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ROTATION OF INDIVIDUALS IN BREEDING POPULATIONS OF DOMINANT SPECIES OF BIRDS IN A PINE FOREST

ABSTRACT: In a pine forest the complete exchange of individuals of particular bird species takes place with a varying frequency: either every year (as in the case of *Erithacus rubecula* (L.)) or it may last even 7 years (*Parus cristatus* L.). A relation is observed between the age and wintering habits of birds and their attachment to the breeding area. Adult individuals which have at least once returned to the breeding area continue doing so in the next years. Other adult and young birds of migratory species and partly migrating ones are less attached to the breeding area than resident species. Individuals of the resident species have more constant breeding territories than individuals of migrating species.

KEY WORDS: Pine forest, bird community, populations, exchange of individuals, migration, attachment to breeding area, ringing of birds.

Contents

1. INTRODUCTION

Birds which in spring form a breeding community in a pine forest do not leave the place for some time after breeding. Then the breeding community becomes dispersed: the majority of

species begin autumn migrations, other species wander in the neighbourhood or move to the forest edge, and only some species remain in the forest for winter. Not all individuals survive till the next breeding period.

The aim of this paper has been to estimate the degree of attachment to breeding area of different species of birds. First, an investigation has been made of whether there is a relation between the wintering habits of individuals of a given species and their exchange in the breeding population. Therefore, species of different wintering habits have been investigated.

Parus cristatus[1] is a resident species (Tomiałojć 1972). *Fringilla coelebs*, *Erithacus rubecula*, *Ficedula hypoleuca* and *Anthus trivialis* fly away for the winter. Only very few individuals of the two first species may remain in Poland mainly in the vicinity of human settlements (Sembrat 1969), but basically all the four species are migrants (Ferens 1971, Tomiałojć 1972).

There are different opinions on how *Parus major* spends the winter. Micheev (1953) observed that on the south of the European part of the USSR on poorly forested areas *P. major* wandered even more than 1500 km to the place abundant in food. He did not observe wanderings in the forested regions of the north of the European part of the USSR and explained it by food abundance. Lichačev (1957) is of the opinion that adult individuals are resident and wander only on small distances towards human settlements. The young ones fly quite far. Mass ringing of *P. major* during migration indicates that at least part of the population wanders every year. As it has been found by Czaja-Topińska (1969) young individuals are the majority of migratory birds ar regards the population of north-eastern Europe. Recapture data on ringed birds prove that *P. major* is a partial migrant; some individuals migrate to various distances, some do not change their place or wander in the closest neighbourhood of breeding areas (Domaniewski 1934, Domaniewski and Kreczmer 1936, Rydzewski 1938, 1939, 1949a, 1949b, Szczepski 1951, 1963, 1965, 1970, 1976, Szczepski and Szczepska 1956, 1957, 1959, Zink 1969. *Parus ater* is also a partly migrating species (Zink 1969), Gibb 1970, Ferens 1971, Löhrl 1974).

Changes in the composition of the whole community of birds in the pine forest in successive years of investigation have been used as a background to show the rotation rate of population composition of chosen species.

The Polish literature has very few papers on the problems of stability of composition of passerine-bird-breeding populations (Jabłoński, Pinowski and Wasilewski 1970). Czarnecki (1975) in his comprehensive paper analysed bird populations of riverside willows. Pielowski and Wasilewski (1972) have carried out studies in a mixed forest and compared the returns to the breeding area of young and adult birds and those considered in the previous season as resident and non-resident. The community of birds in this forest was analysed as a whole without being divided into particular species.

In foreign literature methods of studies and of elaborating material for demographic characteristics of bird populations are given, amongst other, by Bailey (1952), Farner (1952a, 1952b, 1952c) and Jolly (1963). The main technique used here is calculating the size of population on the basis of banding and recapture data.

Studies based on ringing and recapture data can be divided into two groups after Farner (1952a, 1952b, 1952c):

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[1] Full scientific names of bird species are given in Table II.

1. where the data are obtained by extensive ringing and cover a large geographic area and a long period,

2. where the data considered are for a particular population under the direct observation of a scientist.

In the first group of studies the so-called life tables have been elaborated for some species on the basis of recapture data for ringed birds, sent from the whole country or even a greater area. These tables compile the statistical data on the population (Deevey 1947, Eriksson 1970).

