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Effects of urbanization on the breeding bird species richness in Finland: a biogeographical comparison

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Cities represent the extreme of human-modified environments, with only remnants of the original habitats present. To study how increasing urbanization affects breeding bird richness; we compiled literature data on bird assemblages at five different levels of urbanization (forest, countryside, village, small and large city centers) and along an urban gradient (park, residential area and city center in different towns) in the three ornithogeographical zones in Finland. The breeding birds were censused using the territory mapping or study plot method. The estimated number of breeding bird species decreased with urbanization. The highest species richness was found in the countryside (21.8 species in a 50-pair sample) and the lowest in the large city center (7.4 spp.). This finding supports the widely accepted hypothesis that moderate disturbance will increase biotic diversity. The estimated number of breeding bird species was lower in the city centers (6.8 species in a 25-pair sample) than in the urban parks (12.1 spp.). This result points to the important role of trees and shrubs as shelter, and as nesting and feeding places. The species richness was similar at different latitudes, when the level of urbanization was the same. The great productivity (amount of food) and high predictability of resources (food available throughout the year) in the urban habitats may explain why the species richness does not decrease northwards in the urban environments.

1. Introduction

Many ornithological studies have described the temporal and spatial distribution of birds in different kinds of environments. In the literature, however, data from research on urban bird assemblages are scarce and scattered. Most of the urban studies compare bird assemblages in the periphery with those in the city center of a single town. The results have demonstrated that the number and diversity of bird species decline with increasing urbanization (e.g. Batten 1972, Emlen 1974, Huhtalo & Järvinen 1977, Hohtola 1978, Hounsome 1979, Bessinger & Osborne 1982, Bezzel 1985, Jokimäki 1992). The number of bird species also tends to increase with increasing distance from the city center in urban parks (Hounsome 1979, Sukopp et al. 1982).

Nuorteva (1971) compared the bird assemblages of the center of a city, its surrounding agricultural area and uninhabited forest in Finland. He found that, throughout the year the number of species was highest near the rural houses and lowest in the city. In a similar study in Hamburg, Mulsow (1982) also recorded the highest number of breeding bird species in the agricultural area.

This study is part of a project intended to reveal the effects of urbanization on bird species richness and habitat selection. In this article, our main purpose is to examine the effects of urbanization on the species richness of the breeding bird assemblages in Finland.

2. Material and methods

The species richness of breeding bird assemblages was compared at five different levels of urbanization (forest, countryside, village, small and large city centers) (see Table 1; Fig. 1) and along an urban gradient in single towns (park, residential area and city center) (see Table 2) in the three Finnish ornithogeographical zones of Järvinen & Väisänen (1980). Most of the data were extracted from the literature. The rest of the material is derived from our own breeding bird censuses. The breeding birds were censused using the territory mapping or study plot methods; the differences between these two methods are fairly small in urban habitats (Hohtola 1978). The birds were censused in the years 1971–1990, except in Helsinki, where they were censused in 1956. Most of the data are for single years, so that the results may reflect chance annual fluctuations rather than long-term changes in bird populations. Both early and late censuses were available from South and North Finland and also from forest, rural and city areas. For this reason, we believe that variation between the study years has had only a slight effect on our results.

The 17 plots studied were located in spruce-dominated forest, the countryside, villages and

Table 1. The material of this study. Birds were censused by the territory mapping method (M) or the study plot method (P).

