
EKOLOGIA POLSKA - SERIA A

Tom XV

Warszawa 1967

Nr 33

Aleksander WASILEWSKI

THE EFFECT OF INTERSPECIFIC COMPETITION
ON THE NUMBER AND DISTRIBUTION OF BIRDS
IN FOREST BIOTOPES*

In a number of forest biotopes an estimation was carried out of the distribution, abundance dynamics, overlapping of territories of various bird species, as well as of the interactions between species of a community. The interspecific competition has been found to have a significant influence on the numbers and the distribution of birds, its intensity being modified by the environmental conditions. In the community, groups of species have been distinguished with strong competitive interrelations between them. They were given the term of competitive associations. Within the competitive associations a quantitative compensation was found, that is, a stability of numbers in the association, in comparison with the great variability of the abundance of the different components of the association in the successive years during the research.

Contents

1. Introduction
 - 1.1. Purpose and object of study
 - 1.2. Study area and methods
2. Distribution (habitat preference) of individual species, number of individuals in the community and quantitative relations within the community
3. Interspecific competition in a community
 - 3.1. Interactions between species in a community and the method used for studying them
 - 3.2. The effect of interspecific competition on the numbers and on the quantitative relations of the community
 - 3.3. Interspecific competition and the species distribution in the habitat
 - 3.4. The structure of competitive interrelations in a community -- competitive associations
 - 3.5. Quantitative compensation in a competitive association
4. Summary and conclusions

*From the Institute of Ecology, Polish Academy of Sciences, Warszawa.

1. INTRODUCTION

1.1. Purpose and object of study

The aim of the present study is to appraise the extent to which interspecific competition affects the distribution and the number of birds in a community. Competition, as understood by the author, is the interrelations between species of the same trophic level, which lead to the restriction of either the numbers or the territory occupied by the species in the given habitat. The object of study was mainly the small passerine birds found in the forests of the reserve Sieraków near Warsaw. The research was carried out in the years 1960–1963.

In the ecological literature an extensive factual and theoretical material, collected under experimental and field conditions can be found concerning the interspecific competition. There still are, however, many controversial views as to the role interspecific competition plays in natural biocenoses. The problem of interspecific competition is primarily considered in two groups of ornithological studies. The first of these concerns direct facts: antagonistic interactions between species, which often lead to the elimination of individuals of one species from territories occupied by individuals of another species. Although this kind of interactions between species is rather common (numerous data from the literature are quoted in Chapter 3), most authors do not attach much importance to the role of this phenomenon in bird communities. The second group is represented by numerous papers in which the problem of ecological or geographical isolation of closely related species groups is considered. Various forms of isolation are taken into account: geographical isolation (Mayr 1942, Lack 1947), biotopic isolation (Lack 1944, 1947, Moreau 1948), stratum or food isolation within the same biotope (Hartley 1953, 1954, Gibb 1954, Betts 1955, Pielowski 1961a, 1961b).

In general, most authors agree that competition plays some role in the speciation process and in the formation of various kinds of ecological isolation in birds. Ecological isolation is regarded as an adaptation for decreasing the reciprocal competitive pressure by differentiating the ecological niches of the species and thereby losing the reciprocal ecological contact (Hamilton 1962).

The above studies do not explain the actual action of competition, and many authors regard it as a historical process. This view is represented by Udvardy (1951), who thinks that competition is now of no importance in natural multispecies bird communities except hollow nesters. A similar view is held by Bodenheimer (1955) in his studies comprising a wider range of animal groups.

The various interpretation of data obtained in the above two groups of studies results from the fact that it is difficult to simultaneously relate the

information about the interactions of individual species (studies of the first group) to the effects of these interactions upon the distribution and the abundance dynamics of the species (studies of the second group). There are relatively few papers dealing with both these elements simultaneously. The relevant ornithological literature includes studies by following authors: Michelson (1958), Eliseeva (1960), Tompa (1964); among studies dealing with other animal groups – those by Kaczmarek (1953, 1963) should be mentioned, concerned with forest ant associations (1953) and with the soil macrofauna (1963).

Hence the analysis, described in the present study, of the importance of interspecific competition in bird communities has been based on the widest possible range of data concerning habitat preference, distribution, abundance dynamics of individual species, the relationships between the numbers of a population and territorial phenomena, as well as the interactions between the different species.

1.2. Study area and methods

The analysis of the competitive interrelations has been restricted to one bird community. Accordingly, as a study area a habitat was chosen where the range of variation did not prevent the occurrence of the system of species representing the community. At the same time, it was necessary, however, that the variation should involve the basic features of the habitat, affecting the quantitative relations of the community, with the remaining factors retaining a relative homogeneity.

These conditions can be found in the vast, wooded, marsh areas situated between dune ranges within the reserve Sieraków in the Kampinos Forests near Warsaw.

In the study area, comprising a total acreage of about 375 ha, the following plant associations were found:

1. *Carici elongatae-Alnetum* (Tx. et Bod. 1955),
2. *Pino-Quercetum* (Kozłowska 1925),
3. *Tilio-Carpinetum* (Traczyk 1962),
4. *Circaeo-Alnetum* (Oberdorfer 1953).

As regards the area it occupies, *Carici elongatae-Alnetum*, covering the lowest marshes, is the dominant association. The remaining three associations, defined as mixed woods are connected with dispersed islands of drier elevations above the ground water horizon. The highest of the elevated islands, or the highest portions of these, are covered by *Pino-Quercetum* association, whereas their slopes by the *Tilio-Carpinetum* association. The *Circaeo-Alnetum* association is found in areas between the swamps and the islands of drier, sandy elevations, or on those of these islands which are only slightly elevated. On some of the elevated islands three associations occur simultaneously.

In the *Carici elongatae-Alnetum* the tree-stand is made up of the alder (*Alnus glutinosa*¹) with an admixture of birch (*Betula pubescens*). It is a single stratum forest. In the undergrowth the following bushes occur: alder buckthorn (*Frangula alnus*) – the dominant species in this stratum, mountain ash (*Sorbus aucuparia*), here and there the guelder rose (*Viburnum opulus*), and saplings of the alder, birch and willow (chiefly *Salix cinerea*).

This association is characterized by a comparatively great uniformity over the whole area, this uniformity including similarity of the edaphic-hydrological conditions, slight differences in canopy density (0.7 to 0.9) and in quality of tree-stand (from I to III between extreme stations).

Although the tree layer sometimes varied considerably in age (from 30 to 110 years) the differences in height between individual trees are not significant due to the fast growth of the alder.

In comparison with the *Carici elongatae-Alnetum* association the forest associations found on the drier elevated sandy islands are more differentiated both in respect of number of strata and of the number of species in each stratum.

In the *Pino-Quercetum* association the following tree species were found: the pine (*Pinus silvestris*), oak (*Quercus robur*), birch (*Betula verrucosa*), hornbeam (*Carpinus betulus*) and in places the aspen (*Populus tremula*). In the undergrowth the hazel (*Corylus avellana*), alder buckthorn, in places the juniper (*Juniperus communis*) and saplings of oak, hornbeam, and birch are found.

Among the trees in the *Tilio-Carpinetum* association are found: the hornbeam, oak, pine and in small numbers the lime (*Tilia cordata*) and in areas bordering on the *Carici elongatae-Alnetum* the alder occurs. The undergrowth includes bushes: the hazel, the alder buckthorn, the rowan and hornbeam, oak and lime saplings.

In the tree stratum in the *Circaeo-Alnetum* association the alder, birch and here and there the hornbeam occur; in the undergrowth – alder buckthorn, rowan, hazel, bird cherry (*Prunus padus*) and here and there the black current (*Ribes nigrum*) are found.

In the three associations present on the elevated sandy islands usually two or even three tree strata are represented. On individual islands the highest stratum consists of pine or oak, the lower stratum of oak, and the lowest one of hornbeam. The differences in the number of associations and species composition of the tree-stands in the particular mixed woods are connected with their elevation above the ground water horizon and the size of the area, this varying from 1/16 ha to several hectares. The age of the stands found on the elevated mixed-wood islands varies between 85 to about 140 years.

¹Latin names of plant species are given after Szafer, Kulczyński and Pawłowski (1953).

The elevated islands, sometimes scattered in pure alder forest, with the associations' found on them, known under the common term mixed woods, form a mosaiclike habitat — characteristic of the area under study. As alder forests are comparatively homogeneous, the habitat is differentiated chiefly due to the mosaic-diversity proportional to the contribution of the mixed woods in individual portions of the alder forest.

The observations were carried on during the breeding season, that is, from the middle of April till July. The reason for this choice of the period was that the habitat preference of the birds is most evident during the breeding season (Wasilewski 1961). It is during the breeding season that the strongest territorialism occurs within the populations of individual species. It could therefore be expected that the interactions between species, which may affect the sharing of the terrain between the different species and thus limit their numbers, would occur most clearly in the breeding season.

In the observation the strip count method, commonly applied by many authors, was used with some modifications introduced to it. The typical strip census consists of a range of sample areas covering a part of the given station. In the present research the individual sample areas covered the entire station. In Figure 1 a station and the route of observation are shown.

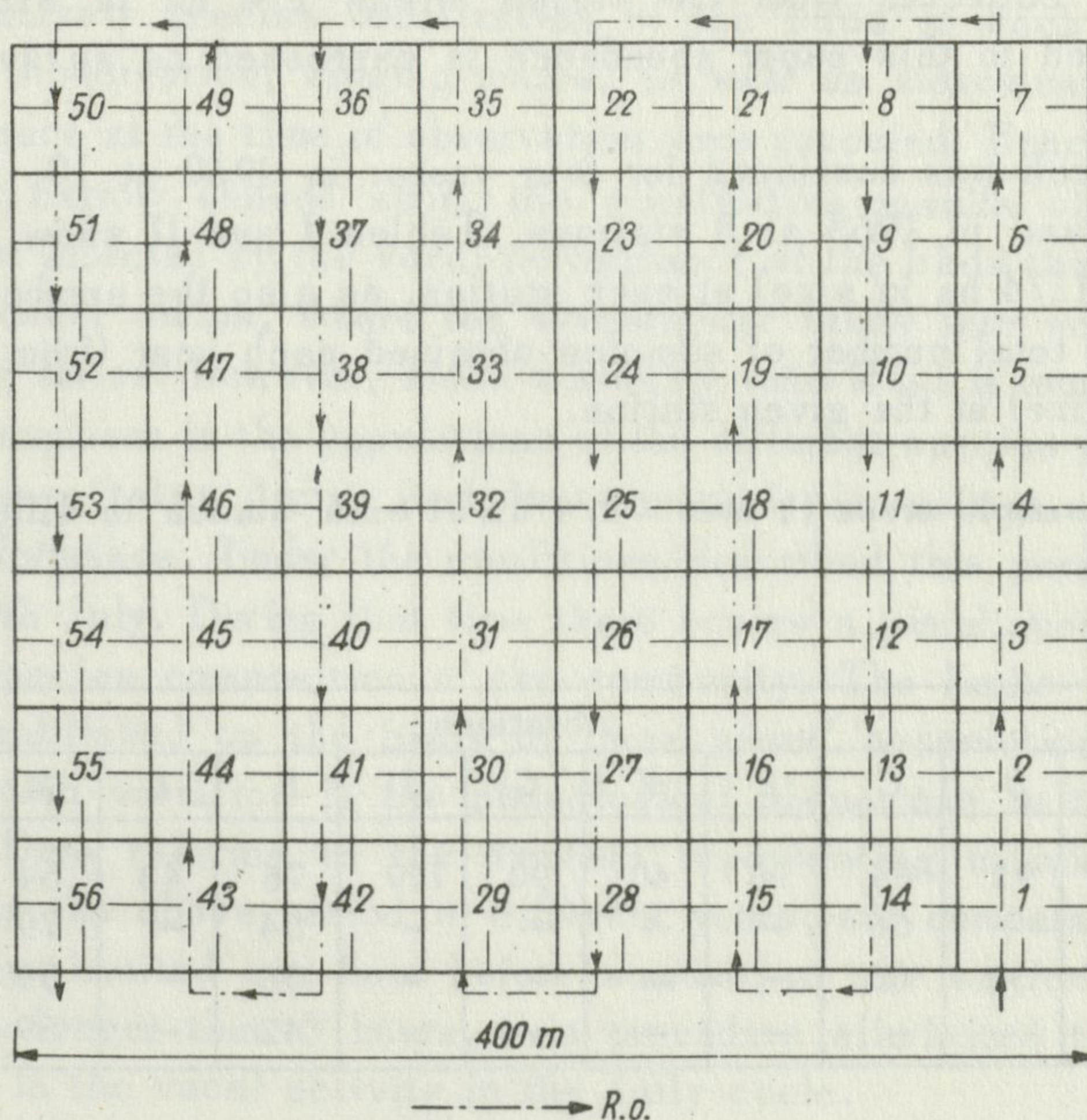


Fig. 1. A diagram showing one of the stations

R.o. — route of observation, 1–56 — consecutive numbers of sample areas of 1/4 ha (within these areas sample areas of the size 1/16 ha were additionally delimited; these are marked with thin line)

Each station was divided into sample areas of the size 50×50 m. At the given station each sample area was marked with a number and exactly the same position was maintained throughout the successive years of research. Owing to the marking of the sample areas it was possible to analyse the distribution of every species in relation to the same, precisely, points in space, in all the many times repeated censuses taken in the successive years of study.

Observation was carried on while passing successively across the middle of each sample area. Observation over one sample area lasted about 3 minutes. Quantitative data obtained during the 3-minutes' observation on one sample area were regarded to be a sample. The number of sample areas at a given station is thus the same as the number of samples obtained during a census. The total number of samples obtained from a station represents the multiple of the sample areas at this station, replicated in the successive censuses. Each sample area of the size 50×50 m ($1/4$ ha) was divided into 4 smaller ones — 25×25 m. This made it possible to analyse, if necessary, the material on the basis of the samples collected from the sample areas of the size 50×50 m ($1/4$ ha), 25×50 m ($1/8$ ha) and 25×25 m ($1/16$ ha).

The size of the populations of the species under study was determined from samples collected from the sample areas $1/4$ ha in size. In all the summaries cited in this paper abundance is expressed as an average density per sample.

The research was continued for four years: in 1960 at 10, in 1961 at 3, in 1962 at 4 and in 1963 at 3 stations. Tables I and II show the number of sample areas ($1/4$ ha in size) at each station, as also the number of censuses taken and the total number of samples obtained each year (from sample areas of $1/4$ ha in size) at the given station.

Number of sample areas (1 area = $1/4$ ha) at each station in different years

Tab. I

Years	Stations											Σ
	A	B	C	E	F	G	J	K	L	M	N	
1960	39	91	64	96	40	90	129	76	43	54	—	722
1961	—	—	66	—	—	—	—	64	—	79	—	209
1962	—	—	66	—	—	—	—	56	—	59	44	225
1963	—	—	—	—	—	—	—	42	—	59	44	145

In 1960 at all the stations a total of 722 samples was collected (from sample areas of $1/4$ ha) and 1,173 occurrences of individuals of different bird species were recorded; during the following years 3,235 samples were collected and 5,992 occurrences of birds were recorded.

Number of censuses and samples taken at individual stations in the years 1961–1963

Tab. II

Years	Stations							
	K		C		M		N	
	number of censuses	number of samples	number of censuses	number of samples	number of censuses	number of samples	number of censuses	number of samples
1961	3	192	5	330	5	385	—	—
1962	8	448	8	528	5	295	5	220
1963	5	210	—	—	5	275	8	352

Most of these investigators who use the strip census for forest biotopes recommend a strip width of 50 m (Breckenridge 1935, Kendeigh 1944, Merikallio 1946, Blagosklonov, Osmolovskaja and Formozov 1952). Šapošnikov (1938) and Novikov (1953) think a strip width of 50 to 100 m is the best, depending on the density of the canopy; Promptov (1932) used in forest studies a strip width of 100 to 200 m. The strip width of 50 m used in the present research ensured a good visibility and a possibility for a comparatively precise localization of the birds in each sample area.

During an observation, singing males, as well as individuals showing no vocal performance at the time of observation were recorded. Hence, considering the relatively narrow census strip, the quantitative results obtained are to a lesser extent affected by the vocal performance of the birds than in censuses taken over broader strips, where the investigator takes into account first of all the singing males. However, since a singing individual is more likely to be recorded, the numbers in the populations of the different species were determined from censuses taken during periods comparable in respect of intensity in the vocal performance. Under the conditions described this period lasts from 8th May to 10th July. During that time there occurs a simultaneous establishment of the species composition of the community. The limits of this period have been established on the basis of three years' observation, taking into account a certain variation in the phenological phenomena in the biology of the species. Data relating to the numbers representing individual species, gathered during the above period in different years, are comparable. Observation was always started one hour before sunrise; at one station the observation lasted no longer than 3 hours, this procedure eliminated the errors due to differences in the vocal activity in the daily cycle.

The strength and frequency of the singing varies with each species. But as the census strips are not wide and as the time of observation at one station was relatively long, compared with the frequency of singing of the individual

species, data concerning the population size of individual species, obtained by using the above-described method, are considered to be comparable with one another.

2. DISTRIBUTION (HABITAT PREFERENCE) OF INDIVIDUAL SPECIES, NUMBER OF INDIVIDUALS IN THE COMMUNITY AND QUANTITATIVE RELATIONS WITHIN THE COMMUNITY

As has been mentioned, the main element responsible for the diversity of the habitat under study is the extent of its mosaic-differentiation. In order to find to what extent this factor affects the numbers in the community a comparison was made of the total density of 6 most abundant species at 10 stations arranged in order of growing mosaic-diversity of the habitat. As a measure of the mosaic-differentiation of the habitat the percentage of sample areas at the given station with mixed-wood associations in them was adopted. This was possible owing to the fact that in the area under study the mixed woods formed islands scattered in pure alder forests, and not large patches. The highest mosaic-differentiation at a station is represented by 50% surface with mixed-wood islands surrounded by pure alder forest.

The data considered in this chapter were collected in 1960 over an area of 372 ha, representing over 50% of the marsh acreage of the nature reserve Sieraków.

The total density of the most abundant species in the community increases with the degree of the mosaic-diversity of the habitat (Fig. 2). This is then the main element of the environment, which determines, under the conditions described, the number of individuals in the community. For this reason a detailed analysis of the quantitative relations and of competitive interrelations in the community was carried out at 4 stations clearly differing in the degree of the mosaic-differentiation: *K*, *C*, *M* and *N*. This order of arrangement of the stations corresponds with the growing gradient of the mosaic-differentiation of the habitat. In Table III a short supplementary description of the above stations is given.

In the years 1961–1963 3 to 8 censuses were taken at each station during each of the seasons under study (Tab. I and II).

