Finnish bird fauna — species dynamics and adaptive constraints

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The adaptive response of Finnish birds to the limits imposed by species dynamics, biological constraints, and environment is described by examining the patterns and underlying mechanisms in the relationships between the number of species, body size, population density, and geographical range size. In the total breeding avifauna the frequency distribution of species with respect to body size was bimodal, while various subsets of species showed unimodal distributions significantly skewed toward the larger body size categories. Abundance distributions of larger sets of species usually followed the canonical lognormal distribution with no significant skewness, while minor groups in general were not normally distributed and exhibited significant left-skewness. The variances of abundance were somewhat higher than the variances of biomass, suggesting that biomass and energy use were more equitably distributed among species than indicated by their abundance. Relatively more large than small species winter in Finland. So, from the energetic point of view, the differences between the summer and winter bird communities were not as great as suggested on the basis of the number of individuals. The average density of birds decreased significantly with increasing body size, but the slope of the relationship was shallower (–0.52) than expected for the energetic equivalence of the species. The Finnish range size of species tended to decrease with increasing body size, partly because the ranges of many larger species have been reduced by human impact. The width of the range increased with density in the total set of species as well as in most of the ecological groups considered, indicating the progress and success of colonization.

1. Introduction

A local bird fauna can be characterized by species dynamics (colonization and extinction) and adaptive constraints (Brown & Maurer 1987). The abundance and the distribution of species are limited, not only by historical reasons, but also by a combination of physical and biotic variables that collectively define their multidimensional niches (Brown 1984). Individual body size, average local population density, and geographical range size provide different measurements of the interactions between a bird species and its environment (Brown & Maurer 1987). The relationships between the number of species in a category and these variables reveal patterns that can be accounted for by various intrinsic and extrinsic factors. These patterns can be expected

to differ, especially between breeding and wintering birds, as well as between resident and migratory species, because of pronounced differences in the year-round constraints.

Distributions of species, in size and abundance, have been explained by the use and division of energy and other resources between the species (e.g., Sugihara 1980, Damuth 1981, Brown & Maurer 1986, Harvey & Godfray 1987, Maurer & Brown 1988, Pagel et al. 1991). Abundances of species often follow the canonical lognormal distribution, in which the most abundant species belong to the class with the highest total number of individuals (Preston 1948, 1962, Ludwig & Reynolds 1988). The variance of species' log-transformed abundances should increase in a precise way with the number of species sampled, being roughly four times the natural logarithm of the number of species in the community (May 1975).

The larger species within the communities are usually found to have lower population densities than the smaller sized ones (Damuth 1981, 1987, 1991), but within guilds the highest densities have been recorded from species of intermediate size (Brown & Maurer 1987, Blackburn et al. 1990). If the number of the intermediate sized species is less than that of the smaller sized species (Blackburn et al. 1990), this may indicate that the smallest species in the communities are less effective competitors or users of resources, or have fewer resources at their disposal (Brown & Maurer 1986, 1987, 1989, Blackburn et al. 1990, Pagel et al. 1991). Contrary to the pattern found in density, the width of the range should increase with increasing body size (Brown & Maurer 1987). The relationship between density and range may be complicated by the size of the species (e.g., Brown & Maurer 1987, Harvey & Godfray 1987, Arita et al. 1990, Blackburn et al. 1990), but, in general, the species restricted to small geographical ranges have lower average population densities than do more widely distributed species (e.g., Hanski 1982, Bock & Ricklefs 1983, Bock 1984, 1987, Brown 1984, Brown & Maurer 1987, Kouki & Häyrinen 1991). These tendencies may be due to various energetic constraints or to interspecific relationships.

The dynamics of the Finnish bird fauna during the last two hundred years seem to be characterized by the continuous immigration of new breeding species and the constancy of old ones (v. Haartman 1973, Järvinen & Ulfstrand 1980, Solonen 1985, 1994a). Some of the old breeding species seem, however, to be on the verge of extinction (Rassi et al. 1992). In this paper the adaptive response of Finnish birds to the limits imposed by species dynamics, biological constraints, and environment is described by examining the patterns and underlying mechanisms in the relationships between the number of species in a category, body size, population density, and geographical range size. To assess the above ideas, a series of predictions are tested using recent literature:

1) Distributions of the number of species in successive logarithmic body size classes, reflecting patterns of energy division among species, are suggested to be unimodal and skewed to the right (e.g., Hutchinson & MacArthur 1959, May 1986, Maurer & Brown 1988).

2) Abundances of species should follow the canonical lognormal distribution (Preston 1948, 1962) skewed to the left (Sugihara 1980, Nee et al. 1991a). Variation among species in population biomass should be less than that in abundance, indicating that biomass (and energy use) should be more equitably distributed across species than the canonical lognormal curve predicts (Harvey & Godfray 1987, cf. Sugihara 1989, Pagel et al. 1991).

