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INTERSPECIFIC COMPETITION IN RELATION TO HOMEOSTASIS
 IN BIRD COMMUNITIES

ABSTRACT

10-year study carried out in the Kampinos National Park shows that the total number of breeding pairs in multispecies bird communities is relatively stable. A particularly high stability in number was found for the group of species forming a competitive association. Analysis of numerical and spatial relationships in the association indicates that the tendency to maintain a stable number of breeding pairs has a character of homeostatic processes based on interspecific competition. The effect of association homeostasis on lower trophic levels is also discussed.

The present contribution is a preliminary analysis of the results obtained in long-term studies on the role of bird communities in forest ecosystems. Thus only basic concepts concerned with homeostatic processes in bird communities will be discussed here, without description of the methods applied.

The analysis is based on the long-term population dynamics of birds inhabiting some habitats of the Kampinos National Park during the breeding seasons of 1964—1973. Generally, the study was conducted in an about 10-ha plot supporting a mosaic of the oak-pine forest (*Pino-Quercetum*), lime-oak-hornbeam forest (*Tilio-Carpinetum*), and alder forest (*Carici-elongatae-alnetum*) (Tab. 1, stand PQ). In addition, data collected in a damp pine forest (*Vaccinio myrtilli-Pinetum*) are used for comparison (Tab. 1, stand VmP).

It has been found that the total number of breeding birds in the community inhabiting stand PQ was relatively stable through ten successive seasons. For hole nesters this stability was in fact maintained only during the period from 1964 through 1967, since in the following years their numbers were artificially increased as a result of supplying many nest boxes; but the stability of the other part of the community was very high, the index of variability over ten years being 7.1% (Tab. 1).

Table 1. Number of breeding pairs and number of species in two stands in the breeding seasons of 1964—1973.

Stands		Number of pairs										$V = \frac{\sigma}{x} 100\%$
		1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	
PQ	Hole nesters	23	26	28	25	38	46	41	44	59	57	32.7
	Others	82	77	70	78	82	81	90	83	88	89	7.1
VmP	Hole nesters	2	4	—	—	2	3	3	4	6	—	92.1
	Others	34	21	—	—	32	31	37	40	45	—	20.6

	Number of species										Cumulative for all years
	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	
PQ	25	25	24	24	24	25	21	27	27	26	33
VmP	9	9	—	—	12	11	12	12	16	—	17

The community under study occupied a highly diversified mature forest, thus it consisted of many species. The comparative data collected in about 50-year-old pine forest (stand VmP), where the number of species was lower by half (Tab. 1), show a considerably higher variability in the number of birds in the community.

A high stability of the total number of birds in communities comprising many species can be an effect of random interferences of independent fluctuations in the component species. In particular, it could be the case of migratory species, since timing, directions and ultimate destinations of migrations considerably differentiate survival rate of particular species, and this can account for independent fluctuations in their numbers from year to year. Conversely, severe climatic conditions in winter can unify population dynamics of many species [2].

Earlier studies conducted in the same area show, however, that only the settled part of the populations of particular species accounts for stability in the number of individuals in the whole community [4]. This suggests that other than casual factors are responsible for number stability in multispecies communities and, in particular, competitive interactions within the community. Hence, number fluctuations of seven species were analysed, which are known to form a competitive association [7].

Stability of the total number of breeding pairs over ten successive seasons was very high in this association, particularly, when compared with a considerable variability in numbers for particular species (Tab. 2). Such a high stability of the association could hardly be interpreted as an effect of random interferences of independent number fluctuations for particular components. It should be rather expected that inter-

Table 2. Variability in the number of pairs of particular species in the competitive association compared with the total number of pairs in this association for 10 years (1964—1973).

Species	Variability range of number of pairs min. max.	Mean number of pairs over 10 years	$V = \frac{\sigma}{x} 100\%$
<i>Fringilla coelebs</i> L.	12 — 22	17.0	20.7
<i>Phylloscopus collybita</i> Vieill.	6 — 19	12.1	28.8
<i>Phylloscopus sibilatrix</i> Bechst.	3 — 14	8.4	39.5
<i>Sylvia atricapilla</i> L.	2 — 12	6.9	46.9
<i>Sylvia borin</i> Bod.	1 — 5	3.0	33.3
<i>Erithacus rubecula</i> L.	5 — 11	8.5	51.9
<i>Troglodytes troglodytes</i> L.	1 — 7	3.3	49.1
Total association:	55 — 61	59.2	3.3

specific, competitive interactions limiting the number of pairs of definite species, are developed among them.

