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Conservation value of nature reserves: do hole-nesting birds prefer protected forests in southern Finland?

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The occurrence of 15 hole-nesting species was studied in 39 nature reserves in southern Finland. The densities of species in forests of nature reserves (size range 0.9–55 km^2) were compared to the species' regional densities outside the protected areas. The two most abundant hole-nesters, *Parus major* and *P. montanus*, did not prefer nature reserves. The density of six other species (*Dendrocopos major*, *Picoides tridactylus*, *Phoenicurus phoenicurus*, *Ficedula hypoleuca*, *Parus cristatus* and *Certhia familiaris*) correlated positively with the proportion of forests over 100 years old in the reserves. The density of this species group increased as the area of old-growth forests increased, suggesting that hole-nesters of old-growth forests prefer large forest areas (>5 km^2). Hole-nesters of lush and deciduous forests are poorly represented in the nature reserve network, although several of these species have declined. Thus far, dry pine-dominated forests in particular have been protected. The present reserve network should be enlarged to include more lush forests in order to better preserve the hole-nesting avifauna.

1. Introduction

The conservation value of nature reserves differs from reserve to reserve. Both size and habitat diversity of a nature reserve affect the occurrence of different species. Thus far much of the protected areas has not been established solely on the basis of ecological reasoning, but often as a consequence of human-mediated recreational, scenic, political and land-ownership goals (see

Terborgh & Winter 1983, Götmark & Nilsson 1992). For this reason, nature reserves may not be a representative sample of the landscape. Some threatened species or communities may not necessarily be found in the existing nature reserves, although a considerable part of the land may be protected (Margules et al. 1988). It is usually the poorly productive land which has been protected, whereas in protected areas lush and productive habitats are under-represented (Nilsson & Götmark 1992). In Finland, as well, especially dry forests, poor-quality forest land and 'waste' land (in terms of forestry) have been protected (Ruhkanen et al. 1992, Virkkala et al. 1994).

In order to evaluate possible deficiencies in the nature reserve network, the value of existing protected areas should be analyzed (Rebelo & Sigfried 1992). Hole-nesting bird species represent an important group for analyzing the significance of such existing protected forest areas, because modern forestry removes dead and dying trees important for hole-nesters (Mannan & Meslow 1984, Zarnowitz & Manuwal 1985, Chadwick et al. 1986). Therefore, protected areas in which such silvicultural practises are not allowed are important for several hole-nesters (Haapanen 1965, Virkkala 1987, Virkkala & Liehu 1990).

The significance of single nature reserves for hole-nesting species can be estimated and reserves can then be ranked according to the occurrence of hole-nesters. This is important as a guideline for the future in establishing protected areas, although scoring procedures might be inefficient in conservation evaluation (see Pressey & Nicholls 1989). The cause is that many reserves might mainly duplicate each other as regards the occurrence of species, and several endangered species might live outside the present reserves. So reserves must also be complementary in terms of species representation (Vane-Wright et al. 1991).

In the present work we compare the densities of hole-nesting birds in single nature reserves with their density in the region where a given reserve is situated. Without information on general regional density of species, the representativeness of single nature reserves cannot be evaluated. The general regional density of a given species outside a protected area has an effect on its numbers within the nature reserve. Our study covers southern Finland, which belongs to the south and mid–boreal vegetational zones (Ahti et al. 1968, Hämet-Ahti 1981). The aim of the work is to take into account the effects of regional scale patterns on a local scale (nature reserves). This kind of approach is necessary in understanding the landscape ecology of boreal forests, because the dynamics of species cannot be explained by processes occurring within separate habitat patches or only on a local scale (Virkkala 1991a, Hansson 1992).

2. Material and methods

2.1. Study areas

The abundance of hole-nesters was studied in southern Finland in 39 protected areas whose forest component ranged from 0.9 to 55 km^2. The density of hole-nesters was calculated in forest and scrub land, which are, respectively, regarded as high and poor quality forestry land (Aarne 1992). Forest and scrub land cover about 70% of the land area in the 39 nature reserves (see Appendix 1); 54% of forests in the protected areas is over 100 years old (Ruhkanen et al. 1992), but only 10% in southern Finland as a whole (Aarne 1992). About 75% of southern Finland is covered by forest land.

The situation of the 39 protected areas is shown in Fig. 1, where southern Finland is divided into four regions (zones I–IV). These regions were selected to compare hole-nesters' density in the reserves to these species' regional density in forests. Size of forest area, the proportion of forests of all land in the protected areas, the length of line transects and census year(s) in the different reserves are presented in Appendix 1. The protected areas comprise 550 km^2 of forest and scrub land, which is about 0.45% of all the forest and scrub land in southern Finland (121 000 km^2, Aarne 1992).

2.2. Bird censuses

The density of hole-nesters was estimated by using line transect censuses of birds (Järvinen & Väisänen 1976, Järvinen et al. 1991). The Finn-