Location	Area ha	Years	Method	Visits	Population	Source
Forest						
Hirsala (60°05′N, 24°37′E)	64.0	1980	M	14	0	Tiainen et al. (1984)
Siilinjärvi (63°07′N, 27°37′E)	32.0	1983	P	1	0	Mönkkönen (1984)
Perta-aapa (65°45′N, 24°50′E)	51.0	1977	P	4	0	Rauhala (1980)
Countryside						
Lammi (61°03′N, 25°03′E)	30.0	1971–77	M	7–8	100	Tiainen & Solonen (1979)
Valamo (62°34′N, 28°48′E)	67.4	1982	M	4–20	50	Knuutinen (1982)
Kaakamojoki (65°51′N, 24°25′E)	26.0	1977	P	4	50	Rauhala (1980)
Village						
Loppi (60°42′N, 24°26′E)	96.0	1987	P	1	6 800	Suhonen unpub.
Järvelä (60°22′N, 25°18′E)	240.0	1990	P	2	2 500	Eronen et al. (1991)
Konnevesi (62°37′N, 26°17′E)	93.6	1985	M	6	3 500	Suhonen (1987)
Tervola (66°05′N, 24°48′E)	53.0	1987	P	1	4 500	Jokimäki unpubl.
Center of small city						
Karkkila (60°32′N, 24°12′E)	10.2	1978	M	5	8 000	Luoto (1981)
Heinola (61°10′N, 26°02′E)	50.0	1971	P	2	15 000	Hietanen (1975)
Kemi (65°44′N, 24°34′E9	80.0	1978	P	4	27 000	Rauhala (1980)
Tornio (65°50′N, 24°10′E)	30.0	1975	M	4	20 000	Huhtalo & Järvinen (1977)
Center of large city						
Helsinki (60°10′N, 24°55′E)	150.0	1956	P	4	426 000	Kajoste (1961)
Kuopio (62°52′N, 27°40′E)	7.5	1972–74	P	3	70 000	Hohtola (1984)
Rovaniemi (66°30′N, 25°42′E)	81.3	1983	M	5	33 000	Jokimäki (1992)

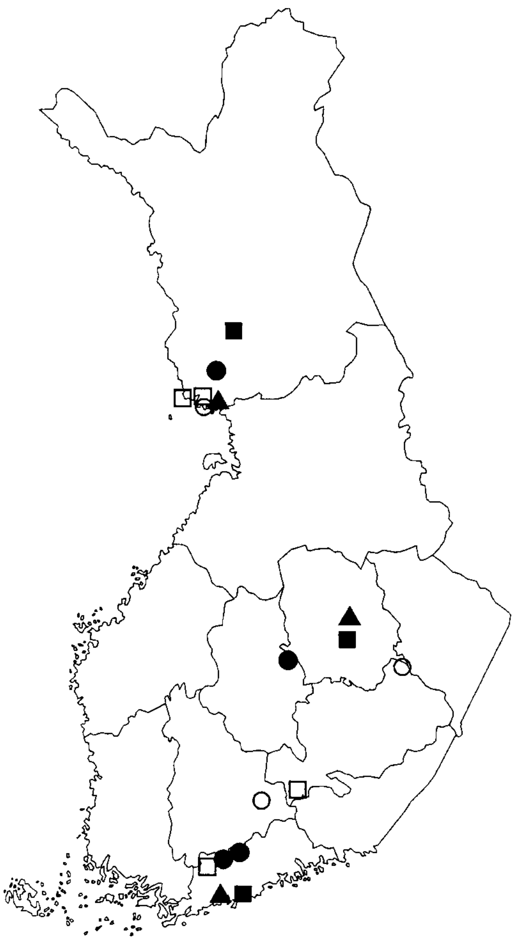

Fig. 1. Situation of the censuses areas in Finland. The symbols indicate different levels of urbanization: Triangle = forest, open dot = countryside, filled dot = village, open square = center of small city and filled square = center of large city.

Table 2. Area (ha) of study plots used for censusing the bird population of different city centers, residential areas and parks.

	City center	Residential area	Parks	Source
Helsinki	150.0	240.0	130.0	Kajoste (1961)
Karkkila	10.2	79.2	13.2	Luoto (1981)
Heinola	50.0	225.0	60.0	Hietanen (1975)
Kuopio	7.5	30.4	6.4	Hohtola (1984)
Rovaniemi	81.3	279.0	12.0	Jokimäki (1992)

the centers of small or large towns. The plots were allocated different levels of urbanization according to the human population living in them and their surroundings.

The general features of the landscape at the different levels of urbanization are as follows:

Forests: Old coniferous forest, dominated by Norway spruce (*Picea abies*) and including some Scots pines (*Pinus sylvestris*) and birches (*Betula spp*). The undergrowth consisted mainly of natural vegetation. The level of natural predation was normal and human interference was limited. No nest-boxes or supplementary food was provided by humans.