Since the number of birds was estimated by Enemar's mapping method, it was also possible to calculate an index of the area occupied by particular species each year. This index is based on the number of 12.5×12.5-m quadrats (the size of the grid used for the mapping of breeding territories) in which individuals of a given species were recorded through 5 censuses. Mapping of these quadrats, characterizing the size of the area utilized by particular species, and their subsequent superposition made it possible to determine the size of the area utilized by the whole association in a given year.

Like in the case of the number of birds, it has been found that the total area occupied by the association showed a high stability, while the area occupied by its particular component species considerably varied from year to year (Tab. 3). In addition, this indicates that spatial relationships among the component species are arranged. This conclusion is based on the fact that although the area occupied by particular species is in fact positively correlated with the number of breeding pairs, yet it does not automatically imply that the total area occupied by the association has to vary with time as little as the total number of pairs in the community does.

Table 3. Variability in the size of the area occupied by particular species and the whole association for 10 years (1964—1973).

Species	Variability range of area size		Mean area size for 10 years	$V = \frac{\sigma}{x} 100\%$
	min.	max.		
<i>F. coelebs</i>	62	— 108	84.2	18.5
<i>Ph. collybita</i>	20	— 64	42.8	33.6
<i>Ph. sibilatrix</i>	16	— 82	52.7	43.7
<i>S. atricapilla</i>	10	— 45	27.7	43.6
<i>S. borin</i>	7	— 16	12.1	26.3
<i>T. troglodytes</i>	1	— 20	12.1	43.0
<i>E. rubecula</i>	29	— 56	43.4	17.7
Total association:	220	— 239	229.2	3.0

At the same time, it is not possible to recognize a competitive background of the relationships described above by, for instance, searching for negative correlations between numbers of pairs of particular species compared on the one-to-one basis. The reason is that within the association there act concurrent competitive impacts but of different intensities [7]. On the other hand, particular species do not occupy their territories simultaneously. Firstly such species appear as *Fringilla coelebs*, *Phylloscopus collybita*, *Erithacus rubecula*, and *Troglodytes troglodytes*, then *Phylloscopus sibilatrix*, and finally *Sylvia*

atricapilla and *Sylvia borin*. Taking into account these time lags in the appearance of particular immigrants, it seems probable that the possible low densities of early settlers will be compensated by high densities of late immigrants, or that the density of the latter group will be limited when early immigrants reach high densities. Consequently, a negative correlation between these two groups of species would verify the hypothesis that stability of the total number of pairs in the association is not casual.

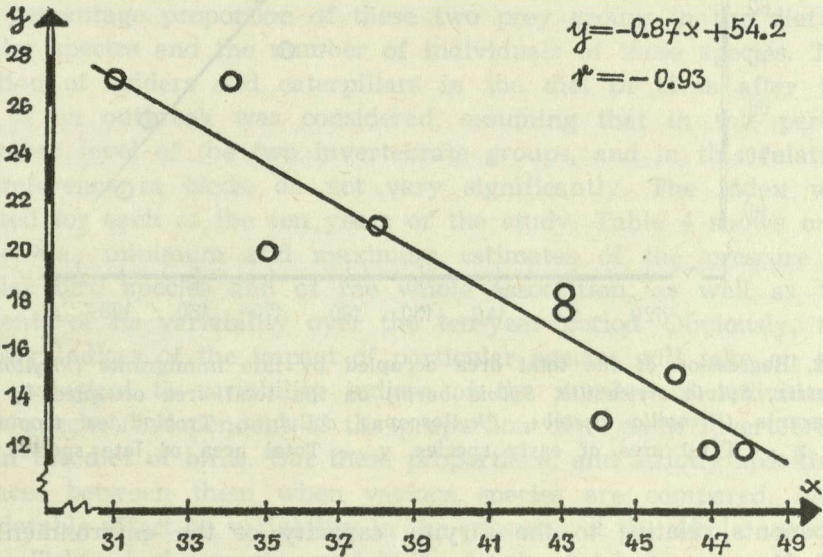


Fig. 1. Regression of the total number of breeding pairs of late immigrants (*Phylloscopus sibilatrix*, *Sylvia atricapilla*, *Sylvia borin*) on that of early immigrants (*Fringilla coelebs*, *Phylloscopus collybita*, *Troglodytes troglodytes*).
 x — Total number of early species, y — Total number of late species

And really, a high, statistically significant negative correlation ($r = -0.93$) was obtained when the total numbers of late immigrants (*Ph. sibilatrix* + *S. atricapilla* + *S. borin*) were plotted against the total numbers of early immigrants (*F. coelebs* + *Ph. collybita* + *E. rubecula* + *T. troglodytes*) in particular years (Fig. 1). A similar analysis was followed to find a relationship between the size of areas utilized by these two groups. Again a high negative correlation was obtained ($r = -0.96$), this relationship being better described by a curvilinear function (correlation ratio $R = 0.98$, Fig. 2).

