Birds in a Farmland — More Species in Small than in Large Habitat Island

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Abstract: *Birds were censused on habitat islands to investigate the effect of vegetation, island size, and isolation on the density and species diversity of birds.*

The density of birds was highest on small habitat islands and in islands close to other islands, especially large ones. We suggest that this is because birds on small habitat islands utilize resources from surrounding fields. After compensating for sampling effect (the fact that we made more observations and there are more territories on large islands), we analyzed the species richness of different islands. We found that there are more territorial species (i.e., bird species whose territories are readily mapped) on small than on large islands. We discuss different causes for this finding. We also found that a given area comprised of many small islands contains more species than the same area comprised of only a few large islands. This is true for both all observed bird species and for all recorded territorial species. We conclude that, when considering conservation from a local perspective, it is important to protect all nonmatrix land in this type of landscape. This will ensure a high local diversity.

Resumen: *Las aves fueron censadas en hábitats aislados para investigar el efecto de la vegetación, del tamaño del área y del aislamiento en la densidad y diversidad de las especies de aves.*

La densidad de aves fue más alta en hábitats aislados pequeños y en áreas aisladas cercanas a otras áreas aisladas, especialmente a las grandes. Sugerimos que ésto se debe a que las aves en hábitats aislados pequeños utilizan los recursos de las tierras que las rodean. La riqueza de las especies de diferentes áreas aisladas es analizada después de tomar en cuenta el efecto que pudo tener el muestreo, por ej. compensando por el hecho de que se hicieron más observaciones y hay más territorios en áreas aisladas grandes. Siguiendo este enfoque, nos encontramos que hay más especies territoriales (por ej. especies de aves cuyos territorios son fáciles de mapear) en las áreas aisladas pequeñas que en las grandes. Diferentes causas para éste hecho son discutidas. También se ha encontrado que las un área dada integrada por muchas áreas aisladas pequeñas, contiene más especies que la misma integrada solamente por algunas áreas aisladas grandes. Esto es verdad tanto como para cuando uno cuenta todas las especies área de aves observadas, como para cuando uno cuenta todas las especies registradas de aves territoriales. Concluímos que, cuando se esté considerando la conservación en una perspectiva local, es importante proteger todas las áreas no utilizadas en éste tipo de terrenos. Esto asegurará una alta diversidad local.

Introduction

The last decade and a half has seen many studies concerned with bird communities on islands, real and "habitat" (Diamond 1975; Moore & Hooper 1975; Forman et al. 1976; Morse 1977; Whitcomb et al. 1981; Ambuel & Temple 1983; Opdam et al. 1985; Cieślak 1985). The studies have focused on the effect of island area on species numbers and on the conservation value of different island types.

Paper submitted November 29, 1989; revised manuscript accepted September 26, 1990.
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The present study is concerned with all bird species living on habitat islands. For methodological reasons, one subset, species with mappable territories, is also treated separately. The aim is to shed light on the value and function of habitat islands in an agricultural area for birds at large.

The purpose of this study is to determine what factors influence the number of bird species found in a set of habitat islands (henceforth referred to as "islands."). The factors considered are island size, island shape, island isolation, and vegetation. Their effect is seen as a two-stage process; effect on density and, given the number of individuals, effect on the number of species.

If species number is found to increase with area this does not, in our opinion, imply any "biogeographic" effect of area per se on species number. The effect may be due simply to the large number of individuals on large islands. To study this aspect properly we need a null hypothesis: what would the species number be on an island if there were no active biogeographic effects (in any sense that we choose to recognize)? Many studies of bird species number in habitat islands have not taken this approach; these studies have simply found in most cases that species number increase with area (Cieślak 1985; Opdam et al. 1984; Opdam et al. 1985; Ambuel & Temple 1983). As the sample sizes usually are larger in larger areas, this is not a very interesting finding. A null hypothesis is therefore necessary.

Studies that have used a null hypothesis have followed two lines of approach. One approach employs a null hypothesis without quantitative data. The species numbers are estimated with methods that are identical in all respects (equal number of point censuses, equal-size study plots, etc.) for both islands and source areas (Forman et al. 1976).

The other approach depends on the existence of quantitative data: number of "individuals" (observations, territories). In this case rarefaction (James & Wamer 1982) can be used. This method involves sampling an equal number of individuals in all study areas. The samples are equal in a statistical sense; the actual data may result from different numbers of observations in the different study areas. This approach has been used by Coleman et al. (1982), Martin (1983), and Haila et al. (1987).

In this study we use two null hypotheses: (1) Density (number of territories or observations per area unit) is the same on all islands, regardless of size and habitat. (2) The number of species can be found by random sampling of individuals from the total pool of birds in all studied islands. These two null hypotheses together imply that the number of species in a single island is completely determined by its size and the pooled distribution of species abundances (Fig. 1).

As an alternative analysis, we recognize that from an applied point of view, the effect of size may be of interest in two different ways. In addition to the effect of a particular island's area on species number, one may study the effect of area on the total bird fauna in a set of small or of large islands. This addresses what has been termed the SLOSS (Single Large Or Several Small) problem (Simberloff & Abele 1976; Simberloff and Abele 1982).