3) Density should decrease reciprocally with the rate by which metabolism increases with body mass (0.75; Kleiber 1972), if there were no overall relationship of size and energy use (the energetic equivalence rule; Damuth 1981, 1987, 1991, Nee et al. 1991b). Below a threshold body size, however, the maximum density should increase, and thereafter decrease with increasing body mass, while the minimum density should stay relatively constant (Brown & Maurer 1987, cf. Blackburn et al. 1990, Blackburn & Gaston 1994).

4) There should be a positive relationship between range size and body size, indicating both the growing spatial requirements and the increasing colonization potential of species (Brown 1981, Brown & Maurer 1987).

The minimum size of the range, reflecting a high probability of extinction, should especially increase with body size.

5) The width of the range should increase with density (Brown & Maurer 1987) and the maximum density should increase with range size (Brown 1984). Threatened species and recent colonists should show low densities and small ranges. Species of large body size are expected to be limited to a smaller region of low density and large range size, while species of small body size vary much more in both respects.

2. Material and methods

The basic data of this paper are published in an up-to-date check-list of Finnish birds (Solonen 1994a). These data were derived from the recent Finnish literature. The most comprehensive source (v. Haartman et al. 1963–72) concerns various aspects of the biology of Finnish birds. Body masses, used to measure the size of birds, are mainly based on this source. The estimates of the average population density (pairs/100 km²) are Finnish population estimates (see Solonen 1985, Koskimies 1989) divided by the measurement used for the Finnish range of the species, i.e. the number of the 100 × 100 km squares in which the species considered was recorded in the Finnish bird atlas (Hyytiä et al. 1983). My rough, tentative estimates of the numbers of wintering birds are based on the average abundance indices of the Finnish winter bird census (A) (published in the journals Ornis Fennica, in 1974–1982, and Lintumies, in 1975–1988), estimates of average winter densities (B) based on the breeding densities of non-migratory species (assuming, for simplicity, that late winter abundances do not differ appreciably from breeding abundances), and arbitrary correction coefficients (C = A/B). Correction factors calculated for the resident reference species were used also for other species of similar main winter habitat and detectability. Subjective modifications were done when the species did not fit well into any of the reference types. In any case, the detectability of birds, including the abundance of species and uniformity of distribution, always affects both the estimates

of density (e.g., Brown & Maurer 1987, Solonen 1994b) and measures of range (cf., e.g., Virkkala 1993). Because of the considerable scatter in the relationships between the body size, density, and range size, in addition to the average slopes (the lines of least squares), the overall shapes of the bivariate distributions were examined (cf., e.g., Brown & Maurer 1987, Lawton 1989). Statistical procedures follow standard methods (Sokal & Rohlf 1981, Ludwig & Reynolds 1988).

3. Results

3.1. Body size and abundance distributions of species

In the total Finnish breeding avifauna the frequency distribution of species with respect to body size was bimodal, while various subsets of species showed an unimodal distribution significantly skewed toward the larger body size categories (Fig. 1). Within minor groups there was less variation in body size, and this predicted pattern was much less evident. Contrary to the general pattern, in the winter there was no skewness ($t_s = 0.82$, ns) and the distribution of species fitted well to the normal distribution (Kolmogorov-Smirnov test, $D_{max} = 0.05$, ns).

Abundance distributions of larger sets of species usually followed the canonical lognormal distribution with no significant skewness, while minor groups, in general, were not normally distributed and exhibited significant left-skewness (Tables 1, 2 and 3). The shares were somewhat different when species, individuals, or biomasses were considered (Fig. 2). Biomass (and accordingly energy use) increased significantly with abundance ($b = 0.81$, $r = 0.85$, $df = 235$, $P < 0.001$), but it was not the higher the larger the species either in the total set of species or in the major taxonomic groups examined. The variances of abundance were slightly (though not significantly) higher than the variances of biomass, both in breeding species (2.24 and 2.09) and in wintering birds (2.21 and 1.93, respectively; log-transformed data).

In total, the number of individuals in winter was about 11% of the number of adult birds in

Breeding birds
n = 237

Passerines
n = 102

Terrestrial species
n = 183

Insectivores
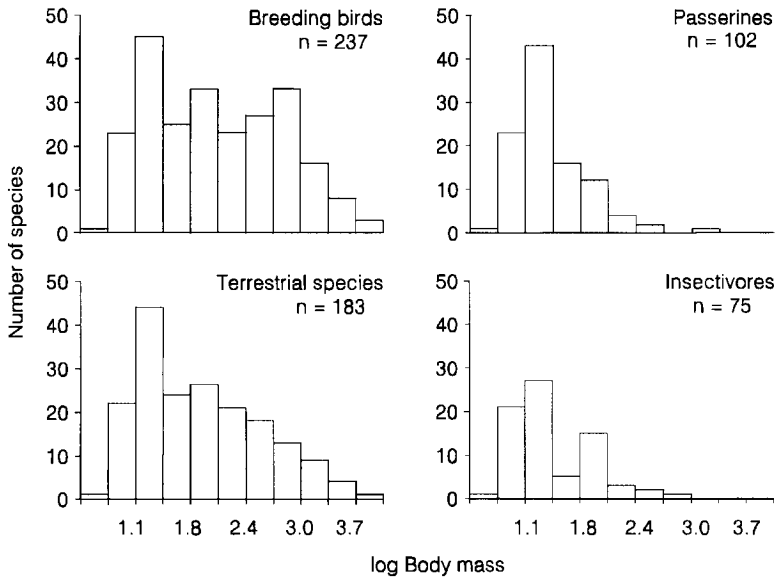n = 75

Number of species

log Body mass

Fig. 1. The size class distributions for some major groups of species of Finnish birds.