In general, at all stations 42 species of small birds, most of which were passeriformes (Tab. IV), were found.

For each study year a comparison was made of the number of individuals of all the species in the community at each of the different stations. The number of birds in the community appeared to increase with the mosaic-differentiation of the environment. This relationship was observed in all the years of the research, although during the period 1961–1963 at individual stations the number of birds decreased considerably (Tab. V).

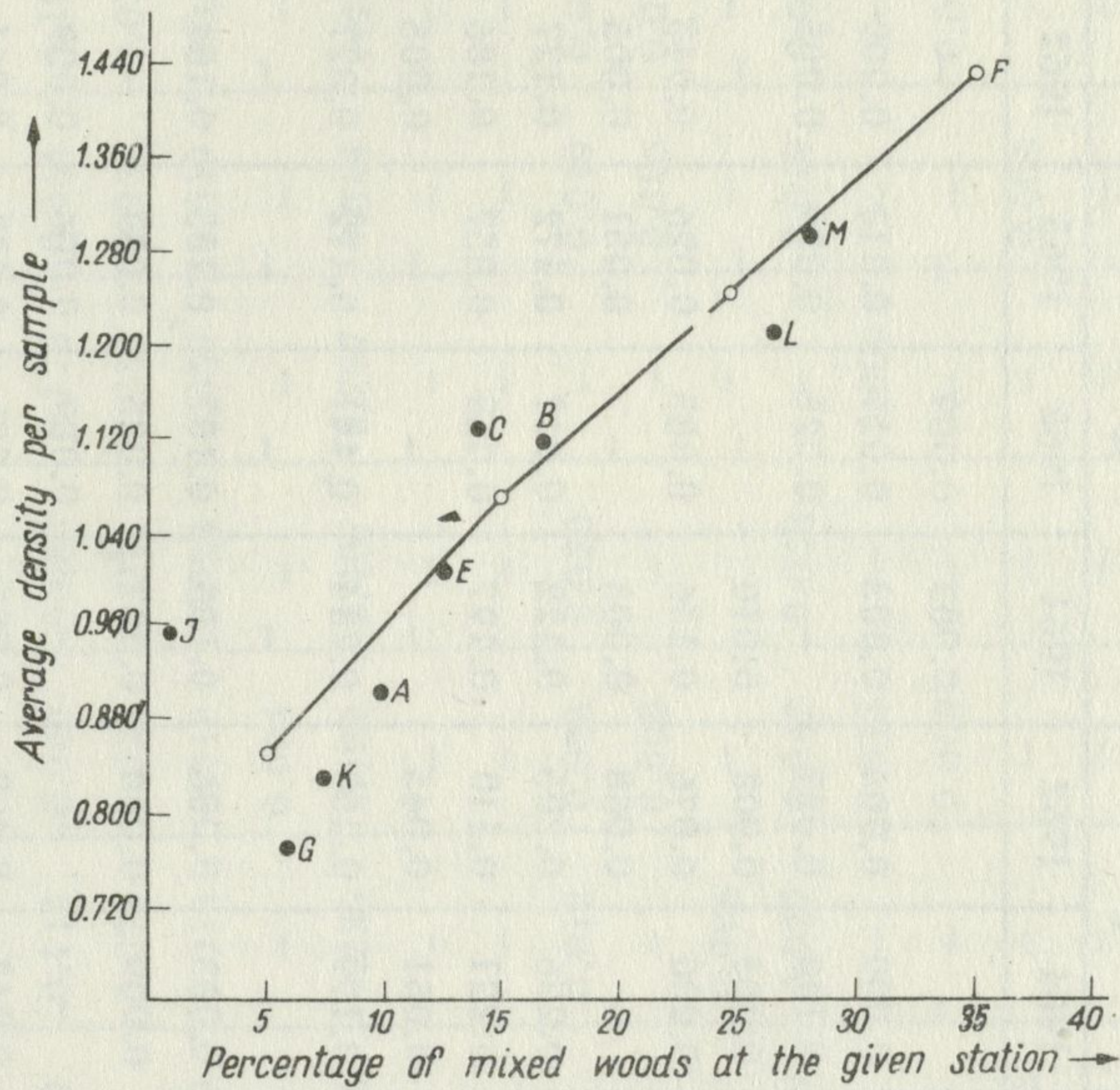


Fig. 2. Relation between the total density of 6 most abundant species of the community (*Sylvia borin*, *S. atricapilla*, *Phylloscopus collybita*, *Ph. sibilatrix*, *Erithacus rubecula*, *Fringilla coelebs*) and the percentage of mixed-wood surface at each station (A-M)

A comparison of the mixed-wood surface, of the age, density and quality of tree-stand, as also of the number of plant associations at individual stations

Tab. III

Stations	Percentage of mixed woods	Age of alder forest in years	Age of mixed woods in years	Canopy density in alder forest (on the scale 0.1-1.0)	Quality (on the scale I-V)	Number of associations
K	4	32-45	103	0.8-0.9	III-II	2
C	14	103	103-138	0.9	II-I	2
M	28	55	115	0.7	III	4
N	55	41-61	85-130	0.6-0.7	III	4

If all the stations analyzed are taken into account, the density of the avifauna in the mixed woods is higher than in pure *Carici elongatae-Alnetum*.

Average density of individuals of the different species at stations K, C, M, N, in successive years

Tab. IV

No.	Species	Stations and years									
		K			C		M			N	
		1961	1962	1963	1961	1962	1961	1962	1963	1962	1963
1	<i>Anthus trivialis</i> L.	—	—	—	—	—	0.003	0.009	—	—	0.023
2	<i>Oriolus oriolus</i> L.	0.005	—	—	0.009	0.004	0.003	0.017	0.013	0.009	0.030
3	<i>Sturnus vulgaris</i> L.	—	—	0.005	0.100	0.027	—	0.025	0.019	0.005	0.091
4	<i>Garrulus glandarius</i> L.	—	—	—	0.003	0.008	0.010	—	—	—	0.015
5	<i>Troglodytes troglodytes</i> L.	0.198	0.030	0.005	0.200	0.076	0.136	0.085	0.026	0.045	—
6	<i>Hippolais icterina</i> Vieill.	0.021	0.036	0.005	—	0.068	0.003	—	0.051	0.005	0.053
7	<i>Sylvia borin</i> Bod.	0.255	0.268	0.219	0.236	0.205	0.122	0.017	0.172	0.127	0.136
8	<i>Sylvia atricapilla</i> L.	0.036	0.089	0.048	0.221	0.110	0.197	0.068	0.057	0.186	0.159
9	<i>Sylvia communis</i> Lath.	0.026	0.054	0.014	0.051	0.045	—	—	—	0.005	—
10	<i>Phylloscopus collybita</i> Vieill.	0.286	0.369	0.329	0.179	0.250	0.234	0.441	0.172	0.327	0.235
11	<i>Phylloscopus trochilus</i> L.	—	—	—	—	—	—	—	—	—	—
12	<i>Phylloscopus sibilatrix</i> Bechst.	0.021	—	0.024	0.033	0.056	0.156	0.187	0.153	0.154	0.227
13	<i>Ficedula hypoleuca</i> Pall.	—	0.036	0.076	0.009	0.038	0.037	0.085	0.089	—	—
14	<i>Ficedula parva</i> Bechst.	—	—	—	—	—	—	0.009	0.006	0.009	0.015
15	<i>Muscicapa striata</i> Pall.	0.026	0.042	0.114	0.043	0.068	0.085	0.025	0.153	0.064	0.106
16	<i>Erithacus rubecula</i> L.	0.146	0.107	0.052	0.248	0.095	0.193	0.127	0.083	0.268	0.167
17	<i>Luscinia svecica</i> L.	0.047	0.059	0.029	—	0.023	0.013	0.017	—	—	—
18	<i>Turdus merula</i> L.	0.087	0.042	0.014	0.070	0.027	0.027	0.009	0.006	0.068	0.061
19	<i>Turdus philomelos</i> L.	0.021	0.024	0.029	0.043	0.034	0.030	—	0.013	0.100	0.015

20	<i>Aegithalos caudatus</i> L.	—	—	—	—	0.008	—	0.009	—	—	—
21	<i>Parus palustris</i> L.	0.010	0.006	—	0.006	0.004	0.034	0.025	—	0.009	—
22	<i>Parus atricapillus</i> L.	—	—	—	—	—	0.003	0.009	—	—	—
23	<i>Parus caeruleus</i> L.	0.073	0.060	—	0.167	0.205	0.186	0.195	0.064	0.168	0.030
24	<i>Parus major</i> L.	0.125	0.054	0.019	0.112	0.083	0.085	0.178	0.064	0.109	0.068
25	<i>Sitta aeuropaea</i> L.	0.021	0.012	—	0.073	0.034	0.071	0.051	0.038	0.032	0.023
26	<i>Certhia familiaris</i> L.	0.005	0.036	0.010	0.015	0.019	0.024	0.059	0.019	0.036	—
27	<i>Certhia brachydactyla</i> Brehm.	—	—	—	—	0.004	—	—	—	—	—
28	<i>Fringilla coelebs</i> L.	0.245	0.155	0.195	0.236	0.189	0.407	0.297	0.344	0.482	0.462
29	<i>Carduelis spinus</i> L.	—	—	—	—	—	—	—	—	—	—
30	<i>Pyrrhula pyrrhula</i> L.	—	—	—	—	—	—	—	—	—	—
31	<i>Coccothraustes coccothraustes</i> L.	0.016	—	—	0.012	0.023	0.020	—	0.019	0.018	0.007
32	<i>Emberiza citrinella</i> L.	—	—	—	—	0.008	—	—	0.006	0.009	—
33	<i>Dryocopus martius</i> L.	—	—	—	0.006	—	—	—	—	—	—
34	<i>Dendrocopos major</i> L.	0.021	0.006	0.005	0.027	0.042	0.058	—	0.019	0.064	0.007
35	<i>Dendrocopos medius</i> L.	—	—	—	—	0.015	—	0.009	—	—	0.015
36	<i>Dendrocopos minor</i> L.	—	—	—	—	0.008	—	—	—	0.005	—
37	<i>Jynx torquilla</i>	—	—	0.005	—	—	—	—	0.006	—	—
38	<i>Cuculus canorus</i> L.	—	—	—	—	—	—	—	—	—	0.007
39	<i>Upupa epops</i> L.	—	—	—	0.006	—	—	—	—	—	—
40	<i>Tringa ochropus</i> L.	—	—	—	—	—	0.010	—	0.006	0.005	0.007
41	<i>Scolopax rusticola</i> L.	0.010	—	—	—	—	—	—	—	—	—
42	<i>Streptopelia turtur</i> (L.)	—	—	—	—	0.008	—	—	—	0.005	—

Community abundance level at stations *K*, *C*, *M*, *N* in successive years of study

Tab. V

Years	Stations			
	<i>K</i>	<i>C</i>	<i>M</i>	<i>N</i>
1960	1.30	1.61	1.85	—
1961	1.68	2.10	2.15	—
1962	1.48	1.78	1.95	2.31
1963	1.20	—	1.60	1.96

In 1962 the average density (per sample) of individuals of all the species found in the *Carici elongatae-Alnetum* association was 0.416, in the mixed-wood associations — 0.603; in 1963 0.341 in *Carici elongatae-Alnetum* and 0.502 in the mixed woods (in order to make a clear distinction between the *Carici elongatae-Alnetum* and the mixed woods the mean values were calculated from samples collected in the sample areas of the size of 1/16 ha).

However, the increase of the number of individuals in the community, proportional to an increase in the mosaic-differentiation of the habitat is caused not only by the increasing proportion of the mixed woods, because the density of the avifauna in pure alder forests also grows with an increasing mosaic-differentiation, and at station *N*, where the mosaic-differentiation was the highest, the density of bird populations was even higher in the *Carici elongatae-Alnetum* than in the mixed woods (Tab. VI). Comparative materials, gathered in 1956 and 1957, relating to the area under study indicate that in mixed woods of comparatively large size smaller numbers of birds are found than in the smaller islands of mixed woods scattered in the alder forests (Tab. VII). This means that the increase of the number of individuals in the community is significantly influenced by the extent of the mosaic-differentiation of the habitat, and not only by the per cent increase of the surface of the mixed-wood islands as such.

An increase in the mosaic-differentiation of the habitat represents a particular case of an increase in the diversity of a habitat. It may be presumed that other types of differentiation would also affect the size of bird populations. This is indicated by the higher density of birds in the mixed-wood islands than in the pure alder forests, and, compared with the latter, the mixed woods represent a more diverse habitat (Chapter 1.2, Tab. III). A distinct influence of the habitat diversity on the numbers of birds has been emphasized by Toropanova and Dubinin (1962) and by Brewer (1963). Comparing the number of birds in various types of habitat characterized by an increasing diversity Hickey (1943) (after Odum 1959) also draws attention to the effect of the differentiation of the habitat on the density of birds. In many cases the action

Comparison of average density of birds in mixed woods and in alder forest at stations *K*, *M*, *N*. Average density was calculated from samples collected at sample areas = 1/16 ha (numbers of samples given in brackets)

Tab. VI

Stations	Years and plant associations					
	1961		1962		1963	
	alder forest	mixed woods	alder forest	mixed woods	alder forest	mixed woods
<i>K</i> *	0.42 (768)	—	0.37 (672)	—	0.30 (840)	—
<i>M</i>	0.46 (1120)	0.67 (420)	0.41 (328)	0.70 (144)	0.33 (436)	0.54 (192)
<i>N</i> *	—	—	0.59 (400)	0.58 (480)	0.51 (240)	0.48 (288)

*The difference between the average density in alder forest at station *K* and the average density in alder forest at station *N* is significant for 1962 and 1963, at a significance level of $\alpha = 0.01$.

A comparison of average density of birds in pure alder forest, in homogeneous large mixed-wood patch and in mixed-wood islands scattered in alder forest

Tab. VII

Years	Habitat		
	alder forest	large mixed-wood patch	mixed-wood islands scattered in alder forest
1956	2.91	4.17	4.63
1957	4.55	4.52	5.30

of the ecotone probably depends upon the effect of habitat differentiation. Within the habitats investigated during the present research the author (Wasilewski 1961) found an increase in number in several bird species over the borderlines between two different types of forest, for instance between *Carici elongatae-Alnetum* and the mixed-wood associations. Beecher (1942) found that the size of the bird populations is proportional to the number of plant associations per unit of surface, as also to the length of the line of contact between these associations. It may be concluded from this that the relationship between the total density of avifauna and the extent of the habitat

differentiation is of a general character. Therefore, shorter and more common term "habitat differentiation" will be used in the next part of this paper.

It follows from the above that the abundance of the whole community increases proportionally to the degree of the differentiation of the habitat. At the same time the distribution of the abundance of individual species varies with the stations arranged according to the degree of the differentiation. An increase of numbers following an increase in habitat differentiation was found in *Fringilla coelebs*, *Parus major* and *Phylloscopus sibilatrix* (Fig. 3). A similar

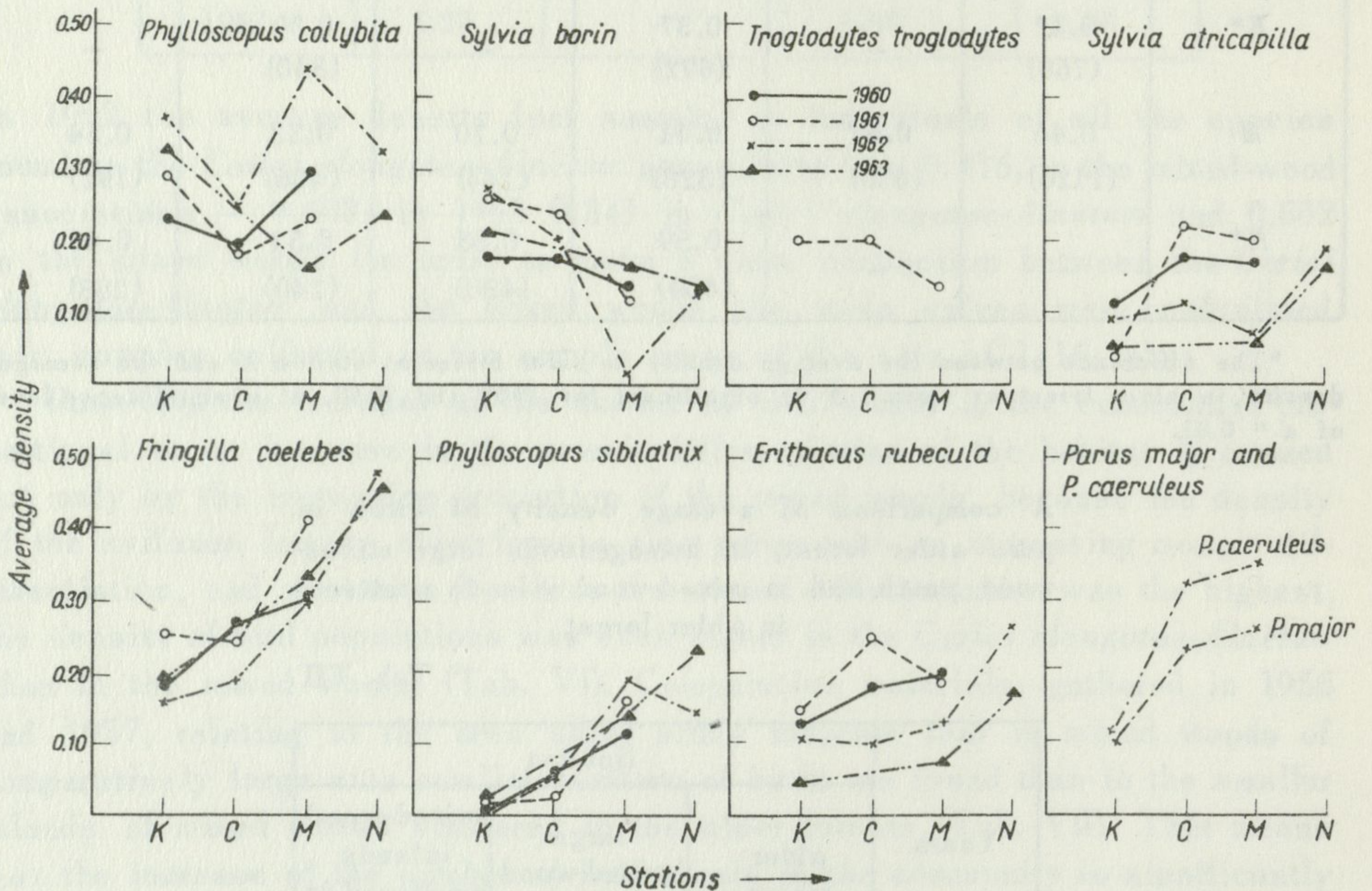


Fig. 3. Distribution of most abundant species of the community at stations K, C, M, N, arranged according to the degree of differentiation of the habitat (data concerning distribution of *Parus major* and *P. caeruleus* come from the period 14th April – 7th May)

distribution of density was found also in *Parus caeruleus*, *Sylvia atricapilla* and *Erithacus rubecula* – the highest density of these species was found at station N. In *Phylloscopus collybita*, *Sylvia borin* and in *Troglodytes troglodytes* a decrease in density was observed as the differentiation of the habitat increased (Fig. 3). In *Phylloscopus collybita* this decrease was not regular, and in 1962, when the density of this species was particularly high, the largest numbers were found at station M. Similar variations in the distribution of individual species at the stations, depending on the size of their populations in the given year will be considered in later chapters.