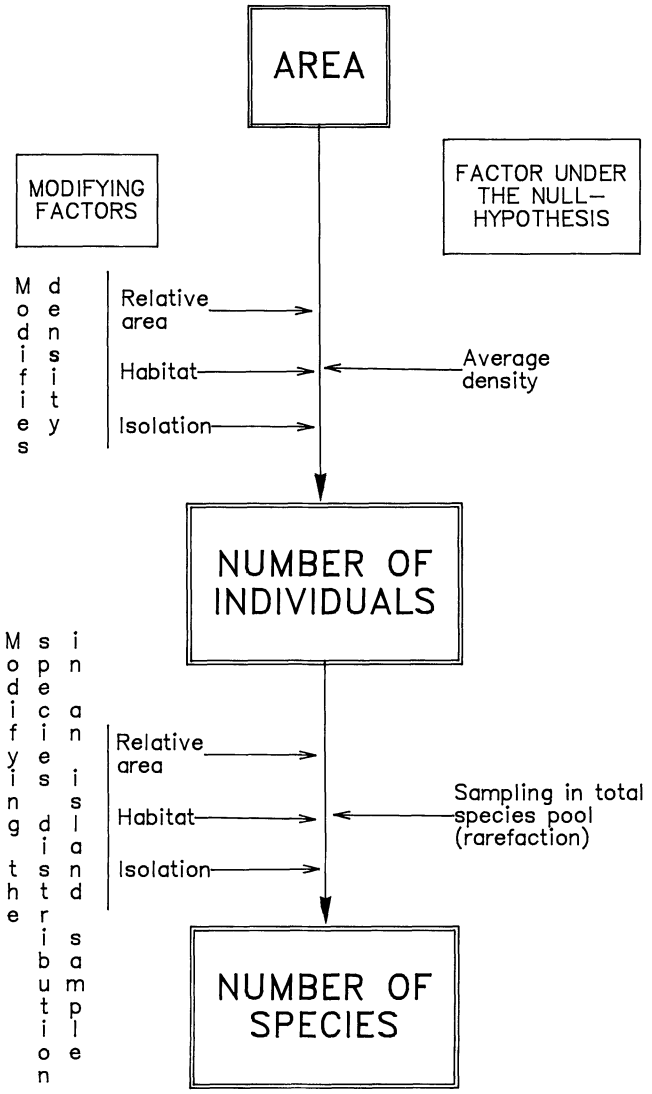

Figure 1. Overview of the factors and processes considered in this study.

Study Areas

The present study was undertaken in an agricultural landscape. Six different study areas scattered over the southwestern part of the southernmost province of Sweden (Skåne) were used. They were (location, year stud-

ied, and number of different islands in parentheses): Ellinge (55° 50′ N, 13° 0′ E, 1982 and 1983, 28 islands), Jordberga (55° 25′ N, 13° 25′ E, 1982 and 1983, 30 islands), Mölleberga (55° 35′ N, 13° 15′ E, 1983, 17 islands), Svenstorp (55° 55′ N, 13° 15′ E, 1982 and 1983, 25 islands), Trolleholm (55° 55′ N, 13° 10′ E, 1982, 16 islands), and ssj (56° 15′ N, 13° 0′ E, 1982 and 1983, 24 islands). All were open landscapes in which more than 70% of the land was ploughed. The size of the studied islands (.01 to 24.0 ha, with most below 1.0 ha) is in the lower range of those studied by previous authors. Types of islands included in the sample are: small woods (ranging in size down to a few trees), hedges, grazed fields, marl pits with a surrounding border of trees and grass, ditches verged by grass, and small marshes. The islands studied are a representative sample of those typically found in the agricultural districts of Skåne. The islands are not biased toward any particular habitat; all habitat islands in the six areas are included (except for the surroundings of houses). This makes the choice of particular interest from an applied conservation point of view. It also makes it possible to study the influence of habitat on density and species numbers. The islands are surrounded by fields of agricultural crops. The most important crops grown are wheat, rye, rape, and sugar beets.

Methods

Bird Census

The analysis was carried out with two types of measurements. One is based on all *observations* of birds, scored by species. This is presumed to be an index of a species' presence that can be used for all species. Detection rate may vary greatly among species. The index is not used to compare different species, however, but to compare the same set of species on different islands. It is not possible to standardize observation rates on islands of different types (of different sizes, for example) so some bias is still possible. Nevertheless, for some applications of the results we consider it important to include as many species as possible. The other type of measurement is based on *territories*. This type can only be used for a subset of all species but it has merits with respect to lack of bias. Because this measurement is based on several visits, few territories remain undetected and there is little room for bias resulting from islands' being of different types.

The field procedure was this. Each year all islands were visited eight to ten times. The visits were spaced from April 21 to June 28. All birds observed on islands (except three species) were scored and noted on maps. One bird observed on one visit was thus one "observation." Birds merely flying over an island were not scored, nor were birds seen in surrounding fields. The number of territories of species suitable for mapping was evaluated (Anon. 1970) (Table 1). The rules for territory mapping were those conventionally used. Essentially, to score a territory there must be at least three observations of a bird with territorial indication (singing, agression) in an area of reasonable size to constitute a territory for the species in question. All Starlings (*Sturnus vulgaris*) and Wood Pigeons (*Columba palumbus*) were excluded. We considered that their highly clumped distribution could introduce more noise in the computation than was justified by the increase in generality of conclusions to be gained when these two species were included. We also excluded the Sky Lark (*Alauda arvensis*) because it can survive in open fields without the support of habitat islands, and its distribution is thus not relevant to the problem at hand. If the mapping suggested that a territory covered several islands it was scored on the island with the most observations or on the island where the nest was located. All islands in an area were visited. This reduced the possibility of bias due to scoring a territory on one island when the main part of the territory really belonged to another island that was not censused.

Four different bird fauna variables were considered for each island. (1) The total number of bird observations divided by the island's area: Density of Observations (DO). (2) The number of territories divided by island area (DT). For both measurements we only considered the island's area exclusive of water.

As stated in the introduction, the expected number of each species in each island was computed by means of rarefaction (James & Wamer 1982). This gives the number of species one would find if one sampled a number of territories equal to that found on the considered island from the total pool of territories. The total pool is represented by the combined observations (or territories) on all islands during both years. An index of species richness that is not affected by the number of observations (or territories) on the different islands is obtained by dividing the actual number of species with the expected number (from rarefaction). This gives (3) the Relative number of Observed Species (ROS) and (4) the Relative number of Territorial Species (RTS).

Structure

The following variables that represent the landscape structure were recorded for each island: (1) Area (LOGAREA). Open water, ponds, and streams were not included in this measure. (2) Closeness (LOGCLOSE). This is an inverse measure of isolation. It was measured as the total area not covered by cropped fields within 200 m of the island. (3) Shape

Table 1. Bird species observed and considered in the study. Territory mapping was only done for birds in the upper group. Below "Islands" are the number of islands where the species was observed or a recognized territory was found given.

