

DISPERSION AND ASSOCIATION OF SOME MARSHLAND-NESTING BIRDS: A MATTER OF SCALE

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Dispersion and association of five abundant passerine bird species (*Acrocephalus arundinaceus*, *A. schoenobaenus*, *A. scirpaceus*, *Locustella luscinioides* and *Emberiza schoenioides*) were studied in a marsh in Hungary, at 7 different levels of spatial scale. The index of dispersion (variance/mean) and Morisita's index gave very similar results for the dispersion of the species. The method block-quadrat variances revealed patterns on much higher scales, connected with the habitat. The Ochiai, Dice, and Jaccard indices, the chi-square test of association, and Kendall's rank correlation coefficient were applied for the measure of association between species. Results on dispersion and association showed a high order dependency on block size. Biological explanation of the results are also discussed.

1. INTRODUCTION

A considerable proportion of ornithological work has focused on the structure of avian communities, by examining several mechanisms like habitat selection, competition, and predation affecting the dispersion of bird populations (CODY 1985, see review in WIENS 1989), but papers on the analysis of spatial pattern are very scarce. Analysis of the spatial pattern of bird populations reveals how individuals are dispersed in space, brought about by mechanisms of intraspecific and interspecific interactions among populations (TAILOR & WORWOD 1982, SHERRY & HOLMES 1985). Interactions with the spatial pattern of habitat could also be in the centre of interest (SHAW & ATKINSON 1990, LÓRINCZ et al. 1990).

Dispersion of organisms in space and time is not only a population characteristic, it is in close connection with community structure. Spatial variation and changes of the patch structure in time can influence the community pattern in numerous ways (WIENS 1989), so dispersion can indicate environmental changes as well.

Ecological patterns suffer from scale dependency. Which is the right scale, how can we interpret our results on community characteristics? Is there any mathematical solution for the scale problem? As WIENS et al. (1987) and WIENS (1989) pointed out, the term "scale problem" covers effects of a wide variety of scales (biogeographical, regional, local, etc.). However, scale is not a property of the object being observed, but a property of the method of observation (ALLEN & STARR 1982). An accurate analysis of a bird community can be achieved by viewing the community at several levels of resolution (MAURER 1985).

Different levels of the local spatial scale are examined in this paper. We asked the following questions:

- How can we determine by simple spatial statistical tools the main characteristics of dispersion of some selected bird species?
- How consistent are the results in spatial pattern analysis obtained by different methods?

- Do dispersion characteristics of selected marshland passerines depend on spatial scale?
- Is there a consistency in the association of some bird species at different levels of spatial scale?
- Is it worth to apply statistical tools for examining spatial patterns when community characteristics are studied?

To answer these questions, we conducted a study in the marshland Kis-Balaton, in W. Hungary in two consecutive years during the breeding season. Although forested areas have been shown to be better for studies on the structure of avian communities (SHERRY & HOLMES 1985), this marshland provided some special advantages, like relatively long transect routes in a more or less homogenous habitat. Our study also revealed some ecological characteristics of certain abundant marshland-nesting migratory passerines.

2. STUDY AREA

The study was conducted in the marsh Kis-Balaton, which is situated around the mouth of the river Zala entering Lake Balaton, West Hungary (46°42' N, 17°21' E). The area is composed of the following plant associations: *Scirpo phragmitetum*, *Typhosum angustifolias*, *Caricetosum elatae*, *C. acutiformis*. Bushes and trees of *Salix alba* and *S. fragilis* were very scarce in the area. Bird surveys were carried out in reed belts (*Phragmitetum communis*) along the small dykes, forming a long continuous transect of circular shape.

3. METHODS

3.1. Bird censuses

Line transect surveys were carried out in May 1989 in the early hours under fine weather conditions. Field surveys were also carried out in 1990. We registered the distance of singing males, or observed specimens/pairs from the starting point of the transect measured in steps (one step was about 0.75 m). Lateral distances of birds from the survey route were also registered. Detections of singing birds dominated over visual observations. Single line transect surveys could not result in well-identified territories, so we examined the dispersion pattern of the location of individual male birds, rather than the dispersion of territories.

3.2. Data manipulation

For the statistical analysis of dispersion and association of bird species we divided the transect data into continuous blocks, and set up a distance limit of 50 m for the width of the transects. In order to study the effect of spatial scale on the results, 7 block sizes were applied: 25, 50, 100, 200, 300, 400, and 500 steps long blocks. Total length of transect was 18000 steps (about 13.5 km).

3.3. Statistical analyses

In vegetation research, plant ecologists generally apply the method quadrat-variance for the detection of dispersion of individuals of a species. The method of block-quadrat variances (BQV) is based on examining changes in the variance and the mean of the number of individuals at different block sizes, as the latter increases in powers of 2 (GREIG-SMITH 1983, KERSHAW & LOONEY 1985). We tried to apply this technique for bird data. Computations were carried out by the program BQV (LUDWIG & REYNOLDS 1988).

We measured the dispersion of the species by the index of dispersion (ID), which expresses the variance-to-mean ratio as a test for agreement with a Poisson model. This index is the most popular among the group of dispersion indices, because we can test it by *chi-square* test statistic, or for large sample size by the *d* statistic (ELLIOTT 1977). The program POISSON was used for computation of the index of dispersion (LUDWIG & REYNOLDS 1988).