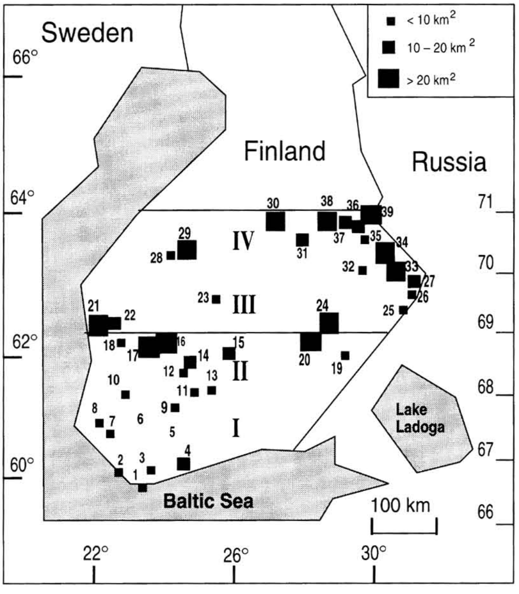

Fig. 1. Situation of the protected areas in the four different zones (grid at the right) in southern Finland. On the left are degrees of northern latitude and at the bottom degrees of eastern longitude. Forest size in protected areas is presented. — N = National Park, S = Strict (restricted access) Nature Reserve, O = other protected area, pl. = yet to be established as a protected area in the near future. — Zone I (grid 66–67): 1 = Tammisaari (N), 2 = Punassuo (O), 3 = Karkali (S), 4 = Nuuksio (N, pl.), 5 = Liesjärvi (N), 6 = Torronsuo (N), 7 = Kurjenrahka (N, pl.), 8 = Vaskijärvi (S), 9 = Aulanko (O). — Zone II (grid 68): 10 = Puurijärvi (N), 11 = Vesijako (S), 12 = Sinivuori (S), 13 = Päijänne (N), 14 = Isojärvi (N), 15 = Haapasuo (O), 16 = Helvetinjärvi (N), 17 = Seitseminen (N), 18 = Häädetkeidas (S), 19 = Punkaharju (O), 20 = Linnansaari (N). — Zone III (grid 69): 21 = Lauhanvuori (N), 22 = Kauhaneva (N), 23 = Pyhä-Häkki (N), 24 = Kolovesi (N), 25 = Petkeljärvi (N), 26 = Ruosmesuo (O), 27 = Koivusuo (S). — Zone IV (grid 70): 28 = Salamanperä (S), 29 = Salamajärvi (N), 30 = Talaskangas (O, pl.), 31 = Tiilikka (N), 32 = Koli (N), 33 = Patvinsuo (N), 34 = Ruunaa (O), 35 = Rasvasuo (O), 36 = Jonkeri (O), 37 = Teerisuo (O), 38 = Hiidenportti (N), 39 = Ulvinsalo (S).

ish line transect method is a one-visit census, in which birds are recorded separately on a 50-m wide main belt and outside it on a supplementary belt; main and supplementary belts together comprise the survey belt.

In calculating bird density (pairs/km^2) survey-belt observations were used by applying species-specific correction coefficients; for details of their calculation, see Järvinen & Väisänen (1983). The species-specific correction coefficient is based on the main/supplementary belt ratio for any given species. This coefficient was calculated according to the pooled data of species' observations in the whole of Finland and in adjacent areas in 1941–92.

Bird censuses in the 39 protected areas consist altogether of 1207 km of transects in southern Finland in 1981–92 (Appendix 1). These data include censuses carried out in all habitats, e. g., those in open peatlands as well. The density of hole-nesters in forests was analyzed by taking into account the proportion of forest and scrub land in every nature reserve (see Appendix 1). Censuses in nature reserves were carried out in the appropriate proportions in the different habitats. The numbers of reserves censused in three periods in 1981–92 in the different zones are presented in Table 1. The mean length of a line transect walked one morning is about 5 km.

The census data from southern Finland covers two periods: 1973–77 and 1986–89 with a total of 2380 km of transects. The total length of the transects and their spatial distribution were equal in the two periods. The two data sets, protected areas and the area of southern Finland, are independent: no censuses of protected areas are included in the south Finnish data. The data on southern Finland were divided into four zones (Fig. 1). The number of transects in the different zones (in km) were as follows:

Zone I (Uniform grid 66–67)	774
Zone II (68)	637
Zone III (69)	521
Zone IV (70)	447

Table 1. Number of nature reserves censused in the three periods in the four different zones. For a reserve counted in years in two periods, only the main census year was taken into account.

Zone	1981–84	85–88	89–92
I	1	4	4
II	3	6	2
III	4	2	1
IV	5	1	6
Total	13	13	13

The average regional density of hole-nesters in forests of the four zones was calculated by taking into account the proportion of forest and scrub land in every zone.

We consider the abundance of 15 hole-nesting species of forests divided into three foraging guilds: (1) woodpeckers (wryneck *Jynx torquilla*, grey-headed woodpecker *Picus canus*, black woodpecker *Dryocopus martius*, great spotted woodpecker *Dendrocopos major*, lesser spotted woodpecker *D. minor*, and three-toed woodpecker *Picoides tridactylus*), (2) flycatchers (redstart *Phoenicurus phoenicurus*, red-breasted flycatcher *Ficedula parva*, and pied flycatcher *F. hypoleuca*) and (3) gleaners (willow tit *Parus montanus*, crested tit *P. cristatus*, coal tit *P. ater*, blue tit *P. caeruleus*, great tit *P. major* and treecreeper *Certhia familiaris*). Gleaners comprising titmice and the treecreeper are considered to be in the tit guild. About 80% of the pairs in the woodpecker guild are of one species, the great spotted woodpecker.

2.3. Statistical analyses

We used an ordination method, the detrended correspondence analysis (DCA, see Hill 1979, Hill & Gauch 1980) to study whether hole-nesting species abundance is distributed differently than are the most abundant forest bird species abundances in our protected and non-protected areas (the four zones of southern Finland). This allowed us to study in more detail the use of hole-nesters in estimating the conservation value of nature reserves. The most abundant forest bird species are mainly habitat generalists not preferring protected areas (Virkkala et al. 1994). Because rare species often appear as statistical outliers in the ordination, we excluded the grey-headed woodpecker, lesser spotted woodpecker and blue tit, which were observed in less than five reserves. In addition to the remaining 12 hole-nesting species we included the 12 most abundant forest passerines: the tree pipit *Anthus trivialis*, dunnock *Prunella modularis*, robin *Erithacus rubecula*, song thrush *Turdus philomelos*, redwing *T. iliacus*, garden warbler *Sylvia borin*, wood warbler *Phylloscopus sibilatrix*, willow warbler *Ph. trochilus*, goldcrest *Regulus regulus*, spotted flycatcher *Muscicapa striata*, chaffinch *Fringilla coelebs* and siskin *Carduelis spinus*. In the DCA we thus had a matrix of the densities of the 24 species in 43 'sites' (39 nature reserves and the four zones of southern Finland), and the aim of this analysis was to study whether the score values (based on densities) of hole-nesting species were distributed differently on the ordination axes from those of the most abundant forest birds.