summer (Table 4). In biomass the corresponding proportion was about 25%, indicating that relatively more large than small species winter in Finland. Also, from the energetic point of view, the differences between the summer and winter bird communities were not so great as suggested on the basis of the number of individuals. So, an "average Finnish bird" weighs about 50 g in summer, but in winter it weighs about 116 g (however, the variation is large).

Table 1. Number of species of breeding birds, characterizing the main habitats of Finland, in different classes of abundance: the Finnish population 0 = less than ten pairs, 1 = tens, 2 = hundreds, 3 = thousands, 4 = tens of thousands, 5 = hundreds of thousands, and 6 = more than a million pairs (Solonen 1985). Each species is included in only one habitat considered as the most characteristic one. The areas of habitats are compiled from or estimated on the basis of the data in the Finnish official statistics (Anon. 1987). Kolmogorov-Smirnov test statistics, D_{max}, for goodness of fit to normal distribution and t_s-values for testing skewness are given. Significance of the test statistics is indicated as follows: * = P < 0.05, ** = P < 0.01, *** = P < 0.001; ns = not significant.

		Number of species									
	Area (km²)	Classes of abundance									
Habitat	(in 1980)	0	1	2	3	4	5	6	Total	D_{max}	t_s
Archipelagoes	1800	–	3	4	7	3	1	–	18	0.27 **	1.56 ns
Oligotrophic waters	31500	–	–	3	2	9	3	–	17	0.35 **	1.98 *
Eutrophic waters	200	–	4	4	7	3	1	–	19	0.26 **	1.29 ns
Shores	1400	–	5	2	2	2	4	–	15	0.23 ns	0.45 ns
Mires	20800	–	2	–	4	8	4	1	19	0.30 **	3.75 ***
Forests	234000	1	6	3	28	23	24	15	100	0.27 **	13.49 ***
Fells	9600	–	6	4	5	1	2	–	18	0.22 *	0.11 ns
Cultivated fields etc.	25400	–	1	1	2	2	4	–	10	0.23 ns	2.34 *
Scrubby open habitats	3400	–	3	1	4	1	4	–	13	0.26 *	1.26 ns
Build-up areas	10000	–	1	1	–	2	3	1	8	0.33 *	2.15 *
Total	338100	1	31	23	61	54	50	17	237	0.05 ns	1.40 ns

Table 2. Finnish birds: number of species in different classes of abundance (see Table 1). Ecological groups after Alerstam (1990) and Solonen (1994a). Kolmogorov-Smirnov test statistics, D_{max}, for goodness of fit to normal distribution and t_s-values for testing skewness are given. Significance of the test statistics is indicated as follows: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$; ns = not significant.

| | Number of species | | | | | | | | D_{max} | | t_s | |
| | Classes of abundance | | | | | | | | | | | |
	0	1	2	3	4	5	6	Total				
All species	1	31	23	61	54	50	17	237	0.05	ns	1.40	ns
Non-passerines	1	22	16	46	34	16	–	135	0.06	ns	1.31	ns
Passerines	–	9	7	15	20	34	17	102	0.10	*	2.85	**
Migratory groups												
Migratory	1	24	18	46	37	37	12	175	0.05	ns	1.03	ns
Partial migrants	–	6	4	5	9	7	3	34	0.07	ns	0.56	ns
Sedentary	–	1	1	10	8	6	2	28	0.06	ns	0.20	ns
Feeding groups												
Shore and mire birds	–	5	3	7	11	5	–	31	0.27	**	2.74	**
Water bottom foragers	–	3	4	6	4	4	–	21	0.23	**	1.71	ns
Terrestrial herbivores	–	1	2	3	4	3	–	13	0.23	ns	2.27	*
Fish eaters	–	5	3	6	5	–	–	19	0.27	**	1.23	ns
Water surface foragers	–	1	1	2	2	–	–	6	0.28	ns	1.63	ns
Birds of prey	1	5	2	15	3	–	–	26	0.36	**	5.94	***
Insectivores	–	6	3	14	16	23	13	75	0.24	**	6.00	***
Granivores	–	5	5	6	4	12	4	36	0.22	**	2.47	*
Omnivores	–	–	–	2	5	3	–	10	0.28	*	0.72	ns

