Ornis Fennica 71:156–169. 1994

Factors affecting the structure of Finnish birds of prey communities

Tapio Solonen

Solonen, T., Department of Zoology, Division of Ecology, P.O. Box 17 (P. Rautatiekatu 13), FIN-00014 University of Helsinki, Finland

Received 29 December 1993, accepted 31 September 1994

The large-sized species tended to occur in lower densities but, contrary to the expectation, their ranges tended to be less extensive than those of the smaller-sized species. Correlation between the density and the size of the range of the species was not significant. Disturbed populations and marginal ranges of many species seemed to explain the deviations from expectations. Environmental factors indicating productivity seemed to be important in explaining density variation in many, but not all of the species considered. The number of species and diversity in local assemblages increased, while the total density decreased with increasing latitude. Tree species composition of forests in combination with latitude explained best the geographical variation in the number of species. The total density of birds of prey was best explained by the combination of those variables that indicated productivity, the contribution of the proportion of fields being the most pronounced. Environmental variables indicating gradients in productivity also explained best the variation in the structure of the local communities as a whole. The availability of forests seemed to explain the large scale difference in the community structure between the central and peripheral parts of the country.

1. Introduction

The structure of a local bird community or assemblage is a result of the occurrence and abundance of species, which in turn are consequences of the distribution and habitat requirements of species. The distribution and abundance of species are constrained both by historical reasons and by a combination of various biotic and abiotic factors (Brown 1984, Brown & Maurer 1987, Solonen 1994). Body size is an important variable in the food axis of community structure (Marti et al. 1993b). Not surprisingly, the availability of food seems to be by far the most important factor in contributing to the numbers of birds (e.g., Newton 1980, Wiens 1989, Marti et al. 1993a). For birds of prey, direct persecution and habitat alterations, especially due to forestry, also seem to have pronounced effects (e.g., Newton 1979, Saurola 1985, Solonen 1993).

For breeding birds, the essential ultimate features of habitat include the availability of suitable food and nest-sites (Hildén 1965, Cody 1985). These resources seem often to be of short supply, especially in birds of prey characterized by relatively large body size (see, e.g., Newton 1979, 1980, Mikkola 1983, Solonen 1993). These features, among other things, make the relationships between body size, local density, and geographical range of birds of prey an interesting special case worthy of closer examination as compared with other avian groups, or birds in general (cf. Solonen 1994).

The aim of this study is to characterize various aspects of interactions between the Finnish birds of prey and their environment by body size, population density, and range size, and to examine how well various environmental factors explain the patterns detected in the community structure at a regional scale. The general expectations are as follows:

1) Population density should decrease and the size of the geographic range should increase with increasing body size. These tendencies should exist, because the larger species need more food, and their spatial requirements and colonization potential are larger than those in the smaller species (Schoener 1968, Newton 1979, Brown & Maurer 1987, Solonen 1994).
2) Range size should increase with density, indicating the spill-over of populations (Brown 1984, Brown & Maurer 1987). This relationship may, however, be complicated by the size of the bird (e.g., Harvey & Godfray 1987, Arita et al. 1989).
3) The number and diversity of birds should increase with increasing productivity and diversity of habitats, while they should decrease

Table 1. Local variations in the Finnish community of birds of prey: density estimates (pairs/1000 km²) in moderate vole years (data derived mainly from Saurola 1985). Widely fluctuating (nomadic) species are marked with an asterisk (*), irregular or sparse nestings with plus (+). A code figure (1–22) and the approximate latitude (°, below) for each local area are given.

	Local areas																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Species	60	61	60	61	61	61	62	61	61	62	62	63	63	64	63	63	63	63	65	65	66	68
Pernis apivorus	5	15	45	15	35	45	10	25	45	25	45	60	15	30	10	20	15	20	10	5	5	3
Milvus migrans	–	–	+	–	–	+	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	+
Haliaetus albicilla	12	1	–	–	–	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	+
Circus aeruginosus	3	2	1	1	5	2	+	4	2	2	5	1	1	1	+	1	1	1	–	+	–	
*Circus cyaneus**	1	–	–	–	+	1	1	–	–	–	2	13	3	20	11	4	5	10	5	14	18	14
Accipiter gentilis	33	35	30	29	54	18	19	35	41	22	44	34	25	44	22	30	21	22	19	21	8	8
Accipiter nisus	33	60	75	60	29	79	12	71	64	30	87	48	13	56	16	34	23	43	10	42	9	7
Buteo buteo	20	25	52	27	69	48	33	71	41	27	54	19	28	48	16	43	30	45	14	21	19	13
*Buteo lagopus**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	+	2	15
Aquila chrysaetos	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	1	1	2
Pandion haliaetus	5	5	8	8	5	5	4	4	7	7	5	3	3	3	1	4	1	1	1	1	1	+
*Falco tinnunculus**	1	3	3	2	11	7	1	4	3	3	6	11	10	20	7	3	8	12	5	7	4	3
Falco columbarius	3	1	1	+	4	4	1	3	4	1	2	4	+	3	1	2	4	7	3	8	1	9
Falco subbuteo	7	15	22	19	20	35	6	16	26	5	10	29	5	4	7	9	9	13	6	2	4	3
Falco rusticolus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Falco peregrinus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	1
Bubo bubo	67	30	21	10	10	7	5	5	17	22	16	17	16	40	19	9	2	3	2	6	1	1
*Nyctea scandiaca**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
*Surnia ulula**	2	–	–	–	+	1	1	+	+	+	+	+	–	1	+	1	1	6	5	7	9	15
Glaucidium passerinum	–	5	15	5	25	18	8	12	14	11	33	4	10	16	19	9	5	10	7	4	7	5
Strix aluco	3	25	60	39	69	35	4	20	26	28	13	3	1	1	+	9	3	3	–	–	–	
Strix uralensis	–	5	9	10	10	7	14	35	37	36	33	6	2	24	33	52	14	7	6	4	1	1
*Strix nebulosa**	–	–	+	–	+	1	1	+	+	+	+	–	–	2	+	1	1	2	5	6	7	5
*Asio otus**	10	28	41	77	59	53	8	25	23	27	18	23	2	12	54	6	5	24	5	3	2	2
*Asio flammeus**	4	1	1	–	3	3	1	1	1	1	6	20	3	35	82	1	8	12	9	10	32	25
*Aegolius funereus**	10	60	67	60	64	75	22	25	23	46	55	21	19	45	82	45	17	25	18	15	52	30

with increasing climatic harshness (i.e., northward) and with various detrimental effects of man (cf., e.g., MacArthur 1972, Wiens 1989). Environmental factors indicating food availability should have major contributions to various aspects of the structure of assemblages of birds of prey (cf. Newton 1979, 1980).