Studies in the second group consider the population as inseparable from the area on which the birds are found in the breeding season. This allows one to observe the long-term history of bird community and changes taking place in it. Apart from the already mentioned paper of Czarnecki (1975) this category includes also the research of Haartman (1951) on *Ficedula hypoleuca*, that of Anven and Enemar (1957) and Paevskij and Vinogradova (1974) on *Fringilla coelebs*.

These works deal generally with species migrating for the winter. The relation between the wintering habits of birds and their attachment to breeding area has not been investigated. And this is one of the main problems of the present paper.

2. AREA INVESTIGATED

The area investigated (Fig. 1) is a part of a large complex of fresh pine forest growing on podzolic soil in the Gostynin Forest District in the Płock province. This is a mainly flat area cut by some dunes several hundred metres long, several metres in width and height. The forest consists of stands of various age, mainly 40–80 years old, and of clearings and pine plantations. Apart from *Pinus sylvestris* L. there are single trees of *Quercus robur* L., *Betula verrucosa* Ehrh. and *Populus* sp. The undergrowth consists of *Juniperus communis* L. In the herb layer dominate mosses, *Calluna vulgaris* (L.), *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L.

Two small fragments of the area examined (of a surface area 1 and 2 ha) have a character of raised bog. On the larger one the tree layer consists mainly of birches, and on the smaller one there are clumps of shrubs, mainly alder buckthorn (*Frangula alnus* Mill.). The ditches dug out on this area have water almost all the year round.

In two other places of the forest there are two 600 m^2 "gardens", where in place of cut off pines, trees and foliaceous shrubs were planted in 1967: *Betula verrucosa*, *Tilia cordata* Mill., *Padus serotina* (Ehrh.) and *Sorbus aucuparia* L. On one of the gardens there is a concrete water stand for birds.

Around the gardens, on the area of several hectares, several piles of dry twigs were placed, and on tree trunks there were about 20 nest-collars made of branches. About 100 nest-boxes were hung in rows at an average density of 6 nest-boxes per ha. In the last year of investigation, early in spring, 350 nest-boxes were placed on an area of 250 ha.

Apart from the above-mentioned sources of water, raised bog and water stand, there are other two water stands dug out for animals: one with a surface area of 20 m^2 and the second – about 100 m^2.

From the north the fragment of forest under investigations is partly bordered by crop fields and in other places passes into a vast forest complex.

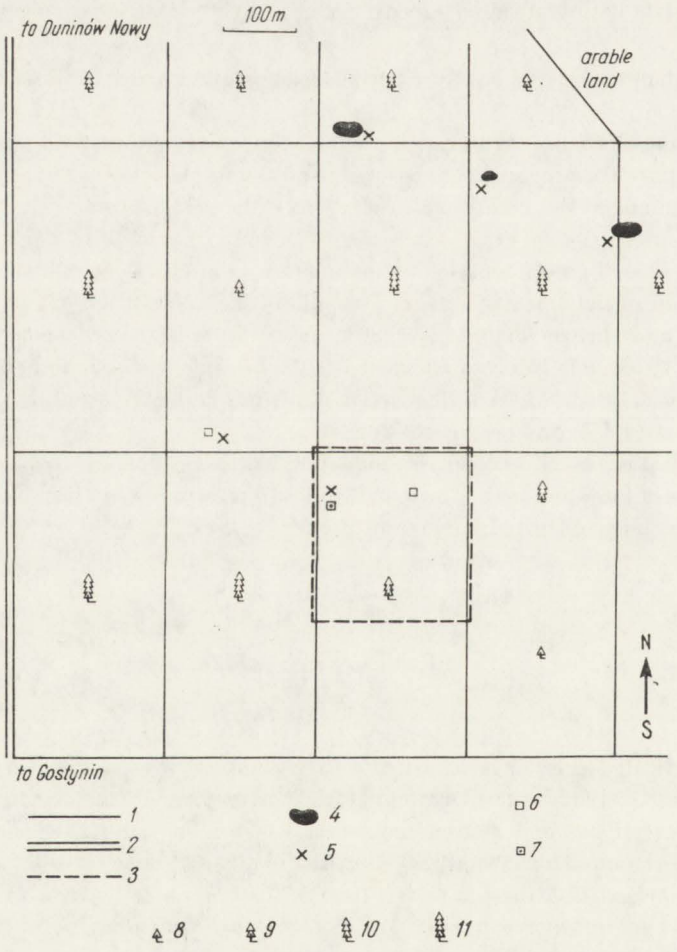

Fig. 1. Plan of the area investigated
1 – line of forest sections, 2 – highway, 3 – borders of the area with greater number of nest-boxes, 4 – water body, 5 – region of net distribution, 6 – "garden" without a water stand, 7 – "garden" with a water stand. Age of forest stand dominating in the given forest section: 8 – pine plantations, 9 – 21–40 years old, 10 – 41–60 years old, 11 – 61–80 years old

