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CERTAIN ASPECTS OF THE HABITAT SELECTION
OF BIRDS

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STUDY AREA AND METHODS

One of the working methods used for this study consisted of the selection of several habitats distinctly differing from each other, which taken together covered a wide range of living conditions of avifauna, while each separate habitat was as far as possible uniform within itself. At the same time the differentiated habitats should be distributed so as to make it possible to connect them by means of one or two observation belts, in such a way that the whole forms one elongated sequence. Transition from one habitat to the next should, however, be completely distinct.

In accordance with the foregoing conditions, two observation belts were chosen, independent of each other, one of which commanded three, and the second four, habitats, distinctly differing from each other as regards the physionomy of the vegetation cover. These habitats are not completely free of a somewhat mosaic-like character, but they nevertheless differed from each other to an extent which made it possible to consider them as separate units.

This permitted, on the one hand, of considering the differentiated habitats independently of each other, and on the other, of classifying them according to the gradient of variations in the defined elements of the habitat. In the first case, it is possible to analyse the distribution of the birds within, and on the boundaries between the biotopes. In the second case definition of the density of bird population in a given habitat makes it possible to determine the degree of the birds attachment to the habitat. The variable density of the birds may also be arranged according to the defined gradient of the habitat.

Linear assessment was used as the method for estimating the numbers of birds.

The observation route led along two independent belts — Belt I embraced four habitats, Belt II — three. The length of the observation belt differed in

[1]

different habitats — the total length of belt I was approximately 3500 m., and of belt·II 2100 m. — width of both belts was 100 m., that is, 50 m. to the left and 50 m. to the right of the route established. Each of the paths was divided into 100 m. sections, each of which was numbered in order. The width was assessed visually.

Each section therefore corresponded to a square hectare in area. Passage on foot through one section, lasting five minutes, was established as being a „sample". The observation route was, wherever the nature of the area permitted, made in a bee-line, or along narrow paths or clearings.

Observations were made during the period of maximum activity of the birds, i.e. at most for four hours after sunrise, and only during good weather.,

The presence of birds in the observation belt was established either visually, or by hearing their song or the sounds they utter. Birds flying above treetops, and therefore totally unconnected with the place of observation, or only to an inconsiderable extent, were not counted.

The observation period lasted from May 1956 to December 1957, with the exception of March and July 1957. From 4 — 7 observations were made each month in each belt; during the winter period the number of observations was less in certain months. The number of observations occuring during the different months, and the corresponding number of samples, are set out in Table I.

The number given above of from 4 — 7 passages made in a relatively short period, permitted of obtaining sufficiently accurate data as to the specific composition and numbers of birds, and their distribution in the space. The empirical data obtained by P a l m g r e n (1930) show that a single transit of the sample area requires the addition of correction equal to 60%, transit made twice — 24%, made three times — 10%, and four times — 4%. In view of this, the number of transits made by the author would, with the exception of several winter months, appear to be sufficient.

The data obtained refer both to the singing male birds, and to the birds which either utter sounds or are silent, which may include males, females and young birds.

Application of linear assessment involves several errors. An exhaustive discussion of this problem is given by P a l m g r e n (1930), K e n d e i g h (1944) and T u r č e k (1956). Here only those points involved by the particular method used will be emphasised.

The diurnal cycle of the activity of the various species may differ. The activity of a given species, where observations of short duration are used, may be subject to variations. As a result the data obtained constitute, to a certain extent, the average of the activity and numbers of the given species. This is even more striking in the seasonal aspect. The above errors are of significance when attempting to make an estimation of the absolute numbers of a population; but the accuracy of the results obtained would appear to be sufficient to obtain relative, comparable data on the numbers and distribution of the species investigated in different habitats.

Comparison of number of samples in the different habitats in successive months
Zestawienie ilości prób przeprowadzonych w poszczególnych środowiskach w kolejnych
miesiącach

Tab. I

Date — Data		Number of samples — Liczba prób						
		Belt I — Pas I			Belt II — Pas II			
		Habitats — Środowiska						
		A	B	C	D	E'	E	F
1956	V	36	24	56	24	16	32	36
	VI	36	24	56	24	16	32	36
	VII	54	30	70	30	16	32	36
	VIII	36	24	64	30	16	32	36
	IX	72	42	84	36	20	40	45
	X	27	18	28	12	12	24	27
	XI	36	24	42	18	12	24	9
	XII	36	24	9	24	12	24	0
1957	I	27	18	42	18	8	16	18
	II	45	30	53	30	20	40	27
	IV	63	42	98	42	28	56	63
	V	36	24	56	24	16	32	36
	VI	45	30	70	30	20	40	45
	VIII	63	42	104	48	28	56	63
	IX	45	30	84	36	20	40	45
	X	45	30	70	30	20	40	45
	XI	18	12	28	12	8	16	18
	XII	36	24	43	18	12	24	19
Total Razem		756	492	1057	486	300	600	604

The investigations covered 24 sub-sections of the Forest Intendancy of
Laski, in the south-east part of the Kampinos Forest. Observation belts passed
through a total of seven habitats, which have been given letters to facilitate
description. The length of the observation routes in the different habitats of
Belt I and II was as follows:

Belt I   Belt II
A — 900 m.   E[1] — 400 m.
B — 600 m.   E — 800 m.
C — 1400 m.   F — 900 m.
D — 600 m.

A short description follows of the habitats under discussion.
Mixed forest (A). Belongs to the *Pineto-Quercetum* association. 85—year
old forest stand is composed of pine, with an admixture of oak, birch and aspen.
The forest consists principally of a single stratum, only in places is

there a second layer where 45-year old oak occurs. The sapling or intermediate layer consist of oak, pine, birch and hornbeam. The undergrowth is dense, with oak, pine, birch, hazel occurring most frequently, with occasional juniper and *Frangula alnus*. The ground vegetation is abundant. The whole is well lighted, although certain spots are shaded where the canopy density is greater. The habitat is fairly varied. In places where the ground rises the habitat is drier, but in the hollows between dunes it is similar to that in *Pineto-Vaccinietum Myrtilli* association. Small pools remain here until the late spring, or even longer.

Pine forest (B). Constituting the *Pineto-Callunetum* association (K o b. 1930). Single stratum forest stand about 67–74 years old, composed chiefly of pine, with some single oaks scattered among the pines. Canopy density varies from 0.5 to 0.7. There is practically no undergrowth, only here and there single junipers or oaks. Heather dominates in the ground vegetation.

Alder (C). This habitat consists of one association — *Cariceto-elongatae-Alnetum* (K o b, 1926). The age of the forest stand varies greatly. The canopy density is fairly considerable, from 0.7 to 0.9. In places, particularly in the central section, the forest is better lighted. Birch occurs sporadically in addition to alder. The saplings consist chiefly of alder, and the undergrowth of willow, *Frangula alnus*, mountain ash, and in the drier places — black currant. The hummocks rising above the water are densely overgrown with moss and marsh fern, while the spaces between hummocks are full of rushes. Reeds grow very abundantly in places where water remains longer.

Mixed Forest (D). Like habitat A, belongs to the *Pineto-Quercetum* association, but is drier. The forest stand is composed of pine and oak, while hornbeam (*Carpinus betulus*) occurs in places. The average age of the stand is about 100 years. The forest is strongly lighted, the canopy density being about 0.2 to 0.4, only reaching 0.7 in a few places. Saplings occupy about 20% of the surface, with oak, hornbeam and pine predominating, and birch in some places. The undergrowth consists of pine, oak and birch. Where the canopy density is greater — juniper, *Frangula alnus* and hazel occur. To the south the habitat is bounded by a *Querceto-Potintelletum albae* association.

Neglected forest land (E[1]) probably belongs to the *Pineto-Cladonietum* association (K o b. 1930). The area is intersected by three belts of dunes, on which groups of old pines grow. In the hollows between the dunes a fairly abundant growth of saplings occurs, composed of pine and birth. The area is very dry.

Pine forest (E). Growing on three belts of dunes. The age of the forest stand is comparatively uniform — from 115 to 135 years, and only at the point of transition from pine to alder is the age different. i.e. 63. From other aspects the habitat is more varied. *Pineto-Vaccinietum Myrtilli* association (K o b, 1930) occupies the hollows between dunes, and the rising ground is occupied by a *Pineto-Cladonietum* association (Kob, 1930). On the boundary between the pine forest and the alders there is the *Sphagnetum medii pinetosum* (Mat, 1952)

associaiton. On this account the different parts differ from each other considerably as to moisture, density of undergrowth and of ground vegetation.