		Observations		*Territories*	
		Total	*Islands*	*Total*	*Islands*
Blackbird	*Turdus merula*	761	103	107	45
Blackcap	*Sylvia atricapilla*	241	28	38	12
Blue Tit	*Parus caeruleus*	147	30	15	11
Brambling	*Fringilla coelebs*	2346	132	355	97
Chaffinch	*Fringilla montifringilla*	1	1	0	0
Corn Bunting	*Miliaria calandra*	1	1	0	0
Dunnock	*Prunella modularis*	590	76	94	42
Garden Warbler	*Sylvia borin*	639	90	134	60
Goldcrest	*Regulus regulus*	74	13	10	6
Golden Oriole	*Oriolus oriolus*	2	1	0	0
Goldfinch	*Carduelis carduelis*	28	6	1	1
Grasshopper Warbler	*Locustella naevia*	19	4	3	2
Great Spotted Woodpecker	*Dendrocopos major*	10	3	1	1
Great Tit	*Parus major*	385	66	60	25
Greenfinch	*Carduelis chloris*	738	72	98	37
Grey Wagtail	*Motacilla cinerea*	3	2	0	0
Hawfinch	*Coccothraustes coccothraustes*	22	6	1	1
Icterine Warbler	*Hippolais icterina*	357	32	81	16
Lesser Whitethroat	*Sylvia curruca*	74	28	11	9
Linnet	*Carduelis cannabina*	376	62	35	23
Marsh Tit	*Parus palustris*	39	16	2	3
Marsh Warbler	*Acrocephalus palustris*	402	95	107	69
Meadow Pipit	*Anthus pratensis*	56	6	7	2
Nuthatch	*Sitta europaea*	58	13	6	5
Ortolan Bunting	*Emberiza hortulana*	3	3	0	0
Pied Flycatcher	*Ficedula hypoleuca*	117	44	12	7
Redstart	*Phoenicurus phoenicurus*	31	19	4	1
Redwing	*Turdus iliacus*	1	1	0	0
Red-backed Shrike	*Lanius collurio*	21	13	1	1
Reed Bunting	*Emberiza schoeniclus*	287	55	34	24
Reed Warbler	*Acrocephalus scirpaceus*	38	15	9	7
River Warbler	*Locustella fluviatilis*	1	1	0	0
Robin	*Erithacus rubecula*	186	39	21	8
Sedge Warbler	*Acrocephalus schoenobaenus*	49	10	11	7
Siskin	*Carduelis spinus*	19	7	0	0
Song Thrush	*Turdus philomelos*	326	53	46	20
Spotted Flycatcher	*Muscicapa striata*	59	20	3	3
Tree Pipit	*Anthus trivialis*	238	46	40	22
Treecreeper	*Certhia familiaris*	27	3	2	1
Trush Nightingale	*Luscinia luscinia*	855	67	170	50
Wheatear	*Oenanthe oenanthe*	23	16	1	1
Whinchat	*Saxicola rubetra*	74	24	7	4
White Wagtail	*Motacilla alba*	131	45	10	8
Whitethroat	*Sylvia communis*	359	98	74	59
Willow Warbler	*Phylloscopus trochilus*	1057	124	199	63
Willow Warbler	*Phylloscopus collybita*	9	7	0	0
Wood Warbler	*Phylloscopus sibilatrix*	33	16	5	5
Wren	*Troglodytes troglodytes*	39	6	8	4
Wryneck	*Jynx torquilla*	1	1	0	0
Yellow Wagtail	*Motacilla flava*	116	24	15	12
Yellowhammer	*Emberiza citrinella*	61	27	6	6
Sky Lark	*Alauda arvensis*	*	*	*	*
Buzzard	*Buteo buteo*	37	17		
Collard Dove	*Streptopelia decaocto*	4	3		
Common Sandpiper	*Actitis hypoleucos*	3	2		
Common Tern	*Sterna hirundo*	14	5		
Coot	*Fulica atra*	57	8		
Crow	*Corvus corone*	96	46		
Cuckoo	*Cuculus canorus*	64	29		
Fieldfare	*Turdus pilaris*	105	10		
Sparrow Hawk	*Accipiter nisus*	8	7		
Great Snipe	*Gallinago media*	1	1		
Grey Heron	*Ardea cinerea*	23	14		
Hobby	*Falco subbuteo*	2	1		
House Martin	*Delichon urica*	25	3		
House Sparrow	*Passer domesticus*	127	17		
Jackaw	*Corvus monedula*	122	12		

Table 1. Continued.

		Observations		Territories	
		Total	*Islands*	*Total*	*Islands*
Jay	*Garrulus glandarius*	5	3		
Kestrel	*Falco tinnunculus*	7	2		
Lapwing	*Vannelus vannelus*	43	8		
Long-eared Owl	*Asio otus*	1	1		
Magpie	*Pica pica*	54	35		
Mallard	*Anas platyrhynchos*	314	50		
Marsh Harrier	*Circus aeruginosus*	3	3		
Moorhen	*Gallinula chloropus*	48	23		
Mute Swan	*Cygnus olor*	8	2		
Oystercatcher	*Haematopus ostralegus*	1	1		
Partridge	*Perdix perdix*	6	2		
Pheasant	*Phasianus colchicus*	204	54		
Pochard	*Aythya ferina*	3	1		
Ringed Plover	*Charadrius hiaticula*	1	1		
Rook	*Corvus frugilegus*	34	2		
Sand Martin	*Riparia riparia*	15	3		
Shelduck	*Tadorna tadorna*	44	13		
Snipe	*Gallinago gallinago*	11	1		
Starling	*Sturnus vulgaris*	*	42		
Stock Dove	*Columba oenas*	73	12		
Swallow	*Hirundo rustica*	15	4		
Tawny Owl	*Strix aluco*	1	1		
Teal	*Anas crecca*	5	3		
Tree Sparrow	*Passer montanus*	295	37		
Tufted Duck	*Aythya fuligula*	4	1		
Wood Pigeon	*Columba palumbus*	*	109		

* *These data were not recorded, for reasons explained in the text.*

(LOGSHAPE). This was calculated as the island's ratio of periphery over area divided by the corresponding ratio for a circular island of the same area. These variables were log transformed in the statistical analyses.

Some analyses were performed on two sets of islands, either all islands or only "rows." "Rows" were defined as islands with a width of at most 10 meters and a length of more than 10 times the width.