The results presented above show that the numerical stability of the association largely depends on competitive interactions among component species. These interactions show a character of regulatory processes, since both compensation and limitation of the number of

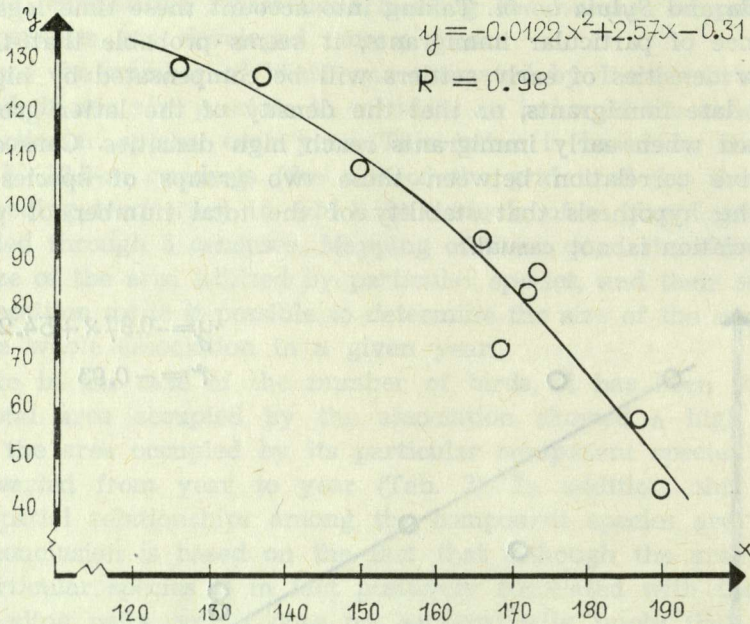


Fig. 2. Regression of the total area occupied by late immigrants (*Phylloscopus sybilatrix*, *Sylvia atricapilla*, *Sylvia borin*) on the total area occupied by early immigrants (*Fringilla coelebs*, *Phylloscopus collybita*, *Troglodytes troglodytes*)
 x — Total area of early species, y — Total area of late species

components relative to the carrying capacity of the environment are involved.

In this case it was possible to analyse competitive relationships within one association. But in multispecies communities there may be more such associations. Another example of a distinct association is the group of hole nesters [3]. It can be expected that the number of possible competitive relationships and, in this relation, the stabilizing effect, will rather be proportional to the number of species in a given association.

All bird species belonging to the analysed association are insectivorous general predators during the breeding season. Thus a question arises about the consequences that the association stability can have to lower trophic levels.

Nutritional relations in the association were analysed on the basis of a relatively large number of samples (about 7000) of food items collected from nestlings by means of the collar ligature method. Food spectrum of 11 bird species was analysed. Comparison of the diet composition in particular species (Renkonen's similarity index modified by Romaniszyn [5] was used) showed a relatively high

similarity of feeding niches in the association. It was due to a high preference for two invertebrate groups: the leaf-eating larvae and the spiders.

It would be interesting to know how the degree of feeding niche overlapping can influence the possibility of a functional replacement of particular species by one another within the association. Basing on the data for four species, a model was constructed to determine variability in the impact of these four species on the group of caterpillars and spiders. The index of this impact was calculated as a product of the percentage proportion of these two prey groups in the diet of particular species and the number of individuals of these species. The proportion of spiders and caterpillars in the diet of birds after the period of an outbreak was considered, assuming that in this period the number level of the two invertebrate groups, and in this relation food preference in birds, do not vary significantly. The index was calculated for each of the ten years of the study. Table 4 shows only extreme, i.e., minimum and maximum estimates of the pressure of particular bird species and of the whole association, as well as the coefficients of its variability over the ten-year period. Obviously, the variability indices of the impact of particular species will take on the values analogical to variability indices of the number of individuals in these species, independent of the proportion of a given invertebrate group in the diet of birds. But these proportions, and strictly speaking, differences between them when various species are compared, have a considerable effect on variability in the pressure of the whole association. As Table 4 shows, the variability in the total pressure of the association is considerably lower than that of its particular components.