Morisita's dispersion index (MORISITA 1971) was also applied to measure dispersion, using a program written by the first author.

Association of the species was measured by association indices (Ochiai, Dice and Jaccard), and by the chi-square statistic with help of the computer program SPASSOC (LUDWIG & REYNOLDS 1988). A rank correlation coefficient, Kendall's tau was also applied for the measurement of interspecific association (see e.g. SOKAL & ROHLF 1981). Rank correlations were computed by the statistical package SPSS/PC+ (NORUSIS 1986).

4. RESULTS

4.1. Bird species selected for analysis

During the transect surveys 24 passerine bird species were detected in 1989, and 18 in 1990. For statistical considerations we selected the five most abundant species for the calculation of spatial characteristics, namely the Great Reed Warbler (*Acrocephalus arundinaceus* L., 1758), the Sedge Warbler (*Acrocephalus schoenobaenus* L., 1758), the Reed Warbler (*Acrocephalus scirpaceus* (HERM.), 1804), Savi's Warbler (*Locustella luscinioides* (SAVI), 1824), and the Reed Bunting (*Emberiza schoeniclus* L., 1758). A total of 707 occurrences were registered for the selected five species, but only observations within a 50 m lateral distance were used for analyses (615 records). In more details, the data set composed of 16 and 26 records for the Great Reed Warbler, 105 and 83 for the Sedge Warbler, 57 and 76 for the Reed Warbler, 54 and 40 for the Reed Bunting, 80 and 78 for the Savi's Warbler in 1989 and 1990, respectively.

4.2. Dispersion patterns

4.2.1. Block-quadrat variance

The method is usually applied when no visual aggregation in the pattern is detected. Peaks in the graph of the variances plotted against the series of block sizes reveal the scale of pattern. For the Sedge Warbler, the Reed Warbler, the Reed Bunting, and Savi's Warbler the initial block size was 50 steps long. We did not calculate block-quadrat variances for the Great Reed Warbler because of insufficient data.

Each of the graph of block-quadrat variances show one or two peaks (Fig. 1), detecting some tendency for aggregation in dispersion. Each of the species show a peak in variance at block size 32 in 1989, although for Savi's Warbler it is not a primary peak. In 1990 two species also showed the peak at block size 32 (Reed Bunting and Savi's Warbler), but the peak was shifted to block size 16 for the Reed Warbler, and peaks were not so evident for the Sedge Warbler. Since the method of quadrat-variances uses block sizes increasing in powers of 2, the result may be somewhat different from the exact scale. For example, for the Sedge Warbler the BQV method showed a peak at 1600

1989

1990

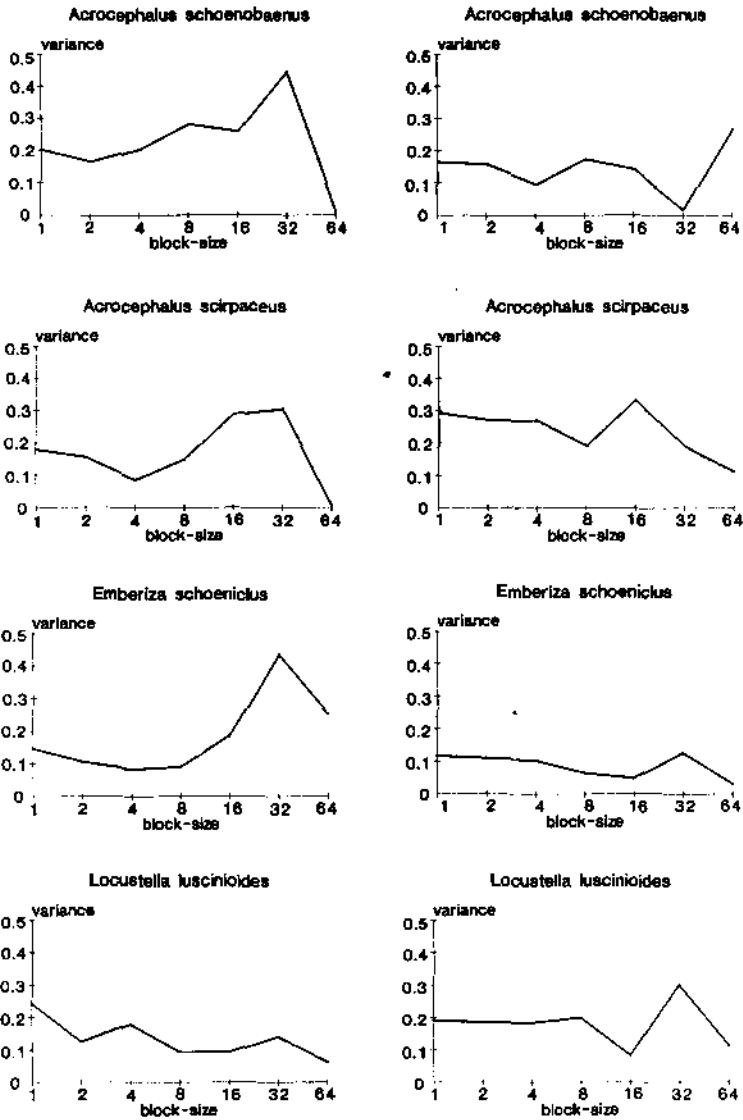


Fig. 1. Plots of variances against block size for the Sedge Warbler (*Acrocephalus schoenobaenus*), Reed Warbler (*A. scirpaceus*), Reed Bunting (*Emberiza schoeniclus*), and Savi's Warbler (*Locustella luscinioides*) in the marsh Kis-Balaton, W. Hungary in 1989 and 1990. (block width = 50 m, block size 1 = 50 steps, 1 step = ca. 0.75 m).