In comparing nature reserves situating in different zones (I–IV), we standardized densities of hole-nesters, because the density of most bird species change latitudinally. Densities of hole-nesters in nature reserves were standardized (divided) by the species' regional density, by which is meant the mean density in the forests in the 100 km zone of any given reserve. A standardized density of 1.00 in a nature reserve means that the density of hole-nesters there equals the mean density in the forests of the 100 km zone.

Because the data obtained did not fulfill the demands of parametric testing, for instance when using standardized density values, only non-parametric tests (sign test, Mann Whitney *U*-test, Kruskall-Wallis analysis of variance, Spearman rank correlation) were adopted.

2.4. Year-to-year variation

Year-to-year variation might have an effect on the results, because several reserves were censused in only one year. There is information on year-to-year variation in birds in the whole of Finland; most of the data are from southern Finland (Väisänen et al. 1989, Väisänen & Routasuo 1991, R. A. Väisänen, unpubl., Hustings 1992). We compared the year-to-year density variation of the six most common hole-nesters (great spotted woodpecker, redstart, pied flycatcher, willow tit, crested tit, great tit) in Finland in 1981–92 (Table 2). These species comprise 90% of all hole-nesting birds in nature reserves. "Normal" density in a given year was regarded within the range of ±20% of the mean in 1981–92. When the density differed more than 20% from the mean, the year was regarded as showing either a low or a high density for a species. There was no significant between-year difference in the abundance of all the six hole-nesting species (Kruskall-

Wallis analysis of variance, $H'_{\text{corrected for ties}} = 3.187$, $df = 11$, ns). Different species seemed to have population lows in different years, and population fluctuations of species were compensated for when all the six species are considered.

The most pronounced population declines, when numbers of species were more than 30% lower than average in the period 1981–92, were observed in the pied flycatcher in 1981–83 and in the crested tit in 1986. As several reserves were counted in these years, we compared the geometric mean in the standardized density of these species between the reserves censused in years of population collapse with the other reserves counted in other years. Eight reserves were counted in 1981–83 and nine in 1986; with the geometric mean in all the areas also presented:

	1981–83	1986	Other years	All areas
Pied flycatcher	2.22		2.53	2.47
Crested tit		0.91	1.28	1.19

Although the densities of the species in nature reserves were slightly lower in these years, neither in the pied flycatcher (Mann-Whitney *U*-test, $z = 0.410$, ns) nor in the crested tit ($z = 1.361$, ns.) did the densities differ significantly from those obtained from other parks in other years. The highest density for the pied flycatcher in all nature reserves was even observed in Salamanperä Strict (restricted access) Nature Reserve, which was counted in 1982 — the lowest year for the species.

We further compared densities for the great spotted woodpecker in different nature reserves during its population lows in 1982–85 and 1991–92 with densities at its population peak in 1986–90 (Table 2). There was no significant difference in density between nature reserves censused during its population low (standardized density, geometric mean = 1.73, $n = 17$) and population peak (geometric mean = 1.57, $n = 16$; Mann-Whitney *U*-test, $U = 127$, ns).

In the previous comparisons there were no proper controls for year-to-year variations. However, year-to-year variation in species seemed not to be so large that it could fundamentally bias the results.

3. Results

3.1. Gradients in species

Results from DCA-ordination of the abundant forest passerines and the hole-nesters on the first two DCA-axes are presented in Fig. 2. The first axis ordinates species according to dominant tree species and latitudinal patterns, whereas the second DCA-axis ordinates species based on forest-age preferences. The distribution of abundance for hole-nesters differed from that of the abundant forest passerines on the second DCA-axis. However, distribution of certain hole-nesters, like the great tit, the willow tit and the black woodpecker, seemed to be rather similar to that of the abundant forest passerines (Fig. 2).

3.2. Density differences

In nature reserves the mean density (pairs/km^2 ± *SE*) of hole-nesters was 34.10 ± 2.51 in forests, and in forests of southern Finland 23.03 ± 1.21.

Table 2. Population fluctuation in Finland of the six most common hole-nesting species in nature reserves. "Normal" density regarded as having a range of ±20% of the mean in 1981–92. When density deviated more than 20% from the mean, the year was considered either a low- or a high-density year for a given species. – = low, 0 = "normal", + = high density.

	1981	82	83	84	85	86	87	88	89	90	91	92
Dendrocopos major	0	0	–	0	–	0	0	0	0	+	–	–
Phoenicurus phoenicurus	+	0	0	0	0	0	0	0	–	–	0	0
Ficedula hypoleuca	–	–	–	0	0	0	+	0	+	0	+	0
Parus montanus	0	0	0	0	0	0	0	0	0	0	0	–
P. cristatus	–	+	0	0	0	–	–	–	0	0	0	0
P. major	0	–	0	–	0	0	0	0	0	0	+	+