Alder wood (F) the age of the forest stand varies from 53 to 68 years. A slight admixture of birch occurs in addition to alders. The intermediate layer consists of alder, and in some parts of birch. Bird-cherry (*Padus avium*), *Frangula alnus* and mountain ash occur in the undergrowth, and in places willows. Both this habitat and habitat C belong to the *Cariceto-elongatae-Alnetum* association and do not differ from it fundamentally, but this particular habitat is drier.

The environments distinguished do not always exactly coincide with plant associations, and are rather physiognomic units. In each of the two observation belts habitats were differentiated which directly bordered on each other — transition from one habitat to the other is very distinct. An especially sharp change in conditions occurs at the boundary between the alders and the pine forests.

The description given of the area is based on data made available by the Forest Intendancy authorities. Definition of the plant associations in the study area was supplied by the courtesy of T. Traczyk M.Sc., of the Forest phytosociological Laboratory of the Botanical Institute, Polish Academy of Sciences, Warsaw.

HABITAT SELECTION BY BIRDS,
AND ITS VARIABILITY DURING THE ANNUAL CYCLE

Differentiation of the elements of the environment deciding on the presence of the given species is difficult, bearing in mind that the most recent research (Svärdson 1949) has revealed that the birds reaction in choosing a habitat is evoked by the group of properties present in the habitat. On this account, an attempt was made, with the aim of investigating the specialisation of different species in their choice of habitat, at analysing to what extent they react to the group of conditions in the habitat which change according to the gradient of moisture. The habitats examined do not constitute, as regards moisture, homogeneous units; the variability within the habitat does not, however, exceed the differences between the various habitats.

Arrangement of the habitats according to the moisture gradient is as follows: the dry limit of the gradient is the neglected forest land (E^1), from which we pass through pine forests (B and E) and mixed forest (D and A), to the wet alder sections, F and C.

<div align="center">

pine forests-mixed forests-alders

$E^1 - B - E - D - A - F - C$

</div>

Calculation was made, in the differentiated habitats, of the averages of

density of the different species of bird in the given month. Calculations were made for the whole bird community, but only the most numerous species will be given further consideration here.

Distribution of the species according to gradient makes it possible to grasp the degree of specialisation of the given species in its habitat preference.

The following species: *Emberiza citrinella, Turdus viscivorus, Parus cristatus, Regulus regulus, Phoenicurus phoenicurus, Lanius collurio, Lullula arborea, Oenanthe/oenanthe* are connected with dry habitats; *Parus caeruleus, Phylloscopus collybita, Turdus merula, Turdus ericetorum, Hippolais icterina, Erithacus rubecula, Sylvia atricapilla, Luscinia luscinia, Sylvia borin, Troglodytes troglodytes, Luscinia svecica, Sylvia communis* occur in damp habitats.

Phylloscopus sibilatrix, Muscicapa striata, Sitta aeuropaea, Certhia familiaris, Dryobates major, Fringilla coelebs, Parus major, Sturnus vulgaris, Anthus trivialis, Coccothraustes coccothraustes occur in the majority of the habitats examined (Fig. 1).

The first two groups of birds may be defined as stenotopic, and the species belonging to the last group as eurytopic.

This division gives only the approximate relation to the different species to the habitat. There are no sudden transitions between the groups differentiated. The distribution of numbers of the different species along the habitat gradient is not interrupted but continuous. As a result variations in the specific composition in the habitats arrangement along the gradient are also continuous. B o n d (1957) found a similar picture of the distribution of birds in relation to the phytosociological gradient within deciduous forests. In our case this proves true for the group of habitats which is even more varied from the phytosociological aspect.

The habitat specialisation of the different species as given above is relative. Very many species (*Sylvia atricapilla, Erithacus rubecula, Hippolais icterina, Turdus ericetorum, Phylloscopus collybita, Lullula arborea*) may considerably enlarge the range of the habitats in which they occur during the post-nesting period. During the nesting period, however, they exhibit a very advanced specialisation in their choice of habitat (Fig. 1).

Certain of the species (*Sylvia communis, Troglodytes troglodytes*) with extreme specialisation may occur altogether outside the area of the forest complex; *S. communis* is a bird typical of groups of trees situated in the middle of fields. *Troglodytes troglodytes* is frequently encountered in the vegetation edging streams flowing through a completely treeless area.

From the point of view of the general distribution of these species they should be included among species adapted to living in varied habitats. In a certain natural group of habitats, in a definite biocenotic situation, they become species specialised as to choice of habitat.

As shown above, habitat preference in the various species is not a constant phenomenon, and is subject to variation. With many of the species examined these variations were repeated over the two years of observations in the same

	C	F	A	D	E	B	E'
Oenanthe oenanthe							
Lullula arborea							
Lanius collurio							
Phoenicurus phoenicurus							
Regulus regulus							
Parus cristatus							
Turdus viscivorus							
Emberiza citrinella							
Coccothraustes coccothraustes							
Anthus trivialis							
Sturnus vulgaris							
Fringilla coelebs							
Parus major							
Dryobates major							
Certhia familiaris							
Sitta aeuropaea							
Muscicapa striata							
Phylloscopus sibilatrix							
Parus caeruleus							
Phylloscopus collybita							
Turdus merula							
Turdus ericetorum							
Hippolais icterina							
Erithacus rubecula							
Sylvia atricapilla							
Luscinia luscinia							
Sylvia borin							
Troglodytes troglodytes							
Luscinia svecica							
Sylvia communis							
	C	F	A	D	E	B	E'

1   2   3

Fig. 1. Habitat selection by birds in the nesting and post-nesting period

Habitat arranged according to moisture gradient; 1 — habitats in which the species constantly occurs (in predominating numbers), 2 — habitats in which the species occurs constantly but in smaller numbers than in others, 3 — habitats occupied in the post-nesting period

Wybiórczość środowiskowa ptaków w okresie lęgowym i polęgowym

Środowiska uszeregowane wg gradientu wilgotności; 1 — środowiska, w których gatunek występuje stale (w przeważającej ilości), 2 — środowiska, w których gatunek występuje stale, lecz mniej licznie niż w innych, 3 — środowiska zajmowane w okresie polęgowym

period each year, and the change of habitat is exactly defined, or at least evinces a tendency in a definite direction.

This kind of variability in habitat selection during the annual cycle was observed in the following species:
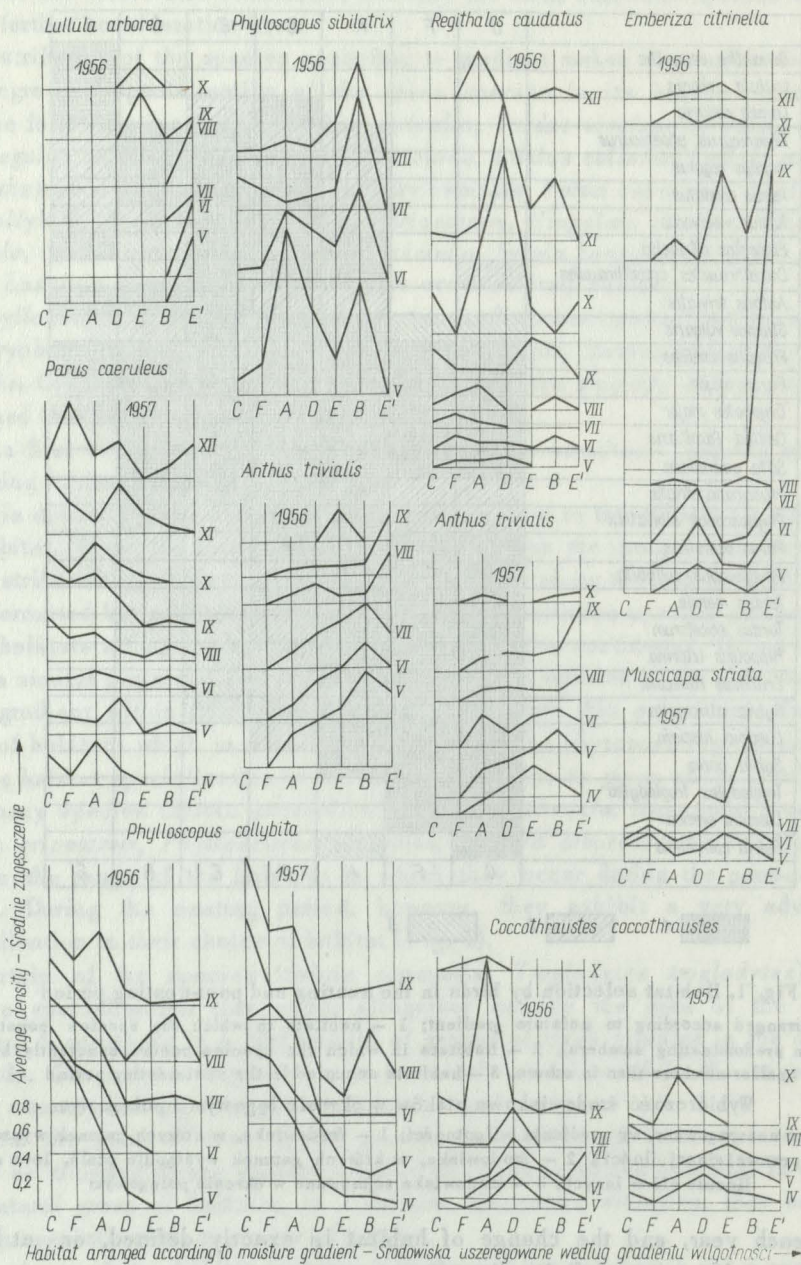
Fig. 2. Variations in habitat selection in the annual cycle