Vegetation

The following variables that represent the vegetation of each island were recorded: (1) Percentage of the ground covered by the canopy of trees or bushes (PCAN). (2) Total stem area (dm^2 per ha) (TSAREA). (3) Mean canopy height (zero heights included) (MCH). (4) Coefficient of variation for MCH (CVCH). (5) Mean stem area (MSAREA). (6) Number of different tree and/or bush species expected in a sample of five (estimated with rarefaction) (TSP5). (7) Tree/bush species diversity from the formula $1/\partial p_i$ where the proportions (p_i) are based on total stem area for the different species (TSPDIV). (8) Percentage bare ground (PBG). (9) Mean height of the field layer (MFH). (10) Coefficient of variation for MFH (CVFH). (11) Stem area per ha for bushes (stems below 4 cm diameter) (BSAREA). (12) Stem area class diversity from the formula $1/\partial p_i$ where the proportions are based on stem area in different stem size classes (0–1 cm, 1–2 cm, 2–4 cm, 4–8 cm, etc.) (STADIV). (13) Number of different field layer species expected in a sample of twelve (rarefaction) (FSP12). (14) Stem area of trees and bushes standing dead (DSAREA). (15) Grass as a percentage of all field layers (PG).

On islands less than .25 ha we made a complete census of *large stems* (more than 4 cm in diameter), recording size and species. On larger islands we censused four .1 ha circulars sample areas (Fig. 2). In "rows," islands longer than 100 m and narrower than 10 m, we censused three to six separate 20 m sample sections.

If the bush layer was sparse, we censused *small stems* in the same sample areas as were used for large stems. In all islands with a dense bush layer, small (less than 4 cm in diameter) stems were only sampled in part of stem sample areas. In small islands this was a cross of 2-m-wide sample lines, each running between diagonal corners of the island. In large islands a cross of 2-m-wide lines was censused on each circular plot, and in "rows" four 2-m-wide subsections were censused in each 20 m section. These procedures gave data for the variables TSAREA, MSAREA, TSPDIV, BSAREA, STADIV, and DSAREA.

On the lines constituting the subsamples for small

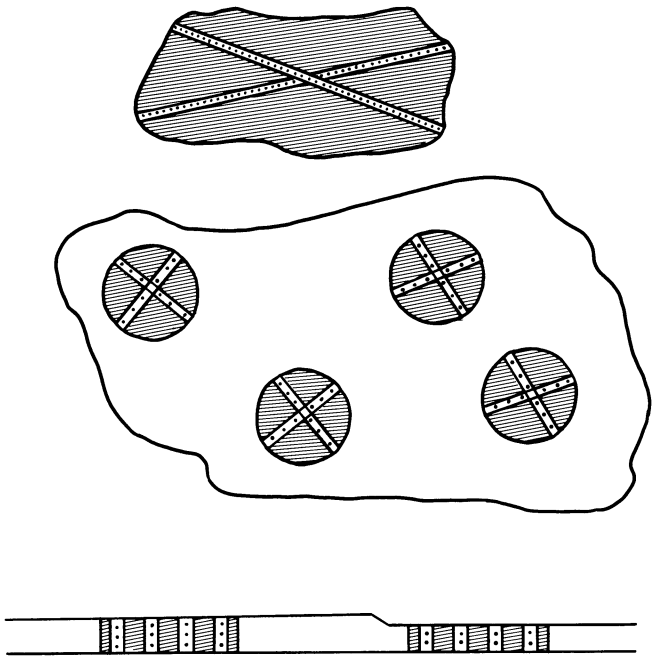

Figure 2. Vegetation sample areas in small, large, and "row" islands, respectively. Stems were sampled on the shaded area. In bushy islands, small stems were only sampled on the "bands." Point samples of tree and field layer heights and species were taken on the dots.

stems we used a sample point for every 5 meters (Fig. 2). In the "rows" there were one to three sample points across the row, the number depending on the width and homogeneity of the row. This gave 40 to 70 sample points for each island. At each point we registered *field layer height* and *species* and also *canopy height* and *species*. This gave data for the variables PCAN, MCH, CVCH, TSP5, PBG, MFH, CVFH, FSP12, and PH.

Several of the vegetation variables are highly correlated both conceptually and statistically. We therefore reduced the 15 variables to 6 independent variables by principal component analysis. Each of these new variables loads mainly on a set of conceptually interrelated original vegetation variables. These new variables are thus easily interpretable in biologically meaningful terms and we have named them accordingly (Table 2). High values of GROUND represent a low and patchy field layer. High values of BUSHY represent a large total amount of bushes and generally great variation in size of woody vegetation. The interpretations of TREE SP. DIVERSITY and FIELDL.-DIVERSITY are obvious. A high value of DEAD means an island with many trees and large trees standing dead. A high value of FOREST indicates a forest with a high and uniform canopy, made up of a large number of thick trees.

Results

Factors Affecting Density: DO and DT

There is a negative correlation between island area and bird density. This applies to density based both on number of observations and on number of territories. There is a positive correlation between closeness and territory density; that is density is lowest on the more isolated islands. Compact islands tend to have higher densities than islands with a more developed periphery. This pattern is only significant for observations, not for territories, and only if all islands are included; excluding the "row" islands considerably reduces variation on this variable (Table 3). There was no aspect of vegetation that significantly affected bird density (Table 3).

Factors Affecting the Number of Species in an Island: ROS and ROT

The relative number of territorial species is highest on the smaller islands (Table 3). Only one vegetation variable is significantly correlated to relative species number; DEAD (which mainly depends on the amount of standing dead trees [Table 2]) is positively correlated to the relative number of species observed (but not to the number of territorial species) (Table 3).

Species Number in Groups of Large and Small Islands (SLOSS)

The islands were ranked according to area. The two largest islands were assigned to one group, the four next in area to a second group, etc. The four groups thus formed had similar total areas. As a group, the small islands contained more species, considering both observations and territories, than did the larger islands (Table 4).

To remove any density effects (due to the fact that smaller islands had more observations and territories per area than large ones), we made a similar analysis in which we based ranking and total group size on number of observations and number of territories. In these analyses, too, there were more species present in the groups of small islands than in the two groups of large islands. There was no difference between the two groups of small islands (Table 4).

The appendix gives an overview of the island size preferences of the different species encountered. Note, however, that without further analysis outside the scope of this report, this information is not reliable for species with a small total number of observations.

Table 2. Principal component loadings. The principal components have been rotated with the varimax method (Wilkinson 1987). "% expl" refers to the percentage of total variance explained by the rotated components.