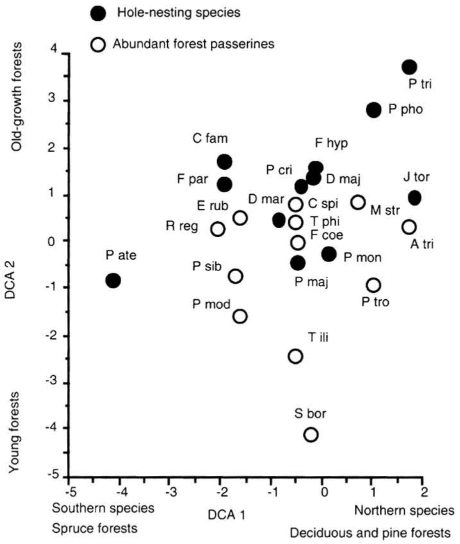

Fig. 2. Ordination of species in protected and non-protected areas (the four zones of southern Finland) based on detrended correspondence analysis (DCA). Score values for 12 hole-nesting species (filled circles) and 12 abundant forest passerines (open circles) on the first two DCA-axes are entered on the axes. Interpretation of factors affecting the first and second DCA-axis on the right. Abbreviations: A tri = *Anthus trivialis*, C fam = *Certhia familiaris*, C spi = *Carduelis spinus*, D maj = *Dendrocopos major*, D mar = *Dryocopus martius*, E rub = *Erithacus rubecula*, F coe = *Fringilla coelebs*, F hyp = *Ficedula hypoleuca*, F par = *F. parva*, J tor = *Jynx torquilla*, M str = *Muscica striata*, P ate = *Parus ater*, P cri = *P. cristatus*, P maj = *P. major*, P mod = *Prunella modularis*, P mon = *Parus montanus*, P pho = *Phoenicurus phoenicurus*, P sib = *Phylloscopus sibilatrix*, P tri = *Picoides tridactylus*, P tro = *Phylloscopus trochilus*, R reg = *Regulus regulus*, S bor = *Sylvia borin*, T ili = *Turdus iliacus*, T phi = *T. philomelos*.

This difference was statistically significant (sign test, $P < 0.01$). The mean density in nature reserves weighted by size of reserve was 28.60 pairs/km^2. The lower weighted density stemmed from the fact that reserves situated in the southernmost zones were smaller and had higher densities than those situated in the northernmost zones. When species were divided into the three foraging guilds (Table 3), the density of woodpeckers and of flycatchers was significantly higher in nature reserves than was their mean density in forests of southern Finland, whereas for the tit guild there was no density difference.

Seven hole-nesting species comprised 96.5% of hole-nesting pairs in nature reserves (great spotted woodpecker, redstart, pied flycatcher, willow tit, crested tit, great tit and treecreeper). Each of these species was observed in at least 36 of the 39 nature reserves. The other eight species (wryneck, grey-headed woodpecker, black woodpecker, lesser spotted woodpecker, three-toed woodpecker, red-breasted flycatcher, coal tit, and blue tit) were each observed in less than 30 areas. The weighted mean density of the seven abundant species in nature reserves was over 1 pairs/km^2 and those of the eight scarce species less than 0.5 pairs/km^2.

Five abundant hole-nesting species were more numerous in the forests of nature reserves than elsewhere in the forests of southern Finland: great spotted woodpecker, redstart, pied flycatcher, crested tit and treecreeper (Table 4). The willow tit was scarcer in the protected areas, and great tit densities did not differ between the nature reserves and forests of southern Finland (Table 4).

Table 5 presents densities of hole-nesters in nature reserves of different zones (I–IV) as standardized by their regional density. Standardized densities of the guilds in every nature re-

Table 3. Mean density (pairs/km^2 ± *SE*) of foraging guilds of hole-nesters in nature reserves and elsewhere in forests of southern Finland. Weighted (by reserve size) mean density in nature reserves in parentheses. Ratio of higher/lower density in nature reserves (n = 39) compared with regional density is presented. Statistical significance based on sign test.

	Nature reserves		Other forests	Ratio	*P*
Woodpecker guild	3.78 ± 2.50	(3.45)	1.81 ± 0.06	32/7	<0.001
Flycatcher guild	11.42 ± 1.06	(11.29)	3.90 ± 0.10	34/5	<0.001
Tit guild	18.64 ± 1.83	(13.74)	17.32 ± 1.06	22/17	ns

Table 4. Mean density (pairs/km^2 ± *SE*) of hole-nesting species in forests of nature reserves and elsewhere in forests of southern Finland. In parentheses the mean weighted (by reserve size) density in nature reserves. For ratio of preferences and the statistical test, see Table 3. Statistical test was carried out for only the most abundant species, observed in at least 36 reserves (see text).

Guild	Species	Nature reserves		Other forests	Ratio	*P*
Woodpecker	*Jynx torquilla*	0.25 ± 0.40	(0.19)	0.16 ± 0.03	–	–
	Picus canus	0.06 ± 0.05	(0.03)	0.04 ± 0.04	–	–
	Dryocopus martius	0.13 ± 0.03	(0.10)	0.07 ± 0.02	–	–
	Dendrocopos major	3.00 ± 0.33	(2.76)	1.52 ± 0.35	31/8	<0.001
	D. minor	0.01 ± 0.10	(0.03)	0.04 ± 0.01	–	–
	Picoides tridactylus	0.35 ± 0.10	(0.36)	0.03 ± 0.01	–	–
Flycatcher	*Phoenicurus phoenicurus*	3.43 ± 0.43	(4.17)	1.05 ± 0.11	31/8	<0.001
	Ficedula parva	0.10 ± 0.05	(0.09)	0.04 ± 0.01	–	–
	F. hypoleuca	8.16 ± 0.81	(7.12)	2.77 ± 0.47	35/4	<0.001
Tit	*Parus montanus*	4.27 ± 0.35	(3.97)	5.61 ± 0.26	8/31	<0.001
	P. cristatus	3.73 ± 0.36	(3.58)	2.97 ± 0.76	27/12	<0.05
	P. ater	0.34 ± 0.13	(0.12)	0.44 ± 0.28	–	–
	P. caeruleus	1.09 ± 0.81	(0.08)	1.04 ± 0.67	–	–
	P. major	6.59 ± 0.35	(4.18)	6.48 ± 1.96	19/20	ns
	Certhia familiaris	2.62 ± 0.40	(1.82)	0.94 ± 0.29	33/6	<0.001

serve are presented in Appendix 2. Density of flycatchers in nature reserves was, on average, 2.5 times and that of woodpeckers 1.7 times their mean regional density in forests, whereas the density of the tit guild was in nature reserves equal to their mean density elsewhere in southern Finland (geometric mean = 0.98, Table 5). Pairwise correlations between the standardized densities of guilds in nature reserves were all positive (Table 6).