2. Material and methods

The data used in this paper come from various published sources, and represent varying levels of accuracy, but they were standardized as far as possible. The average body masses were taken from general handbooks (v. Haartman et al. 1963–72, Newton 1979, Mikkola 1983). As an index of mean density (pairs/100 km^2), I used the estimate of the total Finnish population for each species (Helo 1981, Saurola 1985, 1986a, Stjernberg 1983, Wikman 1983) divided by the measure of the range. As a measure of the geographical range of each species, I used the number of the 100 km^2-squares in which the species was recorded in the Finnish breeding bird atlas (Hyytiä et al. 1983; cf. Virkkala 1993). There was a significant correlation between the area of the Finnish range and that of the Western Palearctic range of the species (Cramp & Simmons 1980, Cramp 1985) ($r_S = 0.69$, $n = 25$, $P < 0.01$).

The local densities of the species (Table 1) were derived from population estimates in 22 sub-areas covering the whole country (Saurola 1985). To reduce the effect of local peculiarities on the regional patterns, in some analyses, a few minor areas of the original data set were combined, resulting in 18 sub-areas. Large, within species variation in the estimates suggests that some of the estimates may be fairly subjective. The bases of the estimates, however, are not clear and show some variation.

The environmental data used to interpret the observed patterns were mainly from the official statistics of Finland (Anon. 1987, Uusitalo 1989). They included measures of climatic harshness and unpredictability, productivity, and general structure of habitats, as well as measures of forests, indicating features and the effects of man (Table 2).

Relationships between the body mass, density, and range of the species were studied by bivariate correlation plots (Brown & Maurer 1987, Solonen 1994). Due to a wide (latitudinal) gradient with strongly non-linear abundance distribution patterns, initial ordinations of local as-

Table 2. Environmental variables that were used to interpret the patterns found in Finnish communities of birds of prey, their correlation (r_S) with latitude, and their primary indications. Significance of the relationship is indicated as follows: * = P<0.05, ** = P<0.01. Sources of the environmental data: Anon. 1987, Uusitalo 1989.

Variable	Correlation (r_S) with latitude		Primary indications
Latitude (°)			Climatic harshness and unpredictability
Size of the local area (km^2)	+	**	Artefact
Forests of >100 yrs old (%)	+	**	Effects of forestry
Dominance of pine (%)	+	*	Habitats
Forest land area (%)	+	ns	Habitats
Deciduous forests (%)	+	ns	Habitats, forestry
Forests of <20 yrs old (%)	+	ns	Effects of forestry
Forests of 20–60 yrs old (%)	–	ns	Effects of forestry
Dominance of spruce (%)	–	*	Habitats, productivity
Proportion of fields (%)	–	**	Productivity, habitats
Mineral forest land (%)	–	**	Productivity
Forests of 60–100 yrs old (%)	–	**	Effects of forestry
Mean volume of the growing stock in forests (m^3/ha)	–	**	Effects of forestry (or productivity)

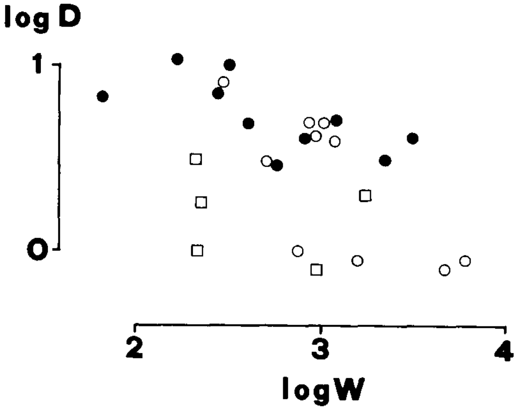

Fig. 1. General population density (D, pairs/100 km²) in relation to individual body mass (W, g) in Finnish birds of prey: hawks (Accipitridae, including Pandion) (open circles), falcons (Falconidae) (open squares), and owls (Strigidae) (solid circles).

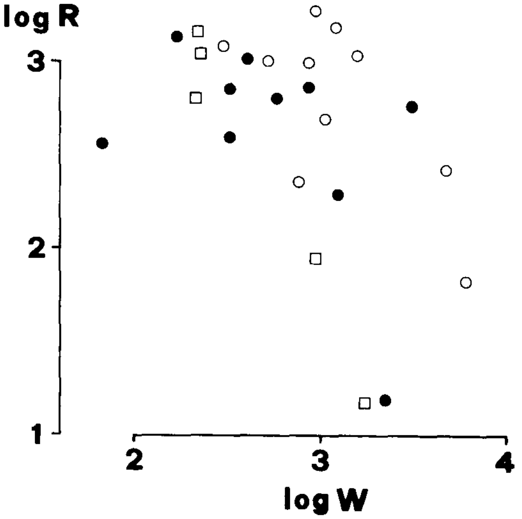

Fig. 2. Area of the Finnish range of the species (R, 100 km²) in relation to individual body mass (W, g) in Finnish birds of prey (for the explanation of the symbols, see Fig. 1).

semblages produced by correspondence analysis (COA) were rearranged by nonmetric multidimensional scaling (NMDS; see Ludwig & Reynolds 1988). In the environmental interpretations of the patterns found I used simple and multiple linear regression analyses and discriminant analysis (Ludwig & Reynolds 1988).

3. Results

3.1. Relationships between bird species and their environment

As expected, the large-sized species tended to occur in lower densities (Fig. 1; $r = -0.48$, $df = 23$, $P < 0.05$), but contrary to the expectation their ranges tended to be less extensive (Fig. 2; $r = -0.47$, $P < 0.05$) than those of smaller-sized species (log-transformed data). These tendencies were consistent both in the diurnal and in the nocturnal species. No significant correlation was found between the density and the size of the range of the species (Fig. 3), either in the total group of species ($r = 0.32$) or in the two subgroups ($r = 0.44$, $df = 13$, and $r = 0.41$, $df = 8$; for raptors and owls, respectively).

In most species, there were several (4–9) significant relationships between the density and the environmental variables considered, but in a few species (*F. tinnunculus, B. bubo, G. passerinum, S. uralensis*) only a single, or no significant relationship was found (Appendix). Environmental factors indicating productivity seemed to be important in explaining density variation in many, though not all of the species considered. In some nomadic species (*C. cyaneus, S. ulula, S. nebulosa, A. flammeus*) the relationships were negative, suggesting that some factors correlating reciprocally with productivity, collectively indicated by latitude, were governing.

Latitude (indicating not only climatic harshness and unpredictability, but also declining productivity) alone explained on an average 33.8% ($r^2 = 0.024$–0.718, $n = 19$) of the variation in the density of the species (Appendix). It also explained considerable proportions of the coefficients of multiple determination (R^2) in various combinations with those environmental variables that indicated productivity and other features of habitats. In many cases, however, the relationships were not significant. Contributions of other factors were higher in a few cases only, the effects of productivity being more probable than those of forestry.