Zmienność wybiórczości środowiskowej w cyklu rocznym

Coccothraustes coccothraustes	*Phylloscopus collybita*
Carduelis spinus	*Phylloscopus sibilatrix*
Emberiza citrinella	*Parus caeruleus*
Lullula arborea	*Aegithalos caudatus*
Anthus trivialis	*Muscicapa striata*

Results are shown in Diagram 2. The horizontal lines represent the axes of habitat gradient in the different months. Each of the habitats in the different months is linked by vertical lines, on which the density value of the birds in each habitat may be read; connection of these values gives us a curve which enables us to observe a tendency in the species to distribution in relation to the gradient in the given month. Diagram 4 is also constructed on the same principle. Where the picture of distribution showed no significant difference during the two years of observations, results are given for one year only. Full data are given for certain species to illustrate the harmony of the variations in distribution over the 2-year period.

Of the species mentioned above, only in the case of *Aegithalos caudatus* and *Coccothraustes coccothraustes* is the variability in habitat selection not exactly defined. With *Anthus trivialis, Lullula arborea, Emberiza citrinella, Carduelis spinus, Phylloscopus collybita* and *Phylloscopus sibilatrix* variations follow in regular succession in both years and for exactly defined habitats. *Parus caeruleus* and *Muscicapa striata* exhibit a tendency to occupy habitats of a certain type. *Parus caeruleus* appears in a certain period in larger numbers in damp habitats, *Muscicapa striata* in dry ones.

Phylloscopus collybita appears in habitats in which it previously occurred in small numbers only, and even occupies one of the dominant positions there.

Anthus trivialis, together with an increase in numbers in some habitats, exhibits a decrease in numbers in the habitats in which it lived previously. *Phylloscopus sibilatrix*, which occupies habitats A and B during the nesting period in uniformly equal numbers, moves from A to the adjoining habitat B in the post-nesting period, only very small numbers continuing to occur in A (Fig. 4).

Carduelis spinus occurs chiefly in pine and mixed forests during the summer. In the autumn it appears in continually increasing numbers in alder woods, while its numbers decrease in pine forests. During the winter period it occurs exclusively in alder woods. This cycle was regularly repeated during the two years of observations (Fig. 3).

In addition cases occur of extension in the range of habitats occupied by species specialised as to choice in habitat, preference consisting in a short--lived penetration of non-typical habitats at points of contact between habitats. This may be observed in the case of *Sylvia atricapilla, Hippolais icterina, Erithacus rubecula, Regulus regulus, Parus cristatus* (Fig. 4).

Variability in habitat selection would appear to be a fairly common phenomenon among birds. Probably in each case the causes producing this phenomenon may differ in character. With certain species variability in habitat selection is connected with variations in population density.
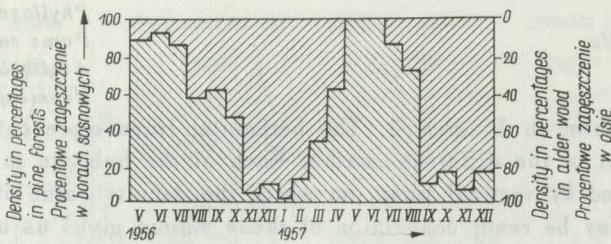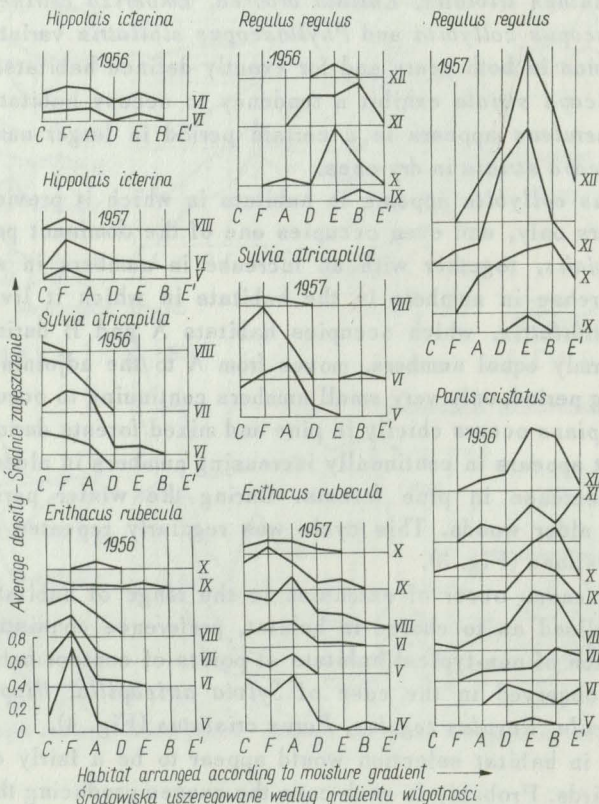
Fig. 3. Comparison of the distribution of *Carduelis spinus* in pine forests and in alder woods in the annual cycle

The total density of birds in both types of habitat in different months was taken as 100%

Data for III and IV 1957 from interpolation

Porównanie rozmieszczenia *Carduelis spinus* w borach sosnowych i w olsie w cyklu rocznym

Za 100% przyjęto sumę zagęszczenia ptaków w obydwu typach środowisk w poszczególnych miesiącach

Dane dla III i IV 1957 r. z interpolacji

Fig. 4. Variations in habitat selection in the annual cycle

Zmienność wybiórczości środowiskowej w cyklu rocznym

Variations which may be termed periodical penetration to habitats in general non-typical of the species, often coincide with an increase in density of the population of this species.

With the fifteen species which may be defined as stenotopic, the connection was investigated between the number of habitats occupied in a given period and the variations in numbers in biotopes optimum for the given species.
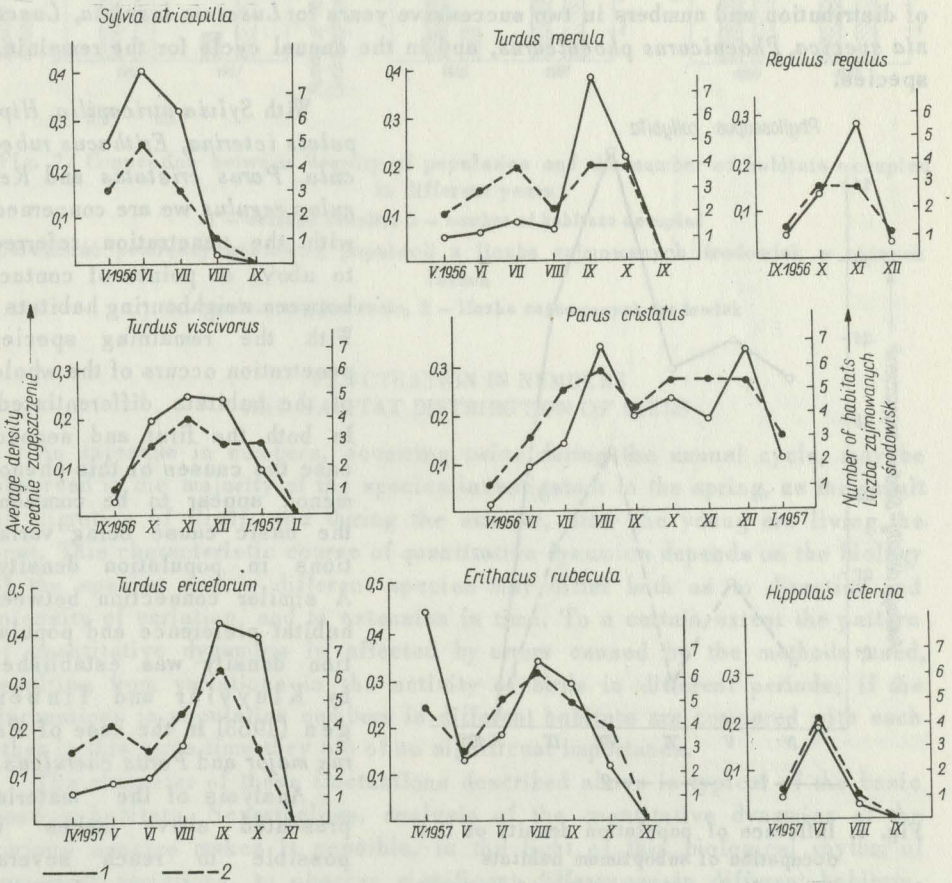