There was no statistical significance among the standardized densities of all the hole-nesters in nature reserves between the four regions (zones) (Kruskall-Wallis analysis of variance, H' = 7.027, df = 3, ns) or in the woodpecker guild (H' = 4.315, ns). The flycatcher (H' = 16.139, P < 0.01) and the tit guild (H' = 8.272, P < 0.05) nature reserves situated in different zones had different densities in relation to their regional density. In the tit guild, however, none of the pairwise comparisons was statistically significant (Dunn's nonparametric a posteriori test with unequal sample sizes, K = 4, P > 0.05). For the flycatchers the northern nature reserves had the highest densities in relation to the regional density (see Table 5).

Table 5. Density of hole-nesters in nature reserves of the different zones (I–IV) as standardized by their regional density in forests in every zone. Density of different guilds are presented, with 1.00 meaning that guild's density in nature reserves is equal to density in that region (zone) of reserve. Geometric mean was calculated for standardized densities in nature reserves in every zone. For standardized density values of every single nature reserve, see Appendix 2.

Zone	All hole-nesters	Woodpecker guild	Flycatcher guild	Tit guild
I	1.11	1.44	1.45	0.95
II	1.30	1.30	1.82	1.12
III	1.97	1.97	4.48	1.28
IV	1.51	2.33	3.50	0.76
Total	1.42	1.72	2.48	0.98

Table 6. Values of Spearman rank correlation coefficient (r_s) between standardized densities of guilds in nature reserves (n = 39). Significance levels: *: P < 0.05, **: P < 0.01.

	Flycatcher		Tit	
Woodpecker	0.531	**	0.323	*
Flycatcher	–		0.432	**

3.3. The significance of old-growth forests

In six species (three-toed woodpecker, great spotted woodpecker, redstart, pied flycatcher, crested tit and treecreeper) standardized density increased parallel to the proportion of old-growth forests (over 100 years) in nature reserves (Table 7). The combined and standardized density of the six species preferring old-growth forests was compared to the size of old-growth forest area (Fig. 3). As the area of old-growth forest in nature reserves became larger, the density of hole-nesters occurring in the forests of reserves increased (Spearman rank correlation).

The amount and proportion of lush and moist forests (mainly spruce-dominated) vary greatly between the reserves. We compared the densities of species preferring old-growth forests and the proportion of lush and moist forests in old-growth forests in a reserve. The numbers for the redstart correlated negatively and those for the treecreeper positively with the proportion of lush and moist forests (Table 8).

Nature reserves were ranked according to the standardized density for the six species occurring in old-growth forests (Table 9). In ten reserves the density of this species group was at least three-fold as great as the group's mean regional density in forests. In Salamanperä Strict Nature Reserve the density of species preferring old-growth forests was seven-fold, and in Pyhä-Häkki National Park over five-fold that of the species' mean regional density in forests. In Salamanperä the densities of woodpeckers and flycatchers were the highest of all the reserves, whereas in Pyhä-Häkki the density of the tit guild was the highest (see Appendix 2).

The size of the reserve was taken into account in analyzing the importance of protected

Table 7. Correlation (Spearman rank, r_s) between standardized density of a given species and proportion of forests over 100 years old in nature reserves. All species observed in at least 17 nature reserves are included.

	r_s	z	P
Jynx torquilla	–0.267	1.65	ns
Dryocopus martius	–0.117	0.72	ns
Dendrocopos major	0.348	2.15	<0.05
Picoides tridactylus	0.519	3.20	<0.01
Phoenicurus phoenicurus	0.717	4.42	<0.001
Ficedula hypoleuca	0.513	3.16	<0.01
Parus montanus	–0.300	1.85	ns
P. cristatus	0.414	2.55	<0.05
P. major	–0.103	0.63	ns
Certhia familiaris	0.477	2.94	<0.01

Table 8. Correlation (Spearman rank, r_s) between density of species preferring old-growth forests and proportion of lush and moist forests (>100 years) in nature reserves.

	r_s	z	P
Dendrocopos major	0.212	1.31	n.s.
Picoides tridactylus	0.043	0.27	n.s.
Phoenicurus phoenicurus	–0.337	2.05	<0.05
Ficedula hypoleuca	0.027	0.17	n.s.
Parus cristatus	–0.118	0.73	n.s.
Certhia familiaris	0.396	2.44	<0.02

Table 9. Nature reserves in which standardized density of hole-nesters preferring old-growth forests was highest. In ten reserves density was at least three-fold that of the regional average density in forests. Standardized density was multiplied by forest area of a nature reserve [log (1+x) transformed]. If area of a nature reserve is taken into account, reserves at the end of the table would be among the ten most significant protected areas for hole-nesters preferring old-growth forests. Size of forest areas (in km^2) and rank number of reserves when reserve size is taken into account are presented in parentheses. Mean density (pairs/km^2) in these nature reserves are presented.