The age structure of forests (sometimes in combination with some aspects of productivity)

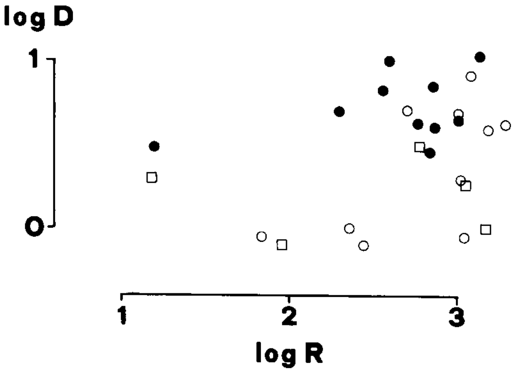

Fig. 3. Relationship between the general population density (D, pairs/100 km²) and the area of the Finnish range (R, 100 km²) for Finnish birds of prey (for the explanation of the symbols, see Fig. 1).

contributed much to the variation in density in many species, while in four species (*F. subbuteo, B. bubo, A. otus, A. funereus*) tree species composition seemed to be of importance (Appendix). In most species, significant combinations of factors were found that explained up to 35–85% of the variation in species' density. In two species (*G. passerinum, S. uralensis*), however, significant combinations were not found.

3.2. Variation in the community structure

The number of species and diversity in the local assemblages of birds of prey increased significantly northward, due to the increasing proportion of diurnal species, while the decrease in the total density was largely due to the decreasing densities of a few dominant species (Tables 1 and 3). The number of species was also affected by the northward increasing size of the local areas, the percent contribution to the coefficient of multiple determination with latitude ($R^2 = 0.713$, $F = 18.66$, df = 2, 15, $P < 0.001$) being 36.5%. The number of species was significantly related to most of the environmental variables considered (Table 3), as well as to their combinations (Table 4). It increased with the proportion of fields and decreased with the proportion of forests. Tree species composition of forests, in combination with latitude, explained best the geographical variation in the number of species

Table 3. Contribution of various environmental variables (cf. Table 2) to the local variations in the number of species, total density, and diversity (H') of Finnish birds of prey: results of simple linear regression analyses (df=17).

Environmental variables	r^2	t	P<
Number of species			
Latitude	0.679	5.81	0.001
Size of the local area	0.618	5.09	0.001
Proportion of fields	0.457	3.67	0.01
Mineral forest land	0.459	−3.68	0.01
Dominance of spruce	0.418	3.39	0.01
Dominance of pine	0.017	0.53	ns
Deciduous forests	0.011	0.42	ns
Forests of <20 yrs old	0.134	−1.57	ns
Forests of 20–60 yrs old	0.492	−3.94	0.01
Forests of 60–100 yrs old	0.008	−0.36	ns
Forests of >100 yrs old	0.390	−3.20	0.01
Forest land area	0.421	−3.41	0.01
Volume of the growing stock	0.655	−5.51	0.001
Total density			
Latitude	0.351	−2.94	0.01
Size of the local area	0.249	−2.30	0.05
Proportion of fields	0.072	−1.12	ns
Mineral forest land	0.115	1.44	ns
Dominance of spruce	0.350	−2.93	0.01
Dominance of pine	0.037	−0.78	ns
Deciduous forests	0.039	−0.80	ns
Forests of <20 yrs old	0.312	2.70	0.05
Forests of 20–60 yrs old	0.288	2.55	0.05
Forests of 60–100 yrs old	0.030	−0.70	ns
Forests of >100 yrs old	0.570	4.60	0.001
Forest land area	0.039	0.80	ns
Volume of the growing stock	0.127	1.52	ns
Diversity			
Latitude	0.515	4.12	0.001
Size of the local area	0.214	2.09	ns
Proportion of fields	0.016	0.51	ns
Mineral forest land	0.034	−0.75	ns
Dominance of spruce	0.114	1.44	ns
Dominance of pine	0.204	2.02	ns
Deciduous forests	0.059	1.01	ns
Forests of <20 yrs old	0.005	−0.27	ns
Forests of 20–60 yrs old	0.358	−2.99	0.01
Forests of 60–100 yrs old	0.003	0.20	ns
Forests of >100 yrs old	0.281	−2.50	0.05
Forest land area	0.336	−2.84	0.05
Volume of the growing stock	0.441	−3.55	0.01

Table 4. Contribution of various sets of environmental variables (A–F) to the local variations in the number of species, total density, and diversity (H') of Finnish birds of prey. Results of multiple linear regression analyses as well as percent contributions of each variable (EV; cf. Table 2) to the coefficients of multiple determination (R^2) are given.

Number of species	Combinations of environmental variables					
	A	B	C	D	E	F
R^2	0.751	0.667	0.799	0.674	0.690	0.535
F	9.79	9.36	18.58	9.66	10.36	3.74
df	4, 13	3, 14	3, 14	3, 14	3, 14	4, 13
P<	0.001	0.01	0.001	0.01	0.001	0.05
EV	Percent contribution of environmental variables					
Latitude	63.3	–	30.7	–	83.1	–
Fields	5.9	36.9	–	–	–	–
Mineral land	4.7	34.7	–	–	–	–
Spruce forests	26.1	28.4	29.8	52.3	–	–
Pine forests	–	–	39.5	46.2	–	–
Deciduous forests	–	–	–	1.5	–	–
Young forests	–	–	–	–	–	3.5
Youngish forests	–	–	–	–	–	14.5
Oldish forests	–	–	–	–	16.7	40.1
Old forests	–	–	–	–	0.2	41.9

Total density	Combinations of environmental variables					
	A	B	C	D	E	F
R^2	0.630	0.571	0.375	0.452	0.403	0.515
F	5.53	6.21	2.80	3.85	3.15	3.46
df	4, 13	3, 14	3, 14	3, 14	3, 14	4, 13
P <	0.01	0.01	ns	0.05	ns	0.05
EV	Percent contribution of environmental variables					
Latitude	40.2	–	40.2	–	50.2	–
Fields	46.9	96.4	–	–	–	–
Mineral land	10.0	1.6	–	–	–	–
Spruce forests	2.9	2.0	33.7	54.1	–	–
Pine forests	–	–	26.1	40.9	–	–
Deciduous forests	–	–	–	5.0	–	–
Young forests	–	–	–	–	–	7.6
Youngish forests	–	–	–	–	–	22.0
Oldish forests	–	–	–	–	0.4	27.3
Old forests	–	–	–	–	49.4	43.4

Diversity	Combinations of environmental variables					
	A	B	C	D	E	F
R^2	0.658	0.622	0.590	0.567	0.671	0.439
F	6.26	7.67	6.71	6.12	9.50	2.55
df	4, 13	3, 14	3, 14	3, 14	3, 14	4, 13
P <	0.01	0.01	0.01	0.01	0.01	ns
EV	Percent contribution of environmental variables					
Latitude	36.0	–	92.7	–	52.8	–
Fields	20.9	35.3	–	–	–	–
Mineral land	32.3	53.0	–	–	–	–
Spruce forests	10.8	11.7	4.4	58.1	–	–
Pine forests	–	–	2.9	38.7	–	–
Deciduous forests	–	–	–	3.2	–	–
Young forests	–	–	–	–	–	14.1
Youngish forests	–	–	–	–	–	4.2
Oldish forests	–	–	–	–	26.8	44.5
Old forests	–	–	–	–	20.5	37.2

($R^2 = 0.799$; Table 4). The total density of birds was best explained by the combination of those variables that indicated productivity ($R^2 = 0.630$), the contribution of the proportion of fields being the most pronounced. The diversity of birds of prey was best explained by the combination of latitude with the proportions of the oldest age classes of forests ($R^2 = 0.671$), though the contribution of other factors than latitude was somewhat higher in the combination with those variables indicating productivity (Table 4).