Fig. 5. Influence of population density on the number of habitats occupied
1 — average density of birds in optimum habitats, 2 — number of habitats occupied in different months
Wpływ gęstości populacji na liczbę zajmowanych środowisk
1 — średnie zagęszczenie ptaków w optymalnych biotopach, 2 — liczba środowisk zajmowanych w poszczególnych miesiącach

In the case of twelve species, the number of habitats occupied do in fact change in proportion to the variations in numbers of birds in optimum habitats — these are as follows:

Sylvia atricapilla	*Turdus viscivorus*
Phylloscopus collybita	*Turdus merula*
Hippolais icterina	*Luscinia luscinia*
Parus cristatus	*Luscinia svecica*
Regulus regulus	*Erithacus rubecula*
Turdus ericetorum	*Phoenicurus phoenicurus*

The above connection is shown in diagrams 5, 6 and 7. Comparison is made of distribution and numbers in two successive years for *Luscinia luscinia, Luscinia svecica, Phoenicurus phoenicurus,* and in the annual cycle for the remaining species.

With *Sylvia atricapilla, Hippolais icterina, Erithacus rubecula, Parus cristatus* and *Regulus regulus* we are concerned with the penetration referred to above at points of contact between neighbouring habitats. With the remaining species penetration occurs of the whole of the habitats differentiated. In both the first and second case the causes of this phenomenon appear to be common, the basic cause being variations in population density. A similar connection between habitat preference and population density was established by Kluyvier and Tinbergen (1953) in the case of *Parus major* and *Parus caeruleus*.

Analysis of the material presented above makes it possible to reach several conclusions of a general nature.

Independently of the causes operating in each case, several species make use of not one, but a whole group of biotopes. Birds living in different habitats of the study area are not
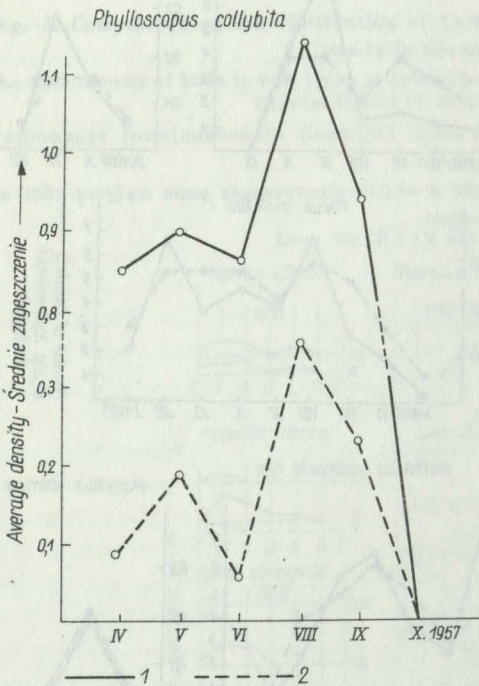
Fig. 6. Influence of population density on the occupation of suboptimum habitats

1 — average density in optimum habitats, 2 — average density in habitats in which the species occurs in small numbers

Wpływ gęstości populacji na zajmowanie suboptymalnych biotopów

1 — średnie zagęszczenie w optymalnych biotopach, 2 — średnie zagęszczenie w biotopach, gdzie gatunek występuje nielicznie

isolated, but form one population, in contact as a result of the passage of part of the population from one set of habitats to another.

The numbers of the population as a whole may decide on settlement in the different biotopes.
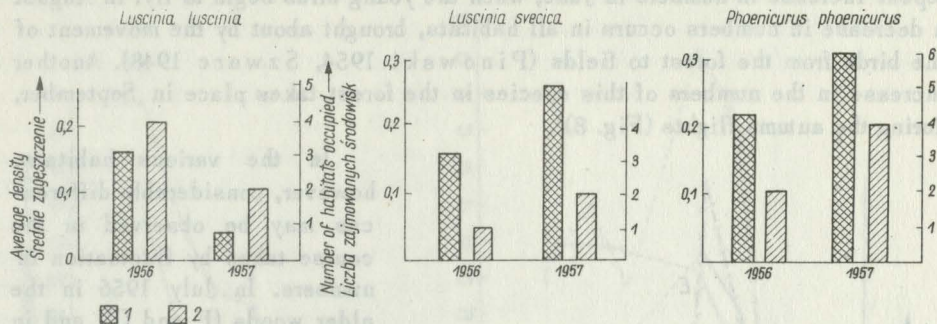
Fig. 7. Connection between density of population and the number of habitats occupied
in different years

1 — average density, 2 — number of habitats occupied

Zależność pomiędzy gęstością populacji a liczbą zajmowanych środowisk w różnych
latach

1 — średnie zagęszczenie, 2 — liczba zajmowanych środowisk

FLUCTUATION IN NUMBERS
AND HABITAT DISTRIBUTION OF BIRDS

An increase in numbers, occurring twice during the annual cycle, may be
observed in the majority of the species investigated: in the spring, as the result
of migration of flight, and during the summer, after the young are living the
nest. This characteristic course of quantitative dynamics depends on the biology
of the species and in different species may differ both as to direction and
intensity of variation, and to extension in time. To a certain extent the pattern
of quantitative dynamics is affected by errors caused by the methods used,
resulting from variations in the activity of birds in different periods; if the
fluctuations in population numbers in different habitats are compared with each
other in this same time they are of no significant importance.

The character of these fluctuations described above is typical of the basic
nesting habitats. Nevertheless, analysis of the quantitative dynamics of the
various species makes it possible, in the light of this biological rhythm of
numerical variations, to observe significant differences in different habitats.
They are not absolutely constant; when comparing dynamics of numbers of
a given species in the same habitat over two years, it was found that this
same type of habitat is not always synonymous in this respect. In different
years the fluctuations in numbers in this same habitat may be completely
different.

Thus, for instance, with *Fringilla coelebs* nesting takes place in all the
habitats differentiated. In each of them a general biological rhythm of dynamics
may be observed, basically similar in all the habitats; high level of numbers in
April, as the result of the flights taking place, a fall in numbers in May and

repeat increase in numbers in June, when the young birds begin to fly. In August a decrease in numbers occurs in all habitats, brought about by the movement of the birds from the forest to fields (P i n o w s k i 1954, S z w a r c 1948). Another increase in the numbers of this species in the forest takes place in September, during the autumn flights (Fig. 8)[1].

In the various habitats, however, considerable differences may be observed in the course taken by fluctuation in numbers. In July 1956 in the alder woods (F and C), and in the mixed forest A, a sudden sharp decrease in numbers occurs, in the pine forest B this decrease is very small, and in habitats E, D and E an increase in numbers takes place. In 1957 the direction taken by quantitative variations in the alder wood differs from the remaining habitats; at the same time considerable differences are to be seen in the dynamics of numbers in the same habitats during the two successive years of observations.