Reserve	Standardized density	Density × area	Mean density
Salamanperä (7.0)	7.00	6.32 (1)	50.3
Pyhä-Häkki (9.8)	5.46	5.65 (3)	39.6
Ruosmesuo (7.4)	4.86	4.49 (7)	35.2
Rasvasuo (7.5)	4.55	4.22 (9)	32.6
Koivusuo (10.0)	4.28	4.46 (8)	31.0
Vesijako (1.1)	3.72	1.20	33.9
Petkeljärvi (3.4)	3.61	2.32	26.1
Patvinsuo (49.1)	3.58	6.08 (2)	25.7
Talaskangas (24.9)	3.54	5.00 (5)	25.4
Sinivuori (0.9)	3.36	0.94	30.6
Ruunaa (34.5)	2.86	5.01 (4)	20.6
Salamajärvi (35.7)	2.91	4.56 (6)	20.9
Kolovesi (22.7)	2.97	4.08 (10)	21.5

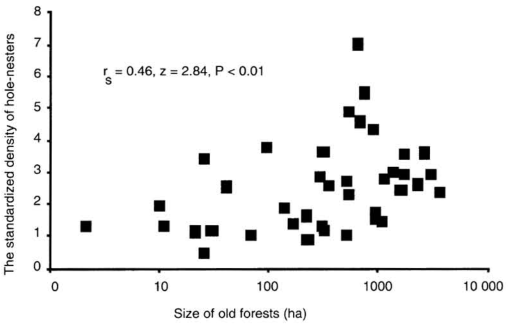

Fig. 3. Relationship between size of old forests (>100 years) in nature reserves and standardized density of hole-nesters preferring old-growth forests. Standardized density of 1.00 means the density in a given reserve equals the density in forests in the zone of the reserve. Value and significance of correlation coefficient (Spearman rank) between size of old forests and standardized density of hole-nesters is presented. Highest standardized densities are in Salamanperä Strict Nature Reserve and in Pyhä-Häkki National Park (see also Table 9). Size of forest area log-transformed.

areas for the hole-nesters: the coefficient of standardized density was multiplied by the log $(x+1)$-transformed forest area of a reserve (Table 9). For this analysis three large areas (Ruunaa, Salamajärvi and Kolovesi) were included in the list of the ten most important protected areas for the hole-nesters of old-growth forests, and the three smallest areas (Vesijako, Petkeljärvi, Sinivuori) were omitted from the list.

4. Discussion

4.1. The importance of regional patterns

Nature reserves are often evaluated only on the basis of site visits. In this kind of analysis only area-effect and species' diversity of a nature reserve can be estimated. However, to study species' rarity, representativeness and naturalness of reserves require detailed knowledge of the surrounding biogeographic region; that is, the reserve should be compared with the region in which it is found (Margules & Usher 1981). In the present work we have tried to take these factors into account in assessing the value of nature reserves to hole-nesters. Without knowledge of the general densities of hole-nesters outside the reserves in different regions it could be difficult or even impossible to evaluate the importance of protected areas to these birds. Average regional densities of species was found to change considerably from south to north in southern Finland. For instance, the southern species, the coal tit and the blue tit, showed an average mean density of 1.2 and 3.0 pairs/km^2 (respectively) in the forests of the southernmost zone (I, uniform grid 66–67), whereas their densities in the two northernmost zones (III and IV, grid 69–70) were only 0.1–0.2 pairs/km^2.

We used hole-nesters to indicate the value of forests for the avifauna in the protected areas of southern Finland. Although difficulties arise in using indicator species (Landres et al. 1987), we consider the present approach as suitable for the evaluation of nature reserves. The distribution of densities of hole-nesters in protected and non-protected areas does differ from that of the most abundant forest bird species, which are more generalized in their habitat selection, and thus do not prefer protected areas in southern Finland (Virkkala et al. 1994). These species are of minor importance in studying the conservation value of nature reserves compared with the value of hole-nesters, because hole-nesters indicate the occurrence of dead and dying trees which are removed systematically from managed forests. Only the woodpeckers are dependent on dying wood in foraging.

4.2. Species and guild-specific preferences for nature reserves

The total density of hole-nesters seemed not to deviate noticeably from that in managed forests outside the protected areas. This was due to the fact that several hole-nesting species, such as the willow tit, coal tit, blue tit and great tit do not prefer the protected areas. The willow tit and great tit are the two most common hole-nesters in Finland, with populations of over 1 million pairs (Koskimies 1989, 1993). The blue tit is a species of lush and deciduous forests, which are under-represented in protected areas (Virkkala et al. 1994). Protected areas are largely covered by dry pine-dominated forests; the willow tit probably occurs in forests having more deciduous trees, because the species usually excavates its nest-hole in a decaying birch (von Haartman et al. 1963–72).

The significance of nature reserves for hole-nesters was most pronounced in the flycatchers, as their density was three-fold in reserves compared to that in other forests in southern Finland. For the woodpeckers, the density difference was about two-fold, but for the tit guild no difference was observed. Among the most abundant hole-nesters, the redstart showed the highest densities in protected areas, on the average four-fold compared to the regional mean density. The abundance of the redstart in nature reserves can in part be explained by the fact that the species prefers particularly dry pine forests which are more common in the protected areas than are moist and lush forests (see Ruhkanen et al. 1992, Virkkala et al. 1994). The redstart has declined considerably both in southern (Järvinen & Väisänen 1978) and northern Finland (Väisänen et al. 1986) during the past 50 years, presumably owing to the cutting of old-growth pine forests (Järvinen et al. 1977, Virkkala 1987). The species occurs also in other kinds of habitats, such as near human settlements (von Haartman et al. 1963–72), but in forests its density is, by far, highest in old-growth pine forests. The high density of flycatchers in nature reserves situated in the northern zones is in part due to the fact that these areas include more dry forests suitable for the redstart.

