference based on vegetational characteristics in the Great Tit, although in southern areas it prefers deciduous forests and breeds more successfully in them than in coniferous forests (e.g. Van Balen 1973, Perrins 1979, Ulfstrand et al. 1981).

The Redstart is confined to coniferous forests in natural habitats south of the forest limit (Pulliainen 1977, Virkkala 1987), but farther north it breeds fre-

quently and successfully in birch forests (e.g. Järvinen 1978, 1983). In our study area the Redstarts did not select the breeding habitat on the basis of the vegetational characteristics studied. As the occurrence of pine forests is also negatively correlated with altitude, the only significant factor which we found, the possibility cannot be excluded that pine is an important habitat characteristic, which in this data set happened to be masked by a stronger correlation with altitude. Another reason for the altitude effect, the importance of which will be seen later, is that the Redstart selects old and lower quality nest-boxes, which are more common at low altitudes. In Kilpisjärvi the species occurs at much higher altitudes than in our study area (Järvinen 1983). The breeding success of the Redstart varied with field layer type and almost significantly with forest type. The trends are best summarized by stating that the breeding success was highest in barren pine forests — an observation that fits with the habitat preference known from other areas. In our study area, birch forest is a suboptimal habitat, which, however, offers the species an adequate breeding environment. In the Kilpisjärvi area, where no pine forests are available, the breeding success of the Redstart is sufficient to maintain the population size (Järvinen 1983).

The preference of the Pied Flycatcher for deciduous forests is well documented over its geographical range (Berndt & Winkel 1967, 1975, Lundberg et al. 1981, Gezelius et al. 1984, Järvinen 1984, Tiainen et al. 1984, Alatalo et al. 1985). In eastern Lapland a

preference for coniferous and mixed forests was reported by Pulliainen (1977), and Järvinen & Lindén (1980) reported a larger clutch size in pine than in mountain birch forest. We found that the preference for the forest type defined by the dominant tree species depended on altitude: at low altitudes birch forest was preferred, as in the south, but at higher altitudes pine forests. This may explain the observation by Pulliainen. In addition, a preference for forests with a luxuriant field layer was evident. Breeding success, on the other hand, was best in birch forests. The observations on habitat preference and breeding success are not contradictory, because forest and field layer types are highly correlated, especially at lower altitudes, from where the majority of our data originate.

In conclusion, the habitat preference of the four species studied in Inari Lapland were similar to those in southern and more central populations. As the data from different areas are not directly comparable, we are unable to determine whether the degree of selectivity is lowered in the north (cf. Krebs 1978, p.46). This is suggested, however, by the observations that at higher altitudes the habitat use of the Siberian Tit and the Redstart is extended into birch forests and that of the Pied Flycatcher into pine forests. The suggestion that selectivity is low in harsh subarctic conditions disagrees with the report that birds at the edge of the species range (all the species in this study, but especially the Great Tit and the Pied Flycatcher which have recently spread to the area) select the optimal habitat (e.g. Hildén 1965, Järvinen 1978). The newcomers were in fact selective — the Pied Flycatcher in the direction that could be expected from studies from more central parts of its range. The selectivity of the Great Tit indicated strong attachment to human settlement, but the species did not select its optimal vegetational habitat. In a large part of Fennoscandia the Great Tit is more or less dependent on man. So, our data support the hypothesis of "selective frontier individuals" rather than the hypothesis of "unselective individuals in harsh conditions".

Järvinen (1983, 1989) has reported that the main factor influencing breeding success in the subarctic is weather. As the effects of weather are the same over large areas, the effects of habitat on breeding parameters might be expected to be low or non-existent. However, habitat was found to influence breeding success in particular. As we analysed standardized values over several years, this must mean that differences in breeding success among habitats show the same trend in different years. The effects of habitat

were also understandable from the evolutionary point of view, because they correlated positively with habitat preference. We suggest that the preferred habitats offer food resources that are not completely governed by weather factors. The existence of such consistent differences among habitats is a prerequisite for a bird to evolve habitat selectivity.

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Selostus: Neljän pönttölintulajin pesimäympäristön valinta ja pesintämenestyksen suhde pesimäympäristöön pohjoisella äärialueella

Tutkimme lapintiaisen, talitiaisen, leppälinnun ja kirjosiiepon pesintää Utsjoella ja Inarin pohjoisosassa, Inarin Lapissa, vuodesta 1983 alkaen. Lajit esiintyvät tutkimusalueella pohjoisella äärialueellaan. Kirjosiieppo ja talitiainen ovat levinneet alueelle vasta viime vuosikymmeninä.

Habitaatin valintaa selvitimme käyttäen log-lineaarisia malleja. Luokitelimme habitaatit neljän ominaisuuden perusteella: metsätyyppi (mänty-, seka- ja koivumetsä), kenttäkerroksen kasvillisuus, korkeus merenpinnasta ja etäisyys ihmisen tarjoamista talviruokailumahdollisuuksista (vain tiAISilla). Lisäksi otimme malleissa huomioon tarjolla olevien pönttöjen määrän.

Tutkimillamme lajeilla habitaattien asutusaste vaihteli. TiAISilla ja leppälinnulla ei kumpikaan kasvillisuutta kuvaava tekijä vaikuttanut habitaatin valintaan. Tämä osoittaa näiden lajien habitaatin valinnan väljentymistä eteläisempiin alueisiin verrattuna. Kirjosiieppo suosi alhaalla eteläisten alueiden tapaan reheviä lehtimetsiä, mutta ylempänä olevilla alueilla mäntymetsiä. Leppälinnun havaittiin selvimmin hakeutuvan alhaalla oleviin metsiin, ja kaikki lajit välttivät kaikkein korkeimmalla sijaitsevia tunturikoivikoita. Talitiaisen pesintä on alueella erittäin selvästi sidoksissa ihmisasutukseen.

Pesintämenestys noudatti pääsääntöisesti habitaattien suosituimmuusjärjestystä lapintiaista lukuun ottamatta. Tämä osoittaa, että halutuissa habitaateissa on tarjolla ravintoresursseja, jotka eivät ole täysin säätekijöiden säätelimiä. Havainto tukee myös teoriaa, jonka mukaan territoriaalisuus estää kaikkia pareja sijoittumasta optimihabitaattiin. Habitaattitekijöillä ei ollut lainkaan vaikutusta lapintiaisen pesintämenestykseen, mutta sen pesyekoko vaihteli habitaatin mukaan ja ainakin osaksi eteläisemmällä alueella todetun suosituimmuuden mukaan. Tämä viittaa siihen, että pohjoiseen hyvin sopeutunut laji voi mukauttaa pesyekokonsa odotettavissa olevan menestyksen mukaan.

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