The NMDS I scores of 18 local assemblages of the Finnish birds of prey were negatively related to the latitude and to the proportion of pine forests, and positively related to the proportion of spruce forests (Table 5). They were positively related especially to those environmental factors indicating positive trends in productivity (proportion of mineral land, mean growing stock in forests, proportion of fields; r^2 up to 67%; Table 5). The most powerful combination of two variables, the proportion of mineral land of forest land and the proportion of fields, explained 85.6% of the variation ($F = 44.53$, $df = 2, 15$, $P < 0.001$). The NMDS II scores were positively related to the forest land area ($P < 0.05$).

Environmental variables indicating gradients in productivity explained best the variation in the NMDS I scores of the 18 communities, both singly (simple linear regression analysis; Table 5) and in combinations (multiple linear regression analysis; R^2 up to 88%; Table 6). The contribution of the latitude to the coefficient of multiple determination (R^2) was relatively minor, about a half of that in the combinations with those variables indicating the tree species composition or the age structure of forests. The variation in the NMDS II scores was best explained by the tree species composition of forests ($R^2 = 0.433$; Table 6).

In a simple discriminant analysis (SDA) of the environmental variables in the original data set of 22 local areas, the availability of forests, most significantly in combination with mean volume of the growing stock, seemed to explain the difference between the centroids of clusters of 11 central and 11 peripheral communities ($D^2 = 2.80$, $F = 7.32$, $df = 2, 19$, $P < 0.01$). Percent of variation between the clusters accounted for by the SDA was 43.5%. The contribution of the former variable (forest land area) to the total multivariate distance (D^2) was 96.5%.

4. Discussion

4.1. Density estimates

Wide-ranging species such as birds of prey are generally inadequately represented in studies on

Table 5. Interpretation of the NMDS scores (Ludwig & Reynolds 1988, see Methods) of 18 Finnish communities of birds of prey by simple linear regression analyses with a set of 13 environmental variables (cf. Table 2) (df=17).

Environmental variables	NMDS I r^2	NMDS I t	NMDS I P<	NMDS II r^2	NMDS II t	NMDS II P<
Latitude	0.580	–4.71	0.001	0.044	0.85	ns
Size of the local area	0.150	–1.68	ns	0.143	1.63	ns
Proportion of fields	0.428	3.46	0.01	0.124	–1.51	ns
Mineral forest land	0.671	5.72	0.001	0.003	0.22	ns
Dominance of spruce	0.477	3.82	0.01	0.059	1.00	ns
Dominance of pine	0.404	–3.29	0.01	0.040	–0.82	ns
Deciduous forests	0.022	–0.60	ns	0.149	–1.67	ns
Forests of <20 yrs old	0.099	–1.32	ns	0.157	1.73	ns
Forests of 20–60 yrs old	0.027	0.67	ns	0.021	–0.59	ns
Forests of 60–100 yrs old	0.544	4.37	0.001	0.037	–0.79	ns
Forests of >100 yrs old	0.206	–2.04	ns	0.000	0.08	ns
Forest land area	0.159	–1.74	ns	0.231	2.19	0.05
Volume of the growing stock	0.648	5.43	0.001	0.010	–0.39	ns

bird communities, and, therefore, they are usually either excluded or included in unrealistic densities or proportions. This is because of deficiencies in the general methodology available to census species of widely varying densities and dispersion patterns (see Ralph & Scott 1981). Methods aimed to take into account all the species of a study area (such as mapping or line transect methods) evidently often give too low density estimates for sparse species due to unrepresentative sampling, but methods based on small study plots may also give unrealistically high values for wide-ranging species.

Birds of prey breed at relatively low densities, their territories are large, and they are usually difficult to detect during the breeding season. Thus, general methods for censusing terrestrial birds are not very applicable for estimating numbers of birds of prey (Fuller & Mosher 1981, Forsman & Solonen 1984, Solonen 1993). Species-specific peculiarities make it difficult to find a single universal census method for all the species. The best available estimates of communities of birds of prey are mainly based on more or less systematic searches for birds over large areas, but the accuracy of estimates still varies from species to species and area to area (e.g., Saurola 1985). Differences in the present estimates partly reflect different "ornithological traditions" between areas (e.g., different species may be popular as study objects in different areas), but probably the main differences are real. In any case, in most species and areas the estimates seem to be quite reasonable, but the recent observations suggest that at least in some areas the densities of *G. passerinum* were higher than formerly believed (e.g., Lagerström 1991).

Because the quality of the data used here varies, both locally and between species, the results in this paper must be considered as provisional. However, they indicate some general patterns and suggest some probable processes behind them. For more detailed and reliable results, more accurate and comparable data are needed (cf. Wiens 1983). In addition, in place of the rough average estimates, the pronounced annual fluctuations in density of the nomadic species should be taken into account. It will be seen how well the Finnish nation-wide raptor grid study, aimed to detect all occupied territories and nests of

Table 6. Interpretation of the NMDS scores of 18 Finnish communities of birds of prey by multiple linear regression analyses with some sets (A–F) of environmental variables (EV) (cf. Table 5). Latitude (Latid), proportions of fields (Field), mineral forest land (Miner), dominant trees (Spruc, Pine, Decid), and the four age classes of forests (Age 1–4) are considered. Percent contributions of each variable (cf. Table 5) to the coefficient of multiple determination (R^2) are given below.

	NMDS I						NMDS II					
	A	B	C	D	E	F	A	B	C	D	E	F
R^2	0.879	0.863	0.682	0.719	0.757	0.640	0.349	0.335	0.330	0.433	0.121	0.421
F	23.54	29.46	10.00	11.95	14.58	5.78	1.74	2.35	2.30	3.56	0.64	2.36
df	4, 13	3, 14	3, 14	3, 14	3, 14	4, 13	4, 13	3, 14	3, 14	3, 14	3, 14	4, 13
P <	0.001	0.001	0.001	0.001	0.001	0.01	ns	ns	ns	0.05	ns	ns
EV	Percent contributions of environmental variables											
Latid	16.1	–	39.8	–	38.0	–	15.7	–	13.9	–	43.6	–
Field	27.9	31.6	–	–	–	–	44.5	57.5	–	–	–	–
Miner	50.6	59.0	–	–	–	–	0.5	2.2	–	–	–	–
Spruc	5.4	9.4	44.0	53.5	–	–	39.3	40.3	53.7	44.6	–	–
Pine	–	–	16.2	44.5	–	–	–	–	32.4	37.3	–	–
Decid	–	–	–	2.1	–	–	–	–	–	18.2	–	–
Age 1	–	–	–	–	–	12.4	–	–	–	–	–	46.4
Age 2	–	–	–	–	–	7.2	–	–	–	–	–	18.4
Age 3	–	–	–	–	40.7	44.2	–	–	–	–	49.9	30.9
Age 4	–	–	–	–	21.3	36.2	–	–	–	–	6.6	4.3

birds of prey in more than one hundred permanent study areas of 100 km^2 every year (Saurola 1985, 1986b), will fulfil these strict requirements.