3. METHODS AND MATERIAL

3.1. METHODS OF FIELD INVESTIGATIONS

The studies were conducted from 1970 to 1976. The main part of material was collected by ringing birds. The birds were caught in mist-nets of a size 6–7 × 2.5 m. About 20 nets were placed irregularly in several places in the forest (Fig. 1). The greatest distance between nets was 1 km. The most attractive places for birds were selected in order to increase their trappability; usually small natural and artificial water bodies, clumps of shrubs, piles of dry twigs.

In order to investigate the possible dispersion of birds from the investigated area to the adjoining ones, additional nets were placed at a distance of 3–4 km to the west from the main

area of investigations in 1972 from July 15 to August 24. The nets were placed in three places near water stands for animals.

After few days the number of birds caught decreased as the birds had learned where the nets had been placed and how to avoid them. This reaction was also observed by P i e l o w s k i and W a s i l e w s k i (1972) and C z a r n e c k i (1975). So the nets were taken away and set out again after few days. Those nets into which many birds were being caught remained, whereas those into which few birds were caught were moved to different places.

The ringing dates (Fig. 2) varied in different years. They always covered a long period of the breeding season and usually (not in all years) lasted as long as the post-breeding period and the autumn one.

The nets were controlled daily about every 2 hours and for the last time after dusk.

An additional number of birds was ringed in nest-boxes and in natural nests. These were either females caught in the nest or nestlings before leaving the nest.

When ringing the species, the age of the bird, the hour and place were recorded. The birds were divided into following age groups: adults (over one year old), young birds in the first year of life that can already fly, and nestlings. If the age was difficult to determine then the bird was defined as a flying one.

The same information, the symbol and number of the ring were recorded when a ringed bird was caught.

In order to check to what extent the dominance structure of a bird community determined on the basis of net catches shows the real one, comparative observations were made in 1975. In the breeding season, when the nets were distributed, the birds on that area were counted in

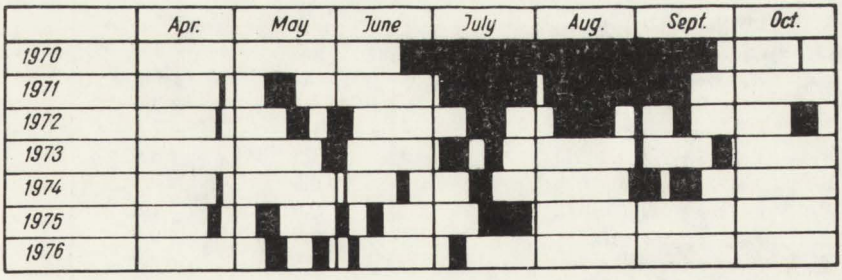

Fig. 2. Dates of ringing birds (intervals of at least four days are taken into consideration)

transects of a width of about 40 m leading in different directions, among other things, joining the ringing points. 230 birds belonging to 32 species were caught in the nets and 222 birds from 29 species were recorded on transects. The dominance structure of the community obtained by these two methods was compared (Table I). Renkonen index was used to measure the similarity of dominance structure which was 80%, i.e., indicated a high similarity. Thus the dominance structure obtained as a result of catching birds in nets can be treated as a real picture of bird community structure. Despite the differences in the behaviour of particular species the probability of catching them in nets was balanced considerably by the fact that the majority of nets were placed close to water bodies. The demand for water by different forest species of passerine birds is similar (G r a c z y k and W ą s 1967, J ę d r a s z k o-D ą b r o w s k a 1978).

Some slight differences in the dominance structure are presumably accidental ones. But unaccidental is probably the recording of a greater number of thrushes (*Turdus merula* and

T. viscivorus) than caught in the nets. Thrushes are strong and vigorous birds and they frequently escape from the nets.

Usually in the nets there was a smaller number of bigger birds than observed in the forest (e.g., *Garrulus glandarius*) and some species were not caught at all (e.g., *Streptopelia turtur*). These birds were usually noticed in the upper forest layer, more rarely in the lower layer where the nets were distributed.