With *Phylloscopus collybita* the course taken by the dynamics of numbers differs both in the various habitats and in different years. In 1956 the trends of variations in alder woods F and C were almost identical; in mixed forests A and D the course of quantitative dynamics is different. In 1957 population trends in alders were in harmony in the previous year, now differ considerably, and the same applies to the mixed forest A (fig. 9).
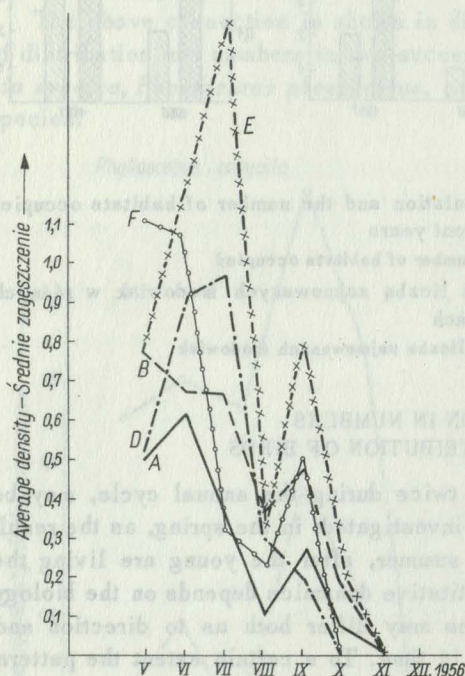
Fig. 8. Dynamics of numbers of *Fringilla coelebs* in different habitats

The symbols used for the different habitats in figs. 8 — — 15 correspond to those used in the text

Dynamika liczebności *Fringilla coelebs* w różnych środowiskach

Symbole poszczególnych środowisk na rysunkach 8 — 15 odpowiadają oznaczeniom w tekście

Phylloscopus sibilatrix occurs numerously in mixed forests A and D, and in the pine forest with heather B. The course of fluctuation in mixed forests and in the pine forest B with heather is however completely different. In the mixed

[1]In order to simplify the diagram, not all of the habitats were taken into consideration.
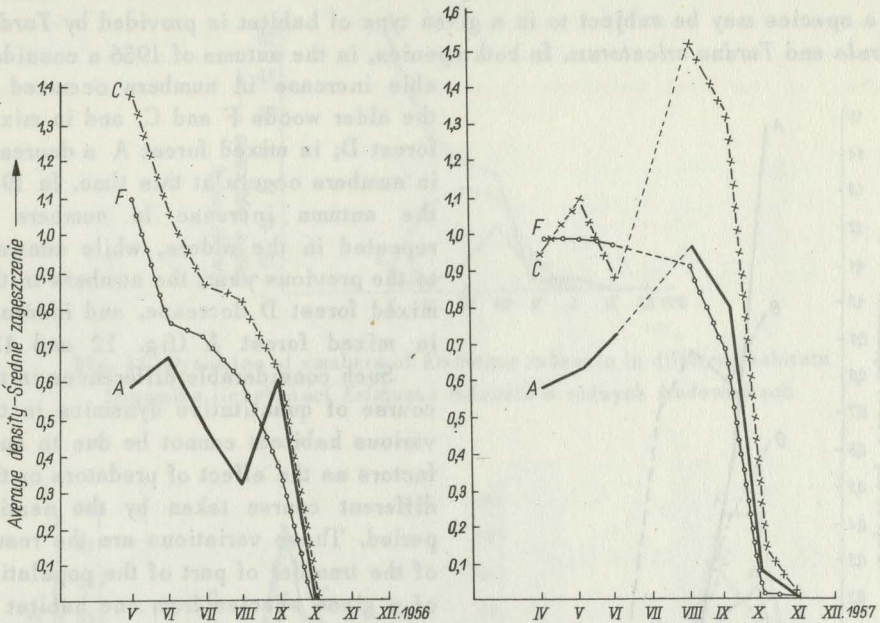
Fig. 9. Dynamics of numbers of *Phylloscopus collybita* in different habitats and years
Dynamika liczebności *Phylloscopus collybita* w różnych środowiskach i latach

forest habitats numbers increase up to May, after which they decrease sharply, while in the pine forest B with heather they remain at a high level until August (fig. 10). In both years the directions of variations are similar, while the level of numbers in the different habitats undergoes variation.

In 1956 *Erithacus rubecula* possessed a distinctly different character of dynamics in each of the nesting habitats in which it occurred. In 1957 the course taken by quantitative variations was uniform in all habitats, with the exception of the alder wood F, where the numbers are greatest in the autumn, while a decrease in numbers takes place in other habitats (fig. 11).

Troglodytes troglodytes exhibited uniformity of the fluctuation in both the nesting habitats which it occupied in 1956, whereas in 1957 fluctuations in these same biotopes differ greatly; the character of the variations is different in these two years.

Parus major exhibits a comparatively uniform trend in variations in all habitats, but the intensivity of the variations is not identical. During the autumn-winter period the differences in the course of dynamics in the different habitats increase.

With *Parus caeruleus, Sitta aeuropaea, Dryobates major,* and *Lanius collurio* the character of their dynamics of numbers is different both in different types of habitat and in different years.

An excellent illustration of what great variations the fluctuation in numbers of a species may be subject to in a given type of habitat is provided by *Turdus merula* and *Turdus ericetorum*. In both species, in the autumn of 1956 a considerable increase in numbers occurred in the alder woods F and C, and in mixed forest D; in mixed forest A a decrease in numbers occurs at this time. In 1957 the autumn increase in numbers is repeated in the alders, while contrary to the previous year, the numbers in the mixed forest D decrease, and increase in mixed forest A (fig. 12 and 13).

Such considerable differences in the course of quantitative dynamics in the various habitats cannot be due to such factors as the effect of predators or the different course taken by the nesting period. These variations are the result of the transfer of part of the population of a given species from one habitat to another. This was emphasised in the previous section; data on the quantitative dynamics of species in different habitats constitute in this way confirmation of data on the variability in habitat selection.
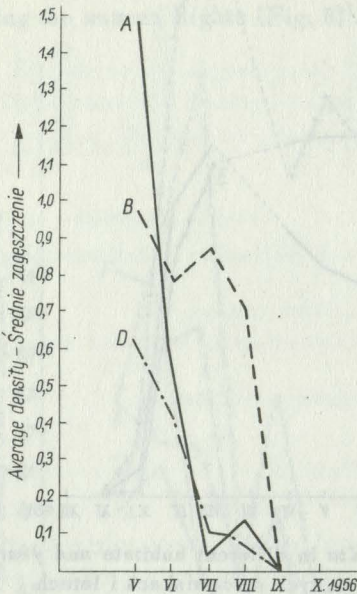

Fig. 10. Dynamics of numbers of *Phylloscopus sibilatrix* in different habitats
Dynamika liczebności *Phylloscopus sibilatrix* w różnych środowiskach

The habitats differentiated in the sense of nesting places, of certain defined spatial structure etc. were not subject to fundamental variations during the relatively short period of the investigations. Differences in the course of quantitative dynamics in the different types of environment are therefore caused by the different biocenotic system in these environments. It appears that with the species *Turdus ericetorum, Turdus merula, Carduélis spinus, Coccothraustes coccothraustes*, food factors take the first place in this system. Exactly which factors play a chief part in each case is not, however, clear and requires detailed investigation.

DISTRIBUTION OF BIRDS WITHIN THE HABITATS

In the foregoing sections the behaviour of several species was traced in relation to a defined habitat gradient. Analysis of the distribution of species within the biotopes included in the composition of this gradient revealed that the spatial distribution of the different species in the biotope is not even. Significant differences were found in the distribution of eurytopic and stenotopic
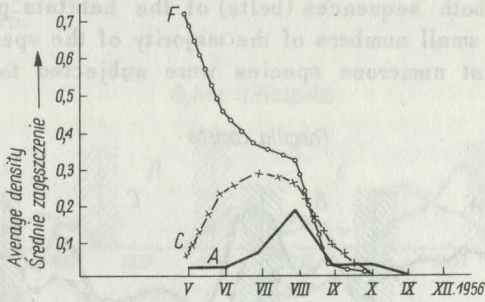
Fig. 11. Dynamics of numbers of *Erithacus rubecula* in different habitats
Dynamika liczebności *Erithacus rubecula* w różnych środowiskach