steps, but a more precise estimation by Hill's two-term local quadrat variance method (HILL, 1973) revealed 1900 steps.

Two interesting conclusions may be drawn from the quadrat-variance analyses: (1) there are tendencies for clumping in each of the species analyzed by the BQV technique at least in one of the years, and (2) the block size of clumping seems to be very large. (See more below.)

Table 1

Dispersion types of five abundant passerine bird species based on index of dispersion in the marsh Kis-Balaton in 1989

(U = uniform, R = random, C = clumped pattern)

Species	Block length (steps)						
	25	50	100	200	300	400	500
<i>Acrocephalus arundinaceus</i>	C, R	C	C	C	C	C	C
<i>Acrocephalus schoenobaenus</i>	U	U	R	R	R	R	R
<i>Acrocephalus scirpaceus</i>	R	R	R	R	R	R	R
<i>Emberiza schoeniclus</i>	R	R	U	R	R	R	R
<i>Locustella luscinioides</i>	R	U	U	U	U	U	U

4.2.2. Dispersion indices

The results of computation of the dispersion index (ID) can be consulted in Tables 1 and 2, and the results of Morisita's index in Tables 3 and 4. Although these indices belong to two basically different groups, the results are very similar. For the Great Reed Warbler both of them revealed a clumped pattern in all of the block sizes in 1989, and for Savi's Warbler both of them mostly revealed uniform pattern. For the other three species (Sedge Warbler, Reed Warbler, and Reed Bunting) there is a tendency for showing a random pattern at larger block sizes.

Table 2

Dispersion types of five abundant passerine bird species based on index of dispersion in the marsh Kis-Balaton in 1990

(U = uniform, R = random, C = clumped pattern)

Species	Block length (steps)						
	25	50	100	200	300	400	500
<i>Acrocephalus arundinaceus</i>	R	R	R	R	R	R	R
<i>Acrocephalus schoenobaenus</i>	R	U	R	R	R	R	R
<i>Acrocephalus scirpaceus</i>	R	R	R	R	R	R	R
<i>Emberiza schoeniclus</i>	C	C, R	R	R	R	R	R
<i>Locustella luscinioides</i>	U	U	U	U	U	U	U

Table 3

Dispersion types of five abundant passerine bird species based on Morisita's index in the marsh Kis-Balaton in 1989

(U = uniform, R = random, C = clumped pattern)

Species	Block length (steps)						
	25	50	100	200	300	400	500
<i>Acrocephalus arundinaceus</i>	C, R	C	C	C	C	C	C
<i>Acrocephalus schoenobaenus</i>	U	U	R	R	C	R	R
<i>Acrocephalus scirpaceus</i>	R	R	R	R	R	R	R
<i>Emberiza schoeniclus</i>	R	R	U	R	R	R	R
<i>Locustella luscinioides</i>	R	U	U	U	U	U	U

Table 4

Dispersion types of five abundant passerine bird species based on Morisita's index in the marsh Kis-Balaton in 1990

(U = uniform, R = random, C = clumped pattern)

Species	Block length (steps)						
	25	50	100	200	300	400	500
<i>Acrocephalus arundinaceus</i>	C	C	R	R	R	R	R
<i>Acrocephalus schoenobaenus</i>	R	U	R	R	R	R	R
<i>Acrocephalus scirpaceus</i>	C	R	R	R	R	R	R
<i>Emberiza schoeniclus</i>	C	C	R	R	C	R	R
<i>Locustella luscinioides</i>	R	U	C	U	U	R	U

The dispersion index (ID) and the Morisita's index of dispersion did not reveal any important tendencies for clumping in the four species analyzed by the BQV method. The scale of clumping for these species revealed by the BQV method (see above) is out of the range chosen for these indices. The limit in block size for these indices was chosen to be 500 steps, but with the BQV method we analyzed variances of blocks up to 3200-step long. We obtained similar results for the interval uncommon.

4.3. Association of individual bird species

4.3.1. Association indices

LUDWIG & REYNOLDS (1988) recommended the Ochiai, Dice, and Jaccard indices to measure interspecific association. These indices are relatively simple ones, easy to use and to understand the rationale underlying them, they use binary (presence/absence) data. Furthermore, their favourable properties have been proven by extensive tests. The three indices applied for Kis-Balaton data

revealed nearly the same associations between species, but the indices Ochiai and Dice gave somewhat higher values than the Jaccard index did (Fig. 2). Values of each of these indices showed an increasing tendency in relation to increasing block size. For the sake of simplicity only the values of the Jaccard index are presented for all pairs of species and for all block sizes (Tables 5 and 6).