Countryside: This area was mixed forest and fields with isolated farm-houses and barns, and may be called 'rural'. As there were many edges of various kinds of habitats, natural predation pressure was high. Some nest-boxes and feeding tables for birds were available near the houses. Ther were about 50 to 100 inhabitants living in the surroundings of the study plots.

Village: Many houses with gardens and a few small blocks of flats. There were also some patches of forest and fields. A large number of nest-boxes and feeding tables were provided for birds. Some human interference existed. The human inhabitants numbered about 3000–7000. Breeding birds were censused only in the center of the village, and the edges of the study plots could be fairly diverse and sharp.

Center of small city: Small blocks of flats predominated. Isolated small parks occurred between the built-up areas. In the parks, the deciduous trees predominated and the undergrowth was managed. The number of nest-boxes and feeding tables was limited. Human interference was fairly high, but the natural predation may have been reduced. The human population was between 8000 and 30 000. The breeding birds were censused in the city center.

Center of large city: Large blocks of flats predominated. The only green areas were small, isolated and strictly managed parks, where the level of human interference was high. Only a few nest-boxes for small passerines and feeding places for pigeons occurred. The human population was over 30 000. The breeding birds were censused in the city center, and there were abundant non-living areas (such as asphalt and buildings) around the study plot.

There is a great variety of habitat types in urban areas. Most parts have an ecotonal or mosaic character (Erz 1966). The general features of the different subhabitats of the towns are briefly as follows:

City centers: The most urbanized area of the town. High and densely located buildings and scant vegetation. Nest-boxes and feeding tables were rare.

Residential areas: Area around the city center. Not so densely populated and built up as the former area. The proportion of single-family houses with gardens increased from the center to the periphery. There were many feeding tables and nest-boxes.

Parks: Mostly rather small and isolated areas between buildings. The undergrowth was strictly managed.

The study plot size varied from 7.5 to 240.0 ha at the different levels of urbanization (Table 1) and from 6.4 to 279.0 ha in the urban gradient series (Table 2). The effect of differences in sample size on species number was eliminated by the method of rarefaction (see Heck et al. 1975). To ensure sufficient replication, we used the expected number of breeding bird species in samples of the same size (50 pairs for the different levels of urbanization and 25 pairs for the urban gradient series) for each study plot as an independent observation for statistical testing. We used both ANOVA and coefficients of correlation to test the effect of increasing urbanization on breeding bird richness. The level of urbanization of different areas was measured by the number of inhabitants living in the study plots and in the areas surrounding them. We used the number of inhabitants (I), after a $\log_e$ (I+1) transformation, in all statistical tests. All post-multiple comparison tests that we performed employed Tukey's honestly significant difference test with $\alpha = 0.05$.

3. Results

3.1. Species richness and urbanization

The expected number of breeding bird species in samples of the same size (50 pairs) decreased with increasing human population ($r = -0.68$, df = 15, $P = 0.002$). When the impacts of urbanization is minor, the number of bird species will increase. After a certain threshold level, however, it declines very rapidly (Fig. 2).

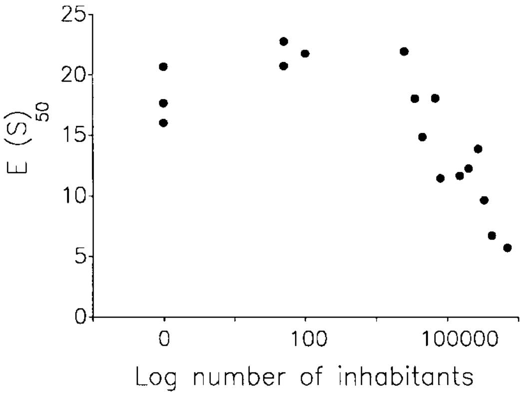

Fig. 2. The number of inhabitants in relation to the estimated species number E(S) in samples of 50 pairs ($r = -0.68$, df = 15, $P = 0.002$).

There were differences in the species richness between the different levels of urbanization (ANOVA, $F = 24.1$, df = 4,12, $P = 0.0001$). The highest species richness was found in the countryside (21.8 species in 50 pairs sample) and the lowest in the large city center (7.4 spp.). The average of the estimated species number in samples of 50 pairs in the small town centers and large town centers was smaller than that in the forests, countrysides and villages (Table 3).