Fig. 12. Dynamics of numbers of *Turdus ericetorum* in different habitats and years
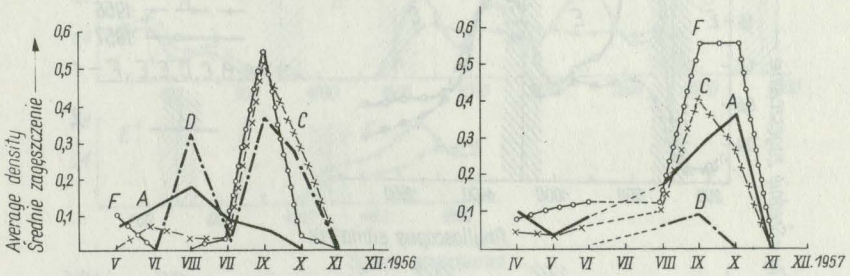Dynamika liczebności *Turdus ericetorum* w różnych środowiskach i latach
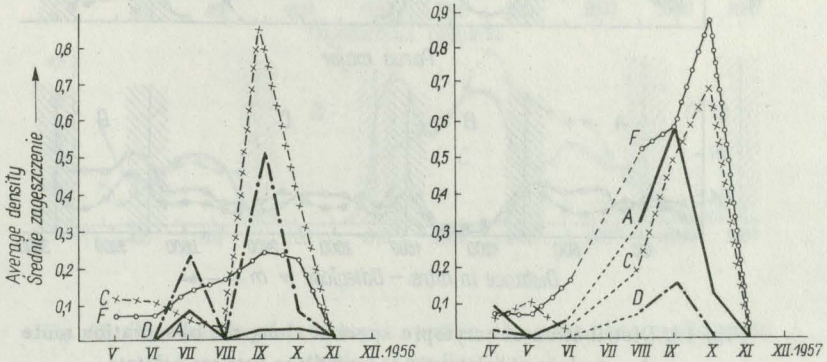
Fig. 13. Dynamics of numbers of *Turdus merula* in different habitats and years
Dynamika liczebności *Turdus merula* w różnych środowiskach i latach

species. The spatial distribution of the various species was considered independently in both sequences (belts) of the habitats previously described. On account of the small numbers of the majority of the species examined, only certain of the most numerous species were subjected to detailed analysis.
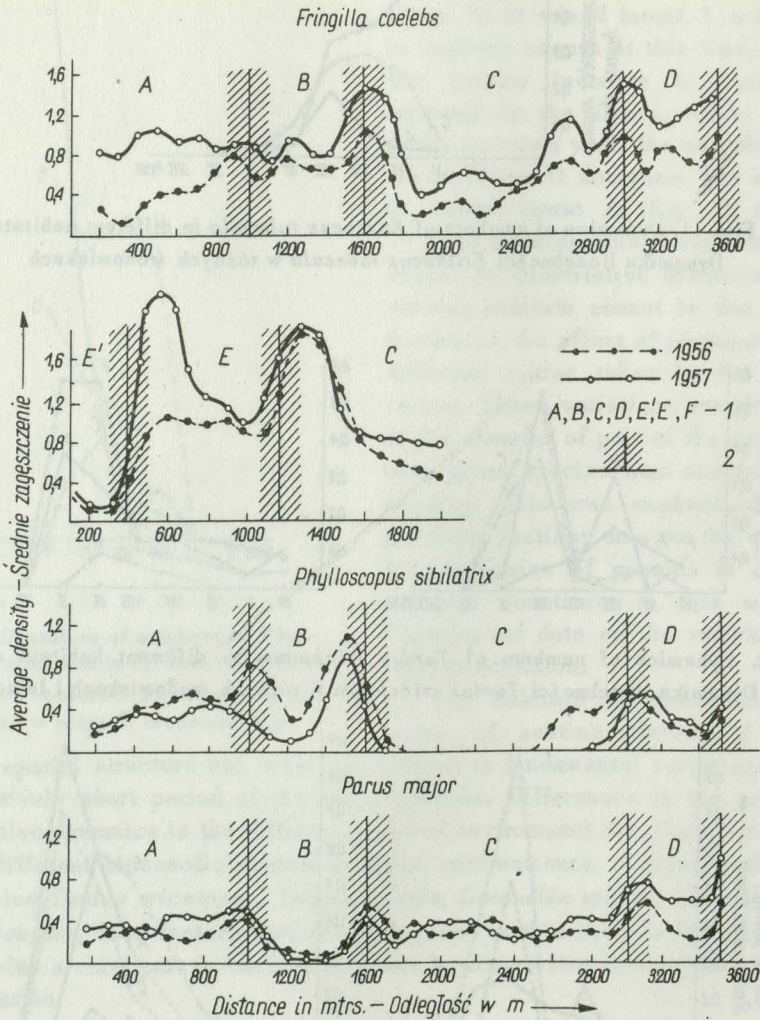
Fig. 14. Distribution of eurytopic species along the observation route
1 — symbols of habitats, 2 — borderlines between habitats
Rozmieszczenie gatunków eurytopowych wzdłuż trasy obserwacji
1 — symbole środowisk, 2 — styki pomiędzy środowiskami

The following were considered as eurytopic species: *Fringilla coelebs*, *Parus major*, *Phylloscopus sibilatrix*, and as stenotopic species, *Sylvia atrica-*

pilla, Sylvia borin, Sylvia communis, Phylloscopus collybita. Results are given
in diagrams 14 and 15.

Fig. 15. Distribution of stenotopic species along the observation route
marking as for fig. 14
Rozmieszczenie gatunków stenotopowych wzdłuż trasy obserwacji
oznaczenia jak na rys. 14

The successive sections of the area through which the observation belt
passes are shown on the horizontal axis of each diagram, while the average
density of birds is given on the vertical axis. The various points of the curve

represent the average numbers of the species in the given section of the area; averages were calculated from the figures for several months. The value of each 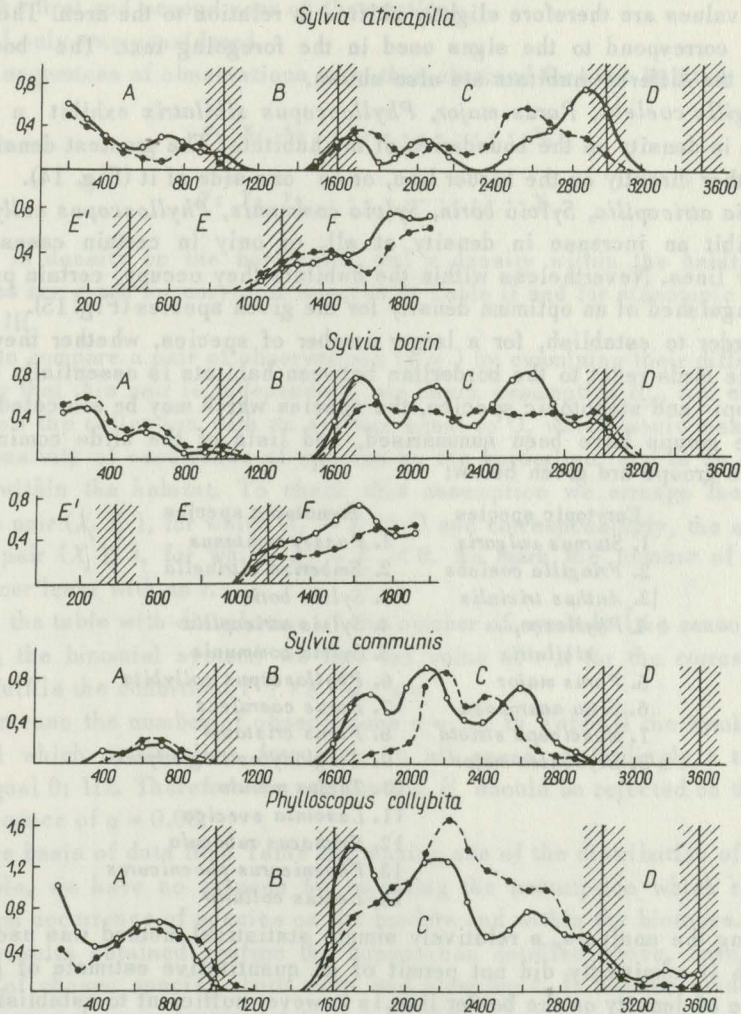point was calculated by means of a moving mean for two 100 m. sections, extreme values are therefore slightly shifted in relation to the area. The habitat symbols correspond to the signs used in the foregoing text. The boundaries between the different habitats are also shown.

Fringilla coelebs, Parus major, Phylloscopus sibilatrix exhibit a distinct increase in density on the boundaries of the habitats. The greatest densities are found either directly on the border line, or on one side of it (Fig. 14).

Sylvia atricapilla, Sylvia borin, Sylvia communis, Phylloscopus collybita do not exhibit an increase in density at all, or only in certain cases, on the boundary lines. Nevertheless within the habitats they occupy, certain parts may be distinguished of an optimum density for the given species (Fig. 15).