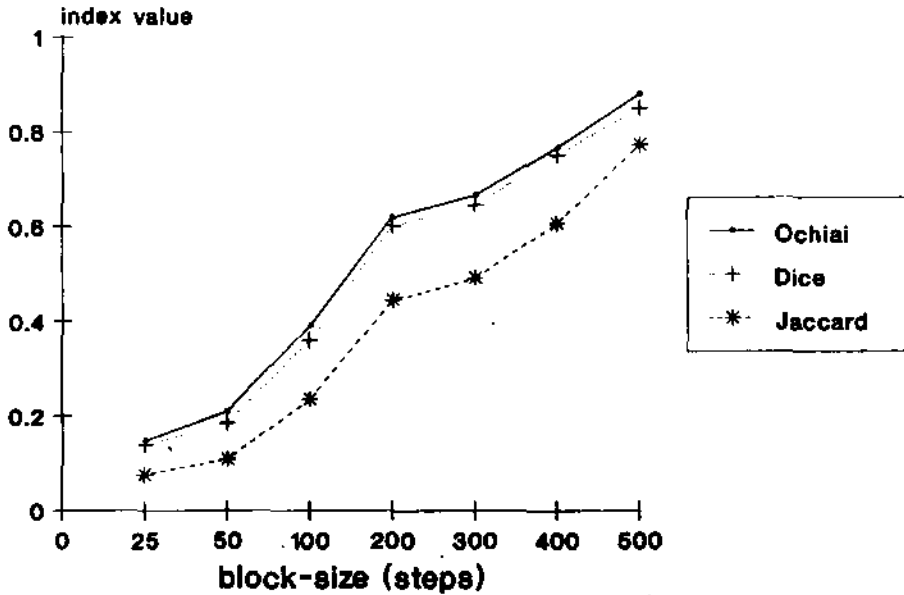


Fig. 2. Behaviour of 3 association indices, Ochiai, Dice, and Jaccard, demonstrated using the Sedge Warbler - Reed Bunting data from 1989.

Table 5

Values of the Jaccard index for pairs of bird species in the marsh Kis-Balaton in 1989 (abbreviations of genera: A. = *Acrocephalus*, E. = *Emberiza*, L. = *Locustella*)

Pairs of species	Block length (steps)							
	25	50	100	200	300	400	500	
A. arundinaceus - A. schoenobaenus	0.00	0.03	0.04	0.10	0.13	0.18	0.27	
A. arundinaceus - A. scirpaceus	0.00	0.02	0.07	0.10	0.16	0.23	0.33	
A. arundinaceus - E. schoeniclus	0.00	0.00	0.05	0.12	0.16	0.19	0.23	
A. arundinaceus - L. luscinioides	0.01	0.01	0.01	0.06	0.07	0.14	0.24	
A. schoenobaenus - A. scirpaceus	0.04	0.08	0.15	0.35	0.44	0.51	0.67	
A. schoenobaenus - E. schoeniclus	0.08	0.11	0.24	0.44	0.49	0.61	0.77	
A. schoenobaenus - L. luscinioides	0.09	0.14	0.28	0.48	0.66	0.78	0.83	
A. scirpaceus - E. schoeniclus	0.03	0.08	0.15	0.28	0.41	0.48	0.65	
A. scirpaceus - L. luscinioides	0.02	0.06	0.19	0.36	0.51	0.59	0.71	
E. schoeniclus - L. luscinioides	0.08	0.11	0.20	0.42	0.51	0.58	0.72	

Table 6

Values of the Jaccard index for pairs of bird species in the marsh Kis-Balaton in 1990
(abbreviations of genera: A. = Acrocephalus, E. = Emberiza, L. = Locustella)

Pairs of species		Block length (steps)						
		25	50	100	200	300	400	500
A. arundinaceus	— A. schoenobaenus	0.02	0.06	0.12	0.19	0.27	0.36	0.44
A. arundinaceus	— A. scirpaceus	0.04	0.08	0.14	0.23	0.28	0.34	0.34
A. arundinaceus	— E. schoeniclus	0.03	0.03	0.09	0.15	0.18	0.34	0.38
A. arundinaceus	— L. luscinioides	0.03	0.12	0.13	0.22	0.33	0.42	0.44
A. schoenobaenus	— A. scirpaceus	0.03	0.08	0.16	0.33	0.45	0.53	0.62
A. schoenobaenus	— E. schoeniclus	0.04	0.11	0.19	0.40	0.48	0.70	0.68
A. schoenobaenus	— L. luscinioides	0.05	0.09	0.23	0.49	0.62	0.68	0.87
A. scirpaceus	— E. schoeniclus	0.00	0.02	0.07	0.20	0.31	0.51	0.59
A. scirpaceus	— L. luscinioides	0.06	0.12	0.20	0.40	0.55	0.62	0.70
E. schoeniclus	— L. luscinioides	0.09	0.10	0.16	0.31	0.40	0.53	0.62

4.3.2. Chi-square test of association

Chi-square test of association has also been applied for binary data. Only few of the chi-square values proved to be significant at the 5% probability level (Tables 7 and 8), which means that the two species in question are associated. Although there are several changes in the sign and value of the