Table 3. Finnish winter birds: number of species in different classes of abundance (for comparison with Table 2, abundances are in individuals × 2; cf. Table 1). For other explanations, see Table 2.

| | Number of species | | | | | | | | D_{max} | | t_s | |
| | Classes of abundance | | | | | | | | | | | |
	0	1	2	3	4	5	6	Total				
All species	5	26	14	25	20	12	2	104	0.08	ns	0.35	ns
Non-passerines	5	20	10	15	6	3	–	59	0.10	ns	1.21	ns
Passerines	–	6	4	10	14	9	2	45	0.06	ns	1.05	ns
Migratory groups												
Mainly migratory	2	20	8	9	–	–	–	39	0.12	ns	1.12	ns
Partial migrants	2	4	4	6	12	6	–	34	0.12	ns	1.67	ns
Sedentary	–	1	1	10	8	6	2	28	0.06	ns	0.20	ns
Feeding groups												
Shore and mire birds	–	1	–	–	–	–	–	1	–			
Water bottom foragers	2	5	4	3	–	–	–	14	0.32	**	2.66	**
Terrestrial herbivores	1	1	–	2	3	2	–	9	0.37	**	3.21	**
Fish eaters	1	5	2	–	–	–	–	8	0.42	**	2.89	**
Water surface foragers	–	–	–	–	–	–	–	–	–			
Birds of prey	1	4	2	9	1	–	–	17	0.30	**	4.36	***
Insectivores	–	2	1	5	8	3	2	21	0.26	**	3.18	**
Granivores	–	4	4	6	5	5	–	24	0.23	**	1.78	ns
Omnivores	–	4	1	–	3	2	–	10	0.28	*	0.25	ns
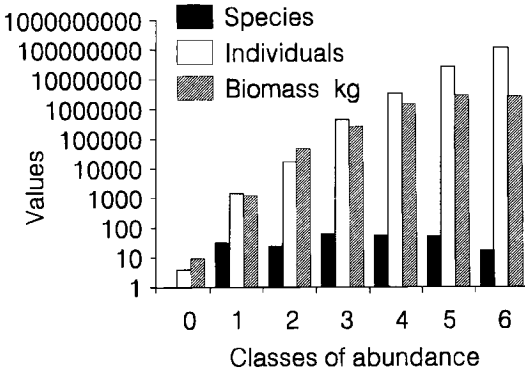
Fig. 2. Distribution of species, individuals and biomass into different classes of abundance (see Table 1) for Finnish birds.
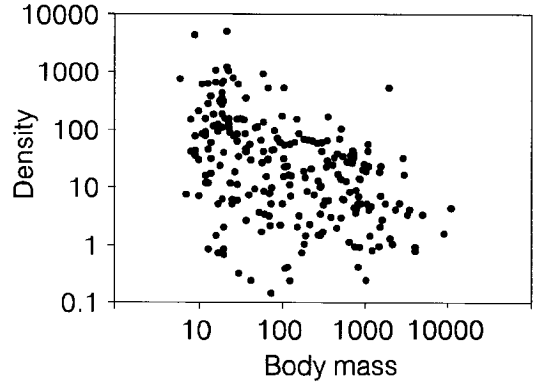

Fig. 3. The relationship between average population density (pairs/100 km²) and body mass (g) for Finnish birds.

3.2. Relationships between the body mass, density, and range

The average density decreased significantly (r = −0.51, df = 235, P < 0.001) with increasing body mass, but the slope of the relationship was flatter (−0.52) than expected for the energetic equivalence of species. There was a similar relationship for birds weighing 100 g or less (mainly passerines; r = −0.27, df = 113, P < 0.01). Within narrower size classes (Fig. 1), there was no significant relationship between size and abundance.

Significant negative relationships between the body mass and density were found in many subsets of species (Table 6). In terrestrial birds the relationship was consistent both in forests and in

open habitats, as well as in various feeding groups of species. However, in species of aquatic habitats there was no correlation between body size and density. To sum up, terrestrial habitats, particularly forests, are densely occupied by small birds, while aquatic habitats are sparsely populated by large species (Table 7).

The bivariate distribution of the body mass and average population density as a whole was relatively uniform and broadly in accordance with the pattern predicted (Fig. 3). Variances in density between size classes were in general relatively similar. In passerines and insectivores there were, however, significant differences (Table 5), indicating that the differences in average densities were real (and not due to differences in the number of species in different size classes).

Table 4. Finnish birds: number of species (Sp.), number of adult individuals (Ind.) and their total biomass (Kg) in various feeding groups in summer and winter.