Table 3. Average of the estimated species number in samples of 50 pairs at different levels of urbanization ($F = 24.1$, df = 4,12, $P < 0.0001$). The capital letters indicate statistically significant differences (Tukey's test at the 0.05 level) between different categories.

	$\bar{x}$	SD	n	
A Forest	18.1	2.4	3	DE
B Countryside	21.8	1.0	3	DE
C Village	18.2	2.9	4	DE
D Center of small city	12.3	1.1	4	ABC
E Center of large city	7.4	2.0	3	ABC

3.2. Species richness within cities

The species richness did not differ between cities (F = 2.14, df = 4, P = 0.17) (Table 4). There were differences in the species richness between the subhabitats of the towns (ANOVA, towns were a block and subhabitats the treatment, F = 7.18, df = 2, P = 0.016). The lowest number of species was found in the city center, except in the city of Helsinki. The average of the estimated species number differs between city centers (6.8 species in 25 pairs sample) and city parks (12.1 spp.). There were no differences in the species richness between the city center and residential area or between the residential area and parks (Table 4).

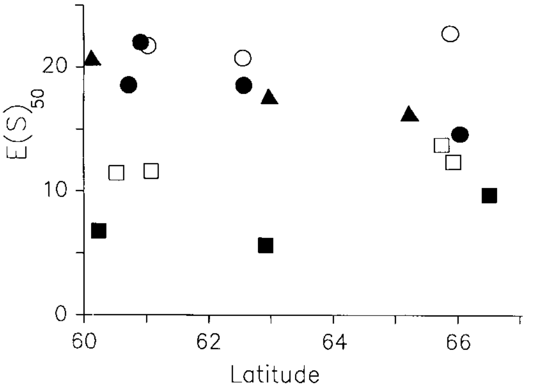

Fig. 3. Relationship between the estimated species number E(S) in samples of 50 pairs and latitude (r = 0.003, df = 13, P = 0.99). For symbols see Fig. 1.

3.3. Species richness and geographical location

Species richness was similar at different latitudes when the urbanization level was the same. The expected number of breeding bird species in samples of the same size (50 pairs) did not correlate with latitude, when both the number of inhabitants (I, after $\log_e$ (I+1) transformation) and the study plot area were controlled (partial correlation r = 0.003, df = 13, P = 0.99) (see Fig. 3).

4. Discussion

Human agricultural activity increases the diversity of the original land and creates opportunities for an increase in the number of bird species (Nuorteva 1971, Møller 1984). Our results suggest that during the first phases of urbanization, the bird assemblages will contain slightly more species, but after that the species richness will decline abruptly. This finding agrees with the widely accepted view that moderate disturbance will increase the biotic diversity of a ecosystem or community (e.g. Connell 1978).

Table 4. Average of the estimated species number in samples of 25 pairs in different parts of towns (F = 7.18, df = 2, P = 0.016). There were statistically significant differences (Tukey's test at the 0.05 level) between the city centers and parks.

	City center	Residential area	Park
Helsinki	5.1	4.1	11.2
Karkkila	8.5	11.6	13.6
Heinola	8.5	10.5	13.5
Kuopio	4.7	12.4	9.7
Rovaniemi	7.2	12.2	10.7
$\bar{x}$	6.8	10.2	12.1
SD	1.8	3.2	2.4

Increased human activity causes drastic changes in the environment, e.g. fragmentation of habitats and decreases in vegetation cover, especially the shrub and tree layers (Bessinger & Osborne 1982, Hooper et al. 1975). However, the urban habitats have many nesting bird species (see e.g. Hounsome 1979, Gilbert 1989), perhaps partly due to the low number of natural predators (Tomiałojć 1982) and the year-round availability of food (Lancaster & Rees 1979).

In northern European land bird communities species number, diversity and density generally decrease northwards (Järvinen & Väisänen 1980). In contrast, an increase in species richness is observed in communities of peatland birds and waders, which is connected with the diversity and amount of available habitats in the north and the large amount of food during the breeding season (see Järvinen & Sammalisto 1976, Järvinen & Väisänen 1978, Boström & Nilsson 1983, Järvinen et al. 1987). In our study, the number of breeding bird species seems to depend more on the level of urbanization than on geographical latitude.