Table 7

Values of the chi-square statistic for associations of pairs of bird species in the marsh Kis-Balaton in 1989 (abbreviation of species: A. aru = Acrocephalus arundinaceus, A. sch. = Acrocephalus schoenobaenus, A. sci. = Acrocephalus scirpaceus, E. sch. = Emberiza schoeniclus, L. lus. = Locustella luscinioides) (When chi-square value > 3.84 reject the hypothesis that the two species are independent; * = biased, chi-square values are considered biased if the expected frequency of any cell in a 2x2 table < 1 and/or the expected frequencies of more than 2 cells < 5 following ZAR (1984))

Pairs of species	Association (— or +) and block length (steps)						
	25	50	100	200	300	400	500
A. aru. — A. sch.	-2.59	-0.15	-0.92	-0.42	-0.01	+0.01*	+1.09*
A. aru. — A. sci.	-1.29	-0.60	+0.20	-0.06	+0.87*	+2.26	+4.00
A. aru. — E. sch.	-1.24	-2.33	-0.10	+0.16	+0.87*	+0.30	-0.06
A. aru. — L. lus.	-0.29	-1.60	-6.41	-5.66	-7.39	-3.12*	-0.12*
A. sch. — A. sci.	-0.68	-1.96	-4.46	-0.67	-2.62	-3.82*	-1.09*
A. sch. — E. sch.	+1.66	+0.01	+0.33	+1.88	-0.14	+0.00*	+0.40*
A. sch. — L. lus.	+1.48	+0.00	-0.18	-0.09	-0.08	-0.68*	-0.30*
A. sci. — E. sch.	-0.40	-0.00	-0.28	-1.12	-0.10	-0.05	+0.06
A. sci. — L. lus.	-1.96	-3.22	-0.31	-0.68	-0.50	-0.21*	+0.12*
E. sch. — L. lus.	+3.40	+0.24	-0.03	+0.28	-0.50	-2.20*	-0.79*

Table 8

Values of the *chi*-square statistic for associations of pairs of bird species in the marsh Kis-Balaton in 1990 (abbreviation of species: A. aru. = *Acrocephalus arundinaceus*, A. sch. = *Acrocephalus schoenobaenus*, A. sci. = *Acrocephalus scirpaceus*, E. sch. = *Emberiza schoeniclus*, L. lus. = *Locustella luscinioides*) (When *chi*-square value > 3.84 reject the hypothesis that the two species are independent; * = biased, *chi*-square values are considered biased if the expected frequency of any cell in a 2 × 2 table < 1 and/or the expected frequencies of more than 2 cells < 5 following ZAR (1984))

Pairs of species	Association (— or +) and block length (steps)						
	25	50	100	200	300	400	500
A. aru. — A. sch.	-0.26	+0.06	+0.13	-0.11	-0.07	+0.00*	+0.61*
A. aru. — A. sci.	+1.26	+1.60	+1.20	+1.04	+0.18	+0.06	-0.26
A. aru. — E. sch.	+0.45	-0.11	+0.05	-0.09	-0.50	+0.30	+0.19
A. aru. — L. lus.	+0.04	+8.51	+0.66	+0.24	+1.37	+2.01*	+0.78*
A. sch. — A. sci.	-0.97	-1.12	-2.57	-4.31	-4.24	-4.09	-1.66*
A. sch. — E. sch.	+0.31	+2.08	+1.50	+4.93	+4.46	+9.88*	+3.13*
A. sch. — L. lus.	-0.28	-0.96	-0.03	+0.00	-0.46	-1.69	-0.13*
A. sci. — E. sch.	-3.92	-4.07	-4.76	-2.56	-0.58	+0.18	+1.33
A. sci. — L. lus.	+0.13	+0.25	-0.10	-0.14	-0.03	-0.01*	-0.38*
E. sch. — L. lus.	+8.20	+1.44	+0.21	+0.01	+0.02	-0.33*	-0.56*

chi-squares between pairs of species along the quadrat series, this technique gives relatively stable results for the significant species considering all of the scales together (Fig. 3) (see also the next paragraph).

4.3.3. Rank correlation

Kendall's rank correlation provides a robust test of association. Although it does not need simplified binary data, this test is based on the rank order of data elements, not on the values of data. Tables 9 and 10 represent the significant associations between species according to Kendall's rank correlation. There is considerable concordance of Kendall's taus with the associations revealed by the *chi*-square tests. Significant associations revealed by rank correlation seem to be fluctuating along the block size series: some of the associations are not apparent at certain levels, but there is no contradiction among the results (Tables 9 and 10, Fig. 4). Most of the associations apparent at a given block size can be revealed by choosing a not so rigorous significance level.

5. DISCUSSION

5.1. Dispersion types of marshland passerines. A question of technique

We studied the spatial pattern of five abundant passerine birds (Great Reed Warbler, Sedge Warbler, Reed Warbler, Reed Bunting, and Savi's Warbler) in the marsh Kis-Balaton. Several methods were applied for the detection of dispersion type and association between species.