Feeding groups		Summer			Winter	
	Sp.	Ind.	Kg	Sp.	Ind.	Kg
Shore and mire birds	31	2882000	447000	–	–	–
Water bottom foragers	21	1217000	1295000	14	20000	27000
Terrestrial herbivores	13	1319000	1241000	9	894000	993000
Fish eaters	19	280000	243000	8	2000	2000
Water surface foragers	6	133000	11000	–	–	–
Birds of prey	26	188000	82000	17	89000	48000
Insectivores	75	86394000	2100000	21	9199000	170000
Granivores	36	51222000	1200000	24	4294000	161000
Omnivores	10	1507000	639000	10	941000	390000
Total	237	145150000	7258000	104	15439000	1791000

In the total set of species examined, the expected positive relationship between the body mass and width of the range was not found, if both variables were log-transformed. Only carnivores and sylvids showed significant, though negative, relationships (Table 8). If only body mass was transformed, the relationship was significant and negative in the total data set ($r = -$ 0.20, P < 0.01). In terrestrial species as a whole the relationship between body mass and range size was significantly negative ($r = -0.16$, P < 0.05) due to such a tendency in the species of open habitats ($r = -0.28$, P < 0.05), but no correlation was evident in forest habitats ($r = -0.05$, ns). There was also no relationship in the species breeding in aquatic habitats.

Table 5. Variance ratio tests of the densities between the median and lowest (LM) and median and highest (MH) size classes (Fig. 1) in some major groups of Finnish birds.

Group	F(LM)	df	P <	F(MH)	df	P <
Breeding species, total	1.05	23, 22	ns	2.32	22, 10	ns
Terrestrial species	1.22	22, 20	ns	1.50	13, 20	ns
Passerines	1.99	42, 23	0.05	2.15	42, 18	0.05
Insectivores	2.89	26, 21	0.01	1.91	26, 20	0.10

Table 6. The relationship between abundance and body mass (log-transformed data) in various species sets of Finnish birds (ns = not significant; cf. Fig. 3).

Species set	Slope (b)	r	df	P <
Breeding species, total	−0.51	−0.45	235	0.001
Phylogenetic groups				
Anseriformes	−0.41	−0.26	2	ns
Charadriiformes	−0.27	−0.24	4	ns
Waders	−0.23	−0.16	2	ns
Skuas, gulls and terns	0.40	0.26	11	ns
Passeriformes	−0.34	−0.19	100	0.10
Turdidae	0.51	0.19	12	ns
Sylviidae	−2.39	−0.46	17	0.05
Fringillidae	−1.42	−0.34	15	ns
Habitat groups				
Terrestrial species	−0.60	−0.52	181	0.00
Forest species	−0.65	−0.51	98	0.00
Species of open habitats	−0.53	−0.49	81	0.00
Aquatic species	0.06	0.06	52	ns
Feeding groups				
Shore and mire birds	−0.16	−0.13	29	ns
Water bottom foragers	0.11	0.08	19	ns
Terrestrial herbivores	−0.83	−0.70	11	0.01
Fish eaters	0.28	0.19	17	ns
Water surface foragers	−0.68	−0.26	4	ns
Birds of prey	−0.45	−0.60	24	0.01
Insectivores	−0.52	−0.27	73	0.05
Granivores	−0.97	−0.39	34	0.05
Omnivores	−1.10	−0.68	8	0.05
Migratory groups				
Long-distance migrants	−0.74	−0.55	71	0.00
Short-distance migrants	−0.47	−0.41	100	0.00
Irruptive and partial migrants	−0.72	−0.71	32	0.00
Nonmigratory species	−0.46	−0.44	26	0.05
Wintering species, total	−0.71	−0.39	99	0.00
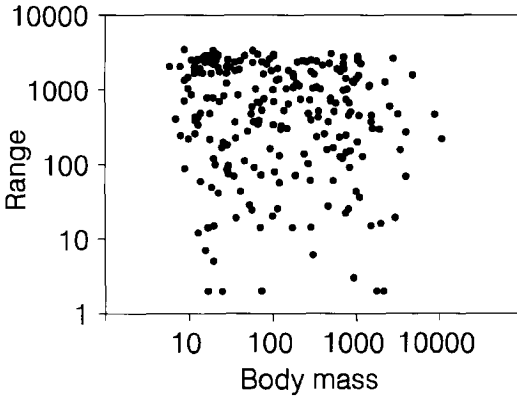
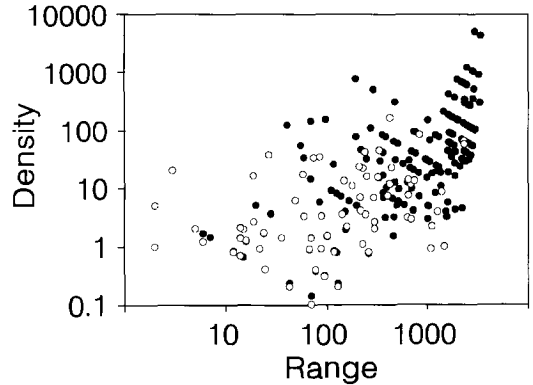Fig. 4. The relationship between the width of the range (100 km²) and body mass (g) for Finnish birds.

Fig. 5. The relationship between the width of the range (100 km²) and average population density (pairs/100 km²) for Finnish birds. Threatened species (Rassi et al. 1992) and recent colonists (Solonen 1994a) are denoted by open circles.