4.2. Relationships between body size, density, and range

Relationships between the body size, density, and range of species suggest that disturbed populations and marginal ranges of many species explain the deviations from the expectations (cf. also Juanes 1986, Damuth 1991, Solonen 1994). Man affects birds by directly changing their numbers, or more often indirectly by decreasing the availability of their essential resources. This may also have additional indirect effects on the interspecific relations of birds (cf. Marti et al. 1993a, b, Solonen 1993). The numbers and ranges of many species of birds of prey are reduced mainly due to various human activities. So, population levels are often lower than they were in undisturbed natural conditions (cf. Newton 1979). Larger-sized species might be more seriously affected than smaller-sized species (e.g., Brown & Maurer 1987, Solonen 1994).

In this study, only the Finnish part of the total range of the species considered was included (cf. Brown 1984, Solonen 1994). In such a restricted area, the probability of extinction of marginal populations is considerable. Strictly speaking, a population or density of a marginal or nomadic species cannot be considered on a similar local or even regional scale than those of other, more stationary species. In any case, density estimates should be representative to the distribution range considered.

4.3. Structuring of communities

Several of the environmental variables considered seemed to explain adequately the density distributions of most species. Major exceptions included the species with pronounced longitudinal gradients in density (especially *B. bubo* and *S. uralensis*; cf. also Solonen 1993), and some species with the most uncertain density estimates (e.g., *G. passerinum*; cf. Saurola 1985 and above). General features of the environment did not explain much of the local variation in density in some of the nomadic species either (*F. tinnunculus, A. funereus*). This was presumably because the local variations in occurrence in these species were due to a food supply that varies not only with the amount, but also with certain special characteristics of habitats, as well as annually.

Annual fluctuations in the range boundaries of some nomadic species (e.g., *S. nebulosa*; Solonen 1986, Hildén & Solonen 1987) seem to be due not only to local food supply, but also to foraging conditions in the more central parts of the species' range. If the food is abundant both in the central and peripheral parts of the general range of the species, there may be no need to expand the distribution to the periphery. So, the peripheral parts of the species' range will be occupied only when there is a shortage of food in the preferred more central parts of the range (cf. also Cornwallis 1961, Lack 1971, Virkkala 1992). Populations of nomadic species clearly "track" food resource variation (see Korpimäki 1985, Korpimäki & Norrdahl 1991, Solonen 1993), but probably not to the saturation level of the resource environment (cf. Karr 1983).

Dynamics of birds of prey assemblages largely depend upon the occurrence and abundance of their prey (e.g., Marti et al. 1993a, cf. however Jaksić et al. 1992, 1993). In the diets of birds of prey there are geographical variations that could be related to changes in the diversity and abundance of their prey species (Herrera & Hiraldo 1976, Korpimäki 1986, Newton 1986, Marti et al. 1993a, b). If changes in the food niche occur in any species, one would expect associated effects on community composition and interspecific relations. Similarities between communities in the number of species and their foraging ecology have been cited as evidence for the role of interspecific competition in structuring communities (Pielou 1979).

It was often evident that the environmental variables studied correlated with some other factors (e.g., the distribution of preferred breeding habitats, the occurrence of heavily fluctuating food resources), or their effects had contributed to the distribution and abundance of the species (e.g., the distribution may be southern or northern for historical reasons originally, or it may be restricted by man). Communities evidently differ due to the differences in habitats and their resources, and also on a more local scale than considered here (e.g., Korpimäki 1987, Solonen 1993). In this study, some characteristics of the resources of species evidently were poorly indicated by the environmental variables examined. For instance, though not shown in this study, *A. gentilis* clearly is a species of old spruce forests in the scale of individual nesting locations (cf., e.g., v. Haartman et al. 1963–72, Solonen 1993). Thus, the unexplained variation may be largely due to more local factors than indicated by the environmental variables studied. In general, productivity, habitat complexity, and diversity of available habitats promote species diversity (Lack 1971, Järvinen & Sammalisto 1976, Järvinen & Väisänen 1978a), and vegetational differences lead to differences between the avifaunas in different areas (Järvinen & Väisänen 1978b, 1980).

In this study, the number of species increased with the proportion of fields and decreased with the proportion of mineral forests. This suggests that some larger scale habitat diversity or heterogeneity were more important to the number of species than productivity. The northward increase of the number of species (see also Herrera & Hiraldo 1976) and diversity contradict the general trend in Northern European bird communities (Järvinen & Väisänen 1973, 1980; cf. also Hanski et al. 1991), but similar gradients have been found in species richness of waders (Järvinen & Väisänen 1978a) and in the diversity of mire birds (Järvinen & Sammalisto 1976, Järvinen et al. 1987). The reversed gradients seem to be correlated with corresponding gradients in habitats. In birds of prey, the trend seems to be largely due to the originally restricted Finnish range of some northern species, and partly due to the present restriction of some declined species to the northern parts of the country (see Hyytiä et al. 1983). In bird-eating species there seems to be a clear southward increase in food supply (e.g., Järvinen & Väisänen 1980). The situation in the vole-eaters is more complicated (see also Hanski et al. 1991). In the south, there are generally more voles in the less intensively cultivated, smaller field areas, while the species of the north have a vole supply of their own that is largely independent of fields.

Acknowledgements. I thank I. Hanski, E. Korpimäki, I. Newton and H. Pietiäinen for their useful comments and suggestions on earlier drafts of the manuscript. The Finnish Cultural Foundation supported the study in its final phases. I dedicate this paper to the memory of Olavi Hildén.

Selostus: **Suomalaisten petolintuyhteisöjen rakenteeseen vaikuttavista tekijöistä**

Suomen petolinnustoa tutkittiin 22 paikallisalueen kannanarvioiden pohjalta. Ruumiin koon, kannan tiheyden ja levinneisyysalueen laajuuden väliset suhteet antoivat viitteitä lintujen ja niiden elinympäristön välisistä vuorovaikutussuhteista. Kookkaat lajit olivat odotusten mukaisesti harvalukuisempia, mutta niiden levinneisyysalue maassamme oli yleensä suppeampi kuin pienemmillä lajeilla. Vastoin odotuksia kannan tiheyden ja levinneisyysalueen laajuuden välillä ei ollut merkitsevää riippuvuutta. Ihmisen aiheuttamat kannan- ja levinneisyydenmuutokset sekä monien lajien esiintyminen meillä levinneisyytensä äärirajoilla näyttivät selittävän poikkeamia odotetuista tuloksista. Ympäristön tuottavuutta ilmentävät tekijät selittivät monien, mutta eivät kaikkien lajien alueellisia tiheydenvaihteluita.