Table 9

Values of Kendall's rank correlation coefficient computed for five passerine bird species in the Kis-Balaton in 1989 (only significant correlations are shown at the probability level <5%) (scale refers to block length measured in steps; 1 step = 0.75 m)

Block-size	Species		Kendall's tau	Significance	n
25	E. schoeniclus	— L. luscinioides	0.068	0.033	720
50	A. scirpaceus	— L. luscinioides	-0.092	0.040	360
100	A. arundinaceus	— L. luscinioides	-0.187	0.006	180
100	A. schoenobaenus	— A. scirpaceus	-0.159	0.012	180
200	A. arundinaceus	— L. luscinioides	-0.265	0.004	90
200	A. schoenobaenus	— E. schoeniclus	0.190	0.021	90
200	A. schoenobaenus	— A. scirpaceus	-0.202	0.015	90
300	A. arundinaceus	— L. luscinioides	-0.316	0.004	60
300	A. schoenobaenus	— E. schoeniclus	0.199	0.034	60
300	A. schoenobaenus	— A. scirpaceus	-0.379	0.000	60
400	A. arundinaceus	— L. luscinioides	-0.380	0.002	45
400	A. schoenobaenus	— E. schoeniclus	0.206	0.047	45
400	A. schoenobaenus	— A. scirpaceus	-0.324	0.004	45
500	A. arundinaceus	— L. luscinioides	-0.441	0.002	36
500	A. schoenobaenus	— A. scirpaceus	-0.493	0.000	36

Table 10

Values of Kendall's rank correlation coefficient computed for five passerine bird species in the Kis-Balaton in 1990 (only significant correlations are shown at the probability level <5%) (scale refers to block length measured in steps; 1 step = 0.75 m)

Block-size	Species		Kendall's tau	Significance	n
25	E. schoeniclus	— L. luscinioides	0.104	0.002	754
25	A. scirpaceus	— E. schoeniclus	-0.072	0.024	754
50	A. arundinaceus	— L. luscinioides	0.148	0.002	377
50	A. scirpaceus	— E. schoeniclus	-0.104	0.021	377
100	A. scirpaceus	— E. schoeniclus	-0.166	0.009	188
200	A. schoenobaenus	— E. schoeniclus	0.187	0.025	94
200	A. scirpaceus	— E. schoeniclus	-0.183	0.027	94
300	—	—	—	—	62
400	A. schoenobaenus	— E. schoeniclus	0.368	0.002	47
400	A. schoenobaenus	— A. scirpaceus	-0.342	0.002	47
500	A. schoenobaenus	— E. schoeniclus	0.310	0.012	37
500	A. schoenobaenus	— A. scirpaceus	-0.279	0.018	37

The method of block quadrat variance revealed the spatial scale of clumping. The block size of clumping was 32 for nearly all of the cases (3200 steps, ca. 2400 m). This value is larger than the average territory size of these species (HUT, 1986), and is possibly connected with habitat structure. In the same study area habitat preferences of passerines were analyzed by the GIS technique (LŐRINCZ et al., 1990). Three main types of vegetation were identified: homogenous reed patch, edge or patch of woody vegetation, and the ecoton of the two former types. This study applied 300 step long blocks of sampling units.

The index of dispersion (ID) and Morisita's index revealed a very similar pattern of dispersion for the five bird species. Although these results show small variations according to block size, they seem to be stable. SHERRY & HOLMES (1985) examined the dispersion of 7 forest passerine birds by the Lloyd's and Morisita's indices, and showed their consistency within a quadrat size.

What are the dispersion types of the bird species studied? Although each of the three basic dispersion types (uniform, random, and clumped) were detected to some extent, we have to punctuate the question. We have to define the circumstances more precisely.

The different methods revealed different aspects of spatial pattern of species. The index of dispersion is applicable for assessing the agreement of the data to the Poisson series. ID has limitations in measuring the degree of clumping, because it is strongly influenced by sample size (ELLIOTT, 1977). Morisita's index is relatively independent of mean density, it is a measure of the departure from randomness based on Simpson's diversity. A number of tests and measures of departure from random expectation are available, but their measures of non-randomness have special characteristics, so they can be considered as relative values (GREIG-Smith, 1983).

All of the results seem to be scale-dependent. For the passerine birds in Kis-Balaton LŐRINCZ et al. (1990) applied the dispersion index proposed by JOHNSON & ZIMMER (1985). It is based on individual-to-nearest-individual distances, so this technique is independent of scale problem. However, the dispersion index of JOHNSON & ZIMMER showed a clear tendency for detecting clumped pattern. According to LŐRINCZ et al. (1990) this distance index applied for all transects revealed only clumped patterns for the same five species analyzed in the present study, but uniform (regular), and random types also occurred in the original transects. Detailed tests and comparisons of dispersion indices based either on blocked or distance data are badly needed, because of the lack of well-defined recipes for field-work and analysis in ornithology. Spatial pattern is an important characteristic of populations, first of all in the landscape ecological viewpoint.