The bivariate distribution of the body mass and width of the Finnish range was generally similar as predicted, but the minimum range did not increase with increasing body mass as clearly as expected (Fig. 4). Species were concentrated to the left and to the upper part of the plot.

There was a highly significant positive correlation between the average population density and the width of the range (Table 9). The pattern was consistent in the birds despite the various habitat and migratory categories. In the feeding groups and taxonomic groups examined, the results, in general, followed the expectation as well. The correlation was not significant, however, in fish eaters, birds of prey that eat mainly mammals, and omnivores.

The bivariate distribution of the variables generally conformed to the predicted relationship, but density maximum increased somewhat unevenly with increasing range size (Fig. 5). Species, in general, were clearly concentrated in the largest range sizes, while threatened species

and recent colonists governed the other boundaries of the distribution.

4. Discussion

4.1. Number of species, size, abundance, and resource use

Heterogeneity of the total species pool of Finnish birds (Solonen 1994a) led to bimodality in the distribution of the number of species in successive body size classes, but the right-skewed unimodal pattern was prevalent in major subsets of species. This latter pattern is more prevalent in samples taken from a large geographical area than within local communities, where distributions may be more symmetric (Maurer & Brown 1988). A symmetric distribution also seems to characterize the assemblage of Finnish wintering

Table 7. Number of species, total number of pairs, density (pairs/km²), and biomass (kg) of birds in terrestrial and aquatic habitats (Table 1) in Finland.

Group	Species	Pairs	Density	Biomass
Forest habitats	100	62561000	267	4550000
Other terrestrial habitats	83	8916000	13	900000
Terrestrial habitats total	183	71477000	235	5450000
Aquatic habitats	54	1093000	33	1810000
Breeding species total	237	72570000	215	7260000

birds. When the number of species is greater in the smaller size categories, the average quantity of energy used by a small species should be less than that used by a large species (Maurer & Brown 1988, cf. also Solonen 1980, Brown & Maurer 1986). The implication is that small species divide up the energy available to them into smaller units than do large species (Hutchinson & MacArthur 1959, Maurer & Brown 1988).

Canonical lognormal distributions of species' abundances in communities have been explained by a sequential, equitable resource division of the species (Sugihara 1980, 1989; cf. Harvey & Godfray 1987, Pagel et al. 1991). The canonicity of abundances, however, does not necessarily imply canonicity across species in the use of resources (Harvey & Godfray 1987). In many communities,

resources seem to be divided more equitably or less equitably as would be inferred from the species' relative abundances (Harvey & Godfray 1987, Pagel et al. 1991). If a community consists of species inhabiting different feeding groups (cf., e.g., Nee et al. 1992), distributions of various resources, as well as those of the species using them, should fit into the model in combination. If the availability of various resources does not vary similarly between habitats and locations (cf. Pagel et al. 1991), this kind of situation would seem to be exceptional rather than general.

In the Finnish bird community, contrary to the common tendency (Pagel et al. 1991), the between-species variation in biomass seems to be somewhat less than that of abundance, suggesting that biomass and energy use were more

Table 8. The relationship between the width of the Finnish breeding range and body mass (log-transformed data) in various species sets of Finnish birds (cf. Fig. 4).

Species set	Slope (b)	r	df	P <
Breeding species, total	−0.13	−0.12	235	ns
Phylogenetic groups				
Anseriformes	−0.51	−0.26	23	ns
Charadriiformes	0.05	0.03	42	ns
Waders	0.27	0.13	26	ns
Skuas, gulls and terns	0.52	0.39	11	ns
Passeriformes		−0.00	100	ns
Turdidae	0.48	0.18	12	ns
Sylviidae	−1.32	−0.47	17	0.05
Fringillidae	0.10	0.02	15	ns
Habitat groups				
Terrestrial species	−0.15	−0.13	181	ns
Forest species	−0.02	−0.03	98	ns
Species of open habitats	−0.22	−0.17	81	ns
Aquatic species	−0.01	−0.01	5	ns
Feeding groups				
Shore and mire birds	0.45	0.27	29	ns
Water bottom foragers	0.19	0.14	19	ns
Terrestrial herbivores	−0.85	−0.33	11	ns
Fish eaters	0.46	0.29	17	ns
Water surface foragers	−0.26	−0.25	4	ns
Birds of prey	−0.72	−0.46	24	0.05
Insectivores	−0.02	−0.01	73	n
Granivores	−0.27	−0.11	34	ns
Omnivores	−0.17	−0.08	8	ns
Migratory groups				
Long-distance migrants	−0.16	−0.14	71	ns
Short-distance migrants	−0.12	−0.10	100	ns
Irruptive and partial migrants	−0.31	−0.33	32	0.10
Nonmigratory species	0.07	0.09	26	ns
Wintering species, total	−0.05	−0.05	99	ns

equitably distributed among species than indicated by their abundance. There is some evidence that a similar relationship also concerns the temporal variation and long-term stability of these parameters in whole communities (Järvinen & Väisänen 1978, Solonen 1986).