Table I. Dominance structure of a community of birds in the breeding period in 1975 obtained by catches in nets and observations on transects

Species	Percentage	
	in nets	on transects
Fringilla coelebs	24.8	22.5
Parus cristatus	12.6	9.9
P. ater	9.6	12.2
Anthus trivialis	8.3	7.2
Ficedula hypoleuca	6.1	4.5
Parus major	4.3	3.2
Coccothraustes coccothraustes	3.9	1.4
Phoenicurus phoenicurus	3.5	3.6
Erithacus rubecula	3.5	3.2
Turdus merula	3.5	7.2
Phylloscopus collybita	2.2	–
Carduelis spinus	1.7	1.4
Phylloscopus trochilus	1.7	0.5
Dendrocopos major	1.3	3.6
Regulus regulus	1.3	1.8
Turdus viscivorus	1.3	3.6
Muscicapa striata	0.9	0.5
Phylloscopus sibilatrix	0.9	1.8
Turdus philomelos	0.9	0.9
Loxia curvirostra	0.9	–
Emberiza citrinella	0.9	–
Lullula arborea	0.9	1.4
Lanius collurio	0.9	–
Certia familiaris	0.9	1.8
Sturnus vulgaris	0.4	0.9
Garrulus glandarius	0.4	1.8
Passer montanus	0.4	0.5
Sylvia communis	0.4	–
Pyrrhula pyrrhula	0.4	–
Carduelis chloris	0.4	–
Motacilla alba	0.4	
Jynx torquilla	0.4	–
Oriolus oriolus	–	0.9
Dryocopus martius	–	0.9
Sitta europaea	–	0.5
Cuculus canorus	–	0.9
Streptopelia turtur	–	1.4

The list of bird species on the area examined (Table II) is completed by species recorded at sporadic observations when collecting the material.

3.2. MATERIAL

Over the 7 years of investigations 3474 birds from 54 species were ringed; 2939 were caught in nets and 535 were ringed in nest-boxes or in natural nests – 75 adult birds and 460 nestlings. At points of additional ringing in 1972, 497 birds were banded.

Recapture data after at least a year from the moment of ringing reached 229 for 185 individuals.

3.3. METHODS OF ELABORATING MATERIAL

When determining the dominance structure on the basis of the percentage of a species in the community, three groups were distinguished: dominants – over 5% of the community, subdominants – 2–5% and influent species – below 2% (P a l m g r e n 1928).

For determining the stability of the composition of bird community in successive years of studies the material was divided into two phenological periods: breeding period lasting from April 23 (date of first catches) to July 14, and the post-breeding period together with autumn period – from July 15 to October 25.

The mean percentage of particular bird species in the whole community was calculated on the basis of data from 6 years; for the breeding period from 1971 to 1976 (in 1970 a very small number of birds was ringed) and the post-breeding period from 1970 to 1975 (in 1976 there were no catches in the post-breeding period).

The variability of the percentage of a given species in the community over several years was expressed by means of a coefficient of variability (W) – the ratio of standard deviation (S) of the character value to its arithmetical mean:

$$W = \frac{S}{\bar{y}},$$

(y is the percentage of a given species in the community in either the breeding or post-breeding period).

The variability coefficient was calculated for the most abundant species in the breeding period: dominants, subdominants and 5 influent species. For the purpose of comparison W was calculated for the same species in the post-breeding period (Table III).

Recapture data were based on information on ringed birds caught in nets. Hole nesting birds with rings caught in nest-boxes were not taken into consideration. Therefore, the data on the percentage of recapture of hole nesting birds could be directly compared with those for birds making open nests and caught only in nets as adults.

In the analysis of return information the material for both phenological periods was considered jointly. This was possible because the percentage of recaptured birds, ringed in the breeding period, did not differ significantly from the analogous percentage of birds ringed in the post-breeding period. A test of two structure indices (G r e ń 1978) was made to examine the significance of differences. This was done on the basis of mean percentage of returns after

Table II. List of species observed on the area investigated in the years 1970–1976

Species caught in nets, arranged in the order of their mean percentage in the breeding period. D – dominant, S – subdominant, I – influent, A – absent