Paikallisten petolintuyhteisöjen lajimäärä ja monimuotoisuus kasvoivat lintujen kokonaistiheyden laskiessa pohjoiseen mentäessä. Lajimäärän maantieteellistä vaihtelua selittivät parhaiten metsien puulajisuhteet yhdessä alueen sijainnin pohjoisuuden kanssa. Petolintujen kokonaistiheyttä selitti tuottavuutta ilmentävien ympäristömuuttujien yhdistelmä, jossa etenkin peltojen määrällä oli huomattava osa. Ympäristön tuottavuutta ilmentävät muuttujat selittivät myös paikallisten yhteisöjen kokonaisrakenteen alueellista vaihtelua. Metsien määrä selitti yhteisörakenteen eroja maan keskiosien ja äärialueiden välillä.

References

Anon. 1987: Environment statistics 1987. — Central Statistical Office of Finland, Helsinki.

Arita, H. T., Robinson, J. G. & Redford, K. H. 1990: Rarity in Neotropical forest mammals and its ecological correlates. — Conserv. Biol. 4: 181–192.

Brown, J. H. 1984: On the relationship between abundance and distribution of species. — Am. Nat. 124: 255–279.

Brown, J. H. & Maurer, B. A. 1987: Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. — Am. Nat. 130: 1–17.

Cody, M. L. (ed.) 1985: Habitat selection in birds. — Academic Press, Orlando.

Cornwallis, R. K. 1961: Four invasions of Waxwings during 1956–60. — Brit. Birds 54: 1–30.

Cramp, S. (ed.) 1985: The birds of the Western Palearctic. Vol. 4. — Oxford Univ. Press, Oxford.

Cramp, S. & Simmons, K. E. L. (eds.) 1980: The birds of the Western Palearctic. Vol. 2. — Oxford Univ. Press, Oxford.

Damuth, J. 1991: Of size and abundance. — Nature 351: 268–269.

Forsman, D. & Solonen, T. 1984: Censusing breeding raptors in southern Finland: methods and results. — Ann. Zool. Fennici 21: 317–320.

Fuller, M. R. & Mosher, J. A. 1981: Methods of detecting and counting raptors: a review. — Stud. Avian Biol. 6: 235–246.

v. Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72: Pohjolan linnut värikuvin. — Otava, Helsinki.

Hanski, I., Hansson, L. & Henttonen, H. 1991: Specialist predators, generalist predators, and the microtine rodent cycle. — J. Anim. Ecol. 60: 353–367.

Harvey, P. H. & Godfray, H. C. J. 1987: How species divide resources. — Am. Nat. 129: 318–320.

Helo, P. 1981: Kotka - lintujen kuningas. — Helo, Kajaani.

Herrera, C. M. & Hiraldo, F. 1976: Food-niche and trophic relationships among European owls. — Ornis Scand. 7: 29–41.

Hildén, O. 1965: Habitat selection in birds: A review. — Ann. Zool. Fennici 2: 53–75.

Hildén, O. & Solonen, T. 1987: Status of the Great Grey Owl in Finland. — In: Biology and conservation of northern forest owls. General Technical Report RM-142: 115–120. USDA Forest Service, Fort Collins.

Hyytiä, K., Kellomäki, E. & Koistinen, J. (eds.) 1983: Suomen lintuatlas. — Lintutieto, Helsinki.

Jaksić, F. M., Jiménez, J. E., Castro, S. A. & Feinsinger, P. 1992: Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. — Oecologia 89: 90–101.

Jaksić, F. M., Feinsinger, P. & Jiménez, J. E. 1993: A long-term study on the dynamics of guild structure among predatory vertebrates at a semi-arid Neotropical site. — Oikos 67: 87–96.

Juanes, F. 1986: Population density and body size in birds. — Am. Nat. 128: 921–929.

Järvinen, O., Kouki, J. & Häyrinen, U. 1987: Reversed latitudinal gradients in total density and species richness of birds breeding on Finnish mires. — Ornis Fennica 64: 67–84.

Järvinen, O. & Sammalisto, L. 1976: Regional trends in the avifauna of Finnish peatland bogs. — Ann. Zool. Fennici 13: 31–43.

Järvinen, O. & Väisänen, R. A. 1973: Species diversity of Finnish birds, I: Zoogeographical zonation based on land birds. — Ornis Fennica 50: 93–125.

— 1978a: Ecological zoogeography of North European waders, or Why do so many waders breed in the North? — Oikos 30: 496–507.

— 1978b: Habitat distribution and conservation of land bird populations in northern Norway. — Holarct. Ecol. 1: 351–361.

— 1980: Quantitative biogeography of Finnish land birds as compared with regionality in other taxa. — Ann. Zool. Fennici 17: 67–85.

Karr, J. R. 1983: Commentary. — In: Brush, A. H. & Clark, G. A. Jr. (eds.), Perspectives in ornithology: 403–410. Cambridge Univ. Press, Cambridge.

Korpimäki, E. 1985: Rapid tracking of microtine populations by their avian predators: possible evidence for stabilizing predation. — Oikos 45: 281–284.

— 1986: Niche relationships and life-history tactics of three sympatric Strix owls in Finland. — Ornis Scand. 17: 126–132.

— 1987: Composition of the owl communities in four areas in western Finland: importance of habitats and interspecific competition. — Acta Reg. Soc. Sci. Litt. Gothoburgensis, Zoologica 14: 118–123.

Korpimäki, E. & Norrdahl, K. 1991: Numerical and functional responses of Kestrels, Short-eared Owls, and Long-eared Owls to vole densities. — Ecology 72: 814–826.

Lack, D. 1971: Ecological isolation in birds. — Blackwell, Oxford & Edinburgh.

Lagerström, M. 1991: The breeding record of owls in Pirkanmaa, 1991. (In Finnish with summary in English) — Lintuviesti 16: 124–133.

Ludwig, J. A. & Reynolds, J. F. 1988: Statistical ecology. — Wiley, New York.

MacArthur, R. H. 1972: Geographical ecology. — Harper & Row, New York.

Marti, C. D., Korpimäki, E. & Jaksić, F. M. 1993a: Trophic structure of raptor communities: a three continent comparison and synthesis. — In: Power, D. M. (ed.), Current Ornithology, Vol. 10: 47–137. Plenum, New York.

Marti, C. D., Steenhof, K., Kochert, M. N. & Marks, J. S. 1993b: Community trophic structure: the roles of diet, body size, and activity time in vertebrate predators. — Oikos 67: 6–18.