4.2. Implications of the relationships between the body mass, density, and range size

The relationship between the body mass and density in Finnish birds was weaker than expected by the energetic equivalence rule, indicating that the larger species use more energy. A community is considered to conform to the energetic equivalence rule, when the amount of energy regionally used by each bird species per unit area of its habitat is independent of body mass. This is indicated by the relationship between density and body size being approximately –0.75 (Damuth 1981, 1987, 1991, Nee et al. 1991b), the opposite of the rate by which metabolism increases with body mass (Kleiber 1972; for lower values, see Calder 1974, Kendeigh et al. 1977, Brown & Maurer 1986, 1987). The

Table 9. The relationship between the width of the Finnish breeding range and the average density in various species sets of Finnish birds (log-transformed data).

Species set	Slope (b)	r	df	P <
Breeding species, total	0.70	0.62	235	0.001
Phylogenetic groups				
Anseriformes	0.41	0.52	23	0.01
Charadriiformes	0.40	0.59	42	0.00
Waders	0.48	0.71	26	0.00
Skuas, gulls and terns	0.88	0.78	1	0.01
Passeriformes	0.70	0.71	100	0.00
Turdidae	0.92	0.88	12	0.00
Sylviidae	1.48	0.81	17	0.00
Fringillidae	0.80	0.82	15	0.00
Habitat groups				
Terrestrial species	0.61	0.60	181	0.00
Forest species	0.91	0.63	98	0.00
Species of open habitats	0.50	0.6	81	0.00
Aquatic species	0.55	0.52	52	0.00
Feeding groups				
Shore and mire birds	0.53	0.69	29	0.00
Water bottom foragers	0.74	0.71	19	0.00
Terrestrial herbivores	0.27	0.60	11	0.05
Fish eaters	0.35	0.38	17	ns
Water surface foragers	2.13	0.83	4	0.05
Birds of prey	0.26	0.54	24	0.01
Small mammal eaters		0.36	10	ns
Insectivores	0.89	0.72	73	0.001
Air-catchers		0.73	7	0.05
Ground/herb-gleaners		0.76	16	0.001
Foliage-gleaners		0.66	13	0.01
Trunk/branch-foragers		0.80	13	0.001
Soil invertebrate eaters		0.56	16	0.05
Granivores	0.77	0.75	34	0.001
Annual plant utilizers		0.71	22	0.001
Omnivores	0.00	0.00	8	ns
Migratory groups				
Long-distance migrants	0.66	0.61	71	0.00
Short-distance migrants	0.59	0.59	100	0.00
rruptive and partial migrants	0.81	0.73	32	0.00
Nonmigratory species	0.55	0.40	2	0.05
Wintering species, total	0.98	0.52	9	0.00

energetic role of even the densest populations of small-sized birds may be minor compared to that of sparse larger species (e.g., Solonen 1980). Within guilds larger species are commonly pointed out to use more energy: both regionally and locally the slopes of the regression tend to be flatter than −0.75 or even positive, showing that the larger guild members usually control more energy (Brown & Maurer 1986, Damuth 1991, Nee et al. 1991b). Thus, resources are not divided as would be inferred from the species' relative abundances, but smaller species that are found at densities below that at which they might be expected to live, use a much smaller share of the community resources than do larger species (Pagel et al. 1991, cf. also Solonen 1980). This suggests that smaller species may be unable to compete sufficiently for community resources (Brown & Maurer 1986, 1987).

The present results showed, in accordance with some other studies (Juanes 1986, Brown & Maurer 1987, Nee et al. 1991b, 1992, Cotgreave & Harvey 1992), that bird species that approach the minimum size (determined primarily by physiological constraints) can exhibit a wide range of population densities. Both maximum and general population densities decreased with increasing body size (cf. Brown & Maurer 1987, Blackburn et al. 1990). This general pattern seems largely to reflect differences between passerines (small body size) and non-passerines (larger body size) (cf. also Cotgreave & Harvey 1992). A similar pattern seems to be common also in various ecological groups, though it does not hold in all subsets of species (see also Brown & Maurer 1987, Nee et al. 1991b, 1992, Cotgreave & Harvey 1992). Among taxonomically close relatives belonging to the same feeding group, the average density and the variance of densities among species are found to be broadly similar for species in different size classes (Blackburn et al. 1990), indicating that, in general, there were no real differences in average densities.

The different aspects of the distribution pattern of the relationship between body size and density have been explained by various energetic constraints (Brown & Maurer 1987; cf. also Juanes 1986, Root 1988a). In local settings birds may, however, occur in considerably greater or smaller densities than those average or general

values used in analyses, which casts some doubt on the explanations, if not on the pattern itself (Wiens 1989). The polymodal distribution of abundances of various size classes of birds in several communities has been explained by the constraints of resource exploitation or food availability (Griffiths 1986).