5.2. Interspecific association of abundant bird species

An easy way for the evaluating of interspecific association is the application of association indices. The Jaccard index revealed close associations between the following pairs of species: Sedge Warbler-Reed Bunting, Sedge Warbler-Savi's Warbler, and Reed Bunting-Savi's Warbler, i.e. all possible combinations of these 3 species. The main problem with association indices like the Ochiai, Dice, and Jaccard-index is that there is no way for testing their significance. As their values increase with block size, they can be considered as relative values. *Chi*-square tests of association gave instable results in relation to block size, but the values of Kendall's tau seem to be more stable. From the results gained in different block sizes we constructed the overall plexus-graphs of the five species (Figs 3 and 4), which demonstrate both the positive and negative relationships between species. No contradictions were found in the results, so we can recommend its usage.

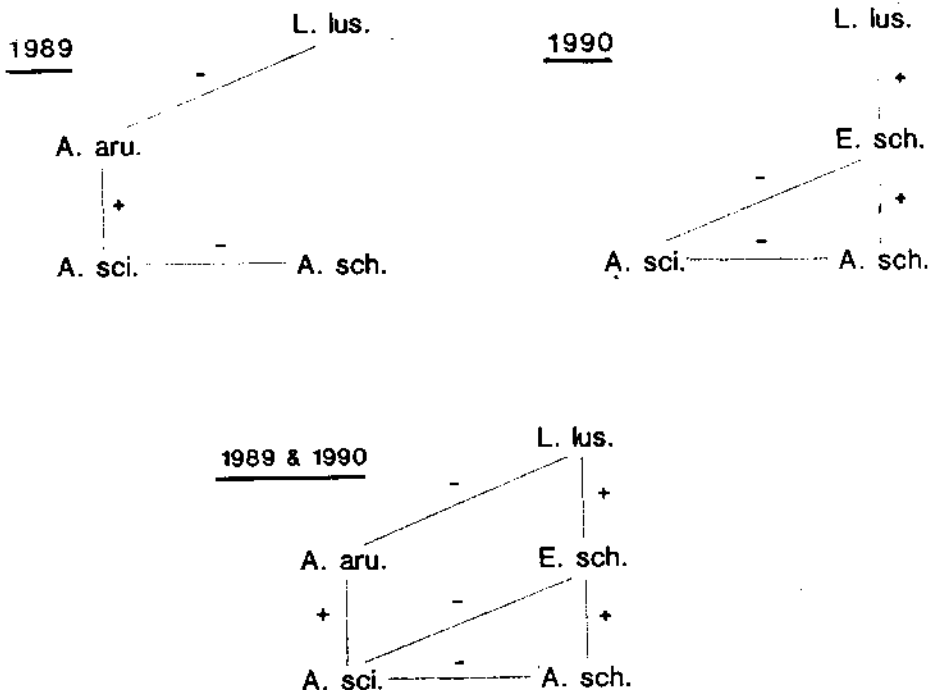


Fig. 3. Associations of five bird species obtained by the *chi*-square test of association. Results at the 7 different spatial scales (block sizes from 50 steps to 500 steps) were pooled into one figure per year, moreover the results from the two years were also pooled to demonstrate the overall association structure. (*A. aru.* = *Acrocephalus arundinaceus*, *A. sch.* = *Acrocephalus schoenobaenus*, *A. sci.* = *Acrocephalus scirpaceus*, *L. lus.* = *Locustella luscinioides*, *E. sch.* = *Emberiza schoeniclus*).

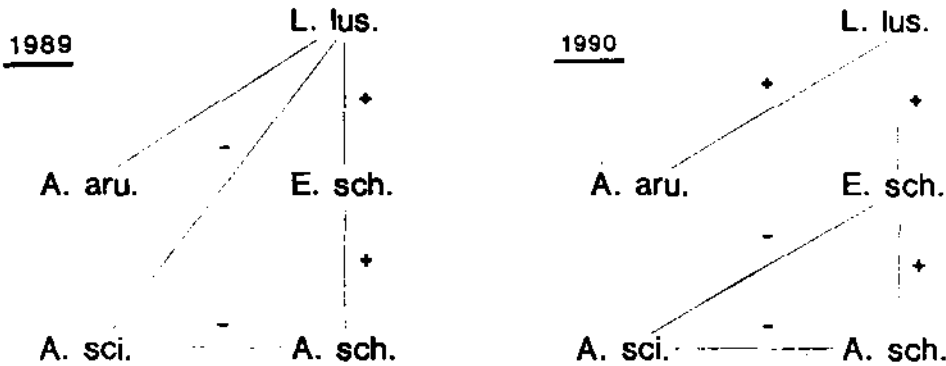


Fig. 4. Associations of five bird species based on the significance of the Kendall's rank correlation coefficient at 5% probability level. Results at the 7 different spatial scales (block sizes from 50 steps to 500 steps) were pooled into one figure per year, to demonstrate the overall association structure. (A. aru. = *Acrocephalus arundinaceus*, A. sch. = *Acrocephalus schoenobaenus*, A. sci. = *Acrocephalus scirpaceus*, L. lus. = *Locustella luscinioides*, E. sch. = *Emberiza schoeniclus*).

Kendall's rank correlation revealed a significant positive association between the Sedge Warbler and the Reed Bunting. This association is likely to be produced by their similarities in habitat preference, because the block-quadrat variance analysis revealed the same spatial scale of clumping for both of these species in 1989 (block size: 32), but in 1990 this similarity was not so evident. The Reed Warbler also showed the highest variance at block size 32, but its relationship was negative with both of these two species.