ALL ISLANDS (N = 238)						
Component no.	*1*	*2*	*3*	*4*	*5*	*6*
Name	*GROUND*	*BUSHY*	*TREE SP. DIVERSITY*	*DEAD*	*FIELDL.-DIVERSITY*	*FOREST*
% expl.	18.8	9.5	13.9	7.5	7.1	18.6
PBG	.91	.08	.01	−.01	.04	.16
CVFH	.88	.07	.03	−.03	.01	.09
MFH	−.78	−.00	−.04	−.08	.15	−.36
BSAREA	.08	.87	−.08	.01	−.16	.05
STADIV	.06	.58	.50	.08	.22	−.07
TSP5	−.03	.01	.91	.00	−.10	.04
TSPDIV	.12	.01	.87	.06	−.10	.09
DSAREA	.01	.04	.11	.92	.11	.07
FSP12	.05	.11	.19	−.11	−.86	−.15
PCAN	.45	.09	.15	.02	.12	.77
MCH	.32	−.15	.23	−.01	.27	.76
TSAREA	.02	.12	−.17	.36	−.05	.74
CVCH	−.26	−.01	−.09	.13	.00	−.72
MSAREA	−.16	−.48	−.08	.05	.08	.59
PG	−.44	−.17	−.29	.34	−.32	−.04

ONLY NON-"ROW" ISLANDS (N = 162)						
Component no.	*1*	*2*	*3*	*4*	*5*	*6*
Name	*FOREST*	*TREE SP. DIVERSITY*	*GROUND*	*BUSHY*	*FIELDL.-DIVERSITY*	*DEAD*
% expl.	20.4	14.0	17.4	10.8	7.4	8.3
PBG	.21	−.03	.89	.03	.08	−.11
CVFH	.10	.01	.86	−.05	.05	−.14
MFH	−.39	−.09	−.76	.00	.11	−.12
BSAREA	.08	−.18	−.11	.85	−.21	.03
STADIV	−.04	.39	.02	.68	.29	.02
TSP5	.07	.92	−.09	.02	−.02	−.03
TSPDIV	.11	.91	.14	.02	−.11	.05
DSAREA	.09	.16	.00	.12	.27	.80
FSP12	−.13	.12	−.03	.06	−.88	−.11
PCAN	.82	.17	.39	.11	.07	−.05
MCH	.78	.29	.26	−.16	.21	−.09
TSAREA	.78	−.16	.10	−.06	−.04	.34
CVCH	−.76	−.09	−.25	−.06	−.04	.19
MSAREA	.54	−.05	−.22	−.57	.09	.09
PG	−.19	−.21	−.36	−.20	−.22	.61

Discussion

Density

We discuss the effect of the different variables on density first, as density itself enters as an independent variable in relation to species number.

In our habitat islands, density (observations and territories per area unit) was highest on the smaller islands. This agrees with the findings by Nilsson (1986) for bird territories on true lake islands and lake-dependent birds on inland lakes. However, opposite results were found by Nilsson (1986) for birds in bogs and by Martin (1983) for forest birds on forested marine islands.

Certain possible biases may or may not have operated and influenced our results. We did not score birds that were foraging outside an island in the surrounding fields. This probably excluded a higher proportion of residents of small than of large islands, and our results are therefore conservative in this respect. It is possible that birds on very small islands (that are part of the only pair of their species on that island) are less involved in territorial encounters in the broad sense (fights, singing), and thus are less easily spotted. In this respect, too, our results err on the safe side, if at all. Finally we tried to search all islands equally thoroughly. This is a subjective judgment and may have introduced bias; if it did, the direction of this bias can not be determined with certainty.

We suggest two explanations for the pattern found. (1) It may be that the border zone is particularly productive. This may, for example, be a reasonable explanation of the findings for shore birds (Nilsson 1986); the shore habitat is likely to be particularly productive. It is also possible that the bog border is not more productive than the bog interior and that marine shores are not particularly productive for forest bird species, which reconciles this hypothesis with the other data cited

Table 3. Coefficients for the partial correlation between bird fauna variables (dependent) and different structure and vegetation variables (independent) when controlling for the other independent variables. N represents the number of observations (different island and year) while d.f. represents the number of different islands involved, whether data are available for one or two years. DO = Observations per area (density), DT = Territories per area, RSO = Relative number of species observed and RST = Relative number of territorial species. The abbreviations of vegetation variables are defined in Table 2.

ALL ISLANDS, N = 238, d.f. = 140.	*DO*	*DT*	*ROS*	*RTS*
LOGAREA	−.170*	−.203*	−.076	−.226**
LOGCLOSE	.050	.196*	−.009	.060
LOGSHAPE	−.169*	−.112	−.018	−.046
FOREST	.051	−.025	.132	.124
TSPDIV	−.111	.010	.129	−.127
BUSHY	.068	.064	.097	−.019
GROUND	.066	.054	.001	.040
FIELDDIV	−.111	.028	.103	−.123
DEAD	−.123	−.049	.247**	−.063
ONLY NON-"ROW" ISLANDS, N = 162, d.f. = 100.				
LOGAREA	−.121	−.197*	−.090	−.248*
LOGCONN	.052	.183	.007	.122
LOGSHAPE	−.174	.055	−.046	−.097
FOREST	.045	−.079	.126	−.029
TSPDIV	−.151	−.039	.151	.066
BUSHY	.096	.118	−.044	−.028
GROUND	−.026	.029	−.048	−.096
FIELDDIV	−.096	.015	.178	−.092
DEAD	−.153	−.163	.295**	−.130

* = $P < .05$.
** = $P < .01$.

above (Nilsson 1986; Martin 1983). (2) An alternative explanation that seems reasonable for the islands in this study is that the fields constitute a productive part of the studied birds' home ranges. The effective island size is thus larger than that measured by us. The situation is analogous to determining population densities of small mammals in a small trapping area. Similar explanations may apply to other studies in landscapes where the "matrix" is productive but does not by itself support the species studied. An example might be lake-dependent birds in inland lakes (Nilsson 1986).

The fact that, among islands of the same size, those with a relatively short periphery have the highest densities does not support the validity of first explanation for our results. Accordingly, we favor the second. It also seems that rather narrow strips of field (in the range of 10 to 100 m) are all that are used, since the presence of other islands within 200 m (LOGCLOSE, Table 3) actually had a positive effect on density.