No.	Species caught in nets*	Breeding period					Post-breeding period				
		mean percentage	in how many out of 6 seasons the bird occurred as:				mean percentage	in how many out of 6 seasons the bird occurred as:			
			D	S	I	A		D	S	I	A
1	*Fringilla coelebs* L.	31.2	6	–	–	–	15.1	5	1	–	–
2	*Anthus trivialis* (L.)	9.8	5	1	–	–	3.2	1	3	2	–
3	*Parus major* L.	9.5	4	2	–	–	13.7	6	–	–	–
4	*P. cristatus* L.	6.3	5	1	–	–	7.4	5	1	–	–
5	*P. ater* L.	4.5	4	1	1	–	10.0	3	3	–	–
6	*Phoenicurus phoenicurus* (L.)	3.6	1	3	2	–	2.8	2	–	2	2
7	*Turdus philomelos* C. L. Brehm	3.0	1	4	1	–	3.4	1	2	3	–
8	*Erithacus rubecula* (L.)	2.9	–	5	1	–	8.0	4	2	–	–
9	*Ficedula hypoleuca* (Pall.)	2.9	1	3	2	–	4.5	3	–	3	–
10	*Turdus merula* L.	2.8	–	3	3	–	1.3	–	1	3	2
11	*Coccothraustes coccothraustes* (L.)	2.8	–	5	–	1	1.3	–	1	3	2
12	*Emberiza citrinella* L.	1.8	1	1	4	–	0.1	–	–	1	5
13	*Turdus viscivorus* L.	1.6	–	2	3	1	4.2	3	–	2	1
14	*Phylloscopus trochilus* L.	1.6	–	3	1	2	1.8	1	1	1	3
15	*Parus caeruleus* L.	1.5	–	2	3	1	4.3	3	1	1	1
16	*Lanius collurio* L.	1.3	–	2	4	–	0.1	–	–	1	5
17	*Muscicapa striata* (Pall.)	1.2	–	1	3	2	0.9	–	1	2	3
18	*Carduelis spinus* (L.)	1.2	–	1	3	2	0.2	–	–	1	5
19	*Phylloscopus collybita* (Vieill.)	1.1	–	1	4	1	1.9	–	3	2	1
20	*Garrulus glandarius* (L.)	1.1	–	1	4	1	1.5	1	1	1	3
21	*Parus montanus* Conr.	1.0	–	1	4	1	3.8	1	3	2	–
22	*Phylloscopus sibilatrix* (Bechst.)	0.9	–	–	5	1	1.2	1	–	2	3
23	*Dendrocopos major* (L.)	0.9	–	–	5	1	1.2	–	1	5	–
24	*Loxia curvirostra* L.	0.7	–	1	3	2	0.0	–	–	1	5

25	*Certia familiaris* L.	0.6	–	1	2	3	1.0	–	1	3	2
26	*Lullula arborea* (L.)	0.5	–	–	4	2	0.1	–	–	1	5
27	*Motacilla alba* L.	0.4	–	–	3	3	0.1	–	–	2	4
28	*Sturnus vulgaris* L.	0.4	–	–	4	2	–	–	–	–	6
29	*Aegithalos caudatus* (L.)	0.3	–	–	2	4	0.6	–	–	3	3
30	*Pyrrhula pyrrhula* (L.)	0.3	–	–	3	3	0.4	–	–	2	4
31	*Regulus regulus* (L.)	0.2	–	–	1	5	2.3	2	–	1	3
32	*Troglodytes troglodytes* (L.)	0.2	–	–	1	5	0.2	–	–	2	4
33	*Oenanthe oenanthe* (L.)	0.2	–	–	2	4	0.2	–	–	1	5
34	*Sylvia curruca* (L.)	0.2	–	–	3	3	0.1	–	–	2	4
35	*Jynx torquilla* L.	0.2	–	–	2	4	0.1	–	–	1	5
36	*Certhia brachydactyla* C. L. Brehm	0.2	–	–	2	4	0.0	–	–	1	5
37	*Sylvia borin* (Bodd.)	0.1	–	–	1	5	0.6	–	–	5	1
38	*Upupa epops* L.	0.1	–	–	1	5	0.3	–	–	2	4
39	*Hippolais icterina* (Vieill.)	0.1	–	–	1	5	0.1	–	–	2	4
40	*Sylvia communis* Lath.	0.1	–	–	2	4	–	–	–	–	6
41	*Carduelis chloris* (L.)	0.1	–	–	1	5	–	–	–	–	6
42	*Passer montanus* (L.)	0.1	–	–	1	5	–	–	–	–	6
43	*Oriolus oriolus* (L.)	0.0	–	–	1	5	0.1	–	–	1	5
44	*Sylvia atricapilla* (L.)	0.0	–	–	1	5	0.1	–	–	1	5
45	*Fringilla montifringilla* L.	–	–	–	–	6	0.4	–	–	2	4
46	*Turdus iliacus* L.	–	–	–	–	6	0.2	–	–	1	5
47	*Dendrocopos minor* (L.)	–	–	–	–	6	0.2	–	–	3	3
48	*Turdus pilaris* L.	–	–	–	–	6	0.2	–	–	2	4
49	*Alcedo atthis* L.	–	–	–	–	6	0.1	–	–	2	4
50	*Tringa ochropus* L.	–	–	–	–	6	0.1	–	–	1	5
51	*Phoenicurus ochruros* (Gmel.)	–	–	–	–	6	0.1	–	–	1	5
52	*Dendrocopos medius* (L.)	–	–	–	–	6	0.0	–	–	1	5
53	*Caprimulgus europaeus* L.	–	–	–	–	6	0.0	–	–	1	5
54	*Accipiter nisus* (L.)	–	–	–	–	6	0.0	–	–	1	5