The other common flycatcher, the pied flycatcher, was numerous in nature reserves. The pied flycatcher also occurs often near human settlements (von Haartman et al. 1963–72), but as regards forests, the species' abundance seems to correlate with the proportion of mature and old-growth forests in nature reserves.

The three-toed woodpecker is a species of old-growth coniferous forests, which have declined considerably due to cutting during recent decades (Järvinen & Väisänen 1979, Väisänen et al. 1986). The density of the three-toed woodpecker in nature reserves is more than ten-fold its level elsewhere in southern Finland, and about 10% of the southern Finnish population is estimated to breed in nature reserves (Virkkala et al. 1994). At present, the three-toed woodpecker is an endangered species in southern Finland (Rassi et al. 1992).

The grey-headed woodpecker and the lesser spotted woodpecker are species occurring mainly in the lush and deciduous forests which are poorly represented in the protected areas (Virkkala et al. 1994).

The black woodpecker was not abundant in the protected areas although the species occurs in mature and old-growth forests (von Haartman et al. 1963–72). The home range of the black woodpecker is, however, very large, covering about 5–10 km^2 (see Tjernberg et al. 1993), so that its preference for or avoidance of the protected areas cannot be properly evaluated by the present data, most of the reserves being smaller than 10 km^2. The black woodpecker forages in forest areas widely separated from each other (Haila et al. 1987, Tjernberg et al. 1993).

4.3. Effect of reserve area and landscape structure

Nature reserves having larger areas of old-growth forests contain higher densities of species preferring such forests. Very small areas of virgin forests are highly susceptible to the influence of the surrounding managed landscape (see Janzen 1983, Väisänen et al. 1986). Areas of old-growth forests larger than 5 km^2, on average, included the highest densities of hole-nesters, whereas areas smaller than that seemed largely to reflect the general regional density patterns of hole-nesters. However, certain very small areas can be important for the hole-nesters, such as Vesijako and Sinivuori, in size only about 1 km^2: Vesijako and Sinivuori include moist and lush forests which are rather rare habitat types in the present reserves. In general, it is in the larger areas of old-growth forest where influence from the surrounding managed landscape might be minimized. In northern Finland the so-called northern taiga species (capercaillie *Tetrao urogallus*, three-toed woodpecker, pine grosbeak *Pinicola enucleator*, Siberian tit *Parus cinctus*, and Siberian jay *Perisoreus infaustus*), preferring old-growth forests, had not declined in old-growth forests which are part of a very large virgin forest tract, about 1000 km^2 in size (Virkkala 1991b). However, the species had disappeared or declined in much smaller virgin forest areas and patches which were isolated as a consequence of forest cutting (Väisänen et al. 1986, Virkkala 1987).

In addition, several species may have rather large home ranges and therefore cannot inhabit very small reserves. It should also be noticed that density estimates for small nature reserves are based on small samples more susceptible to stochastic variations than are the larger samples in larger nature reserves.

When area was taken into account in estimating the significance of protected areas for hole-nesters, larger forest areas were especially significant. Because larger areas contain various types of forests, larger nature reserves include more diverse forests, their spatially greater heterogeneity thus probably affecting the occurrence of hole-nesters. In general, spatial heterogeneity increases the numbers of forest birds (Raivio 1992). Several forest birds utilise different kinds of habitat patches: capercaillie leks are situated in old-growth forests where the birds also over-winter. However, both sexes of the species use younger stages of forests during part of the year, and during summer females move their brood to mires to exploit an abundant invertebrate fauna (Rolstad & Wegge 1990, Sjöberg & Ericson 1992). Forest passerines also utilise different kinds of forests within their home range (Haila et al. 1989, Hanski & Haila 1988).

Titmice, treecreeper and woodpeckers (excluding the wryneck) are mainly sedentary, whereas flycatchers are tropical migrants. Thus, species of the tit and woodpecker guild do not colonize nature reserves every year as migratory species do, and the effects of the surrounding landscape and the size of old-growth forest can be more straightforward regarding the occurrence of sedentary than that of migratory species (Haila 1986).

4.4. Conservation value and complementarity of reserves

Salamanperä Strict Nature Reserve and Pyhä-Häkki National Park offered the highest density indices for hole-nesters preferring old-growth forests. In Pyhä-Häkki National Park the wood-decomposing insect fauna (Coleoptera) consists of several endangered and rare species of primeval forests (Biström & Väisänen 1988, Väisänen et al. 1993), and Pyhä-Häkki is highly important among nature reserves in preserving wood-decomposing beetles (Rassi & Väisänen 1987). Therefore, the abundance of hole-nesters might also be used as a rough indicator of the general conservation value of forests in nature reserves.

The conservation value of individual nature reserves should not, however, be over-emphasized. Scoring procedures neglecting the complementarity of sites in analyzing reserve networks can be highly inefficient (Pressey & Nicholls 1989, Pressey et al. 1993). A small reserve can be important for a particular organism, which might not be observed in other reserves at all.

In the present study the pairwise correlations between hole-nesting guilds in nature reserves were all positive, whereas complementarity should be reflected as negative correlations. Between the hole-nesting guilds of this work no complementarity could be observed; different guilds had their highest densities in the same reserves. This is not to say that complementarity of different reserves should not be taken into account in founding reserve networks. If several bird and animal groups had been compared complementarity certainly would have been essential. In the hole-nesters there is an example of the lack of complementarity in the present reserve network. Endangered or declining species of woodpeckers occurring in lush and deciduous forests — the white-backed woodpecker *Dendrocopos leucotos* (Virkkala et al. 1993), the grey-headed woodpecker, and the lesser spotted woodpecker — are poorly represented in the present reserves. Therefore, the lush and deciduous forests of southern Finland in particular should be protected in future to preserve the hole-nesting avifauna.