The unexpected trend for range size to decrease with increasing body size in this study may be explained by the fact that only the Finnish part, as compared with the total geographical range of the species, was considered (cf. Brown & Maurer 1987, Solonen 1994b; also note the effect of different transformations). Larger species may be more susceptible to human impact as well, and this may have reduced their ranges. Since species of large body size are constrained to have low population densities, such species with small geographical ranges have a high probability of extinction (in spite of the fact that they may have more stable populations than do those of smaller species), because the total species population is small (Brown & Maurer 1987). Consequently, the minimum size of the geographic range should increase with body size.

The width of the range increased with density, indicating the spill-over of populations, as well as the progress and the success of colonization (Brown & Maurer 1987). The density maximum increased with geographical range size, suggesting that few species have small geographical ranges, and these species tend not to have high average population densities. Heterogeneity of species (Root 1988b, Arita et al. 1990) and the marginal and partial ranges of birds (cf. also Bock & Ricklefs 1983, Wiens 1989, Ford 1990, Solonen 1994b) may lead to unexpected relationships. Densities of a species can be expected to be high in the central portion of its range and to decrease toward the periphery (see Grinnell 1922, Bock & Ricklefs 1983). So, species on the edge of their range in Finland might be expected to occur at low density. A logical assumption also is that nearby sites tend to have more similar environments than do distant ones. So, ecological conditions should be most favourable for a species (and density correspondingly greatest) in one area and abundance should decrease with increasing distance in any direction from that location (Brown 1984, Root 1988b).

In reality, this is evident on a broad scale, but spatial heterogeneity and geographical variations in the requirements of species may cause exceptions at any level (e.g., Root 1988b, Wiens 1989).

4.3. Concluding remarks

There are several ecological advantages of large body size (see, e.g., Brown & Maurer 1986). Large birds tend to have more efficient homeostatic mechanisms and greater mobility, so they are able to tolerate a wider range of environmental conditions and are able to seek out more favourable locations. An increase in size enables an individual to spend less energy per unit biomass on maintenance and to become more efficient at extracting usable energy from low-quality foods. Consequently, the same amount of available energy can support a greater biomass of a large species than of a small one. Large species are usually dominant in interspecific aggression, which may result in exclusion of small species from preferred resources (e.g., Solonen 1993).

The distribution patterns of bivariate plots between the body size, population density, and width of the range in Finnish birds were largely similar to those of the North American land birds (Brown & Maurer 1987). It can be concluded, that few resources, a high probability of extinction, or recent colonization were represented by a low number of combinations, while abundant resources exploited by many species were reflected by a high number of combinations.

Selostus: **Suomen linnusto — lajidynamiikkaa ja sopeutumisrajoituksia**

Jatkuva uusien lajien ilmestyminen ja vanhojen pesimälajien vakaus ovat luonnehtineet Suomen linnustoa ainakin parin viimeksi kuluneen vuosisadan ajan. Joidenkin vanhojen pesimälajien kannat ovat kuitenkin nykyisin uhanalaisia. Tässä kirjoituksessa tarkastellaan lintujen sopeutumista lajidynamiikan, biologisten tekijöiden ja ympä-

ristön asettamiin rajoituksiin lajimäärän, ruumiin koon, kannan tiheyden ja levinneisyysalueen laajuuden välisten suhteiden avulla.

Koko linnuston lajien jakautuminen kokoluokkiin on kaksihuippuinen, mutta pienemmissä ryhmissä lajit jakautuvat yleensä yksihuippuisesti, vinosti suurempien kokoluokkien suuntaan. Suurempien lajiryhmien runsausjakaumat ovat tavallisesti log-normaaleja, pienempien taas voimakkaasti vinoja pienten runsausluokkien puolelle. Lintujen biomassa ja sen perusteella myös energian käyttö näyttävät olevan yksilörunsautta tasaisemmin jakautuneita eri lajien kesken. Koska Suomessa talvehtii suhteellisesti enemmän kookkaita kuin pienikokoisia lintulajeja, myös kesä- ja talvilinnustot eroavat biomassaltaan ja energian käytöltään huomattavasti vähemmän kuin yksilömäärien perusteella. Lintujen yksilömäärä on talvella n. 11 % aikuislintujen kesäisestä kokonaismäärästä; biomassana vastaava osuus on 25 %.

Lajien runsausjakaumien perusteella eräät linturyhmät näyttävät jakavan ympäristön tarjoamat voimavarat tasapuolisesti. Tiheyden ja ruumiin koon välinen suhde ei kuitenkaan viittaa yleisesti lajien koosta riippumattomaan energiataloudelliseen vastaavuuteen. Keskitiheys ja levinneisyysalueen laajuus Suomessa pienenevät merkitsevästi linnun koon kasvaessa, mikä viittaa ympäristötekijöiden rajoittavaan vaikutukseen. Monissa elintavoiltaan erilaisissa linturyhmissä keskitiheys on sitä suurempi, mitä laajempi lajin levinneisyysalue on, mikä ilmentää lajien leviämisen edistymistä ja menestymistä.

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