In order to establish, for a larger number of species, whether they way in which the birds react to the borderline between habitats is essentially different in eurytopic and stenotopic species, the species which may be allocated to each of these groups have been summarised, and lists of the birds coming within these two groups are given below:

Eurytopic species	Stenotopic species
1. *Sturnus vulgaris*	1. *Passer montanus*
2. *Fringilla coelebs*	2. *Emberiza citrinella*
3. *Anthus trivialis*	3. *Sylvia borin*
4. *Phylloscopus sibilatrix*	4. *Sylvia atricapilla*
5. *Parus major*	5. *Sylvia communis*
6. *Sitta aeuropaea*	6. *Phylloscopus collybita*
7. *Muscicapa striata*	7. *Parus caeruleus*
8. *Dryobates major*	8. *Parus cristatus*
	9. *Troglodytes troglodytes*
	10. *Turdus merula*
	11. *Luscinia svecica*
	12. *Erithacus rubecula*
	13. *Phoenicurus phoenicurus*
	14. *Lanius collurio*

In making the analysis, a relatively simple statistical method was used, which although it admittedly did not permit of an quantitative estimate of growth or decrease of density on the border line, is however sufficient to establish whether the phenomen on examined takes place in a regular manner. Comparison was therefore made between the density of birds on the borderline sections with the average density occurring in sections lying within the given biotope. Both values constituted averages of monthly periods for the total of densities of the species concerned in each group. In this connection the nearest 100 m. of the habitat directly adjoining the boundary between two habitats were considered as borderline sections. Both sides of the boundary were considered separately, which increased the value of the data obtained.

On the basis of an analysis of the distribution of the various species, the

following months were regarded as comparable: IV, V, VI, VII, VIII, IX. Data from the two years of observations were treated jointly. This was facilitated by the very close agreement in the distribution of species within the habitats in both the first and second year of observations.

Belt I only was considered.

Two sequences of observations were thus obtained for each habitat:

$$x_1 \ x_2 \ x_3 \ \cdots\cdots\cdots\cdots \ x_n$$

$$y_1 \ y_2 \ y_3 \ \cdots\cdots\cdots\cdots \ y_n$$

where x is density on the borderline, and y density within the habitat. Both sequences are given for eurytopic species in Table II and for stenotopic species in Table III.

Let us compare a pair of observations $(x_i \ y_i)$ by examining their differences. Assuming that this pair is independent, we check assumption H_o, i.e. each pair comes from the collection with an average equal to O, which would mean a uniform intensity of occurrence of species on the borderline, and in an optional section within the habitat. To check this assumption we arrange the symbol + for this pair $(X_i \ Y_i)$, for which $X_i - Y_i > O$ and correspondingly, the symbol − for this pair $(X_i \ Y_i)$, for which $X_i - Y_i < 0$. We mark the number of symbols which occur least with an r.

From the table with distribution of the number of symbols (the reasoning is based on the binomial system) we find the value of $r \ a$ for the corresponding a which fulfils the condition: $P \ / \ r \leqslant r \ a \ / \leqslant a$

In our case the number of observations $n = 10$. In Table II the symbol − is a symbol which occurs less frequently in all cases; accordingly r takes on values equal 0; 1; 2. Therefore the assumption H_o should be rejected on the level of significance of $a = 0.05$.

On the basis of data from Table III, making use of the distribution of number of symbols, we have no grounds for rejecting the assumption which refers to the uniform occurrence of species on the borders and within the biotopes.

The results obtained confirm the supposition detailed above, based on an analysis of chosen species, both eury- and stenotopic. It became evident that the first group does in fact react to the borderline between two habitats by an increase in density, while the second group does not exhibit this response.

In generally accepted ecological terminology, borderlines between two or more community are called ecotons; this term is usually taken to mean the borderline between such community as, for instance, prairie and deciduous forest; a belt such as this is usually of considerable width and may be regarded as a separate habitat (Allee, Emerson, P. Park, T. Park, Schmidt 1950, Dice 1952, Odum 1959). Borderlines of this kind are occupied not only by the species belonging to both of the adjoining habitats, but also by other species proper only to themselves (Wolczaniecki 1950).

Comparison of density of birds on borderlines with the average density within the habitats
(calculations for eurytopic species)

Porównanie zagęszczenia ptaków na stykach ze średnim zagęszczeniem wewnątrz biotopów
(obliczenia dla gatunków eurytopowych)

Tab. II

Date — Data		Habitats — Środowiska																	
		A			B					C					D				
		Y_1	X_1-Y_1	X_1	X_2	X_2-Y_2	Y_2	X_3-Y_2	X_3	X_4	X_4-Y_3	Y_3	X_5-Y_3	X_5	X_6	X_6-Y_4	Y_4	X_7-Y_4	X_7
1956	V	2,6	+	4,0	4,2	+	2,7	−	2,5	4,1	+	0,9	+	1,8	3,1	+	1,7	+	1,9
	VI	1,4	+	3,5	2,6	+	1,9	+	3,4	1,8	+	1,1	+	3,1	2,6	+	2,0	+	4,1
	VII	1,2	+	1,6	3,4	+	1,8	+	2,2	1,8	+	1,5	+	2,6	3,4	+	1,8	+	3,4
	VIII	0,8	+	1,2	4,4	+	1,6	+	3,4	2,4	+	0,6	+	1,4	1,0	−	1,2	+	5,6
	IX	1,4	+	2,5	1,1	+	0,9	+	1,2	1,9	+	1,2	−	1,0	3,3	+	1,2	+	4,5
1957	IV	2,2	+	5,1	1,8	+	1,3	+	3,4	3,4	+	1,3	+	5,2	3,7	+	2,4	+	4,9
	V	2,5	+	5,1	2,2	+	1,8	+	6,0	3,8	+	1,8	−	1,3	3,4	+	2,5	+	5,9
	VI	2,5	+	2,8	1,2	−	1,7	+	4,4	2,4	+	0,9	+	2,2	1,4	−	1,9	+	4,8
	VIII	1,5	+	2,2	2,2	+	1,6	+	5,2	3,3	+	0,7	+	1,2	3,4	+	2,2	+	5,2
	IX	2,1	−	0,8	2,0	+	0,7	+	1,4	2,4	+	1,2	+	2,5	2,4	+	1,4	+	6,2
			$r=1$			$r=1$		$r=1$			$r=0$		$r=2$			$r=2$		$r=0$	

Comparison of density of birds on borderlines with the average density within the habitats
(calculations for stenotopic species)

Porównanie zagęszczenia ptaków na stykach ze średnim zagęszczeniem wewnątrz biotopów
(obliczenia dla gatunków stenotopowych)

Tab. III

| Date — Data | | Habitats — Środowiska | | | | | | | | | | | | | | | | | |
| | | A | | | B | | | | | C | | | | | D | | | | |
		Y_1	X_1-Y_1	X_1	X_2	X_2-Y_2	Y_2	X_3-Y_2	X_3	X_4	X_4-Y_3	Y_3	X_5-Y_3	X_5	X_6	X_6-Y_4	Y_4	X_7-Y_4	X_7
1956	V	1,3	−	1,2	0,0	−	0,3	−	0,0	2,1	−	2,8	−	1,8	0,3	−	0,5	−	0,3
	VI	1,6	−	0,0	0,3	−	0,4	−	0,3	3,3	+	3,2	−	2,6	1,9	+	1,1	0	1,1
	VII	1,5	+	1,9	0,6	+	0,4	−	0,2	3,2	+	2,7	−	2,2	1,0	−	1,6	−	1,0
	VIII	0,5	+	2,1	1,8	+	0,8	−	0,3	1,5	−	1,6	−	0,6	0,0	−	0,4	+	0,8
	IX	0,8	+	1,0	0,5	+	0,3	−	0,1	0,6	−	2,6	+	2,9	3,1	+	1,2	+	1,7
1957	IV	2,0	−	1,2	0,9	+	0,2	+	0,6	4,5	+	2,3	−	1,9	0,9	+	0,7	+	1,1
	V	1,7	−	0,8	0,0	−	0,4	+	2,3	4,1	·	3,0	+	3,8	2,3	+	0,8	+	1,6
	VI	2,4	−	1,4	0,6	+	0,3	+	1,2	4,7	+	3,3	+	3,4	1,8	+	0,8	+	1,0
	VIII	2,1	−	1,6	1,4	+	0,9	+	1,5	4,5	+	2,8	−	1,8	0,6	−	0,9	−	0,5
	IX	2,1	−	0,8	1,0	+	0,7	−	0,6	2,7	+	2,7	+	4,9	1,0	+	0,6	+	1,3
			$r = 3$			$r = 3$		$r = 4$			$r = 3$		$r = 4$			$r = 4$		$r = 3$	

In our case the borderline forms a narrow belt, in which a sudden change in habitat conditions, both abiotic and biotic, takes place. It has not, however, proved possible to establish a species confined exclusively to the border, at least not as far as birds are concerned, and from this aspect it has no typically ecotonic character. The classic work by Beecher (1942) treats the problem of borderlines in the same way, since the author states there in that the number of birds in a certain area increased proportionally to the number of plant associations coming within a unit of area.