Our results imply that by scattering small habitat islands in an agricultural land it is possible to turn wasteland (from a bird's point of view) into productive land to a higher degree than would be expected from the area of the habitat island itself. Using small islands is a more efficient way to cropped land productive for birds than is using larger ones. It is possible that birds of many species can utilize cropped fields if they have close access to habitat islands that provide nesting sites, perches, and close cover. We also find that, because closeness to other islands positively influences density, a given set of islands is maximally utilized if they are distributed in groups, with short interisland distances. The findings in this section are summarized in Figure 3.

Area Effects on Species Number—Single Islands

In contrast to what has been found in most other studies on species-area richness (Moore & Hooper, 1975; Howe et al. 1981; Opdam et al. 1984; Cicślak 1985; Rafe et al. 1985), this study demonstrates that area per se can be negatively correlated with species richness, in this case measured as number of territorial species. Martin (1983), who compensated for sample sizes, found a positive correlation between species numbers and marine island size, while Forman et al. (1976), who also used a null hypothesis approach, found higher relative species numbers in habitat islands compared to an extensive forest. However, Forman et al.'s highest values were for a large habitat island, not for the smaller ones, as ours were. Coleman et al. (1982) found no correlation, either positive or negative, in sets of wood lots.

We suggest three mechanisms that may have produced the observed pattern.

(1) It is often pointed out that large islands may contain more species than small ones because there is a lower limit to the size of islands acceptable for many species (Moore & Hooper 1975; Howe et al. 1981; Ahln & Nilsson 1982; Nilsson 1986). This limit should contribute to a tendency for larger islands to contain more species. However, whether this tendency really dominates over possible opposing tendencies can not be determined in the absence of a null hypothesis. However, the phenomenon may well have contributed to the lack of a positive correlation in our study. The largest islands studied were 16 and 24 ha, respectively. This may be below the lower limit of acceptable are for such species as Black Woodpecker (*Dryocopus martius*), Green Woodpecker (*Picus viridis*), Long-tailed Tit (*Aegithalos caudatus*), Willow Tit (*Parus montanus*), Crested Tit (*Parus cristatus*), Crossbill (*Loxia curvirostrata*), and Bullfinch (*Pyrrhula pyrrhula*) (Ahln & Nilsson 1982; Van Dorp & Opdam 1987). None of these species were recorded on any island in this study and their absence from small islands can therefore not give a negative correlation.

(2) It may be that the small islands on average are suitable for more bird species than are the large ones. In this context, "on average" has two different meanings. It means not only "the average small island" but also the "average habitat" in the islands. Suppose that a large island is composed of 10% border zone (habitable for many species) and 90% interior (habitable for a few species) and that a small island contains 50% of each

Table 4. Number of species in bird faunas that are pooled on basis of island size. The islands are ranked according to size and divided into groups with approximately the same size.

Size class	*1*	*2*	*3*	*4*
Ranked according to area				
Number of different islands	1	2	12	147
Observations (islands x years)	2	3	21	212
Total area	48.0	46.2	51.3	47.3
Largest island (ha)	24.0	16.2	7.6	1.0
Smallest island (ha)	24.0	15.0	1.2	.01
Number of observed species	50	59	73	77
Number of territorial species	23	30	36	36
Number of observations	3133	2812	3628	5435
Number of territories	467	348	484	597
Ranked according to number of observations				
Number of different islands	2	3	19	51
Observations (islands x years)	2	4	23	64*
Total number of observations	3225	3621	3410	3349
Largest island (ha)	24.0	24.0	16.2	2.0
Smallest island (ha)	15.0	7.6	.2	.04
Number of observed species	55	62	72	71
Ranked according to number of territories				
Number of different islands	1	2	16	75
Observations (islands x years)	2	4	25	118*
Total number of territories	467	463	474	464
Largest island (ha)	24.0	15.0	16.2	2.0
Smallest island (ha)	24.0	7.6	.3	.02
Number of territorial species	25	29	33	32

** To create equal-size groups we truncated the full set of islands for the last two groupings. Only 92 and 149, respectively, of the total 238 islands were used.*

habitat. Although both islands contain both habitats, the smaller island is on average (in the second sense) suitable for more species. When the lower total number of individuals is corrected for, the smaller island will be found to have relatively more species present. It seems that the high proportion of border zone may be a positive quality of the small islands. This may be true, but according to our results, it should not be the only explanation because the increase in species number with decreasing area was found employing a partial correlation analysis in which indirect habitat effects were canceled. Furthermore, if the border habitat is particularly favorable for some species, one would also expect an increase in species number with the development of the periphery, which was not found. It may also be that the nearby presence of open fields is favorable for several bird species.

(3) Lastly, intraspecific competition in small islands may increase species number above that expected by chance. The null hypothesis chosen here assumes that territories are sampled independently of each other. However if an island is smaller than two acceptable territories for a species, no more than one territory of this species may be present, leaving room for other species (assuming the total number of territories to be fixed). Note that an acceptable "apparent" territory may be smaller on a small island than on a large one because of the possible inclusion of surrounding fields. This is a possible explanation for the pattern found. It also fits the finding that the area effect was only found for territories, not for observations.

Area Effects—SLOSS

In equal-size samples of large and small islands, there were more species on the small islands. This was not a result of the smaller islands having higher overall densities.

Apart from points (1) and (2) above, a third consideration is relevant when explaining this pattern. It is likely that a large island contains more habitats than a small (as shown by Rafe et al. [1985] for English fauna reserves). However, it is quite conceivable that a number of small islands collectively would be more diverse and contain more biotopes than a few large islands. That such a pattern can have a positive effect on species number is clear, and was shown by a semiartificial method, by Boecklen (1986).