An observation was carried out to find to what extent the distribution of the above-discussed species, depending on the degree of differentiation of the habitat, is related to the utilization by them of the alder forests and the mixed-wood associations. For each of these species an average density in homogeneous alder forests and in the mixed woods at each of the different stations was calculated. To make a thorough distinction between the alder forest and the mixed woods the average density was calculated from samples collected at sample areas of the size 1/16 ha.

Species that prefer habitats with a high degree of differentiation, namely, *Fringilla coelebs*, *Phylloscopus sibilatrix*, *Sylvia atricapilla* and *Erithacus rubecula* occur in larger numbers in the islands of mixed woods; however, at station *N*, characterized by the highest degree of differentiation, the mean densities of these species in the mixed-wood islands and in homogeneous alder forest were similar (Tab. VIII). In species predominating numerically in habitats with a slight differentiation — *Phylloscopus collybita* and *Sylvia borin*, a highest density of numbers is observed in pure alder forests. However, the difference between density of these species in the mixed woods and in the alder forest decreases with an increase in the diversity of the habitat. With an increase in the differentiation of the habitat a more intense utilization of the mixed woods by species that predominate numerically in the alder forest, and of the alder forest — by species showing a higher density of individuals in the mixed-wood associations is seen. Thus the distribution (distribution of numbers) of the species discussed, over the range of habitats under study is not determined by their preferences with regard to the elements of the islands of mixed woods or the alder forest, but by the degree of the differentiation of the habitat.

During the three years the following numbers of species were found at the particular stations: *K* — 33, *C* — 34, *M* — 36, *N* — 37.

The number of species is somewhat higher in habitats with higher differentiation, but the species composition appears to be in essence similar in all the habitats. The number of the species common to all stations was 27. The differences in species composition between the different habitats are due to the low density of some of the species in the area under study, owing to which there is little chance of their occurring simultaneously in every habitat. The species occurring exclusively in habitats with high differentiation, associated with the elevated mixed-wood islands, are *Ficedula parva* and *Anthus trivialis*. Approached from this point of view, the species found in the area considered form one community, whereas the particular habitats are differentiated not by the species composition, but by the quantitative relations within one and the same community.

Comparison of average density of individual species in mixed woods and in the alder forest at stations *K*, *C*, *M* and *N* (average density was calculated from samples collected at sample areas = 1/16 ha)

Tab. VIII

Species	Stations							
	<i>K</i>		<i>C</i>		<i>M</i>		<i>N</i>	
	alder forest	mixed woods	alder forest	mixed woods	alder forest	mixed woods	alder forest	mixed woods
<i>Sylvia borin</i>	0.062	—	0.060	0.027	0.041	0.036	0.038	0.037
<i>Phylloscopus collybita</i>	0.082	—	0.058	0.025	0.077	0.055	0.076	0.062
<i>Sylvia atricapilla</i>	0.014	—	0.036	0.078	0.024	0.064	0.043	0.047
<i>Fringilla coelebs</i>	0.050	—	0.050	0.075	0.061	0.141	0.116	0.121
<i>Erithacus rubecula</i>	0.025	—	0.040	0.057	0.026	0.041	0.054	0.055
<i>Phylloscopus sibilatrix</i>	0.005	—	0.006	0.044	0.018	0.095	0.033	0.067

Differences in the quantitative relations between the species found at the different stations consist in the occurrence of larger numbers of relatively abundant species (influents and dominants) in habitat with a higher differentiation (Tab. IX). The influential and the dominant species have been distinguished on the basis of the distribution of the number of species in abundance classes. This distribution reveals a characteristic discontinuity due to a lack or only a small number of species in certain abundance classes, and their increase in number in the next classes. As an example of this the distribution of the number of species in abundance classes at one of the stations (*M*) in different years has been presented (Fig. 4). Above a density of 0.100–0.150 the number of species grows again at all stations. The species occurring in higher abundance-classes have been termed dominants and influents.

The increase in the number of the fairly abundant species with an increase in the differentiation of the habitat indicates that this differentiation influences also the quantitative relations of the community.

3. INTERSPECIFIC COMPETITION IN A COMMUNITY

3.1. Interactions between species in a community and the method used for studying them

In the preceding chapter it has been stated that the level of density, the quantitative relations of a community and the distribution of individual species in a habitat depend upon the extent of the differentiation of the latter. Further

List of dominant and influential species at stations K, C, M and N

Tab. IX

Years	Stations			
	K	C	M	N
1961	1. <i>Phylloscopus collybita</i> 2. <i>Sylvia borin</i> 3. <i>Fringilla coelebs</i> 4. <i>Troglodytes troglodytes</i>	1. <i>Erithacus rubecula</i> 2. <i>Sylvia borin</i> 3. <i>Fringilla coelebs</i> 4. <i>Sylvia atricapilla</i> 5. <i>Troglodytes troglodytes</i> 6. <i>Phylloscopus collybita</i> 7. <i>Parus caeruleus</i>	1. <i>Fringilla coelebs</i> 2. <i>Phylloscopus collybita</i> 3. <i>Sylvia atricapilla</i> 4. <i>Erithacus rubecula</i> 5. <i>Parus caeruleus</i> 6. <i>Phylloscopus sibilatrix</i>	—
1962	1. <i>Phylloscopus collybita</i> 2. <i>Sylvia borin</i> 3. <i>Fringilla coelebs</i>	1. <i>Phylloscopus collybita</i> 2. <i>Sylvia borin</i> 3. <i>Parus caeruleus</i> 4. <i>Fringilla coelebs</i>	1. <i>Phylloscopus collybita</i> 2. <i>Fringilla coelebs</i> 3. <i>Parus caeruleus</i> 4. <i>Phylloscopus sibilatrix</i> 5. <i>Parus major</i>	1. <i>Fringilla coelebs</i> 2. <i>Phylloscopus collybita</i> 3. <i>Erithacus rubecula</i> 4. <i>Sylvia atricapilla</i> 5. <i>Parus caeruleus</i> 6. <i>Sylvia borin</i>
1963	1. <i>Phylloscopus collybita</i> 2. <i>Sylvia borin</i> 3. <i>Fringilla coelebs</i>	—	1. <i>Fringilla coelebs</i> 2. <i>Phylloscopus collybita</i> 3. <i>Sylvia borin</i> 4. <i>Phylloscopus sibilatrix</i> 5. <i>Muscicapa striata</i>	1. <i>Fringilla coelebs</i> 2. <i>Phylloscopus collybita</i> 3. <i>Phylloscopus sibilatrix</i> 4. <i>Erithacus rubecula</i> 5. <i>Sylvia atricapilla</i> 6. <i>Sylvia borin</i>

on, an analysis was made to find the role of the interspecies relations in the formation of these fundamental elements of community organization.

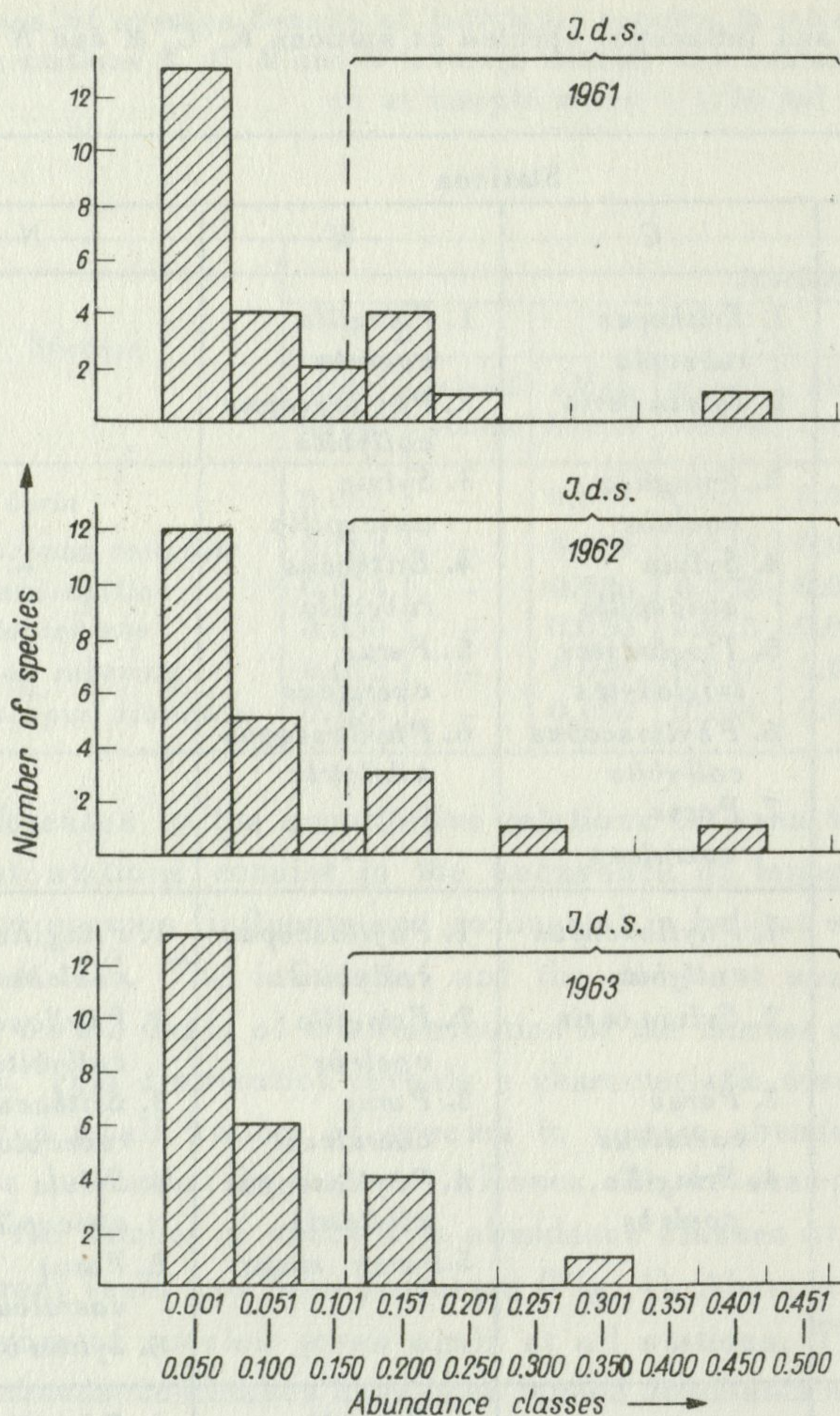


Fig. 4. Distribution of the number of species in abundance classes (expressed as average density per sample)

I.d.s. — influential and dominant species

As has been mentioned in the introductory notes, studies, published so far, dealing with various bird communities do not give in this respect any univocal answer. Examples indicating, beyond any doubt, that there exists an influence of the competitive interactions on the abundance of the species are known among separate group of species, namely the hollow nesters. Here the interaction between individuals belonging to different species generally is restricted to the well-known struggle for tree hollows or for their immediate surroundings, and it seldom includes protection of the entire territory.

Michelson (1958), who studied birds populating nest boxes, found within several hollow-nester species a clear influence of species interaction on the population size and distribution of these species. Analogous results were reported by Eliseeva (1960) from her studies on the hollow nesters in the forest belts in the Ukraine. In woods of this type, where natural hollows in tree trunks are very scarce, tree sparrows, the object of Eliseeva's (1960) research, did not successfully compete with other species. After a large number of nest boxes had been introduced, the tree sparrows were able to defend themselves and then to attack other, sometimes stronger, species of hollow nesters. Consequently, within the three years following the installation of the nest boxes nearly all the other hollow nesters were eliminated from the woods subjected to the experiment. Creutz (1955) relates the rapid increase in number of *Muscicapa hypoleuca* in Germany to a decrease in abundance of *Parus major*. Haartman (1956) recorded violent battles for holes in trees between *Muscicapa hypoleuca* and the two other species: *Parus major* and *Passer montanus*.

The data cited above refer to comparatively simple systems consisting of a small number of species and, moreover, the competition concerns a conspicuous requisite, that is, the hollow in the tree. Concerning other species many examples of antagonistic interactions, very often of territorial nature, can be cited, but no estimation has yet been made of the effect of these interactions upon the population size and distribution of individual species.

Simmons (1951), for instance, found territorial behaviour among individuals belonging to various species of the genus *Oenanthe* (wheatears): *O. leucopyga*, *O. lugens*, *O. monacha*, *O. oenanthe* and *O. pleschanka*; between the wheatears and *Monticola solitarius*; *Lanius collurio* and *L. nubicus*. Besides, the same author (Simmons 1953) states the existence of territorial combats between individuals of *Charadrius dubius* and *Charadrius hiaticola*, as well as between *Charadrius alexandrinus* and *Ch. hiaticola* (the above findings concern the post-breeding period).

Kendeigh (1941) describes violent combats between *Troglodytes aëdon* and 20 other species only 11 of which are hollow nesters, like *T. aëdon*.

Lack (1946a) reports on cases of *Erithacus rubecula* attacking, within the territory occupied by it, members of other species: *Prunella modularis*, *Fringilla coelebs*, *Certhia familiaris*, *Parus caeruleus*, *Parus major* and *Phylloscopus collybita*.

Pitelka (1951) studied the relationship between two species with similar ecology — *Calypte anna* and *Selaphorus sasin*. As a result of territorial combats, in places where their areas overlapped, the species appeared to drive away one another from their territories.

Andrew (1956) observed *Emberiza citrinella* attacking, within the territory, intruders of other species: *Emberiza schoeniclus*, *Carduelis cannabina*, *Fringilla coelebs*, *Passer domesticus*, *Alauda arvensis*. In combats against individuals of different species members of *Emberiza citrinella* do not show the behaviour typical of territorial fighting with individuals of the same species. *Emberiza calandra*, however, attacks intruders of other species such as, for instance, *Emberiza citrinella*, *Carduelis cannabina*, *Alauda arvensis*, *Anthus pratensis*, *Sturnus vulgaris*, as well as the males of its own species.

Marler (1956) recorded cases of *Fringilla coelebs* attacking individuals of *Parus caeruleus* and *Prunella modularis* near its own nest.

Durango (1956) found an outstanding intolerance in *Lanius collurio* towards other species. The males of that species attack, in their territory, almost all other species — *Fringilla coelebs*, *Emberiza citrinella*, *Anthus trivialis*, *O. oenanthe*, *Jynx torquilla*, as well as tits, warblers and flycatchers, but they tolerate the presence of *Sylvia nisoria*.

Brewer (1963) describes numerous examples of territorial fighting between *Parus atricapillus* and *Parus carolinensis* against a number of other species. Brewer (1963) also emphasizes that the strength of territorial combats was not proportional to the taxonomic relationship between the species investigated.

In summing up it may be stated that the above-cited examples of antagonistic interactions between species indicate: 1) their being common in the avian communities; 2) a common occurrence of antagonistic interactions between species of comparatively distant taxonomic relationship.

As regards the various systems of species, it is often difficult to specify the requisite, or a number of requisites, for which the species are competing. The object of competition may be food, space, or some specified spatial elements in the environment. However, regardless of the environmental element or elements for which the birds are in the given case competing, the competition ought to be reflected by the avoidance of the members of the different species in a specified habitat, in time or space, as well as in the general distribution of the particular components of the system of competitive species in the given association of habitats.

Using those assumptions an attempt was made to analyze the interrelations between species within the community concerned. They were studied by analyzing the distribution of individuals of various species in relation to one another, in time and place, in a given habitat.

The ratio of the recorded occurrence of two different species together, in a sufficiently large series of samples, to the number of such joint occurrences calculated by the probability calculus was regarded to be a measure of the interactions between the species. For this purpose the index of "asso-

ciation" $(S)^2$, applied by Dice (1945) for analyzing the occurring-together of species, was applied.

If a total number (N) of samples was collected in the terrain, with species A occurring in n_A , and species B in n_B samples, the theoretically probable number of samples in which the two species will occur together is equal to the product of the probability of occurrence, in a sample, of species A , probability of occurrence of species B , and the number N of samples (if a random distribution, in place and time, of the species considered is assumed).

For species A the probability of occurrence in a sample is:

$$P_A = \frac{n_A}{N}$$

for species B :

$$P_B = \frac{n_B}{N}$$

The probability of the two species occurring together simultaneously in a sample (P_{AB}) is equal to the product of the probability for each of the species separately:

$$P_{AB} = P_A \cdot P_B = \frac{n_A \cdot n_B}{N^2}$$

The number of samples in the series in which species A and species B would be expected to occur together by chance is therefore:

$$N_P = N \cdot P_{AB} = \frac{n_A \cdot n_B}{N^2} N = \frac{n_A \cdot n_B}{N}$$

If n_{AB} is the number of real simultaneous occurrences, the comparison of the quantities: n_{AB} and N_P gives ground for conclusions regarding the relations between the species under study in the given habitat.

If both the species have the tendency to simultaneous occurring with each other, then $n_{AB} > N_P$, if they show a tendency to keep away from each other, then $n_{AB} < N_P$ if they are, however, distributed indifferently in relation to each other, $n_{AB} = N_P$.

The following ratio was calculated as an index of these tendencies:

²Denotations are used after Tarwid (1960).

$$S_{AB} = \frac{n_{AB}}{N_P}$$

This index, here termed the index of association (S) of two different species, ranges between 0 and ∞ . When $0 < S < 1$, the species tend to avoid each other, when $S = 1$, the species concerned have a random distribution with regard to each other and when $S > 1$ — they show an association greater than that determined theoretically.

The index is based on the assumption that the species under study have a random distribution in relation to each other in the habitat. This makes the index rather difficult to interpret. For instance, an index smaller than one, that is, indicating that each of the species is passing-by the other, may be due to an active avoidance between the two species, or to different preferences with regard to the specified spatial elements of the habitat.

Even if we are dealing with a relatively homogeneous environment, there are no methods of analyzing it, methods that would be sufficiently accurate to enable us to state that the habitat is really homogeneous in relation to the needs of the various species.