Mikkola, H. 1983: Owls of Europe. — Poyser, Calton.

Newton, I. 1979: Population ecology of raptors. — Poyser, Berkhamsted.

— 1980: The role of food in limiting bird numbers. — Ardea 68: 11–30.

— 1986: The Sparrowhawk. — Poyser, Calton.

Pielou, E. C. 1979: Biogeography. — Wiley, New York.

Ralph, C. J. & Scott, J. M. (eds.) 1981: Estimating numbers of terrestrial birds. — Stud. Avian Biol. 6: 1–630.

Saurola, P. 1985: Finnish birds of prey: status and population changes. — Ornis Fennica 62: 64–72.

— 1986a: The Ospreys, Pandion haliaetus, in Finland 1971–1985. (In Finnish with summary in English) — Lintumies 21: 67–80.

— 1986b: The raptor grid: an attempt to monitor Finnish raptors and owls. — Vår Fågelvärld, Suppl. 11: 187–190.

Schoener, T. W. 1968: Sizes of feeding territories among birds. — Ecology 49: 123–141.

Solonen, T. 1986: Breeding of the Great Grey Owl Strix nebulosa in Finland. (In Finnish with summary in English) — Lintumies 21: 11–18.

— 1993: Spacing of birds of prey in southern Finland. — Ornis Fennica 70: 129–143.

— 1994: Finnish bird fauna – species dynamics and adaptive constraints. — Ornis Fennica 71: 81–94.

Stjernberg, T. 1983: The reproductive success of the White-tailed Eagle in Finland during 1970–82. (In Swedish with summary in English) — Lintumies 18: 35–43.

Uusitalo, M. (ed.) 1989: Yearbook of forest statistics 1988. Folia Forestalia 730. — The Finnish Forest Research Institute, Helsinki.

Virkkala, R. 1992: Fluctuations of vole-eating birds of prey in northern Finland. — Ornis Fennica 69: 97–100.

— 1993: Ranges of northern forest passerines: a fractal analysis. — Oikos 67: 218–226.

Wiens, J. A. 1983: Avian community ecology: an iconoclastic view. — In: Brush, A. H. & Clark, G. A. Jr. (eds.), Perspectives in ornithology: 355–403. Cambridge Univ. Press, Cambridge.

— 1989: The ecology of bird communities. — Cambridge Univ. Press, Cambridge.

Wikman, M. 1983: Changes in the Finnish Peregrine population 1970–1982. (In Finnish with summary in English) — Lintumies 18: 31–34.

Appendix. Relationships between some environmental variables (EV; cf. Table 2) and the densities of birds of prey (for species codes, see the footnote) in 18 local areas: the contribution (the coefficients of determination, r^2 or R^2), and the sign (+/–) and significance (P; ns = not significant) of the t- or F-statistics (simple and multiple linear regression analyses, respectively). The coefficients of determination (r^2) of the EVs included in the "best" combination of EVs examined in each species (below) are italicized.

	P api			C aer			C cya			A gen		
EV	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<
1. Latitude	0.264	–	0.05	*0.461*	–	0.01	0.598	+	0.001	0.452	–	0.01
2. Fields	*0.401*	+	0.01	0.170		ns	0.129		ns	*0.527*	+	0.001
3. Mineral land	0.085		ns	0.337	+	0.01	*0.736*	–	0.001	0.099		ns
4. Spruce forests	0.327	+	0.05	0.183		ns	*0.471*	–	0.01	0.103		ns
5. Pine forests	*0.307*	–	0.05	0.138		ns	0.363	+	0.01	0.088		ns
6. Decid. forests	0.002		ns	0.020		ns	0.130		ns	0.006		ns
7. Young forests	0.003		ns	0.048		ns	0.008		ns	0.060		ns
8. Youngish forests	*0.226*	+	0.05	0.098		ns	0.002		ns	*0.446*	+	0.01
9. Oldish forests	*0.220*	+	0.05	*0.221*	+	0.05	*0.326*	–	0.05	*0.242*	+	0.05
10. Old forests	0.322	–	0.05	*0.157*		ns	0.183		ns	0.355	–	0.01
11. Forest land	0.001		ns	0.053		ns	0.001		ns	0.080		ns
12. Growing stock	0.148		ns	0.371	+	0.01	*0.759*	+	0.001	*0.226*	+	0.05
Combination of EVs	R^2		P<	R^2		P<	R^2		P<	R^2		P<
1, 2, 3, 4	0.525		0.05	0.471		ns	0.803		0.001	0.620		0.01
2, 3, 4	0.515		0.05	0.400		ns	0.775		0.001	0.544		0.01
1, 4, 5	0.382		ns	0.468		0.05	0.725		0.001	0.467		0.05
4, 5, 6	0.395		ns	0.438		0.05	0.605		0.01	0.528		0.05
1, 9, 10	0.343		ns	0.486		0.05	0.652		0.01	0.494		0.05
7, 8, 9, 10	0.375		ns	0.281		ns	0.407		ns	0.615		0.05
"Best" combination	0.618		0.01	0.486		0.05	0.820		0.001	0.722		0.01

	A nis			B but			P hal			F tin		
	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<
1. Latitude	0.343	–	0.05	*0.287*	–	0.05	0.632	–	0.001	0.057		ns
2. Fields	*0.441*	+	0.01	0.105		ns	*0.439*	+	0.01	0.000		ns
3. Mineral land	0.091		ns	0.146		ns	*0.538*	+	0.001	*0.331*	–	0.05
4. Spruce forests	0.166		ns	0.223	+	0.05	*0.391*	+	0.01	0.089		ns
5. Pine forests	0.142		ns	0.215		ns	0.316	–	0.01	0.051		ns
6. Decid. forests	0.001		ns	0.000		ns	0.031		ns	0.138		ns
7. Young forests	0.145		ns	0.016		ns	0.051		ns	0.023		ns
8. Youngish forests	*0.536*	+	0.001	0.266	+	0.05	0.183		ns	0.122		ns
9. Oldish forests	*0.216*		ns	*0.159*		ns	*0.367*	+	0.01	0.118		ns

	A nis			B but			P hal			F tin		
	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<
10. Old forests	0.293	–	0.05	*0.400*	–	0.01	0.303	–	0.05	0.031		ns
11. Forest land	0.076		ns	0.023		ns	0.077		ns	0.042		ns
12. Growing stock	0.158		ns	0.192		ns	*0.592*	+	0.001	*0.214*		ns

	R^2	P<	R^2	P<	R^2	P<	R^2	P<
1, 2, 3, 4	0.494	ns	0.367	ns	0.763	0.001	0.428	ns
2, 3, 4	0.459	0.05	0.251	ns	0.758	0.001	0.370	ns
1, 4 5	0.352	ns	0.341	ns	0.682	0.001	0.184	ns
4, 5, 6	0.326	ns	0.295	ns	0.655	0.01	0.195	ns
1, 9, 10	0.375	ns	0.475	0.05	0.635	0.01	0.397	ns
7, 8, 9, 10	0.647	0.01	0.474	ns	0.469	ns	0.366	ns
"Best" combination	0.654	0.01	0.475	0.05	0.809	0.001	0.346	0.05