Island Isolation and Shape—Effects on Species Number

Although different measures have been employed, isolation has repeatedly been shown to affect bird species

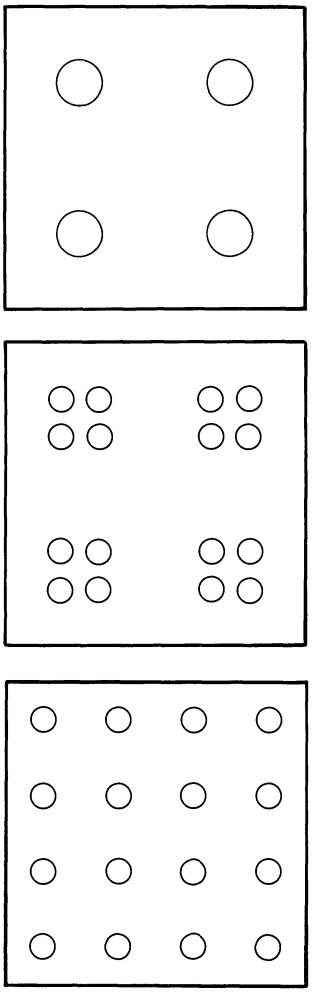

Figure 3. Three patterns of allocating a given area into habitat islands. The central pattern is that predicted to support the highest number of birds according to this study.

numbers on habitat islands (Howe et al. 1981; Cieślak 1985; Opdam 1984; Opdam et al. 1985; Van Dorp and Opdam 1987). No such effect could be found on the number of observed bird species in this study, where all effects of covariation between independent variables have been removed before testing the significance of the correlation.

Cieślak (1985) found an increase in species number on islands with a relatively long periphery (oblong islands and islands with a convoluted periphery). Neither of these patterns was confirmed in the present study.

Vegetation

Only one vegetation component affected relative species number — the amount of trees and bushes standing dead. This supports the findings of Nilsson (1979). The lack of other correlations is surprising. It should be stressed that our study refers to all bird species observed or territory mappable, respectively, with no habitat preference bias. This suggests that the local bird community is well-adapted to the habitat islands present; there is no habitat with particularly few species adapted to it.

Conservation Considerations

Fauna conservation has several different aims. The differences are mainly related to scale. If the main concern is to prevent species extinction on a global or regional scale, local measures should mainly be directed to protect and support globally and regionally rare species. In such cases the value of different habitat islands for conservational purposes can only be assessed after evaluating the different species involved. However, if a local scale is considered, a reasonable goal should be to maintain a high species diversity, with less emphasis on the identity of the different species.

The present study is relevant mainly from this local point of view. Due to the choice of study landscape, only small islands that are the typical result of the old human-caused fragmentation processes are studied. This is intentional — knowledge of how to manage these islands is important in a landscape where they represent the only remaining "natural" habitat.

With these points in mind we draw two conclusions for conservation in this landscape. First, very small habitat islands may, per area, be as valuable or even more valuable than medium-size islands. Also, there is no clear reason to discriminate between the islands on the basis of their vegetation. Protective measures should be directed to all habitat islands left in this landscape. However, the findings may be relevant to all landscapes characterized by the same sort of heterogeneity: habitat islands that contain some crucial resource for the organisms under consideration but that are surrounded by a matrix that is also productive for these organisms.

Acknowledgments

Help with field work came from Valde Holmgren, Anders Jonsson, Nils Kjelln, Jan-Ake Nilsson, Olof Persson and Henrik Smith. The presentation has been improved by comments from Olof Liberg and Thomas Madsen. The work has been financed by the National Swedish Environment Protection Board and the Swedish Council for Forestry and Agricultural Research. We thank them all.

Appendix 1A. Distribution of bird observations on islands of different size. Rel. is the number observe a percentage of the number expected. Expected is computed as (total number of species total number of area class/grand total). (This is the method used to obtain X-square expectancies.) The species have been ranked according to preference.

Number of islands:	*LARGE Above 10 ha* 5		*MEDIUM 1 to 10 ha* 21		*SMALL Below 1 ha* 212		
	Rel	*N*	*Rel*	*N*	*Rel*	*N*	*TOTAL*
Golden Oriole	251	*2*	0	*0*	0	*0*	2
Tawny Owl	251	*1*	0	*0*	0	*0*	1
Snipe	251	*11*	0	*0*	0	*0*	11
Redwing	251	*1*	0	*0*	0	*0*	1
Wryneck	251	*1*	0	*0*	0	*0*	1
Treecreeper	242	*26*	0	*0*	11	*1*	27
Wren	225	*35*	19	*2*	15	*2*	39
Rook	222	*30*	43	*4*	0	*0*	34
Fieldfare	218	*91*	49	*14*	0	*0*	105
Jackdaw	185	*90*	15	*5*	67	*27*	122
Kestrel	179	*5*	0	*0*	86	*2*	7
Blackcap	178	*171*	80	*52*	23	*18*	241
Icterine Warbler	177	*251*	91	*88*	15	*18*	357
Great Spotted Woodpecker	176	*7*	74	*2*	30	*1*	10
House Martin	171	*17*	89	*6*	24	*2*	25
Goldfinch	170	*19*	119	*9*	0	*0*	28
Meadow Pipit	161	*36*	92	*14*	32	*6*	56
Hawfinch	160	*14*	134	*8*	0	*0*	22
Robin	158	*117*	79	*40*	47	*29*	186
Goldcrest	153	*45*	110	*22*	29	*7*	74
Stock Dove	148	*43*	96	*19*	45	*11*	73
Starling	144	*229*	48	*52*	90	*119*	400
Blue Tit	140	*82*	90	*36*	60	*29*	147
Trush Nightingale	139	*474*	111	*257*	44	*124*	855
Nuthatch	134	*31*	134	*21*	31	*6*	58
Song Thrush	133	*173*	86	*76*	71	*77*	326
Great Tit	127	*194*	76	*79*	88	*112*	385
Chaffinch	119	*1109*	103	*651*	75	*586*	2346
Greenfinch	116	*341*	83	*165*	95	*232*	738
Blackbird	116	*351*	111	*229*	72	*181*	761
Buzzard	115	*17*	100	*10*	82	*10*	37
Whinchat	115	*34*	55	*11*	118	*29*	74
Redstart	105	*13*	60	*5*	127	*13*	31
Dunnock	102	*240*	109	*174*	90	*176*	590
Cuckoo	98	*25*	150	*26*	61	*13*	64
Pied Flycatcher	94	*44*	139	*44*	75	*29*	117
Willow Warbler	92	*387*	117	*335*	96	*335*	1057
Tree Pipit	87	*82*	151	*97*	75	*59*	238
Lesser Whitethroat	85	*25*	80	*16*	135	*33*	74
Garden Warbler	85	*215*	142	*245*	85	*179*	639
Marsh Harrier	84	*1*	123	*1*	101	*1*	3
Ortolan Bunting	84	*1*	0	*0*	201	*2*	3
White Wagtail	82	*43*	85	*30*	134	*58*	131
Sedge Warbler	82	*16*	143	*19*	86	*14*	49
Tree Sparrow	82	*96*	43	*34*	169	*165*	295
Wood Warbler	69	*9*	134	*12*	110	*12*	33
House Sparrow	67	*34*	61	*21*	171	*72*	127
Mallard	63	*79*	109	*93*	137	*142*	314
Goshawk	63	*2*	185	*4*	75	*2*	8
Wood Pigeon	62	*304*	89	*298*	155	*635*	1237
Willow Warbler	56	*2*	82	*2*	168	*5*	9
Pheasant	54	*44*	145	*80*	118	*80*	204
Marsh Warbler	54	*86*	83	*90*	170	*226*	402
Grasshopper Warbler	53	*4*	272	*14*	16	*1*	19
Marsh Tit	52	*8*	133	*14*	132	*17*	39
Teal	50	*1*	148	*2*	121	*2*	5
Reed Bunting	40	*46*	113	*88*	161	*153*	287
Shelduck	40	*7*	168	*20*	117	*17*	44
Siskin	40	*3*	194	*10*	95	*6*	19
Red-backed Shrike	36	*3*	53	*3*	216	*15*	21
Spotted Flycatcher	34	*8*	119	*19*	164	*32*	59
Crow	34	*13*	100	*26*	179	*57*	96
Reed Warbler	33	*5*	136	*14*	151	*19*	38
Magpie	33	*7*	21	*3*	246	*44*	54