The method used in this study for collecting the material for the analysis of the association between species eliminates the above difficulty. After a series of censuses the sample areas, in which the occurrence of the species considered had been found, were marked on the map of the given habitat. This was possible owing to the marking of all the sample areas with numbers. To illustrate this a diagram has been presented of one of the stations with the marked sample areas in which *Phylloscopus collybita* and/or *Fringilla coelebs* were found after a series of 8 censuses (Fig. 5).

To estimate the degree of association between the different species samples were taken from only those sample areas in which a given number of censuses revealed the presence of both the species simultaneously. Since the sample areas are comparatively small, it may be assumed that the sample areas so selected, representing some fragments of the habitat, are suitable to both the species, whose degree of association we are studying.

In Figure 6, an example is shown of the occurrence of two species: *Phylloscopus collybita* and *Fringilla coelebs* in sample areas selected in the consecutive censuses, in the described way. For this purpose 10 sample areas, selected at random from among 30 (shown in Fig. 5), were used. *Ph. collybita* and *F. coelebs* were regarded to have met when they were found simultaneously in a specified sample area, during a census, i.e. when they occurred simultaneously in a sample.

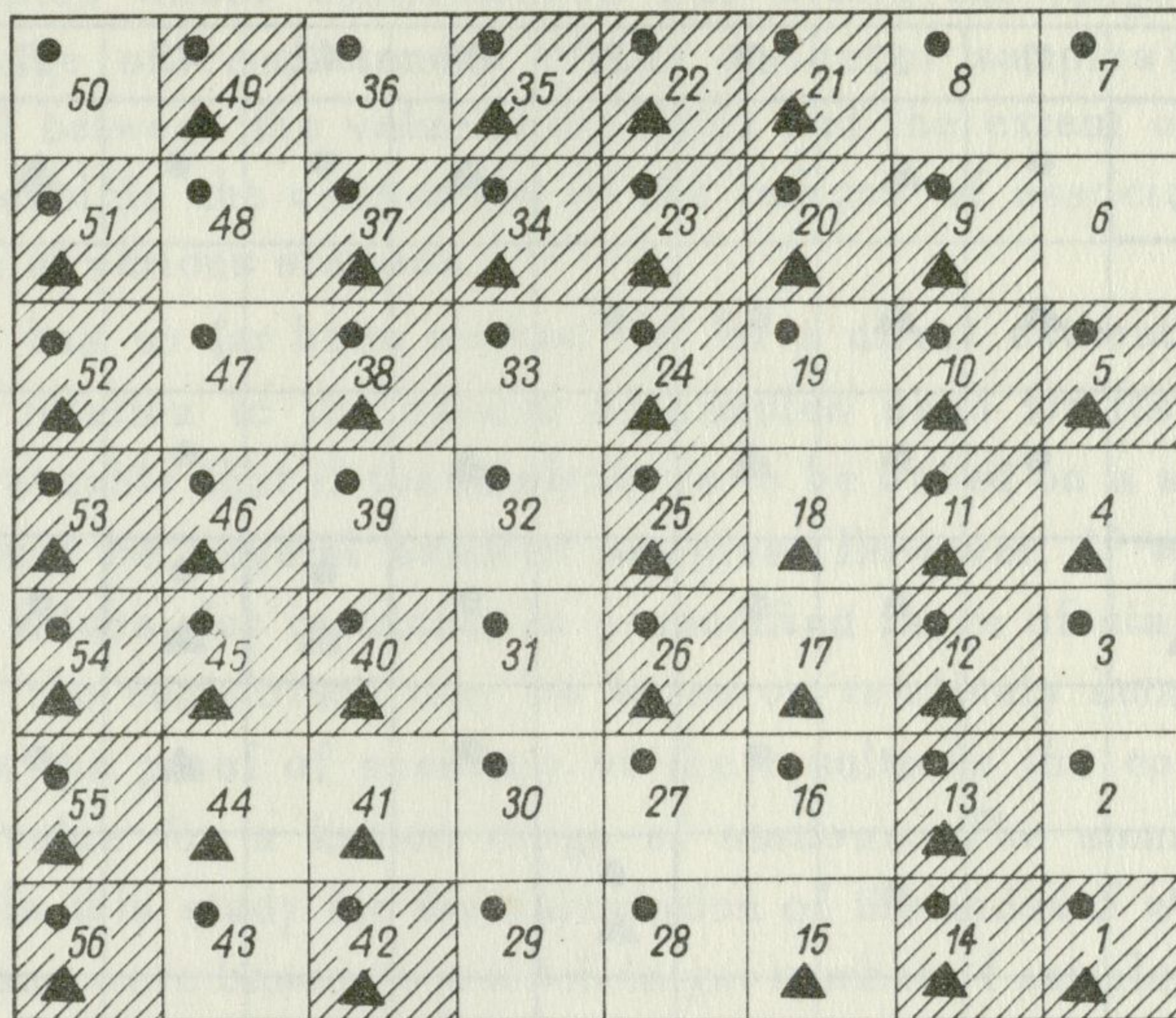


Fig. 5. A diagram showing a station with sample areas on which *Phylloscopus collybita* (circles), *Fringilla coelebs* (triangles) and both the species (hachure) were found after a series of 8 censuses

1-56 — consecutive numbers of sample areas. The association index of *Ph. collybita* and *F. coelebs* was calculated from samples obtained from only those sample areas in which both the species were found

The S index was thus calculated from series of samples obtained by repeated observations in successive censuses taken in those sample areas in which both species occurred during the research. If index S , calculated from such a series of samples took a value below one, it would univocally indicate that each of the species actively avoids the other in time and space. All the values of S , cited in the paper, were calculated according to the above-presented scheme.

When the association-index method is to be used, the material must be collected in a special way. The problem has been widely discussed by Dice (1945) and then by Tarwid (1960). For this reason the present paper only takes into account those points which are significant for the study in question, namely the completion of a series of samples and the size of the series used for the calculation of the index.

Both the too complete and the too incomplete series of samples are disadvantageous. If the series are too complete, significant changes in the degree of association correspond to the disproportionately small variations in the value of the index. A converse situation occurs when the series are too incomplete. Series of samples to be regarded as the best ones have a completeness of about 30% (Tarwid 1960).

$B \backslash A$	9	10	20	25	26	38	40	45	51	56
1	● ▲	●	▲			▲	●	●	▲	▲
2	●	▲	▲	●	●					●
3		●	●	▲		▲		●		▲
4	● ▲		●	●		●	● ▲	● ▲	●	
5				●		●		▲	●	
6	●		●		● ▲					▲
7	▲	▲	●	▲		▲	●		▲	● ▲
8		▲		▲	▲	●	▲	▲	●	

Fig. 6. The occurrence of *Phylloscopus collybita* (circles) and *Fringilla coelebs* (triangles) in selected sample areas, in successive censuses
 A - numbers of sample areas, B - consecutive numbers of censuses. Squares represent samples: double line denotes samples in which in a given census both species occurred together

The completion of a series of samples with material may be regulated by selecting a proper size of the area from which the sample will be taken. As regards the material here considered, the selection of the size of the sample area was determined not only by the need of the best possible completion of the series of samples, but, moreover, the size of the area could not exceed the limit over which the species cease to react to each other. It has been found empirically that the upper range of the size of an area to be sampled, useful for the analysis of the interspecies interactions, is, in the conditions of the present study, 1/4 ha. At the same time, series of samples taken from sample areas of this size are sufficiently complete, their completeness ranging between 20 and 40%.

A significant problem is the completion with material of the series of samples collected at different stations. The indices of association, calculated from series of samples clearly differing in degree of completeness are not comparable. It is for this reason that the study taken into account indices from

series of samples whose completeness was within the range of 20 to 40%. Within this range of completeness of the series of samples no relationship could be found between the value of the index and the extent of completeness. This makes possible the comparison of the indices of association of a given pair of species at various stations.

No method has so far been worked out for a direct estimation of the error of index S in relation to the number of samples used for its calculation. It may be stated roughly that if the analysis is to be based on a single numerical value there must be several hundred samples. However, if we can compare several index values, for instance, in a specified range of stations, as in the present study, the comparison may be based on relatively smaller numbers of samples. Then the proof of accuracy of the results is the correct variations of the index value for a known range of stations. The smallest number of samples used in this study for the calculation of the index S was 60, although most calculations were based on a much larger number of samples. The average number of samples used for the calculation of the index was 122.

As far as yet no method has been developed for the estimation of the range of error of index S . We can, however, estimate the significance of the deviation of the index value from one. For this purpose an additional χ -square test (the "fourfold" table) was applied. The theoretical χ^2 values were found in χ^2 tables for one degree of freedom.

The index of association of a given pair of species was calculated for each of the stations. Where a sufficient number of data permitted it, calculations were made for three different categories of samples: collected in the sample areas of the size 1/4, 1/8 and 1/16 ha.

Using the above-described analysis of the degree of association between species, data have been gathered regarding the interrelations between the species of a total of 29 pairs, representing different combinations of the nine most numerous species of the community.

No relationship (S index value equal to one, or not differing significantly from one, on any of the stations) was found between the following species pairs: *Sylvia atricapilla* and *Troglodytes troglodytes*, *Sylvia borin* and *Troglodytes troglodytes*, *Sylvia borin* and *Parus major*, *Sylvia borin* and *Parus caeruleus*, *Phylloscopus sibilatrix* and *Parus major*, *Fringilla coelebs* and *Troglodytes troglodytes*, *Fringilla coelebs* and *Parus caeruleus*, *Erithacus rubecula* and *Parus caeruleus*, *Erithacus rubecula* and *Parus major*, *Phylloscopus collybita* and *Parus major*.

In 17 pairs of species the S index values indicate an active reciprocal avoidance, in time and place. For those pairs similar S index values were found at particular stations in the successive years of research. Therefore

Comparison of association indices (S) of individual species pairs at stations K , C , M and N (in upper line are given indices calculated from sample areas = 1/4 ha, in middle line = 1/8 ha, and in lower line = 1/16 ha)

Tab. X

Pairs of species	Stations			
	K	C	M	N
<i>Sylvia atricapilla</i> and <i>Sylvia borin</i>	0.00 — —	0.44* 0.20** —	0.75 0.88 0.50	1.25 — —
<i>Sylvia atricapilla</i> and <i>Phylloscopus collybita</i>	— — —	— 1.00 —	1.09 0.50*** 0.33	1.21 0.80 —
<i>Sylvia atricapilla</i> and <i>Fringilla coelebs</i>	— — —	0.83 0.83 —	0.96 1.13 —	0.83*** 1.00 —
<i>Sylvia atricapilla</i> and <i>Erithacus rubecula</i>	— — —	0.83 0.70 —	0.86 0.57 0.40***	0.50*** — —
<i>Sylvia borin</i> and <i>Phylloscopus collybita</i>	0.92 0.64*** 0.56	0.87* 0.65* —	1.10 1.00 —	0.86 — —
<i>Sylvia borin</i> and <i>Fringilla coelebs</i>	0.54** 0.50 0.00	0.93 0.75 0.40	0.94 0.67*** 0.43**	— — —
<i>Sylvia borin</i> and <i>Erithacus rubecula</i>	0.75 — —	0.78 0.75 0.60	0.57 0.60 —	— — —
<i>Phylloscopus collybita</i> and <i>Phylloscopus sibilatrix</i>	— — —	— — —	0.81* 0.73 —	0.85 — —
<i>Phylloscopus collybita</i> and <i>Fringilla coelebs</i>	0.49* 0.43** 0.43	0.80*** 0.67*** 0.33**	0.85 0.96 0.62***	1.00 1.07 —
<i>Phylloscopus collybita</i> and <i>Erithacus rubecula</i>	— — 0.67	1.00 1.00 —	0.89 0.72 0.58	1.09 1.00 —

Tab. X (cont.)

Pairs of species	Stations			
	K	C	M	N
<i>Phylloscopus collybita</i> and <i>Parus caeruleus</i>	— — —	1.05 0.77 0.71	1.00 1.08 —	1.00 — —
<i>Phylloscopus collybita</i> and <i>Troglodytes troglodytes</i>	0.80 — —	0.89 — —	0.57*** — —	— — —
<i>Phylloscopus sibilatrix</i> and <i>Fringilla coelebs</i>	— — —	— — —	0.91 0.68** 0.29*	1.07 1.19 —
<i>Phylloscopus sibilatrix</i> and <i>Erithacus rubecula</i>	— — —	— — —	1.29 — —	0.75 — —
<i>Fringilla coelebs</i> and <i>Parus major</i>	0.75 0.67 —	1.03 0.71 —	1.33 1.25 —	1.10 — —
<i>Erithacus rubecula</i> and <i>Troglodytes troglodytes</i>	0.80 — —	1.06 0.63*** 0.40***	1.25 0.50 —	— — —
<i>Parus major</i> and <i>Parus caeruleus</i>	0.80 — —	0.77 0.50*** —	0.91 0.86 —	1.00 — —

*, **, *** Deviation of S index value from 1 significant at a significance level of $\alpha = 0.01$ (*), at a level of $\alpha = 0.05$ (**), at a level of $\alpha = 0.1$ (***)

for each of these pairs the mean values of S index are given, calculated from data for individual years (Tab. X).

When the association index is to be calculated within a larger number of species, a danger arises of erroneous interpretation of its values, due to the fact that some of the species may keep away seemingly from each other. A situation like this may arise when we obtain for a species a value indicating that it shuns two or more other species, which are, with regard to each other, indifferent. If in a combination, the simplest possible, consisting of three species: A , B , C , species A keeps away from B and C , the last named showing no reaction towards each other, the interaction between A and B may appear to be significant, and only apparent between A and C (or vice versa), due to

the association of the species *C* with species *B*. In the material analyzed, several such combinations may occur. This problem has been solved by additional calculations of *S* index, after the elimination of all those samples in which another component might occur. In all those cases the value of the association index remained much lower than one, which means that in these combinations there was no apparent interspecies interaction. The values of index *S*, as shown in Table X, thus indicate a real interaction between the species in the community.

The area size of 1/4 ha represents the upper range of the sample area size with which interactions between species may be observed under the conditions described, using the method applied in the present research. It may be presumed that in samples collected from smaller areas those interactions would be stronger and as a consequence the values of *S* index, obtained for samples of this kind, would be lower. In Table X are given *S* index values, calculated from a series of samples collected from sample areas 1/4, 1/8, 1/16 ha. Indeed, in 14 out of 17 pairs, at one, at least, station the *S* index value decreases with the decreasing surface of the sample areas. In considering the results for individual years this regularity was found in 82% of cases (in 41 out of 51). As the variations in *S* index value, in relation to the size of the sample areas, appear to be similar both at the various stations and in the various years of study, the general character of this relationship has been illustrated by the mean values calculated from all cases for each category of samples (taken from areas of the size 1/4, 1/8 and 1/16 ha), taking into account all the combinations of species (Fig. 7).

A rapid fall in the mean value of *S* index, with the decreasing surfaces of the sample areas from which the samples were taken, permits the presumption that the strength of interaction between individuals of different species is inversely proportional to the distance between them.

The result of this interaction between individuals of different species is their avoiding to occur together in a unit of space. This mode of interaction is not necessarily connected with active territorial fighting, but with regard to certain species it probably is brought about by alone the presence of individuals of one of the species, which are dominant in relation to the individuals of the other species. A similar kind of interactions between species, consisting in an active reciprocal avoidance, in time and place, was found by Moynihan (1963) among four closely related species: *Diglossa lafrasnayeri*, *D. carbonaria aterrima*, *D. cyanea cyanea* and *Conirostrum cinereum fraseri*.

A comparison of *S* index values for the different stations reveals a regular increase in the value of the index with a growth in the degree of the differentiation of the habitat, for most of the species pairs – this relationship was found in 12 pairs (Tab. X).

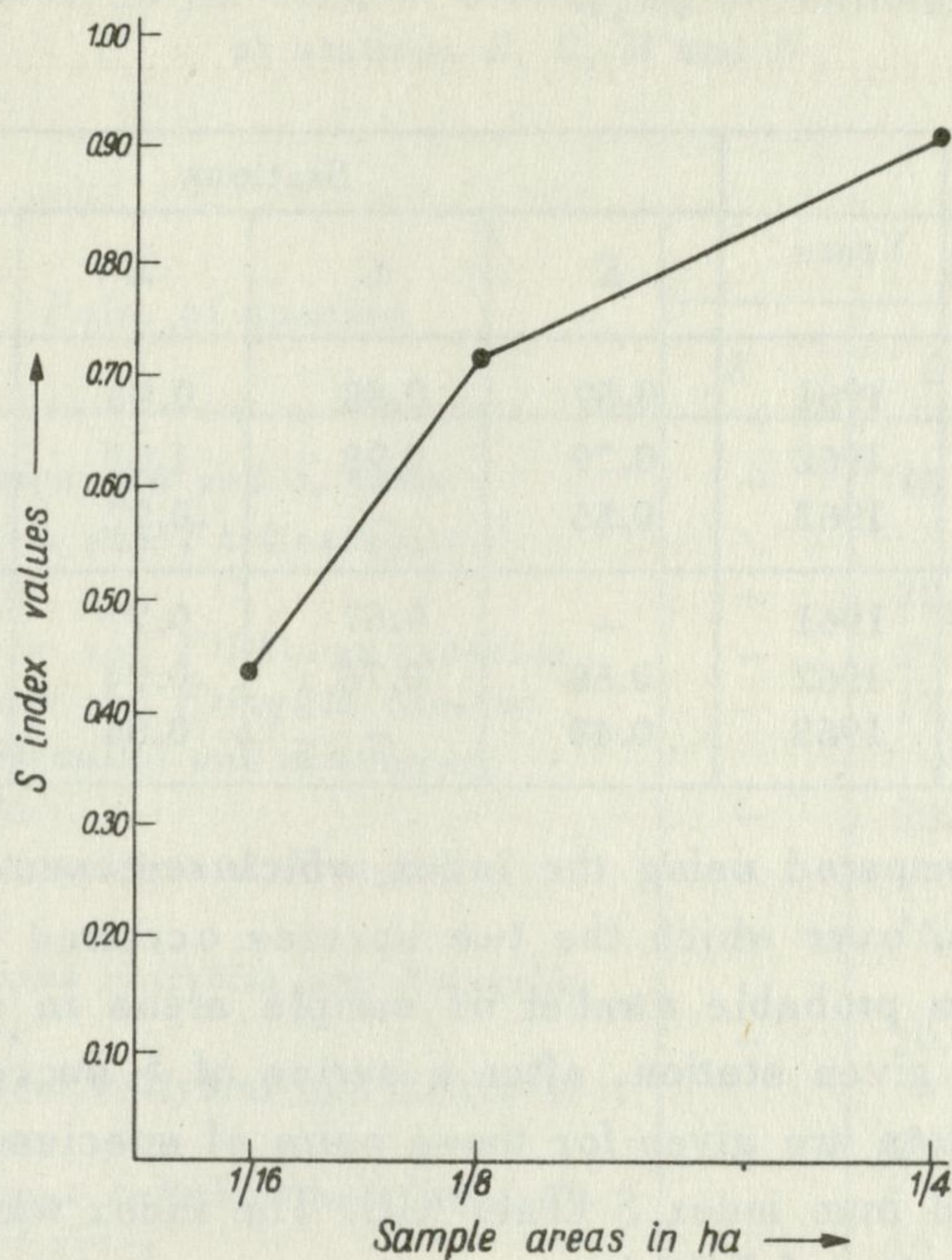


Fig. 7. Relation between sample area size and index S

To illustrate the general tendency in the intensity of the interactions between species, against the growing gradient of diversity of the habitat, average S index values were calculated for individual habitats in the different years of study, taking into account the data for all the species pairs at a given station (for series of samples collected from sample areas $1/4$ and $1/8$, respectively).