In Finnish urban parks, the number of breeding bird species was also independent of latitude (Suhonen & Jokimäki 1988). The urban habitats decrease northwards in Finland, and the northern towns are more isolated from each other than southern ones. So, some other reason than the diversity of available habitats must be responsible for the high species richness in the northern towns.

Sasvári & Moskát (1988) presume that settlement of a species in a human habitat depends upon adaptation to the exploitation of available food sources and/or competition with similarly adapted species. The urban habitats are so new in an evolutionary sense, that most bird species are not yet well adapted to living in them. It is characteristic of urban bird assemblages that from three to five species are dominant, but these comprise about 65–90% of the individuals in the cities (e.g. Huhtalo & Järvinen 1977, Bezzel 1985). These superabundant bird species, nesting mostly in the buildings, have adapted early to the urban habitat and are superior in competition to the other species (Lancaster & Rees 1979). As these species are the same in the south and north, the number of bird species in urban habitats does not decrease to the north.

Under natural conditions, the number of species is influenced mainly by the climate (weather) and seasonal changes in the kind and amount of food (e.g. Bezzel 1982, 1985). In northern regions, with seasonally severe climates, the availability of food during winter is considered a crucial factor affecting the winter survival of birds (Lack 1954, Fretwell 1972). The cities have fewer days with snow and a higher average temperature, especially in the cold season, than the surrounding habitats (see e.g. Erz 1966). Thus, the differences in climatic variables between south and north are not so great in urban habitats as in natural areas. The decrease of productivity (amount of food) and predictability of resources (food available throughout the year) to the north is smaller in an urban environment than in more natural areas. These observations may explain why the number of breeding bird species does not decrease northwards in the urban environments.

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Selostus: **Kaupungistumisen vaikutus lintujen lajimäärään Suomessa: eläinmaantieteellinen vertailu**

Tutkimme lintujen lajimäärän maantieteellistä vaihtelua erilailla kaupungistuneilla alueilla (metsä, maaseutu, kylä, pieni ja suuri kaupunki) sekä "kaupungistumisgradientissa" (puisto, asutusalue ja ydinkeskusta). Aineisto kerättiin pääosin suomalaisesta lintukirjallisuudesta (Taul. 1–2). Laskentamenetelminä on käytetty joko kartoitusta tai koealamenetelmää.

Kaupungistumisen myötä lajimäärä laski (Kuva 2). Lajimäärä oli suurin maaseudulla (21.8 lajia 50 parin näytteessä) ja pienin suurten kaupunkien keskustoissa (vastaavasti 7.4 lajia) (Taul. 3). Tulos tukee hypoteesia, jonka mukaan kohtuullinen häiriö lisää eliöyhteisön monimuotoisuutta. Kaupunkien puistoissa oli enemmän lajeja (12.1 lajia 25 parin näytteessä) kuin keskustassa (vastaavasti 6.8 lajia) (Taul. 4). Tulos korostaa viheralueiden merkitystä kaupunkilinnuston monimuotoisuuden lisääjänä.

Yleensä sekä lintujen lajimäärä että tiheys laskevat pohjoista kohti. Tämän on selitetty johtuvan pohjoisten elinympäristöjen epävakaudesta ja alhaisesta tuottavuudesta. Tässä työssä maantieteellinen sijainti ei vaikuttanut lajimäärään kaupungistumisasteen ollessa vakioitu (Kuva 3). Kaupunkihabitaattien suuri tuottavuus (ravintoa runsaasti) ja hyvä ennustettavuus (ruokaa tarjolla läpi vuoden) voinevat selittää sen, ettei lajimäärä laske pohjoista kohti kaupunkihabitaateilla. Toisaalta kaupungit ovat linnuille evolutiivisesti uusia elinympäristöjä, joten niihin on sopeutuneet vain harvat lajit, ns. kaupunkilinnut. Nämä lajit ovat usein samoja sekä etelässä että pohjoisessa.

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