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Appendix 1. Size of forest area (forest and scrub land, km^2), percentage of forest area in the protected area, length of line transects (km) and census years. Location of protected areas in the different zones is presented. N = National Park, S = Strict Nature Reserve, O = other protected area. Protected areas yet to be established are included. Line transect kms cover all habitat types, but censuses were carried out in appropriate proportions in the different habitats.

Protected area	Zone	Area	%	Trans.	Year
Tammisaari (N)	I	3.9	97	16.3	90
Punassuo (O)	I	1.2	43	5.0	89
Karkali (S)	I	1.0	99	4.0	86
Nuuksio (N, planned)	I	13.1	96	30.0	91
Liesjärvi (N)	I	6.6	98	21.8	81,82
Torronsuo (N)	I	5.2	21	32.4	86
Vaskijärvi (S)	I	4.5	41	15.0	86
Kurjenrahka (N, planned)	I	3.6	54	14.0	86
Aulanko (O)	I	0.9	91	4.9	92
Puurijärvi (N)	II	1.6	33	25.4	86
Vesijako (S)	II	1.1	99	4.8	86
Sinivuori (S)	II	0.9	99	3.8	86
Päijänne (N)	II	6.0	98	11.0	92
Isojärvi (N)	II	18.5	99	33.0	83
Haapasuo (O)	II	14.2	68	21.7	88
Helvetinjärvi (N)	II	20.1	97	31.2	82
Seitseminen (N)	II	32.0	81	79.2	81,82, 87
Häädetkeidas (S)	II	5.2	92	7.8	86
Punkaharju (O)	II	1.8	93	9.2	92
Linnansaari (N)	II	32.2	93	44.3	83,87
Lauhanvuori (N)	III	20.9	79	38.8	81,82
Kauhaneva (N)	III	11.2	35	35.7	86
Pyhä-Häkki (N)	III	9.8	82	36.8	82
Kolovesi (N)	III	22.7	99	27.8	88
Petkeljärvi (N)	III	3.4	91	16.2	82,84
Ruosmesuo (O)	III	7.4	45	21.9	89
Koivusuo (S)	III	10.0	48	53.2	84,85
Salamanperä (S)	IV	7.0	58	20.4	82,83
Salamajärvi (N)	IV	35.7	64	62.2	82,83
Talaskangas (O, planned)	IV	24.9	80	46.4	89
Tiilikka (N)	IV	14.0	65	29.1	84
Koli (N)	IV	8.5	98	5.1	92
Patvinsuo (N)	IV	49.1	54	102.7	83,84, 88
Ruunaa (O)	IV	55.1	84	73.3	90,92
Rasvasuo (O)	IV	7.5	65	20.5	89
Jonkerinsalo (O)	IV	12.2	93	20.5	91
Teerisuo (O)	IV	16.3	79	40.4	89,92
Hiidenportti (N)	IV	36.9	90	74.2	83,84
Ulvinsalo (S)	IV	22.9	91	67.0	84,85

Appendix 2. Density of hole-nesters in different protected areas as standardized by regional density in forests in every zone. Density of different guilds presented. 1.00 means that the species' density in a nature reserve equals the density in that region (zone) of the reserve.

Protected area	Zone	All	Woodpecker	Flycatcher	Tit
Tammisaari	I	0.76	0.18	1.29	0.72
Punassuo	I	0.93	1.63	0.67	0.91
Karkali	I	1.60	1.96	3.53	1.24
Nuuksio	I	1.05	1.71	1.63	0.90
Liesjärvi	I	0.69	1.38	0.44	0.67
Torronsuo	I	1.10	1.40	1.99	0.92
Vaskijärvi	I	1.72	5.62	1.53	1.07
Kurjenrahka	I	0.74	1.34	1.29	0.60
Aulanko	I	2.28	1.87	3.24	2.15
Puurijärvi	II	0.80	0.73	0.72	0.83
Vesijako	II	2.23	2.76	3.14	1.95
Sinivuori	II	2.48	3.22	3.72	2.10
Päijänne	II	0.96	0.49	1.03	0.99
Isojärvi	II	1.21	0.83	2.00	1.06
Haapasuo	II	0.87	2.99	0.93	0.63
Helvetinjärvi	II	1.16	0.32	1.54	1.16
Häädetkeidas	II	1.93	3.48	3.95	1.27
Seitseminen	II	1.07	1.72	1.61	0.87
Punkaharju	II	1.53	0.86	2.99	1.24
Linnansaari	II	1.09	1.35	1.58	0.94
Lauhanvuori	III	1.59	1.20	3.73	1.12
Kauhaneva	III	0.90	1.22	1.92	0.60
Pyhä-Häkki	III	3.72	4.11	4.79	3.40
Kolovesi	III	1.82	1.57	4.53	1.19
Petkeljärvi	III	2.01	1.47	4.88	1.38
Ruosmesuo	III	2.64	3.32	8.05	1.19
Koivusuo	III	2.20	2.45	5.95	1.23
Salamanperä	IV	3.82	6.32	8.55	2.18
Salamajärvi	IV	1.82	3.81	3.37	1.16
Talaskangas	IV	1.60	2.94	4.43	0.64
Tiilikka	IV	1.68	4.07	3.32	0.95
Koli	IV	0.71	0.61	0.83	0.69
Patvinsuo	IV	1.79	3.07	4.58	0.84
Ruunaa	IV	1.45	2.04	3.18	0.88
Rasvasuo	IV	2.05	1.55	7.78	0.47
Jonkerinsalo	IV	1.23	1.46	3.66	0.51
Teerisuo	IV	1.12	2.02	3.10	0.45
Hiidenportti	IV	1.23	2.30	2.68	0.69
Ulvinsalo	IV	1.21	2.25	2.75	0.63