The mean value of S index appears to grow with the growing extent of the differentiation of the habitat; this regularity was observed during three years (Tab. XI). Higher S index values, approximating one, found for the most differentiated stations: M and N indicate an increase in the reciprocal tolerance between individuals belonging to different species, as compared with the habitats with lower diversity — K and C .

3.2. The effect of interspecific competition on the numbers and on the quantitative relations of the community

An increase in the differentiation of the habitat is accompanied by a growth of the extent of overlapping of territories of the species pairs under study. The extent of overlapping of territories of two different species at each of

Comparison of mean values of S index at stations K , C , M and N

Tab. XI

Sample area in ha	Years	Stations			
		K	C	M	N
1/4	1961	0.59	0.88	0.93	—
	1962	0.79	0.98	1.02	1.09
	1963	0.55	—	0.97	0.94
1/8	1961	—	0.67	0.77	—
	1962	0.58	0.76	0.94	0.96
	1963	0.49	—	0.88	0.99

the stations was compared using the index which represents the percentage of the sample areas, over which the two species occurred together, in relation to the maximum probable number of sample areas in which they might occur together at a given station, after a series of 5 successive censuses.

The respective data are given for those pairs of species, for which interactions were inferred from index S (Tab. XII). The index was calculated from sample areas of the size of 1/16 ha.

In most of the species pairs analyzed in Table XII the extent of overlapping of territories grows with the increase in the diversity of the habitat, this regularity could be observed for three years during the research. In the case of *Phylloscopus collybita* and *Sylvia borin* an inverse relationship was observed in 1962.

This probably results from the fact that station K constitutes habitat-optimum for both the species. A higher extent of overlapping of territories between *Phylloscopus collybita* and *Sylvia borin* at station K in comparison with the remaining stations was seen in 1962, when a considerable increase in number was observed in *Phylloscopus collybita*, and it probably resulted from the mutual pressure of these species. This is confirmed by a comparison of the degree of overlapping of territories of these species at individual stations, with the percentage of the sample areas in which no individuals of *Phylloscopus collybita* were found and which were at the same time suitable for *Sylvia borin*. Sample areas in which members of *Sylvia borin* occurred at least once, in the course of two years, were regarded as suitable for *Sylvia borin*. The comparison was made for 1962.

At station K the proportion of sample areas suitable for *Sylvia borin* and not occupied by *Phylloscopus collybita* is almost twice as low as at station C (Tab. XIII), which situation, when combined with the fact that station K

Comparison of indices (in per cent) of overlapping of territories of different species at stations K, C, M and N

Tab. XII

Years	Pairs of species	Stations			
		K	C	M	N
1961	<i>Sylvia atricapilla</i> and <i>S. borin</i>	—	18.2	21.8	—
	<i>Sylvia borin</i> and <i>Phylloscopus collybita</i>	—	22.7	23.5	—
	<i>Sylvia borin</i> and <i>Erithacus rubecula</i>	—	22.4	29.4	—
	<i>Sylvia borin</i> and <i>Fringilla coelebs</i>	—	17.2	35.3	—
	<i>Sylvia atricapilla</i> and <i>Erithacus rubecula</i>	—	29.1	39.5	—
	<i>Sylvia atricapilla</i> and <i>Fringilla coelebs</i>	—	16.4	44.2	—
	<i>Phylloscopus collybita</i> and <i>Fringilla coelebs</i>	—	20.5	37.7	—
	<i>Phylloscopus collybita</i> and <i>Erithacus rubecula</i>	—	25.0	21.6	—
	<i>Phylloscopus collybita</i> and <i>Troglodytes troglodytes</i>	—	22.7	14.7	—
<i>Parus major</i> and <i>P. caeruleus</i>	—	14.3	28.0	—	
1962	<i>Sylvia atricapilla</i> and <i>S. borin</i>	—	6.9	—	16.0
	<i>Sylvia atricapilla</i> and <i>Phylloscopus collybita</i>	—	20.7	—	16.7
	<i>Sylvia atricapilla</i> and <i>Fringilla coelebs</i>	28.5	41.4	—	44.4
	<i>Sylvia atricapilla</i> and <i>Erithacus rubecula</i>	—	20.7	—	36.1
	<i>Sylvia borin</i> and <i>Phylloscopus collybita</i>	58.5	37.0	—	20.0
	<i>Sylvia borin</i> and <i>Fringilla coelebs</i>	12.2	13.0	—	44.0
	<i>Sylvia borin</i> and <i>Erithacus rubecula</i>	14.7	17.6	—	28.0
	<i>Phylloscopus collybita</i> and <i>Fringilla coelebs</i>	12.2	18.6	37.5	40.4
<i>Phylloscopus collybita</i> and <i>Erithacus rubecula</i>	29.4	23.5	43.6	34.8	
1963	<i>Sylvia atricapilla</i> and <i>S. borin</i>	0.0	—	—	12.5
	<i>Sylvia borin</i> and <i>Phylloscopus collybita</i>	30.5	—	—	31.3
	<i>Sylvia borin</i> and <i>Fringilla coelebs</i>	15.2	—	—	31.3
	<i>Phylloscopus collybita</i> and <i>Fringilla coelebs</i>	27.3	—	26.0	37.5

Index of overlapping of territories of *Phylloscopus collybita* and *Sylvia borin* (A) and the percentage of sample areas, at the given station, not occupied by *Ph. collybita* but favourable for *S. borin* (B), at stations K, C, N

Tab. XIII

Values of A and B	Stations		
	K	C	N
A	58.5	37.0	20.0
B	11.6	19.7	—

constitutes an optimum habitat for both these species, explains the increased overlapping of territories at this stations.

Another information about the reciprocal pressure of *Phylloscopus collybita* and *Sylvia borin* is provided by the comparison, at stations K and C, of the percentage of sample areas with *Sylvia borin* present in them, among the sample areas from which *Phylloscopus collybita* had left before the arrival of the next species. This is 76.9% at station K and only 37.5% at station C.

The extent to which the overlapping of territories of the various species depends upon the differentiation of the habitat was also studied in another way, namely, the relationship between the number of occurrence of one of the species in each sample area and the number of occurrences of the other species was studied by using the principle of correlation. A negative coefficient of correlation would in the given case indicate a considerable separation of the territories of two species; a correlation coefficient approximating 0, or a higher one — would indicate a lack of correlation between the occurrence of one species and that of the other, in each of the sample area.

The calculations were made regarding 3 pairs of species: *Phylloscopus collybita* and *Fringilla coelebs*, *Sylvia atricapilla* and *Sylvia borin*, and *Parus major* and *Parus caeruleus*, at stations K, C and M.

At stations where the habitat diversity is small (K and C) a negative coefficient of correlation was found, amounting, for individual pairs: -0.306 , -0.311 and -0.220 , with $\alpha = 0.05$. At station M, where the differentiation of the habitat was higher, the coefficients of correlation for the successive pairs were: -0.075 , $+0.155$ and $+0.330$ (in the first two cases the correlation was not significant). The above-given data indicate a clear separation of territories of the species considered, at stations at which the differentiation is low in comparison with a station characterized by a higher degree of differentiation of the habitat.

This is all the more surprising that, contrary to what is found, a separation of territories of the various species might seem more likely to occur at stations

with considerable diversity of the habitat, i.e. consisting of elements of the alder forest and of the mixed-wood islands, than at stations with pure alder forests or with only a slight admixture of mixed woods.

On the other hand, the varying degree of the overlapping of territories of the different species at each of the stations results from the interactions between these species, as revealed by the index of association. At stations for which low values of the index are obtained (individuals of different species keeping away from one another) there occurs a considerable separation of individual territories; at stations with an index value approximating one (tolerance between different species) the territories of the different species overlap to a considerable degree.

Parallel to the variations in the association index (S), with an increasing differentiation of the habitat, are changes in the quantitative relations of the community. The largest numbers of influential and dominant species are found at stations with a high degree of differentiation (Chapter 2, Tab. IX), that is, where the intensity of the interactions between species is the lowest. Here we can see a co-dominance of pairs of species between which interaction has been found to exist; by contrast to this, at stations with a low differentiation of the habitat, usually one component of a given pair is dominating.

Quantitative relations of this kind at stations differing in the degree of habitat differentiation have been found for the following species pairs: *Phylloscopus collybita* and *Fringilla coelebs*, *Phylloscopus collybita* and *Phylloscopus sibilatrix*, *Sylvia borin* and *Sylvia atricapilla*. The first named hold the position of dominants or influents at stations which are relatively homogeneous (with only a slight admixture of mixed woods), and the second — in habitats with the highest degree of differentiation. However, in these habitats a co-dominance is often found of both the components of the above-named species pairs (Fig. 8 A, B and C).

This is further confirmed by data from comparisons of the quantitative relations between these species at stations studied in 1960. The percentages of *Phylloscopus collybita* and *Fringilla coelebs* are most equalized in a group of stations with a high degree of differentiation — L, M, B. The percentage of *Phylloscopus collybita* in the total abundance including that of *Fringilla coelebs* appears to be at those stations 52, 46 and 47%, respectively, whereas at stations with lower degree of differentiation — K, J, E and G this percentage is higher — 58, 63, 60 and 61%, which indicates a stronger dominance of one of the species.

Analogous results have been obtained for *Phylloscopus collybita* and *Phylloscopus sibilatrix*, as also for *Sylvia borin* and *Sylvia atricapilla*. The percentage of *Phylloscopus collybita* in the total abundance including its own numbers

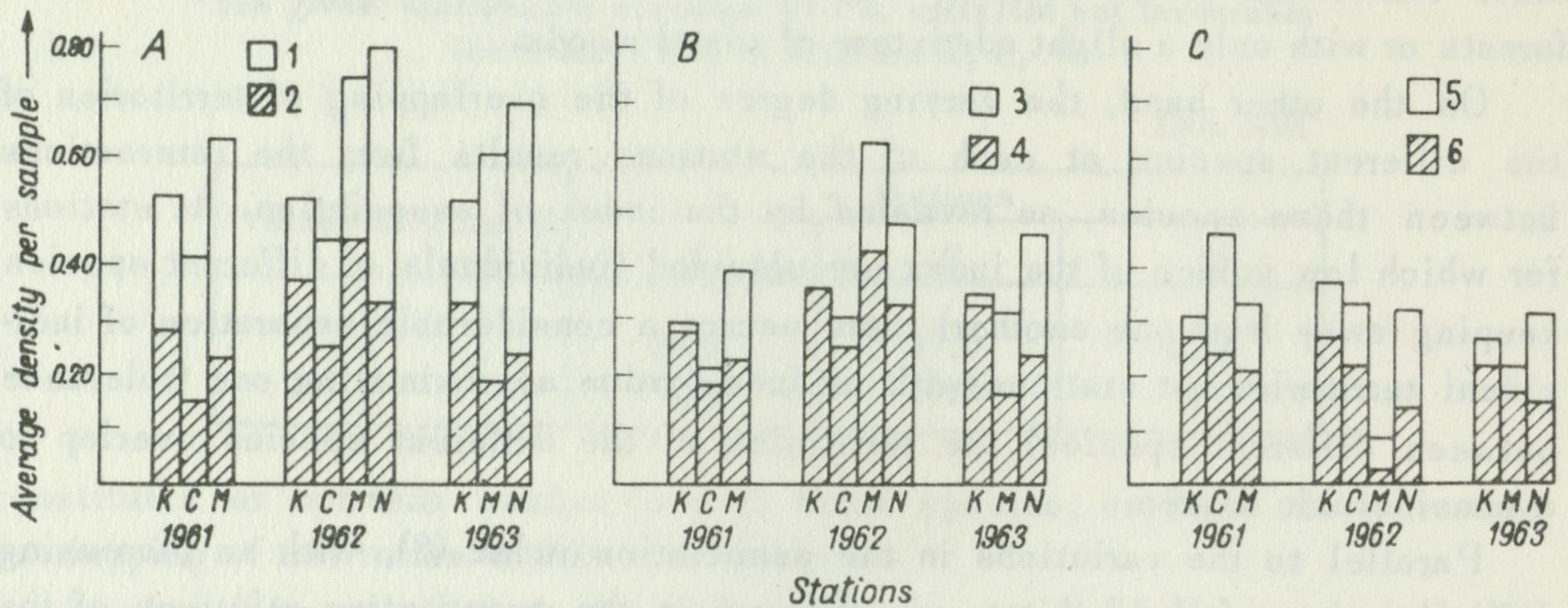


Fig. 8. Comparison of summary abundance and quantitative proportions of *Phylloscopus collybita* and *Fringilla coelebs* (A), *Ph. collybita* and *Ph. sibilatrix* (B) and also *Sylvia atricapilla* and *S. borin* (C) at stations K, C, M, N, arranged according to degree of the differentiation of habitat

1 - *Fringilla coelebs*, 2 - *Phylloscopus collybita*, 3 - *Ph. sibilatrix*, 4 - *Ph. collybita*, 5 - *Sylvia atricapilla*, 6 - *S. borin*

and those of *Phylloscopus sibilatrix*, in a group of stations with highly differentiated habitat, is: at station B - 59, F - 72, L - 50, M - 69%; at homogeneous stations: K - 100, G - 78, J - 95, E - 86%. The percentage contribution of *Sylvia borin* to the total abundance including that of *Sylvia atricapilla*, in a group of stations with a high diversity on the average amounts to 47%, and in a group of comparatively homogeneous stations (with a low degree of diversity) - 65%. A similar kind of relationship (a dominance of one species in a simplified habitat and a co-dominance of a number of species in a differentiated habitat) was found by Tompa (1964) for a combination of species including *Melospiza melodia* and some other species whose ecology is similar to that of *Melospiza melodia*.

As a result of an increased overlapping of territories of different species at stations with higher diversity, there eventually occurs an increase in the number of individuals in the community, correlated with an increase in the index of association (which indicates an increased tolerance between the species present at those stations (Fig. 9)).

Interspecies interactions could only be observed among comparatively abundant species. These interactions probably involve a larger number of species in the community, so a comparison of the abundance level of the whole community with the average values of index S, calculated for individual stations from a restricted group of species, seems to be justified. An analogous interde-

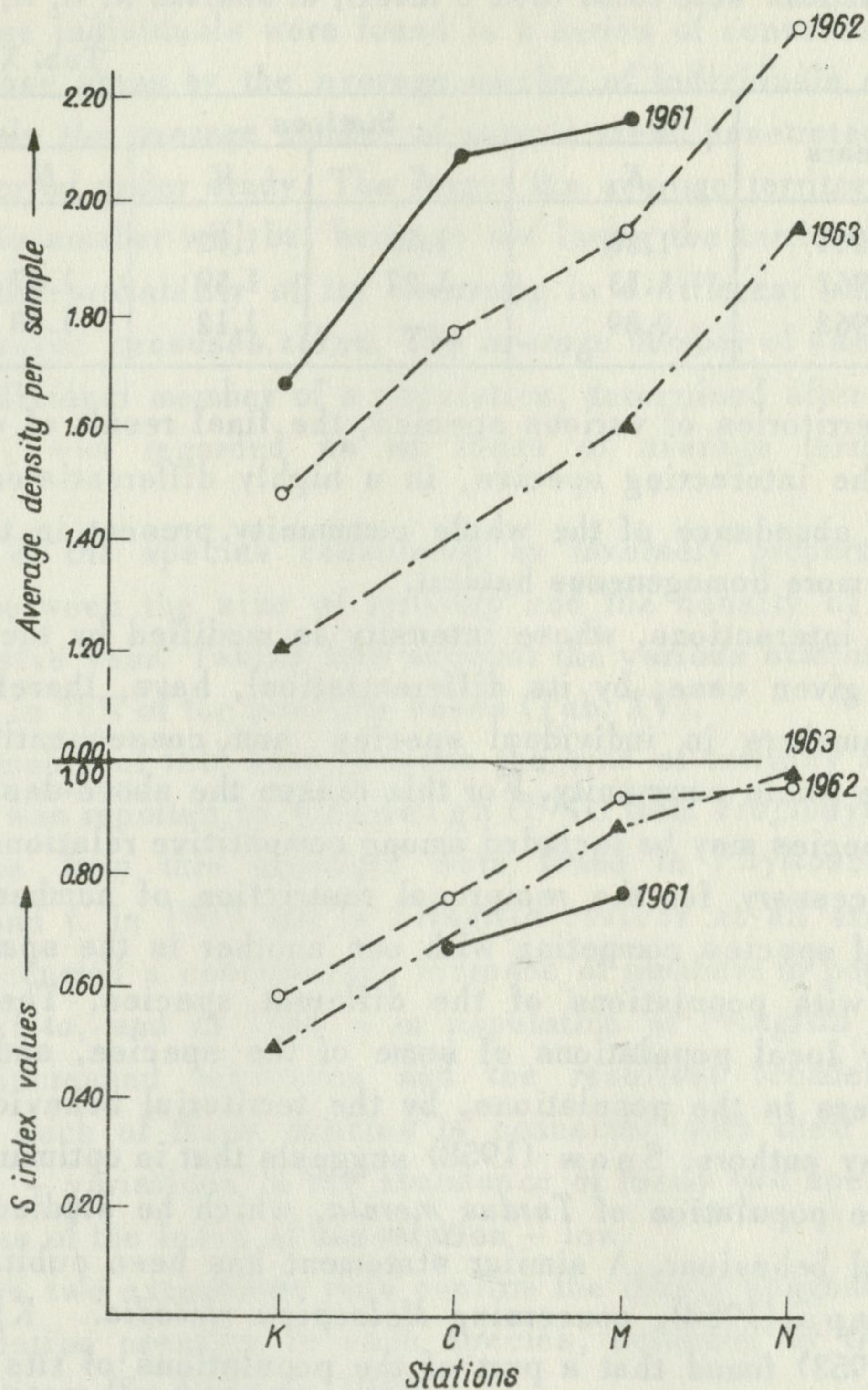


Fig. 9. Comparison of mean values of index S and the abundance level of the community (expressed as average density per sample) at stations K , C , M , N , arranged according to degree of differentiation of habitat

pendence is seen when the index S is compared with the abundance level of only those species between which interspecies interaction was found (Tab. XIV).