Table 4. Simulation model of the variability in the impact of particular bird species and of the whole association on caterpillars and spiders during the period following an outbreak (upper figures — caterpillars, lower figures — spiders).

Bird species	Proportion of prey groups in diet (%)	Variability range of impact for 10 years	$V = \frac{\sigma}{x} 100\%$
<i>F. coelebs</i>	65	780—1430	20.7
	28	336—616	
<i>Ph. collybita</i>	50	300—950	28.8
	35	210—665	
<i>Ph. sibilatrix</i>	21	63—294	39.5
	20	60—280	
<i>S. atricapilla</i>	20	40—240	46.9
	25	50—300	
Total association:		1672—2329	9.9
		1129—1329	5.5

Although this is a hypothetical model (a constant food preference in time is assumed), it indicates that not only numerical compensation can occur within an association, which stabilizes the level of the number of individuals in this association, but also a functional compensation, due to which matter transfer from lower trophic levels is stabilized in the period after an outbreak, independent of number fluctuations in particular components of the association. Thus we have here the case when one of the principles determining homeostasis of a biocoenosis operates, namely, the principle of the conservation of matter cycling and energy flow at the level of a competitive association [6].

A system of the consumers of a higher order can perform its regulatory function in relation to lower trophic levels only when the pressure of predators increases adequately to the rise in the density of their prey. In the case of bird communities, which are characterized by an extremely high stability of number, it cannot be expected that the outbreak of a pest might stimulate an increase in the density of birds, at least in forest communities. And so, the outbreak of *Operophtera brumata* and other accompanying leaf-eaters in the study area in 1971 was not followed by an increase in the density of birds [1]. One may ask, however, whether there is not a shift in food preference during pest outbreaks, which could compensate, to some extent, for lack of the numerical response.

To get an answer, a comparison was made of the character of feeding relationships in the bird community for periods of high numbers (1971, 1972) and low numbers (1973, 1974) of leaf-eating entomofauna (Tab. 5).

Indices of similarity in the diet of birds were considerably higher during outbreaks than in the years of low number of leaf-eating entomo-

Table 5. Trophic relationships in the bird association during the periods of an outbreak and a low density of leaf-eating insects.

	Outbreak period			Postoutbreak period	
	1971	1972		1973	1974
Number of bird species analysed	7	8		6	7
Number of two-species pairs	20	27		15	21
Mean values of the index of similarity in diet	29.9%	36.7%	>	18.1%	26.2%
Mean proportion of leaf-eating larvae in diet	45.0%	57.5%	>	29.2%	33.7%
Mean proportion of spiders in diet	14.8%	10.3%	<	19.8%	21.5%

fauna. This is due to the fact that the average proportion of caterpillars in the diet of birds was considerably higher and the proportion of spiders considerably lower, as compared with the period of low pest numbers. Therefore, during the outbreaks food preference in birds is shifted to mass-occurring prey.

If we calculate the impact of the association (basing on the data for ten bird species) on leaf-eating larvae and on spiders during and after the outbreak, the impact on caterpillars will be 1.8 times higher, while on spiders 1.8 times lower in the former period. Thus the bird community tended to stabilize definite relationships within lower trophic levels.

Although it does not seem probable that birds as a group can control a large outbreak, the data on other groups of general predators show that they have similar effects, stabilizing trophic relationships through shifting directions of matter flux [8, 9].

Obviously, the data presented above are of indicatory character, nevertheless, they seem to suggest that in bird communities there are mechanisms having an effect on homeostasis of trophic relationships in forest ecosystems.

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KONKURENCJA MIĘDZYGATUNKOWA A ZJAWISKA HOMEOSTATYCZNE W ZESPOŁACH PTAKÓW

STRESZCZENIE

W ciągu 10-letnich badań nad zgrupowaniem ptaków na stanowisku obejmującym mozaikę boru mieszanego, grądu i olsu, stwierdzono w okresie lęgowym stosunkowo wysoką stabilność liczebności tego zgrupowania, liczącego ogółem 33 gatunki. Szczególnie wysoką stabilność stwierdzono w odniesieniu do łącznej liczebności 7 gatunków, które na podstawie poprzednich badań zaliczono do zespołu konkurencyjnego. Zmienność sumarycznej liczebności tego zespołu, wyrażona wskaźnikiem zmienności V , w okresie 10 lat wynosiła 3,3%, natomiast zmienność liczebności poszczególnych komponentów zespołu była znacznie wyższa — od 20,7 do 57,9%. Stwierdzono również, że nie tylko liczebność ale i powierzchnia stanowiska zajmowana łącznie przez zespół zmieniała się w ciągu 10 lat w niewielkich granicach ($V = 3\%$), przy wysokiej zmienności wielkości powierzchni zajmowanej przez poszczególne gatunki ($17,7 = 43,7\%$).