An increase in the numbers of birds on the border is most often attributed to the accumulation of birds belonging to each of the neighbouring habitats (Odum 1959). In the present case it was found that increase in density on the border may also be observed in different species as the result of the specific reaction of these species to the border between the habitats. The way in which the birds react to the border depends in this case on the degree of specialisation of the given species in selection of habitat.

In general it may be stated that certain optima of occurrence may be distinguished in the case of each species, within the given habitat: with eurytopic species they are situated on the borders of the habitat, and with stenotopic species within the given habitat.

The spatial distribution of the species examined within the habitats is strikingly similar in both years of observation; when compared with the considerable lability of the fluctuation in numbers of these species in different years this suggests that, apart from the population numbers, those portions of the given habitat optimum for the given species and characterised by the maximum density of population, are the ones chiefly occupied.

CONCLUSIONS

1. A different degree of specialisation in habitat selection was found in different species: the following species were differentiated: eurytopic species, occurring in the majority of the habitats studied, and stenotopic species — peculiar to strictly defined habitats only. The habitat selection of the various species is relative; the species, which may be defined as eurytopic on the basis of their general distribution, behave in the given group of habitats like species with highly developed specialisation in the habitat selection.

2. With the majority of species, the distribution on numbers along the habitat gradient is continuous; in consequence changes in the specific composition in habitats classed according to moisture gradient are also continuous.

3. The habitat selection of the species is not absolutely constant, being most distinct in the nesting period. In later periods the habitat selection of the given species may undergo fundamental changes. In the case of certain species, the nesting season is followed by penetration of exactly defined habitats, this phenomenon being repeated during the same period in both years of observation. Other species in different periods of the annual cycle penetrate the whole of the

habitats investigated, while certain other species were observed to penetrate non-typical habitats on the borders.

4. The majority of the species examined make use of not one but a whole group of habitats. Birds occupying different habitats in the study area are not isolated from each other; they form one population in contact with each other owing to the fact that some of the individuals within this population pass from one habitat to another.

5. The numbers of a population formed by a given species may affect the settlement of the different habitats; several species were observed to widen the scope of the habitats they occupied as their numbers increased.

6. The fluctuation in numbers of the various species take a different course in different habitats. The character of the dynamics in the annual cycle in this same habitat over the period of two successive years may also differ. These differences are caused by local migration of part of the population from one biotope to another. The cause of these migrations is, on the one hand, the state of the population, and on the other, the differences in the biocenotic system of the various biotopes, and the variability, both seasonal and occurring from year to year, of this system.

7. The spatial distribution of the different species was examined within the biotopes occupied. It was found that each species exhibits within the given habitat, optima of occurrence peculiar to the species, characterised by maximum density. With eurytopic species the maximum density was observed on the borders of the habitat, and with stenotopic species — within the biotope.

8. Distribution of the various species within their habitats closely agrees in both years; in comparison with the great lability of the dynamics of numbers this suggests that the optimum parts of the habitat are those primarily occupied regardless of population numbers.

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NIEKTÓRE ASPEKTY WYBIÓRCZOŚCI ŚRODOWISKOWEJ PTAKÓW

Streszczenie

Przeprowadzone w 1956 i 1957 r. badania miały na celu charakterystykę rozmieszczenia przestrzennego oraz dynamiki liczebności ptaków w cyklu rocznym w szeregu środowisk, typowych dla kompleksu lasów Puszczy Kampinoskiej.

W badaniu uwzględniono najbardziej charakterystyczne biotopy, obejmujące w sumie dużą rozpiętość warunków środowiskowych. Ogółem wyróżniono siedem środowisk wyraźnie różnych pod względem fizjonomii szaty roślinnej.

Przez wybrany teren przebiegały dwa niezależne pasy obserwacyjne, z których jeden obejmował cztery, a drugi trzy środowiska. W każdym pasie środowiska sąsiadowały ze sobą bezpośrednio; granice pomiędzy poszczególnymi środowiskami były wyraźne i ostre. Łączna długość obu pasów wynosiła 5700 m.

W badaniu posługiwano się metodą taksacji liniowej. Obecność ptaków w pasie stwierdzano wizualnie oraz po śpiewie lub głosie. Za próbę przyjęto przejście odcinka pasa długości 100 m w ciągu pięciu minut. Na każdym pasie prowadzono od czterech do siedmiu obserwacji w ciągu miesiąca. Opierając się o średnie z serii prób uzyskanych w ciągu każdego miesiąca, badano liczebność poszczególnych gatunków w różnych środowiskach oraz ich rozmieszczenie wewnątrz danego biotopu.

Badane środowiska uszeregowano według gradientu wilgotności. Uzyskano w ten sposób ciąg środowisk, składający się z suchych borów sosnowych, borów mieszanych i olsów.

Celem określenia specjalizacji poszczególnych gatunków w wyborze środowiska zbadano, w jakim stopniu reagują one na zespół warunków środowiska, zmieniających się zgodnie z gradientem wilgotności.

Stwierdzono różny stopień specjalizacji środowiskowej u poszczególnych gatunków. Wyróżniono gatunki eurotopowe — występujące w większości badanych środowisk oraz gatunki stenotopowe — właściwe tylko ściśle określonym środowiskom. Stwierdzono, że rozkład liczebności poszczególnych gatunków wzdłuż gradientu środowiskowego nie jest przerywany lecz ciągły. W rezultacie zmiany w składzie gatunkowym poszczególnych środowisk wzdłuż gradientu są również ciągłe (fig. 1).

Porównanie rozmieszczenia ptaków w różnych okresach cyklu rocznego w ciągu dwu kolejnych lat wykazało, że wybiórczość środowiska poszczególnych gatunków nie jest stała i ulega zmianom. Najsilniej jest ona wyrażona w okresie lęgowym; w okresach późniejszych zakres biotopów, w jakich występuje dany gatunek, może znacznie się powiększać.

U szeregu gatunków zmiany wybiórczości środowiskowej polegają na zajmowaniu po okresie lęgowym dalszych, ściśle określonych biotopów, względnie na zajmowaniu biotopów pewnego typu, (fig. 2 i 3). Zmiany następują przy tym regularnie w obu latach. U innych gatunków penetracja nietypowych środowisk następowała na stykach (fig. 4).

U szeregu gatunków zbadano zależność pomiędzy liczebnością populacji a zakresem zajmowanych środowisk. Stwierdzono, że w cyklu rocznym liczba zajmowanych przez dany gatunek środowisk — była proporcjonalna do zagęszczenia populacji w biotopach

optymalnych (fig. 5 i 6). Porównanie rozmieszczenia i liczebności niektórych gatunków w ciągu dwu lat wykazało, że zakres zajmowanych środowisk był większy w tym roku, w którym liczebność populacji również była większa (fig. 7).

Na podstawie dwuletnich obserwacji stwierdzono, że dynamika liczebności poszczególnych gatunków przebiega odmiennie w różnych środowiskach (fig. 8—13). W cyklu rocznym charakter dynamiki liczebności w tym samym biotopie w dwu kolejnych latach również może być różny. Różnice te tłumaczy autor lokalnymi migracjami części populacji z jednych biotopów do drugich. Przyczyną tych migracji jest z jednej strony liczebność populacji a z drugiej różnice w układzie biocenotycznym poszczególnych biotopów oraz zmienność tego układu tak sezonowa, jak i przebiegająca z roku na rok. W rezultacie lokalnych migracji większość badanych gatunków wykorzystuje nie jeden, lecz cały zespół biotopów. Dzięki przechodzeniu części populacji z jednych biotopów do drugich, ptaki zamieszkujące różne siedliska badanego terenu, nie są izolowane i stanowią jedną populację.

W obrębie poszczególnych środowisk oraz na granicach między nimi zbadane zostało rozmieszczenie gatunków zarówno eurytopowych jak i stenotopowych. Stwierdzono, że każdy gatunek wykazuje w danym biotopie właściwe sobie optimum występowania, charakteryzujące się maksymalnym zagęszczeniem. U gatunków eurytopowych maksymalne zagęszczenie występowało na stykach środowisk, u gatunków stenotypowych — wewnątrz biotopów (fig. 14 i 15).

Rozmieszczenie poszczególnych gatunków wewnątrz biotopów było bardzo zgodne w obydwu latach obserwacji. Porównując tę zgodność rozmieszczenia wewnątrz biotopów z dużą labilnością dynamiki liczebności w tych samych środowiskach, autor wnioskuje, że w danym biotopie, niezależnie od liczebności populacji zajmowane są przede wszystkim jego fragmenty optymalne dla danego gatunku.