	F col			F sub			B bub			S ulu		
	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<
1. Latitude	0.438	+	0.1	0.349	–	0.01	0.169		ns	0.681	+	0.001
2. Fields	0.340	–	0.05	0.281	+	0.05	0.121		ns	0.459	–	0.01
3. Mineral land	0.178		ns	0.234	+	0.05	0.080		ns	0.173		ns
4. Spruce forests	0.124		ns	*0.387*	+	0.01	*0.043*		ns	0.282	–	0.05
5. Pine forests	0.097		ns	*0.316*	–	0.05	*0.047*		ns	0.261	+	0.05
6. Decid. forests	0.012		ns	*0.042*		ns	*0.040*		ns	0.002		ns
7. Young forests	*0.038*		ns	0.000		ns	0.140		ns	*0.032*		ns
8. Youngish forests	*0.016*		ns	0.015		ns	0.041		ns	*0.137*		ns
9. Oldish forests	*0.312*	–	0.05	0.338	+	0.05	0.023		ns	*0.623*	–	0.001
10. Old forests	*0.324*	+	0.5	0.241	–	0.05	0.001		ns	*0.738*	+	0.001
11. Forest land	0.000	–	ns	0.003		ns	0.393	–	0.01	0.016		ns
12. Growing stock	0.338	–	0.05	0.316	+	0.05	0.094		ns	0.505	–	0.001

	R^2	P<	R^2	P<	R^2	P<	R^2	P<
1, 2, 3, 4	0.478	ns	0.492	ns	0.556	0.05	0.846	0.001
2, 3, 4	0.410	ns	0.480	0.05	0.548	0.01	0.533	0.05
1, 4, 5	0.439	0.05	0.488	0.05	0.471	0.05	0.711	0.001
4, 5, 6	0.243	ns	0.538	0.05	0.582	0.01	0.576	0.01
1, 9, 10	0.452	0.05	0.389	ns	0.334	ns	0.819	0.001
7, 8, 9, 10	0.507	0.05	0.365	ns	0.272	ns	0.852	0.001
"Best" combination	0.507	0.05	0.538	0.05	0.582	0.01	0.852	0.001

	G pas			S alu			S ura			S neb		
	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<
1. Latitude	*0.024*		ns	0.406	–	0.01	0.057		ns	*0.718*	+	0.001
2. Fields	*0.117*		ns	*0.335*	+	0.05	0.056		ns	0.437	–	0.01
3. Mineral land	*0.025*		ns	*0.328*	+	0.05	0.005		ns	0.458	–	0.01
4. Spruce forests	*0.029*		ns	*0.268*	+	0.05	*0.208*		ns	0.400	–	0.01
5. Pine forests	0.011		ns	0.179		ns	*0.172*		ns	0.338	+	0.05
6. Decid. forests	0.064		ns	0.149		ns	0.047		ns	0.011		ns
7. Young forests	0.004		ns	0.021		ns	0.020		ns	0.009		ns
8. Youngish forests	0.129		ns	0.147		ns	0.055		ns	0.008		ns
9. Oldish forests	0.034		ns	*0.231*	+	0.05	0.116		ns	*0.686*	–	0.001
10. Old forests	0.089		ns	0.229	–	0.05	*0.198*		ns	*0.468*	+	0.01
11. Forest land	0.018		ns	0.040		ns	*0.134*		ns	0.009		ns
12. Growing stock	0.001		ns	*0.273*	+	0.05	0.074		ns	0.675	–	0.001

	R^2	P<	R^2	P<	R^2	P<	R^2	P<
1, 2, 3, 4	0.286	ns	0.514	0.05	0.338	ns	0.767	0.001
2, 3, 4	0.237	ns	0.513	0.05	0.286	ns	0.701	0.001
1, 4, 5	0.107	ns	0.515	0.05	0.235	ns	0.752	0.001
4, 5, 6	0.122	ns	0.462	0.05	0.230	ns	0.702	0.001
1, 9, 10	0.156	ns	0.405	ns	0.217	ns	0.800	0.001
7, 8, 9, 10	0.232	ns	0.317	ns	0.206	ns	0.726	0.01
"Best" combination	0.286	ns	0.578	0.05	0.353	ns	0.800	0.001

	A otu			A fla			A fun		
	r^2	+/–	P<	r^2	+/–	P<	r^2	+/–	P<
1. Latitude	0.283	–	0.05	0.151		ns	0.054		ns
2. Fields	0.321	+	0.05	*0.000*		ns	0.251	+	0.05
3. Mineral land	0.063		ns	*0.344*	–	0.05	0.003		ns
4. Spruce forests	*0.068*		ns	*0.223*	–	0.05	*0.000*		ns
5. Pine forests	*0.020*		ns	0.242	+	0.05	*0.017*		ns
6. Decid. forests	*0.189*		ns	0.002		ns	*0.301*	–	0.05
7. Young forests	0.004		ns	0.007		ns	0.007		ns
8. Youngish forests	0.040		ns	0.002		ns	0.034		ns
9. Oldish forests	0.237	+	0.05	0.043		ns	0.087		ns
10. Old forests	0.181		ns	0.072		ns	0.073		ns
11. Forest land	0.001		ns	0.009		ns	0.006		ns
12. Growing stock	0.120		ns	0.250	–	0.05	0.001		ns

	R^2	P<	R^2	P<	R^2	P<
1, 2, 3, 4	0.382	ns	0.422	ns	0.320	ns
2, 3, 4	0.331	ns	0.417	0.05	0.318	ns
1, 4, 5	0.460	0.05	0.282	ns	0.408	ns
4, 5, 6	0.481	0.05	0.244	ns	0.417	0.05
1, 9, 10	0.298	ns	0.176	ns	0.090	ns
7, 8, 9, 10	0.245	ns	0.178	ns	0.226	ns
"Best" combination	0.481	0.05	0.417	0.05	0.417	0.05

Key for the names of the species: P api = *Pernis apivorus*, C aer = *Circus aeruginosus*, C cya = *Circus cyaneus*, A gen = *Accipiter gentilis*, A nis = *Accipiter nisus*, B but = *Buteo buteo*, P hal = *Pandion haliaetus*, F tin = *Falco tinnunculus*, F col = *Falco columbarius*, F sub = *Falco subbuteo*, B bub = *Bubo bubo*, S ulu = *Surnia ulula*, G pas = *Glaucidium passerinum*, S alu = *Strix aluco*, S ura = *Strix uralensis*, S neb = *Strix nebulosa*, A otu = *Asio otus*, A fla = *Asio flammeus*, A fun = *Aegolius funereus*