From the facts described in this chapter it may be concluded that: the nature of the habitat influences the interactions between the different species — an increase in the diversity causing an increase in the interspecies tolerance. A growth of the interspecies tolerance in its turn makes possible a higher

Comparison of total abundance level of species among which interactions were found (from *S* index), at stations *K*, *C*, *M*, *N*

Tab. XIV

Years	Stations			
	<i>K</i>	<i>C</i>	<i>M</i>	<i>N</i>
1961	1.38	1.63	1.72	—
1962	1.13	1.27	1.59	1.87
1963	0.89	—	1.12	1.48

overlapping of territories of various species, the final result of which is a co-dominance of the interacting species, in a highly differentiated habitat, and a growth in the abundance of the whole community present in that habitat, as compared with a more homogeneous habitat.

Interspecies interactions, whose intensity is modified by the nature of the habitat (in the given case, by its differentiation), have, therefore a limiting effect on the numbers in individual species and, consequently — upon the abundance of the whole community. For this reason the above-described interactions between species may be included among competitive relations.

A factor necessary for the reciprocal restriction of numbers to occur in a combination of species competing with one another is the spatial saturation of the habitat with populations of the different species. The existence of overcrowding by local populations of some of the species, and the resultant control of numbers in the populations, by the territorial behaviour, have been stressed by many authors. Snow (1958) suggests that in optimum biotopes the abundance of the population of *Turdus merula*, which he studied, was limited by the territorial behaviour. A similar statement has been published by Nice (1964) and Tompa (1964), concerning *Melospiza melodia*. Kluyver and Tinbergen (1953) found that a part of the populations of tits migrated from optimum biotopes, which were overcrowded, to suboptimum biotopes, where population density was lower. The author of the present paper (Wasilewski 1961) has found that the number of biotopes occupied by the populations of a number of species is directly proportional to the population density of the given species in optimum biotopes.

In this case, the spatial saturation in the populations of the species under study was inferred from the comparison of approximative sizes of territories and the population density of the different species in different years.

A direct determination of the size of territories of individual species could not be performed by the methods used in the present research. An index was, therefore, worked out, giving comparative data as to the size of the territories of a species in different years.

At each station the mean number of males in a species, occurring that year, was calculated. Subsequently, the number was determined of the sample areas in which those individuals were found in a series of censuses. By dividing the number of these areas by the average number of individuals occurring at a station, we obtain the average number of sample areas penetrated by an individual during the period under study. The larger the average territory of a population, the larger this number will be, because the larger the territory of an individual, the greater the probability of its occurring in a different sample area in each of the successive censuses taken. The average number of sample areas penetrated by an individual member of a population, determined after a definite number of censuses, was regarded as an index of average territory size of the population.

In most of the species considered an inversely proportional relationship was found between the size of territory and the density of the population in each successive year. Taking into account the various stations, this regularity can be found in 78% of the possible cases (Tab. XV).

A relationship of this kind between the size of territory and the density of a population was reported by Kendeigh (1941) from *Troglodytes aëdon*.

Deviations from this principle were found in *Phylloscopus collybita* at stations K and C in 1962 and in *Fringilla coelebs* at all stations in 1963. In 1962 there occurred a considerable increase of numbers in population of *Phylloscopus collybita*, and in 1963 – in population of *Fringilla coelebs*. In both cases the increased territories and the resultant broadening of the area occupied by each of these species is connected with their competitive interrelationships – variations in the abundance of these two species are opposite, and the values of the index of association – low.

The above two exceptions thus confirm the thesis suggesting the existence of intrapopulation pressure in each species, balanced by the biotic pressure of the competitors (Svårdson 1949).

3.3. Interspecific competition and the species distribution in the habitat

As has been mentioned, the abundance of a community and the numerical proportions of different species are determined, among other factors, by the competitive interactions between species. It may, therefore, be expected that the distribution of species at stations arranged, in this case, according to the growing gradient of diversity of the habitat, depends upon, besides habitat preferences of the species, the interactions between them.

Comparison of trends of population-density changes (*X*) and the index of territory-size (*A*) of some species in successive years at stations *K*, *C*, *M* and *N**

Tab. XV

Stations	Years	Species															
		<i>Fringilla coelebs</i>		<i>Phylloscopus collybita</i>		<i>Sylvia borin</i>		<i>Sylvia atricapilla</i>		<i>Erithacus rubecula</i>		<i>Troglodytes troglodytes</i>		<i>Parus major</i>		<i>Parus caeruleus</i>	
		<i>X</i>	<i>A</i>	<i>X</i>	<i>A</i>	<i>X</i>	<i>A</i>	<i>X</i>	<i>A</i>	<i>X</i>	<i>A</i>	<i>X</i>	<i>A</i>	<i>X</i>	<i>A</i>	<i>X</i>	<i>A</i>
<i>K</i>	1961/1962	-	-	+	+	+	-	+		-	+	-	+	-	+	-	+
	1962/1963	+	+	-	+	-	+	-		-		+		-		-	
<i>C</i>	1961/1962	-	+	+	+	-	+	-	+	-	+	-	+	-	+	+	-
<i>M</i>	1961/1962	-	+	+	-	-		-		-		-	+	+	+	0	+
	1962/1963	+	+	-	+	+		0		-		-		-	+	-	+
<i>N</i>	1962/1963	0	+	-	+	+	-	-	+	-	+	0		-	+	-	+

*+ = increase; - = a decrease in numbers or in territory-size index as compared with the preceding year; 0 = no clear changes from year to year.

In Chapter 2 have been described those species whose abundance increases, or decreases, with an increase in the differentiation of the habitat.

However, the distribution of individual species in relation to the gradient of the differentiation of the habitat varies considerably from year to year (Fig. 3).

The short distances between the stations and their considerable similarity do not permit the interpretation that this phenomenon is the result to different variations in environmental factors at each of the stations in the successive years of research. This suggests that the distribution of population abundance of the individual species occurring over the range of stations under study, is also determined by the interactions between the competing species. In support of the above suggestion the fact may be mentioned that the species here considered occur over a wider range of habitats than that represented by the stations covered by this research. This has been found by an analysis of the distribution of the species discussed in this paper, in a number of biotopes, typical for the Kampinos Forest (Wasilewski 1961).

The particular distribution of numbers of the individual species over a range of stations arranged in order of growing degree of the differentiation of the habitat cannot also be regarded as a result of preferences with regard to the two basic elements of the environment under study — the islands of mixed woods and the pure alder forest. If this were the case, the preferences of a given species with regard to alder forest and the mixed woods would be equally clear at all the stations, which only differ in the proportions of these two environmental elements. Contrary to this, the preferences are strongly marked at stations with a low degree of differentiation, and with considerable intensity of competitive interactions, whereas only slightly at stations with higher degree of differentiation, where the intensity of competitive interactions is lower (Chapter 2, Tab. VIII).

A detailed analysis of the effect of competition on the distribution of a pair of species is usually impossible, since it must be remembered that there may exist a complex interaction among a larger number of species. An analysis of this kind was attempted concerning *Phylloscopus collybita* and *Fringilla coelebs*; these two bird species are the first to occupy the area after arrival, so at that time the habitat is shared mainly by these two and only to a much lesser extent by other species of the community.

The four years' observation on the total abundance of these two species and on their distribution over a range of stations, arranged in order of habitat diversity, revealed the following relationships:

1. The variations in number of *Phylloscopus collybita* and *Fringilla coelebs*, in each of the successive years, are opposite. In 1960 and 1962 a low level

of numbers of *Fringilla coelebs* corresponded with relatively high numbers in the population of *Phylloscopus collybita*. In 1961 and 1963 a high population density of *Fringilla coelebs* corresponded with a low abundance of *Phylloscopus collybita* (Fig. 10).

2. Changes in numbers of both the species are not equal at all stations.

The smallest quantitative variations of population of *Phylloscopus collybita* were found at station K, and those of *Fringilla coelebs* at stations M and N, that is, at stations which are the most favourable for the population of these species (Tab. XVI).

As a result of the unequal intensity of variation in numbers at the different stations in the successive years, a change in the distribution of each of the species is observed over the range of stations considered, from year to year (Fig. 11). When a species occurs in small numbers, the highest density of its population is observed at optimum stations, when the abundance of the species is high, large densities can also be found at other stations, this being particularly clear in *Phylloscopus collybita*. These changes in the distribution are correlated not only with the variations in

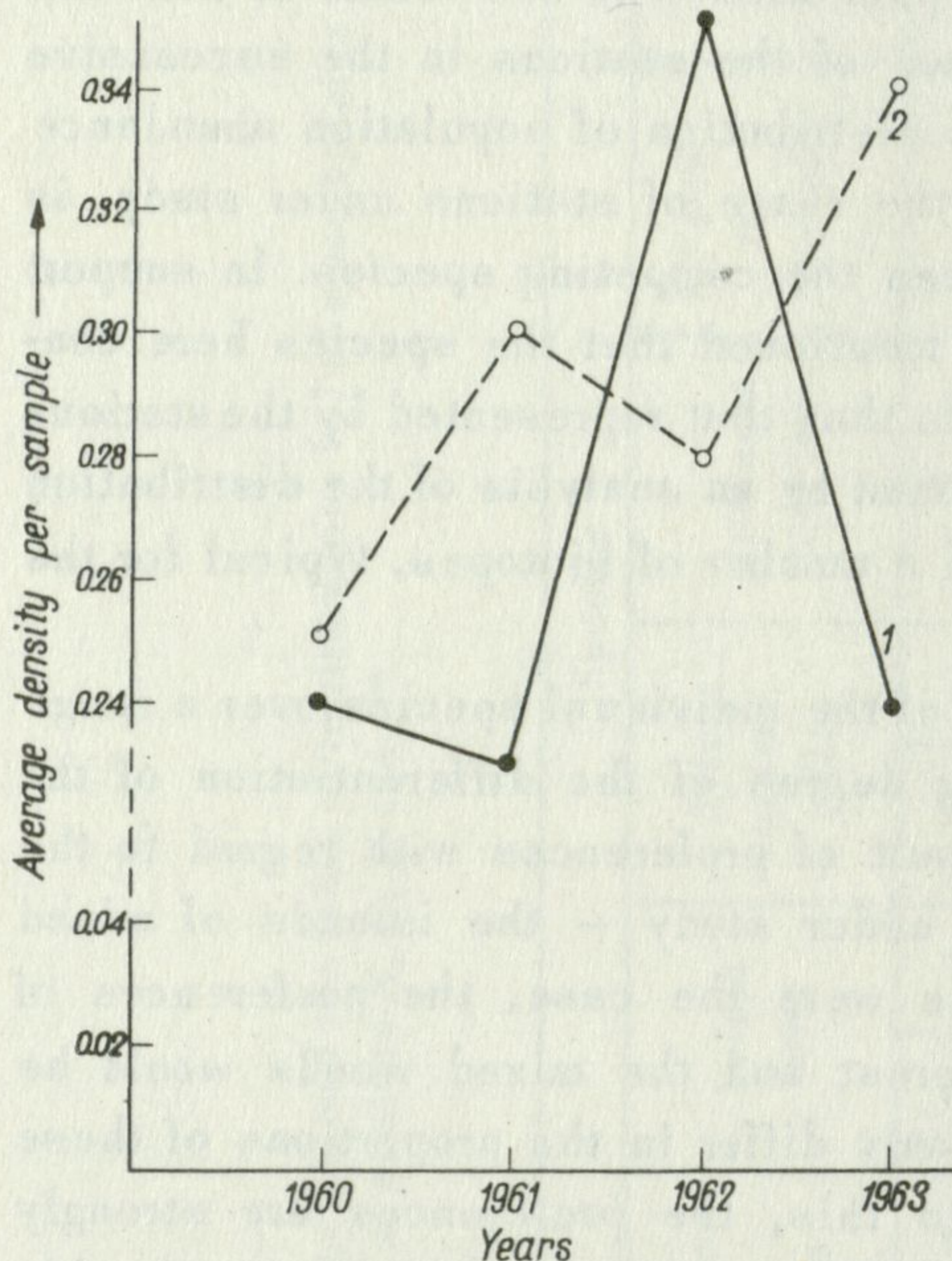


Fig. 10. Comparison of density of *Phylloscopus collybita* (1) and *Fringilla coelebs* (2) in different years

number of individuals of one species, but also with the opposite variations in the abundance of the other species. In 1961 the distribution of the population of *Phylloscopus collybita* was diametrically different from that in 1960, although the difference between the total number at all stations in 1960 and in 1961 was only 3%. The change in the distribution of *Phylloscopus collybita* was thus the result of the increase of the population of *Fringilla coelebs*.

From the above data the following conclusion can be drawn: the distribution of *Phylloscopus collybita* and *Fringilla coelebs* at stations arranged according to the degree of diversity of the habitat is determined, apart from the habitat preferences specific to each of the species, by their mutual competitive interactions, and by the existence of an intrapopulation pressure favouring the spreading of the species over a comparatively wide range of habitats.

Changes in abundance level of *Phylloscopus collybita* and *Fringilla coelebs* at stations K and M (in percent) in relation to preceding year

Tab. XVI

Years	Stations and species			
	K		M	
	<i>Ph. collybita</i>	<i>F. coelebs</i>	<i>Ph. collybita</i>	<i>F. coelebs</i>
1960/1961	+26	+47	-23	+17
1961/1962	+28	-20	+91	-27
1962/1963	-11	+33	-61	+13

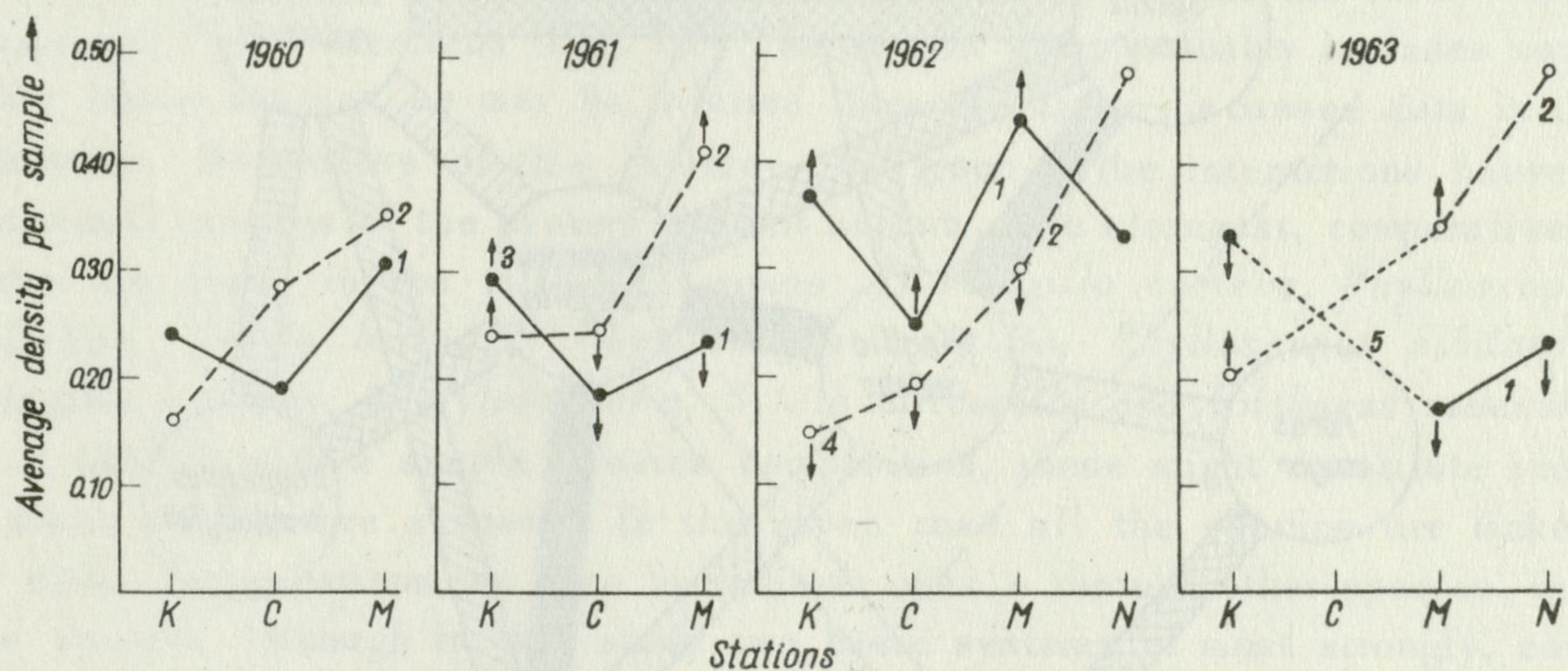


Fig. 11. Changes in the distribution of *Phylloscopus collybita* and *Fringilla coelebs* at stations K, C, M, N, arranged according to degree of the differentiation of habitat 1 - *Ph. collybita*, 2 - *F. coelebs*, 3-4 - arrows represent increase (3) or decrease (4) in population density at a station, in comparison with the previous year, 5 - interpolated data

Taking into account the above-mentioned considerations, the conclusion concerning the effect of competitive interrelations between *Phylloscopus collybita* and *Fringilla coelebs* on the distribution of those species may be extended also to the other species of the community, linked up by competitive relations.

3.4. The structure of competitive interrelations in a community - competitive associations

From index S data have been obtained concerning the interaction of a total of 29 combinations of species pairs. As has been stated above, these interactions reflect the competitive interrelations between species. Due to the lack of a sufficiently extensive (representative) material, it was not possible to establish the relationships for all species of the community under study. Nevertheless, when competitive interrelations have been found, even if for only

a limited species group, it is possible to draw conclusion concerning the structure of these relations, understood as an intensity of interactions between individual species, depending on their role in the community and their taxonomic position.