Możliwość utrzymywania się stabilnej liczebności zespołu warunkował silnie zróżnicowany, dojrzały drzewośtan, określający stałą pojemność środowiska dla badanego zespołu. Z drugiej strony, mechanizm stabilizujący liczebność zespołu stanowi konkurencja pomiędzy poszczególnymi jego komponentami. Wskazuje na to wysoka ujemna korelacja pomiędzy liczebnością gatunków, które stosunkowo późno zajmują tereny lęgowe a sumaryczną liczebnością gatunków zajmujących terytoria lęgowe w pierwszej kolejności. Analogiczna zależność zachodzi w przypadku korelowania powierzchni stanowiska zajmowanej przez te grupy gatunków w poszczególnych latach. Opisane tu zjawisko stabilizacji liczebności zespołu ma charakter procesu homeostatycznego, obejmuje bowiem zarówno ograniczanie wzrostu jak też i kompensowanie spadku liczebności określonych gatunków w zespole przez pozostałe gatunki.

Analiza zależności pokarmowych w zespole wskazuje, że stabilność liczebności zespołu wywiera stabilizujący efekt na przepływ materii z poprzedzającego poziomu troficznego. Porównanie składu pokarmowego poszczególnych gatunków wykazało stosunkowo wysoką zbieżność nisz pokarmowych w zespole, uwarunkowaną wysoką wybiórczością pokarmową w stosunku do dwóch grup bezkręgowców: larw liściożernych i pajaków. W warunkach przeciętnego zagęszczenia fitofagów ten poziom zbieżności nisz pokarmowych wystarcza aby przy stabilnej liczebności zespołu, niezależnie od wahań liczebności jego komponentów, utrzymywała się stała presja w stosunku do obu grup bezkręgowców. Z kolei w przypadku zaistnienia gradacji, następuje znaczny wzrost presji na larwy roślinożerne, a spadek presji zespołu na pająki, czyli tendencja do przywrócenia istniejących uprzednio stosunków w obrębie niższych poziomów troficznych.

МЕЖВИДОВАЯ КОНКУРЕНЦИЯ И ГОМЕОСТАТИЧЕСКИЕ ЯВЛЕНИЯ
В СООБЩЕСТВАХ ПТИЦ

РЕЗЮМЕ

В течение 10-летних исследований, проводимых в гнездовом периоде над сообществом птиц (в общем 33 вида), населяющих Кампиносский национальный парк, констатировалась значительная устойчивость численности этого сообщества. Особенно высокой стабильностью характеризовалась группа видов, составляющих конкурентное сообщество.

Анализ количественных соотношений и пространственной организации в сообществе указывает на то, что стабильность его численности носит характер гомеостатического процесса, обусловленного межвидовой конкуренцией. Обсуждены последствия гомеостатического состояния в пределах сообщества для предшествующих трофических уровней.

ABSTRACT

The stability of the population size of various species, comprising the avian community of the Kampinoski National Park, was studied during a 10-year period. It was found that the population size of the avian community was stable. The stability of the population size of the avian community was particularly high in the case of the competitive community. The analysis of the quantitative relationships and the spatial organization in the community indicates that the stability of its population size is a characteristic of a homeostatic process, caused by interspecific competition. The consequences of the homeostatic state in the community for the preceding trophic levels are discussed.

It is generally accepted that there exists a connection between the stability of a community and the number of species in the community. For instance, the stability of an ecosystem usually increases with increasing in species number. A particular stage in succession sequence, homeostasis, is not the only factor determining an efficient functioning of an avian community. Depending on the relationships between the numbers of species and the stability of a biocoenosis, a practical method of forest protection was developed which consists in the introduction of "biocides" of avian origin (birds) (Budyakova 1971). The introduction of new plant species was followed by changes in the existing ecological systems and, as a result, by an increase in the stability of the whole system. Due to this, for instance, outbreaks of larch pests were eliminated in this area.