5.3. Biological aspects versus mathematical solution for the scale problem

Spatial scale affects the distributional pattern of organisms. On a sufficiently large scale, many animals tend to be aggregated (TAYLOR et al., 1978, TAYLOR & WOJWOD, 1982). SHERRY & HOLMES (1985) found that dispersion patterns of several forest bird species changed with the size of the area analyzed. These changes were the consequences of both interspecific and intraspecific social interactions and fine-scale habitat patchiness. For all species we also found that the dispersion detected by dispersion indices is highly scale-dependent: the dispersion of individuals show a uniform (regular) or a random pattern on a small scale, but aggregation peaks occur at the higher scales. This is more a property of the habitat than the species itself. If the scale analyzed exceeds greatly the extent of the habitat patches, the individuals will tend to be gathered in the habitats most suitable for them for feeding and nesting. Within each habitat patch territoriality will lead to a more uniform dispersion of pairs.

The same applies to association indices, too. Species with similar habitat affinities show a tendency to occur together when other habitat patches are considered at a greater scale. In our study the Sedge Warbler, Savi's Warbler and the Reed Bunting are such species. According to the results of HUT (1986), these species show a marked overlap in their habitat choice. There are generic differences in their morphologies, however, which enable them to utilize different resources where they co-occur. On the other hand, species with high morphological similarity differ in their habitat selection. LEISLER analyzed the foot morphology of Central European *Acrocephalus* and *Locustella* species and stated that the Reed and the Great Reed Warblers are well adapted for clinging to vertical stems, but the Sedge Warbler is well adapted for more heterogenous vegetation structure. Although the foot of Savi's Warbler is adapted for walking, its long hind toe and large claws provide high clinging ability for climbing vertical stems when choosing song perches (LEISLER, 1975). Multivariate analysis of habitat separation in Central European *Acrocephalus* species revealed greater similarity of habitat occupancy between the Reed and the Great Reed Warblers than between the Sedge and the Reed Warblers. The latter two species were separated by the presence or the absence of a dense vegetation layer between 1 and 2 m, while the former pair of species are separated by different densities of the lowest vegetation layers and by differences in vegetation height (LEISLER, 1981). SVENSSON (1978) reported the territorial exclusion of the Sedge Warblers by the Reed Warbler. Dissimilarities in habitat occupancy and a possible background process (territorial exclusion) are reflected by the high negative association between the Reed and the Sedge Warblers revealed by the present study.

At the population scale we have two species, which seem to be scale-independent in their dispersion. For Savi's Warbler in the blocks of up to 500 steps length the dispersion of individuals is uniform. This suggests that this species is highly territorial and very aggressive intraspecifically. The other species, the Great Reed Warbler shows the opposite in dispersion type. The males were clumped at every scale in the 1989 analysis. This can be explained in several ways. One can hypothesize that (1) the food resource they utilize is either very abundant or unpredictable in time so that they are not worth to be defended. Another possibility that (2) the microhabitat suitable for nesting is so rare that individuals are forced to breed in close proximity and forage to higher distances. Which explanation is closer to reality cannot be decided because of the small number of individuals recorded in this year (16 singing males within the belt of 50 m lateral width), as the Great Reed Warbler was the least abundant species among the five species selected for analysis. In 1990, when more birds were counted (26), the pattern disappeared when the dispersion index (ID) was used. The second hypothesis seems to be supported by Csörcső (1983) in some marshes in Hungary. He frequently observed Great

Reed Warblers feeding in the reed far from their nests. Nests of the birds were found close to the reed/water edge. KOSTYRKO (1989) studied the habitat selection of *Acrocephalus* and *Locustella* species on small lakes in the surroundings of Posnan, and stated that the Great Reed Warbler was specialized in habitat selection with respect to vegetation structure. The Great Reed Warblers nested in littoral reeds close to water. A similar result was obtained by LEISLER (1981): principal component and discriminant analyses of six *Acrocephalus* species in Central Europe revealed that the Great Reed Warbler inhabit the extreme edge of a marshland habitat gradient.

Although statistical techniques are effective tools in the study of scale problems, they have limitations. We can ask if all of the scales having biological importance could be determined by statistical analyses, or all of the scales revealed have any biological meaning? Most of the results gained in the present study showed great agreement with the statistical and biological aspects, but further research in the methodology of spatial pattern analysis for birds is badly needed.

5.4. Methodological conclusions

We can recommend the parallel use of some alternative techniques both for the characterization of spatial pattern and to reveal interspecific associations. All of the dispersion and association indices (index of dispersion, Morisita's dispersion index, Ochiai, Dice and Jaccard indices of association), and the *chi*-square test of association are powerful tools for detecting patterns. All the methods applied proved to be scale-dependent, so the application of different scales (block sizes) is desirable. The method of block-quadrat variances (BQV), generally applied in vegetation research, is also applicable for bird data. While dispersion and association indices work at the territorial or on somewhat greater fine scales, the method BQV is applicable for the detection of larger, habitat-type scales.

A c k n o w l e d g e m e n t s

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