Appendix 1A. Continued.

Number of islands:	LARGE Above 10 ha 5		MEDIUM 1 to 10 ha 21		SMALL Below 1 ha 212		
	Rel	N	Rel	N	Rel	N	TOTAL
Lapwing	29	5	60	7	218	31	43
Linnet	29	43	127	129	164	204	376
Whitethroat	25	36	52	51	229	272	359
Swallow	17	1	345	14	0	0	15
Moorhen	10	2	92	12	214	34	48
Yellow Wagtail	6	3	178	56	148	57	116
Jay	0	0	370	5	0	0	5
Pochard	0	0	370	3	0	0	3
Tufted duck	0	0	370	4	0	0	4
Common Sandpiper	0	0	370	3	0	0	3
River Warbler	0	0	370	1	0	0	1
Brambling	0	0	370	1	0	0	1
Grey Wagtail	0	0	370	3	0	0	3
Common Tern	0	0	317	12	43	2	14
Collares Dove	0	0	277	3	75	1	4
Grey Heron	0	0	225	14	118	9	23
Sand Martin	0	0	197	8	141	7	15
Coot	0	0	149	23	180	34	57
Mute Swan	0	0	92	2	226	6	8
Partridge	0	0	62	1	252	5	6
Yellowhammer	0	0	48	8	262	53	61
Wheater	0	0	32	2	276	21	23
Long-eared Owl	0	0	0	0	302	1	1
Oystercatcher	0	0	0	0	302	1	1
Ringed Plover	0	0	0	0	302	1	1
Corn Bunting	0	0	0	0	302	1	1
Hobby	0	0	0	0	302	2	2
Great Snipe	0	0	0	0	302	1	1

Appendix 1B. Distribution of bird territories on islands of different size. Rel. is the number of territories as percentage of the number expected. The data is and computed and ordered as in Table 5a.

Number of islands:	LARGE Above 10 ha 5		MEDIUM 1 to 10 ha 21		SMALL Below 1 ha 212		
	Rel	N	Rel	N	Rel	N	TOTAL
Redstart	230	4	0	0	0	0	4
Hawfinch	230	1	0	0	0	0	1
Treecreeper	230	2	0	0	0	0	2
Great Spotted Woodpecker	230	1	0	0	0	0	1
Wren	201	7	0	0	47	1	8
Goldcrest	184	8	67	2	0	0	10
Blackcap	169	28	62	7	30	3	38
Meadow Pipit	164	5	96	2	0	0	7
Robin	164	15	64	4	36	2	21
Icterine Warbler	162	57	91	22	9	2	81
Song Thrush	135	27	80	11	65	8	46
Whinchat	131	4	48	1	107	2	7
Blue Tit	123	8	89	4	75	3	15
Trush Nightingale	117	86	101	51	71	32	169
Spotted Flycatcher	115	1	167	1	0	0	2
Pied Flycatcher	115	6	167	6	0	0	12
Nuthatch	115	3	112	2	63	1	6
Great Tit	111	29	95	17	88	14	60
Willow Warbler	110	94	97	57	88	46	197
Chaffinch	108	165	95	99	92	86	350
Sedge Warbler	105	5	91	3	102	3	11
Blackbird	103	47	118	37	75	21	105
Dunnock	99	40	101	28	101	25	93
Greenfinch	95	40	97	28	112	29	97
Tree Pipit	83	14	146	17	77	8	39
Grasshopper Warbler	77	1	223	2	0	0	3
Cuckoo	66	2	191	4	54	1	7
Garden Warbler	66	38	133	53	119	42	133

Appendix 1B. Continued.

Lesser Whitethroat	63	*3*	122	*4*	137	*4*	11
Marsh Warbler	56	*24*	85	*25*	190	*50*	99
Linnet	53	*8*	143	*15*	129	*12*	35
White Wagtail	46	*2*	134	*4*	150	*4*	10
Reed Bunting	46	*6*	134	*12*	150	*12*	30
Reed Warbler	29	*1*	167	*4*	141	*3*	8
Whitethroat	24	*7*	40	*8*	291	*52*	67
Goldfinch	0	*0*	335	*1*	0	*0*	1
Yellow Wagtail	0	*0*	201	*9*	150	*6*	5
Wood Warbler	0	*0*	67	*1*	300	*4*	5
Yellowhammer	0	*0*	56	*1*	313	*5*	6
Marsh Tit	0	*0*	0	*0*	376	*2*	2
Total		*789*		*542*		*483*	1814

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