The nature of these interrelations is presented diagrammatically in Figure 12. The diagram contains data, based on the index of association, concerning

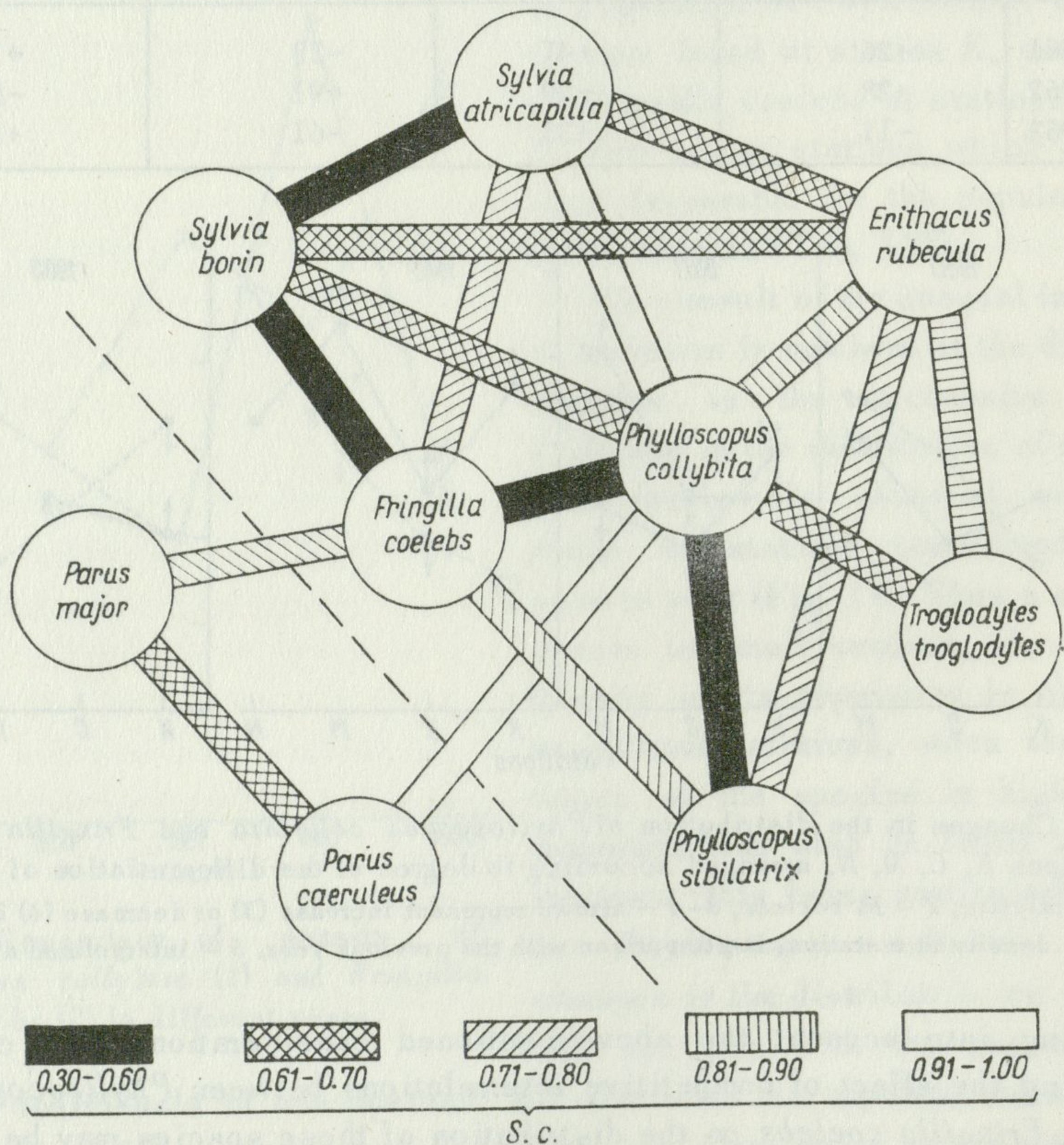


Fig. 12. A diagram to show competitive interrelations in the community S.c. - classes of S index value, expressing intensity of competition between species. Dotted line divides two different competitive associations

the occurrence of competitive interrelations between species, and their intensity. For this purpose mean values of the index S from sample areas $1/4$ and $1/8$ ha in size, collected in the course of 3 years, were utilized for each pair of species. In this case, stations with the lowest values of index S of the species pairs concerned were considered. Although this is only an approximative diagram, it reveals the presence of certain structure of the competitive interrelations in the community.

During the breeding season almost all the species considered in this study belong to the same trophic level. Nevertheless, the species food specialization, which no doubt exists in the community, regarding food, as well as the penetration of the habitat in search of food, and the differentiation of habitat requirements, determine the varying degree of overlapping of the ecological niches of the different species, and thereby the various strength of the competitive interrelations.

From the number of competitive links and their intensity two groups of species may be distinguished, which may be regarded as specific, distinct units in the community. One of these includes the following species: *Fringilla coelebs*, *Phylloscopus collybita*, *Sylvia borin*, *Sylvia atricapilla*, *Phylloscopus sibilatrix*, *Erithacus rubecula* and *Troglodytes troglodytes*; and the other: *Parus major* and *Parus caeruleus* (Fig. 12). The second group probably includes some other hollow nesters, as may be inferred from the above-discussed data in the literature. Regardless of this division, in group 1 the interactions between individual species of the system are not uniform. The strongest, comparatively, links are found in the following groups: 1) *Fringilla coelebs*, *Phylloscopus collybita*, *Sylvia borin*; 2) *Phylloscopus collybita*, *Phylloscopus sibilatrix*, *Fringilla coelebs*; 3) *Sylvia borin*, *Sylvia atricapilla* and *Erithacus rubecula*. In a habitat with a simple species composition, these might constitute independent competitive systems. In the given case all the species are linked, by direct interrelations, as also by indirect ones — through other species, into one system. Although in this study two basic systems of most strongly, comparatively, linked species are distinguished, this does not exclude the existence of other systems, which cannot be established due to the lack of evidence, concerning the nature of interrelations, for all the species present in the community considered. It should be expected that the number of such systems is proportional to the degree of differentiation and thereby to the number of species in the habitat.

Within the species groups here described, competition is the factor affecting the number of individuals of the different components, as also their distribution within the habitat occupied by these groups. This justifies the description of these groups of species as competitive associations, in the same sense as used by Lityński (1938), Tarwid (1952) and then by Kaczmarek (1953).

Individual associations are not separate ecologically; the components of one association may simultaneously be members of other competitive associations. The species linking up the individual associations are probably those characterized by a comparatively wide ecological valency. In fact the two associations here distinguished are linked together on the one side by *Fringilla coelebs* and on the other — by *Parus major*. Both these species may be termed eurytopic (Wasilewski 1961); they are at the same time polysynusal species

in respect of their stratified distribution (Pielowski 1961a), thus fulfilling the condition of euryvalency in relation to the environmental conditions, and probably to food conditions as well.

In his studies on the competitive system of macrofauna Kaczmarek (1963) ascribes to the euryvalent species the role of factors responsible for the integration of the system, which is established through the linking by species with relatively high specialization of the narrowly specialized species, which do not compete directly with one another. In the given case *Fringilla coelebs*, a typically euryvalent species, does not play such a role, because the remaining species of the community also are connected by numerous direct interactions. It is probable, however, that in other competitive systems of avifauna euryvalent species may function as factors integrating the community, especially where the environmental conditions favour the occurrence of large number of bird species.

Of 17 combinations of pairs of species, between which competitive interactions were found, there are only three pairs of species closely related taxonomically, belonging to the same genus. These are: *Sylvia atricapilla* and *S. borin*, *Phylloscopus collybita* and *Ph. sibilatrix*, and *Parus major* and *P. caeruleus*. The remaining combinations consist of species with relatively distant taxonomic positions.

In the studies hitherto published, competitive interrelations were sought for primarily within closely related species groups. The ground for this approach is the belief that between such species a most advanced convergence of ecological niches, and in consequence — a strong competition exist. However, within many such groups of closely related species spatial isolation is often so great that the species are, at least during the breeding season, out of contact, occupying quite different habitats, an example of which is the species belonging to the genus *Anthus*. This kind of isolation results from the way of speciation, most frequent in birds, through differentiation due to geographical isolation (Mayr 1942). On the other hand, a secondary contact between forms that have originated through geographical isolation, leads to a competition between them and to the formation of stronger or weaker ecological isolation — occupancy of different biotopes in the same region, to the differentiation of the trophic niche, when the same biotope is occupied, or to the occurrence in different strata in the same biotope (Lack 1944 and 1947).

Many studies analyzing the distribution or the trophic niches of closely related species are aimed chiefly at finding isolation between species (Lack 1945, 1946b, Moreau 1948, Hartley 1953, 1954, Gibb 1954, Betts 1955, Pielowski 1961a and 1961b). As a result, many authors suggest that there is no competition within groups of closely related species, or that if there is some competition its intensity is not great.

However, if closely related species occur in one habitat, their isolation as a rule is not complete. Owing to the fairly plastic nature of the trophic niche, and the habitat preferences of the species a possibility exists for these species to contact one another, and in consequence a possibility of interspecies competition.

Pielowski (1961b) carried out a detailed analysis of the various forms of isolation of *Phylloscopus collybita* and *Ph. sibilatrix*, as also of *Parus major* and *P. caeruleus*. He found a considerable isolation between these species, consisting in different penetration of the particular plant strata, different penetration of individual tree species, or in the species' passing by one another in space. Simultaneously, this isolation was not complete: at different periods there occurred a considerable overlapping of the spatial distribution of these species, whereas at the same time the forms of isolation varied with the types of biotopes. These facts indicate real interactions between these species, which has been confirmed by the results of the present study.

Competitive interrelations also occur between species of comparatively distant taxonomic relationship, the competition may then assume the same strength as between species belonging to one genus (Fig. 12).

Competition between taxonomically distant species seems to be a frequent phenomenon in a biocenosis, as pointed out by Kaczmarek (1963). Breymer (1966) studies the relationship between wandering spiders and other predatory arthropods and found competitive interrelations even between species representing different taxonomic groups.

The possibility of competition in such combinations of species is determined by a partial overlapping of the ecological niches of individual species, which, in addition to their trophic and environmental plasticity, leads to the maintenance of interspecies contact in the community.

It should be expected that in homogeneous habitats the overlapping of ecological niches of different species will be greater than in the more differentiated habitats; significantly greater will also be the strength of competitive interactions. This has been confirmed by the results concerning the strength of interactions between species in habitats with a varying degree of differentiation.

3.5. Quantitative compensation in a competitive association

By quantitative compensation in an association we mean a relative stability of the quantitative level of a particular group of species, resulting from their quantitative replacing one another.

In a system of species, quantitative compensation may only occur if a func-

tional replacement of one species by another is possible, based on the convergence of ecological niches of individual species of the system, and on the resultant competitive relations. Consequently, compensation phenomena may be expected in a group of species with the strongest competitive ties between them, here described as associations.

From the comparison of the number of individual species at different stations in the course of four years, an analysis was carried out to determine the extent to which quantitative compensation is realized within the associations distinguished in the study. For this purpose an association was considered, consisting of a comparatively large number of species connected by competitive interrelations. This association included the following species: *Fringilla coelebs*, *Phylloscopus collybita*, *Sylvia borin*, *Phylloscopus sibilatrix*, *Sylvia atricapilla*, *Erithacus rubecula* and *Troglodytes troglodytes*.

There are a number of circumstances under which quantitative compensation may occur in an association. These concern: 1) the size of the populations of the species in the association, 2) the phenology of their occupying the habitat, 3) concrete competitive ties in the association. The resulting consequences are considered below.

1. When the density of one, or more, species of the association decreases considerably, the decrease may only be compensated by those species which occur in that year in relatively large number of individuals.

2. A decrease in numbers of the species which occupy the habitat earlier may be compensated by those species which arrive later, if the latter occur in sufficiently large number, and not vice versa.

3. Since the competitive interrelations in an association are of a graded nature (Fig. 12), a decrease in numbers of a species may be compensated, in the first place, by those species which are connected with it by the strongest competitive links, the greater the number of competitive links between the species and the association, the greater the probability of occurrence of this phenomenon.

As regards the association here considered, these circumstances are formed as follows:

1. A decrease in the abundance of species arriving at a later time — *Sylvia atricapilla* and *S. borin*, cannot be compensated by those that arrive earlier.

2. The number of individuals of *Erithacus rubecula* and *Troglodytes troglodytes* have decreased regularly since 1961, so these species cannot compensate a decrease in each other's numbers, or in the numbers of the other components of the association.

3. A decrease in the number of *Erithacus rubecula* cannot be compensated by species such as *Fringilla coelebs*, which are not connected with it by com-

petitive links. As the territories of *Fringilla coelebs* and those of *Erithacus rubecula* overlap considerably, a compensation of a decrease in numbers of *Erithacus rubecula* by its possible competitors – *Phylloscopus collybita* and *Sylvia borin*, or by *Phylloscopus sibilatrix* at stations *M* and *N*, is difficult, because these species compete with *Fringilla coelebs*. The same applies of *Troglodytes troglodytes*, which is connected by competitive links only with *Phylloscopus collybita* and *Erithacus rubecula*.

As a result, during the period considered the following systems of species compensating one another could occur at each of the different stations:

1. At stations *K* and *C* – *Phylloscopus collybita*, *Fringilla coelebs*, *Sylvia borin*.

2. At stations *M* and *N* – *Phylloscopus collybita*, *Fringilla coelebs*, *Sylvia borin*, *S. atricapilla*, *Phylloscopus sibilatrix*.

In fact, in spite of a considerable decrease in numbers of the whole community (Tab. V), between 1961 and 1963, a relatively stable level of abundance was maintained within the group of the species distinguished above.

With that relatively high stability of the total abundance of the system of species considered there occurred a striking variability of the abundance of the individual components (Tab. XVII). This indicates that there really exists a quantitative compensation in associations of species. The reality of this phenomenon, in a different way, emphasized the importance of competition for the formation of quantitative relations in the community.

An analysis of the conditions under which compensation may occur in an association shows that, depending on the type of the habitat, one and the same species may, or may not, play the role of a compensating element in an association of competing species. This is determined by both the number of individuals in the species present in the habitat, and the number of species in the association and the nature of the interrelations that link them. This means that the number and the composition of the species forming an association, whose members compensate one another, may vary both with places and time.

In multi-species communities, probably more than one compensating system may occur, depending on the number of the associations distinguishable in the community. The biocenotic importance of the compensated systems consists in a relatively stable utilization of the same trophic level, regardless of the variations in the abundance of individual species in the community. The number of compensated associations of species plays an important role in the total number of individuals in the community. It may be expected that the degree of stability of the whole community will be proportional to the number of associations present in it.

Comparison of variations in abundance of individual species of the association (A) with variations in their total abundance (B) in the successive years at stations K, C, M, N (variations are expressed in per cent, in relation to the preceding year)

Tab. XVII

Stations	Species	Years					
		1960/1961		1961/1962		1962/1963	
		A	B	A	B	A	B
K	<i>Sylvia borin</i>	—	—	3.8	—	18.5	—
	<i>Phylloscopus collybita</i>	—	—	27.6	0.0	10.8	5.0
	<i>Fringilla coelebs</i>	—	—	37.5	—	33.3	—
C	<i>Sylvia borin</i>	20.0	—	12.5	—	—	—
	<i>Phylloscopus collybita</i>	5.3	1.5	38.9	1.5	—	—
	<i>Fringilla coelebs</i>	14.3	—	20.8	—	—	—
M	<i>Sylvia borin</i>	33.3	—	83.3	—	750.0	—
	<i>Phylloscopus collybita</i>	23.3	—	91.3	—	61.4	—
	<i>Fringilla coelebs</i>	17.1	3.7	26.8	8.9	13.3	12.7
	<i>Sylvia atricapilla</i>	5.3	—	65.0	—	14.3	—
	<i>Phylloscopus sibilatrix</i>	6.7	—	18.8	—	21.1	—
N	<i>Sylvia borin</i>	—	—	—	—	7.7	—
	<i>Phylloscopus collybita</i>	—	—	—	—	27.3	—
	<i>Fringilla coelebs</i>	—	—	—	—	4.2	3.9
	<i>Sylvia atricapilla</i>	—	—	—	—	15.8	—
	<i>Phylloscopus sibilatrix</i>	—	—	—	—	53.3	—

4. SUMMARY AND CONCLUSIONS

A comparison of the density of species, abundance level and quantitative relations of the community at each of the stations revealed the following relationships:

1. The level of the abundance of the whole community grows with an increase in the diversity of the habitat.

2. The number of influential and dominant species also grows with the increase in the differentiation of the habitat.

3. At each of the stations the species analyzed increase or decrease their numbers, depending on the growth of the differentiation of the habitat. In some of the species considerable variations in their distribution over the range of the stations investigated were observed in the different years. The variations were connected with the considerable increase in size of the populations of these species.

Subsequently, the role of interspecies interactions in the formation of quantitative relations of the community was studied.

For the estimation of interactions between species the index of association, informing about the avoidance or tolerance between individuals of two different species, was used.

1. The calculation of indices of the association between 9 of the most numerous species of the community (according to the principle each with each) showed interactions between the 17 pairs of species. These interactions consist in an active avoidance, in place and time, of individuals belonging to different species, and are inversely proportional to the distance between these individuals.

2. A comparison of the index of association between the species considered, at different stations, has shown that the interactions between species depend on the degree of differentiation of the habitat. A growth in the differentiation of the habitat is followed by an increase in the reciprocal tolerance between individuals of different species.

3. Simultaneously with the increasing degree of differentiation of the habitat an increase was observed in the overlapping of territories of the different species, among which competitive interactions occur.

4. An increase in the overlapping of territories of the different species, with an increasing degree of the differentiation of the habitat, is followed by an increase of the abundance of the community, and a co-dominance of interacting species.

5. The degree of the differentiation of the habitat does not, therefore, affect the quantitative relations of the community directly, but through the interspecies relations: a growth in the differentiation of the habitat causes an increase in the tolerance between the different species, owing to which a wider overlapping of territories of these species is possible. This results in a co-dominance of different species, and in an increase of the numbers of the community, following a growth in the differentiation of the habitat. The interactions between species thus restrict the numbers in the community, they have, therefore, been described as competitive interactions.

6. The restricting effect of interspecies competition on the numbers of a community is possible due to the spatial saturation of the habitat by the populations of the species here considered. This is indicated by the inversely proportional relationship between the density and the average size of territories of the populations of these species during each of the successive years of the research.

7. The distribution of numbers of the individual species at stations, arranged according to the degree of differentiation of the habitat, is determined, apart from their specific habitat-preferences, also by interspecies competition.

8. The formation of the abundance level of individual species, as also of

their distribution in the habitat, is carried out within groups of competing species, known under the term of competitive associations.

Within the associations, quantitative compensation was found, that is, a stability of numbers in the whole association, as compared with the considerable variation of numbers in individual species, members of the association, during the successive years of study.

The above-stated regularities indicate a significant influence of interspecies competition on the formation of the level of abundance, of the quantitative relations of the community, and of the distribution of individual species. Both the level of abundance of the community and its quantitative relations are to a considerable extent determined by competitive interspecies relations, the strength of which was modified, under the conditions described, by the differentiation of the habitat.

I wish to express my cordial thanks to Prof. Dr. K. Petruszewicz for many valuable comments throughout the elaboration of the material, and for discussing the main theoretical problems of this study. For the same reason thanks are due also to Prof. Dr. K. Tarwid, Dr. W. Kaczmarek and Dr. F. J. Turček. I wish to extend my thanks to T. Wierzbowska, M.Sc., for her kind assistance in the statistical elaboration of the material, and to Dr. T. Traczyk for describing the plant associations of the biotopes under study.

REFERENCES

1. Andrew, R. J. 1956 — Territorial behaviour of the yellow-hammer *Emberiza citrinella* and corn bunting *E. calandra* — *Ibis*, 3: 502–505.
2. Beecher, W. J. 1942 — Nesting birds and the vegetation substrate — Chicago, 69 pp.
3. Betts, M. M. 1955 — The food of titmice in oak woodland — *J. Anim. Ecol.* 24: 282–323.
4. Blagosklonov, K. N., Osmolovskaja, V. I., Formozov, A. N. 1952 — Učet čislennosti vorob'inyh, dжатловых i rakšeobraznyh ptic (Metody učeta čislennosti i geografičeskogo raspredelenija nazemnyh pozvonočnyh) — Moskva.
5. Bodenheimer, F. S. 1955 — Précis d'écologie animale — Paris, 315 pp.
6. Breckenridge, W. J. 1935 — A bird census method — *Wilson Bull.* 47: No. 3.
7. Brewer, R. 1963 — Ecological and reproductive relationships of blackaped and Carolina chickadees — *Auk*, 80: 9–47.
8. Breymeyer, A. 1966 — Relations between wandering spiders and other epigeic predatory *Arthropoda* — *Ecol. Pol. A*, 14: 27–71.
9. Creutz, G. 1955 — Ver trängt der Trauerfliegenschnäpper die Kohlmeise? — *Vögel der Heimat*, 9: 3–6.
10. Dice, L. R. 1945 — Measures of the amount of ecological association between species — *Ecology*, 26: 297–302.
11. Durango, S. 1956 — Territory in the red-backed shrike *Lanius collurio* — *Ibis*, 98: 476–484.

12. Eliseeva, V. I. 1960 — Vzaimootnošenija meždu polevym vorob'em i melkimi duplognezdnikami pri zaselenii iskustvennykh gnezdovij — Trudy centr. — černozem. gos. Zapov. 4: 321–331.
13. Forbes, S. A. 1907 — On the local distribution of certain Illinois fishes. An essay in statistical ecology — Bull. Ill. Lab. nat. Hist. 7: 273–303.
14. Gibb, J. 1954 — Feeding ecology of tits with notes on tree-creeper and goldcrest — Ibis, 96: 513–543.
15. Haartman, L. 1956 — Territory in the pied flycatcher *Muscicapa hypoleuca* — Ibis, 98: 460–475.
16. Hamilton, T. H. 1962 — Species relationships and adaptations for sympatry in the avian genus *Vireo* — Condor, 64: 40–68.
17. Hartley, P. H. T. 1953 — An ecological study of feeding habits of the English titmice — J. Anim. Ecol. 22: 261–288.
18. Hartley, P. H. T. 1954 — Wild fruits in the diet of British thrushes. A study in the ecology of closely allied species — British Birds, 47: 97–107.
19. Kaczmarek, W. 1953 — Badania nad zespołami mrówek leśnych — Ekol. Pol. A, 1: 69–96.
20. Kaczmarek, W. 1963 — An analysis of interspecific competition in communities of soil macrofauna of some habitats in the Kampinos National Park — Ekol. Pol. A, 11: 421–483.
21. Kendeigh, S. C. 1941 — Territorial and mating behaviour of the house wren — Ill. biol. Monogr. 18: 1–120.
22. Kendeigh, S. C. 1944 — Measurement of bird populations — Ecol. Monogr. 14: 67–106.
23. Kluyver, H. N., Tinbergen, L. 1953 — Territory and the regulation of density of titmice — Arch. néerl. Zool. 10: 265–289.
24. Lack, D. 1944 — Ecological aspects of species formation in passerine birds — Ibis, 86: 260–286.
25. Lack, D. 1945 — The ecology of closely related species with special reference to the cormorant (*Phalacrocorax carbo*) and shag (*P. aristotelis*) — J. Anim. Ecol. 14: 12–16.
26. Lack, D. 1946a — The life of the robin — London.
27. Lack, D. 1946b — Competition for food by birds of prey — J. Anim. Ecol. 15: 123–129.
28. Lack, D. 1947 — Darwin's finches — Cambridge.
29. Lityński, A. 1938 — Biocenoza i biosocjacja — Arch. Hydrob. Rybact. 11: 1–209.
30. Marler, P. 1956 — Territory and individual distance in the chaffinch *Fringilla coelebs* — Ibis, 98: 496–501.
31. Mayr, E. 1942 — Systematics and the origin of species — New York.
32. Merikallio, E. 1946 — Über regionale Verbreitung und Anzahl der Landvögel in Süd- und Mittelfinnland, besonders in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen. — Ann. zool. Soc. zool.-bot. fenn. „Vanamo”, 12:1–143.
33. Michelson, G. A. 1958 — Obzor obščich rezultatov raboty po privlečeniju melkich leśnych ptic-duplognezdnikov v Latvijskoj SSR — Trudy Akad. Nauk Lit. SSR, Orn. Issledov. 1: 5–72.
34. Moreau, R. E. 1948 — Ecological isolation in a rich tropical avifauna — J. Anim. Ecol. 17: 113–126.
35. Moynihan, M. 1963 — Inter-specific relations between some andean birds — Ibis, 105: 327–339.

36. Nice, M. M. 1964 — Studies in the life history of the song sparrow — New York, 246 pp.
37. Novikov, G. A. 1953 — Polevye issledovanija po ekologii nazemnych pozvonočnych životnych — Moskva, 502 pp.
38. Odum, E. P. 1959 — Fundamentals of ecology — Philadelphia, London, 562 pp.
39. Pielowski, Z. 1961a — Über die Vertikalverteilung der Vögel in einen *Pineto-Quercetum* Biotop — Ekol. Pol. A, 9: 1–23.
40. Pielowski, Z. 1961b — Untersuchungen über die Struktur der Vogelgesellschaften einiger Waldbiotope — Vogelwelt, 82: 65–84.
41. Pitelka, F. A. 1951 — Ecologic overlap and interspecific strife in breeding populations of Anna and Allen Hummingbirds — Ecology, 32: 641–661.
42. Promptov, A. N. 1932 — Kačestvennyj i količestvennyj učet fauny ptic „Izmajlovskogo Zverinca” pod Moskvoy — Zool. Ž. 11: No. 1.
43. Šapošnikov, F. D. 1938 — Opyt količestvennogo učeta ornitofauny v lesnom zakaznike Pustynskoj Biologičeskoj Stancii GGU — Uč. Zap. gorkovsk. gos. Univ. 8: 118–141.
44. Simmons, K. E. L. 1951 — Interspecific territorialism — Ibis, 93: 407–413.
45. Simmons, K. E. L. 1953 — Some aspects of aggressive behaviour of three closely related plovers — Ibis, 95: 115–127.
46. Snow, D. W. 1958 — A study of blackbirds — Glasgow, 191 pp.
47. Svärdson, G. 1949 — Competition and habitat selection in birds — Oikos, 1: 157–177.
48. Szafer, W., Kulczyński, S., Pawłowski, B. 1953 — Rośliny polskie — Warszawa, 1020 pp.
49. Tarwid, K. 1952 — Próba charakterystyki zespołów komarów Puszczy Kampinoskiej — Studia Soc. Sci. Toruń, 3: 1–29.
50. Tarwid, K. 1960 — Szacowanie zbieżności nisz ekologicznych gatunków drogą oceny prawdopodobieństwa spotkania się ich w połowach — Ekol. Pol. B, 6: 115–130.
51. Tompa, F. S. 1964 — Factors determining the numbers of song sparrows, *Melospiza melodia* (Wilson), on Mandarte Island, B.C., Canada — Acta zool. fenn. 109: 1–73.
52. Toropanova, G. A., Dubinin, A. P. 1962 — Pticy sosnovych, elovych i listvennych lesov v podzone smešannogo lesa i južnoj tajgi — Bjull. mosk. Obšč. Isp. Prir. (Bull. Soc. Nat. Moskva), 57: 50–60.
53. Udvardy, M. D. F. 1951 — The significance of interspecific competition in bird life — Oikos, 3: 98–123.
54. Wasilewski, A. 1961 — Some aspects of the habitat selection of birds — Ekol. Pol. A, 9: 111–137.

WPŁYW KONKURENCJI MIĘDZYGATUNKOWEJ NA LICZEBNOŚĆ I ROZMIESZCZENIE PTAKÓW W BIOTOPACH LEŚNYCH

Streszczenie

Celem pracy była ocena wpływu konkurencji międzygatunkowej na rozmieszczenie i liczebność ptaków danego zgrupowania. Przez konkurencję rozumie autor zależności

pomiędzy gatunkami należącymi do tego samego poziomu troficznego, które prowadzą do ograniczania liczebności bądź przestrzeni zajmowanej przez gatunek w danym środowisku.

Obiekt badań stanowiły głównie drobne wróblowate występujące w lasach rezerwatu Sieraków, w Kampinoskim Parku Narodowym. Teren badań, o łącznej powierzchni około 375 ha, obejmował nisko położone, zabagnione obszary lasów, na których występowały następujące zespoły roślinne:

1. ols – *Carici elongatae-Alnetum*,
2. bór mieszany – *Pino-Quercetum*,
3. grąd – *Tilio-Carpinetum*,
4. łęg – *Circaeo-Alnetum*.

Ols, porastający najniższej położone obszary bagien, stanowił zespół dominujący. Pozostałe zespoły związane były z rozrzuconymi wyspami w olsie grądami, wyniesionymi ponad poziom wód gruntowych. Rozrzucone w olsie wysepki grądów, wraz z występującymi na nich zespołami, stwarzają charakterystyczną dla badanego terenu mozaikowość środowiska. Wobec stosunkowej jednolitości olsów, stopień tej mozaikowości, proporcjonalnie do udziału powierzchni grądów w poszczególnych partiach olsu, różnicował w pierwszym rzędzie badane środowisko.

Badania prowadzone były w okresie lęgowym kiedy zależności konkurencyjne pomiędzy gatunkami występują szczególnie wyraźnie. Badania prowadzono w ciągu czterech lat: w 1960 na 10, w 1961 na 3, w 1962 na 4 i w 1963 na 3 stanowiskach. Powierzchnia poszczególnych stanowisk wahała się od 11 do 25 ha. Każde stanowisko podzielone było na powierzchnie próbne o wymiarach 50 × 50 m (fig. 1). Powierzchnie te były oznaczone numerami, a ich położenie pozostawało niezmiennym w ciągu kolejnych lat badań. Obserwacje prowadzono stosując metodę taksacji liniowej, to znaczy: idąc kolejno środkiem każdej powierzchni próbnej. Podczas obserwacji notowano dostrzeżone lub usłyszane na danej powierzchni próbnej osobniki różnych gatunków. Obserwację prowadzoną w ciągu 3 minut na danej powierzchni próbnej traktowano jako próbę. Stąd liczebność poszczególnych gatunków określano jako średnie zagęszczenie na próbę w danym stanowisku. W 1960 roku na każdym z 10 stanowisk przeprowadzono po 1 taksacji; w latach następnych przeprowadzono na poszczególnych stanowiskach od 5 do 8 taksacji w ciągu każdego sezonu. Na wszystkich stanowiskach wykonano łącznie 67 taksacji podczas których pobrano 3 957 prób, w których zanotowano 7 165 spotkań osobników różnych gatunków.

Na podstawie zastosowanej metodyki uzyskano dane co do zagęszczenia poszczególnych gatunków oraz ich rozmieszczenia na każdym ze stanowisk. Umożliwiło to szczegółową analizę:

1. wybiórczości środowiskowej poszczególnych gatunków,
2. stosunków ilościowych pomiędzy gatunkami,
3. zmian zagęszczenia rozpatrywanych gatunków w kolejnych latach badań,
4. zależności wielkości areałów osobniczych danego gatunku od zagęszczenia populacji,
5. stopnia pokrywania się areałów osobniczych różnych gatunków w różnych sytuacjach środowiskowych,
6. oddziaływań międzygatunkowych.

Podstawowym elementem różnicującym badane środowisko był stopień jego mozaikowości. Porównanie stosunków ilościowych oraz oddziaływań pomiędzy gatunkami przeprowadzono stąd na stanowiskach uporządkowanych według wzrastającego stopnia mozaikowości środowiska.

Na wszystkich stanowiskach stwierdzono występowanie ogółem 42 gatunków ptaków. Poszczególne stanowiska nie różniły się istotnie pod względem składu gatunkowego. Uznano stąd, że występujące na badanym terenie gatunki stanowiły jedno zgrupowanie.

Porównanie stosunków ilościowych tego zgrupowania na poszczególnych stanowiskach wykazało następujące zależności:

1. Łączna liczebność całego zgrupowania rośnie odpowiednio do wzrostu mozaikowości środowiska (fig. 2, tab. V).

2. Zagęszczenie analizowanych gatunków rośnie lub maleje odpowiednio do wzrostu mozaikowości (fig. 3). Tym niemniej zaobserwowano, w przypadku niektórych gatunków, znaczne zmiany ich rozmieszczenia w obrębie badanych stanowisk w różnych latach. Zmiany te związane były ze znacznym wzrostem zagęszczenia populacji tych gatunków.

3. Liczba gatunków influentnych i dominujących jest wyższa na stanowiskach o dużej mozaikowości (tab. IX).

Zbadano następnie, jaką rolę odgrywają oddziaływania międzygatunkowe w kształtowaniu przedstawionych wyżej stosunków ilościowych zgrupowania. Dla oceny oddziaływań międzygatunkowych wykorzystano wskaźnik informujący o wzajemnym unikaniu się przestrzenno-czasowym, bądź też tolerancji pomiędzy osobnikami dwóch różnych gatunków.

Wskaźnik ten, określony jako wskaźnik spotykalności (S) stanowi iloraz pomiędzy zaobserwowaną liczbą spotkań osobników dwu różnych gatunków w odpowiednio dużej serii prób a liczbą spotkań obliczonych na podstawie rachunku prawdopodobieństwa. Jeśli liczba zaobserwowanych spotkań osobników dwu różnych gatunków jest mniejsza od spodziewanej teoretycznie, oznacza to, że osobniki te unikają się wzajemnie; gdy liczba spotkań zaobserwowanych jest równa liczbie spotkań spodziewanych, lub nie różni się od niej istotnie, wskazuje to na wzajemną tolerancję pomiędzy osobnikami tych gatunków.

Obliczenie wskaźnika spotykalności dla 9 najliczniejszych gatunków zgrupowania (na zasadzie każdy z każdym) wykazało występowanie oddziaływań międzygatunkowych u 17 par gatunków (tab. X). Oddziaływania te polegają na unikaniu jednoczesnego przebywania osobników należących do różnych gatunków w określonej jednostce przestrzennej i są odwrotnie proporcjonalne do odległości pomiędzy tymi osobnikami (fig. 7).

Porównanie spotykalności rozpatrywanych gatunków na różnych stanowiskach wykazało, że oddziaływania międzygatunkowe zależne są od stopnia mozaikowości środowiska: wraz ze wzrostem mozaikowości środowiska następuje odpowiednio wzrost tolerancji pomiędzy gatunkami (tab. XI).

Ze wzrostem tolerancji pomiędzy osobnikami różnych gatunków skorelowany jest wzrost poziomu liczebności całego zgrupowania (fig. 9). W grupie oddziaływających na siebie gatunków stwierdzono przy tym ich współdominowanie na stanowiskach o wysokim stopniu mozaikowości, gdzie występuje jednocześnie najwyższa w porównaniu z innymi stanowiskami tolerancja pomiędzy tymi gatunkami.

Wraz ze wzrostem mozaikowości środowiska stwierdzono jednocześnie wzrost pokrywania się areałów osobniczych różnych gatunków (tab. XII).

Stopień mozaikowości środowiska nie wpływa więc na stosunki ilościowe zgrupowania bezpośrednio, lecz poprzez zależności międzygatunkowe: wzrost mozaikowości środowiska powoduje wzrost tolerancji pomiędzy osobnikami należącymi do różnych gatunków, dzięki której możliwe jest odpowiednio większe pokrywanie się areałów osobniczych tych gatunków. W efekcie następuje wzrost poziomu liczebności całego zgrupowania wraz ze wzrostem mozaikowości środowiska. Oddziaływania międzygatunkowe ograniczają tym samym liczebność zgrupowania i dlatego określono je jako oddziaływania konkurencyjne.

Ograniczające działanie konkurencji międzygatunkowej możliwe jest dlatego, że w populacjach rozpatrywanych gatunków występuje często zjawisko przegęszczenia. Wskazuje na to odwrotnie proporcjonalna zależność pomiędzy zagęszczeniem a przeciętną wielkością areałów osobniczych populacji szeregu gatunków w kolejnych latach badań (tab. XV).

Na podstawie porównania zmian liczebności niektórych konkurujących gatunków w ciągu 4 lat badań, a charakterem ich rozmieszczenia na badanych stanowiskach, stwierdzono, że rozkład liczebności (rozmieszczenie) poszczególnych gatunków na stanowiskach uszeregowanych według stopnia mozaikowości, obok właściwej tym gatunkom wybiórczości środowiskowej, uwarunkowany jest również przez konkurencję międzygatunkową.

Kształtowanie poziomu liczebności poszczególnych gatunków oraz ich rozmieszczenie w środowisku realizuje się w grupach konkurujących wzajemnie gatunków, które określono jako zespoły konkurencyjne (fig. 12). W obrębie zespołów stwierdzono występowanie (z roku na rok) kompensacji ilościowej, to jest – stabilności poziomu liczebności całego zespołu w zestawieniu z dużą zmiennością liczebności poszczególnych gatunków stanowiących zespół (tab. XVII).

Stwierdzone wyżej prawidłowości wskazują na istotny wpływ konkurencji międzygatunkowej na liczebność, stosunki ilościowe zgrupowania oraz rozmieszczenie poszczególnych gatunków ptaków. Poziom liczebności zgrupowania oraz stosunki ilościowe pomiędzy gatunkami tego zgrupowania określone są w znacznym stopniu przez konkurencyjne zależności międzygatunkowe, których nasilenie było z kolei modyfikowane w danych warunkach przez stopień mozaikowości środowiska.

AUTHOR'S ADDRESS:

Dr. Aleksander Wasilewski,
Institute of Ecology,
Polish Academy of Sciences,
Warszawa, ul. Nowy Świat 72,
Poland.