*Species observed but not caught in nets: (55) *Accipiter gentilis* (L.), (56) *Buteo buteo* (L.), (57) *Strix aluco* L., (58) *Dryocopus martius* (L.), (59) *Dendrocopos leucotos* (Bechst.), (60) *Streptopelia turtur* (L.), (61) *Columba palumbus* L., (62) *Cuculus canorus* L., (63) *Sitta europaea* L.

Table III. Variability coefficient (W) for the most abundant species in the breeding period Place in the dominance structure (mean for 6 periods): D – dominant, S – subdominant, I – influent

Species	Breeding period		Post-breeding period	
	place	W (%)	place	W (%)
Fringilla coelebs	D	12.3	D	35.8
Anthus trivialis	D	30.9	S	52.8
Parus major	D	50.3	D	39.5
P. cristatus	D	23.5	D	40.8
P. ater	S	29.5	D	77.5
Phoenicurus phoenicurus	S	50.8	S	100.0
Turdus philomelos	S	50.5	S	62.7
Erithacus rubecula	S	44.4	D	52.9
Ficedula hypoleuca	S	45.0	S	111.1
Turdus merula	S	44.6	I	113.8
Coccothraustes coccothraustes	S	50.5	I	115.7
Emberiza citrinella	I	102.0	I	129.1
Turdus viscivorus	I	69.6	S	78.8
Phylloscopus trochilus	I	69.0	I	130.2
Parus caeruleus	I	60.4	S	66.2
Lanius collurio	I	50.2	I	267.7

1 year of birds ringed in each of the two phenological periods (Table IV). As the limit value of the function read from tables of normal distribution at a risk of error 0.05 is higher (1.96) than that of test function (0.25) the null hypothesis that the per cent of return information for the breeding period does not differ significantly from that for the post-breeding period cannot be turned down.

Table IV. Return information for the breeding and post-breeding period (total for all years for all species together)

Number of ringed birds in the period:		Ringed birds caught after one year from the period:			
		breeding		post-breeding	
breeding a	post-breeding b	number c	$\frac{c}{a}$ (%)	number d	$\frac{d}{b}$ (%)
1406	1614	66	4.7	72	4.5

Thus, the material on return information for the whole period of investigations can be treated as homogeneous and analysed together.

Birds caught in nets on the investigated area did not reach 100%. In order to estimate the trappability of birds the following method was used: ringed birds living in nest-boxes were considered as a representative sample of the community of birds on the area investigated. The per cent of birds caught in the same year in which they lived in nest-boxes was calculated. The data for the years 1971–1976 were treated jointly and the mean number of birds from

nest-boxes was calculated (the per cent in relation to ringed birds). It was 18.6% with a confidence interval at a probability level 0.95 contained between 11.6 and 27.5%. According to this it was assumed that birds caught in nets between 1971 and 1976 were 11.6–27.5% of the community of birds found on the area investigated. Such an assumption can be made if all birds are being caught to the same extent as those inhabiting nest-boxes. The intensity of catching birds decreases, of course, with the increasing distance from breeding areas to nets. Thus, it should be remembered that these are only approximate data indicating the order of value.

Another reason for using the relative values here is the fact that the area investigated is in a large forest complex of the same nature. Therefore, it is impossible to determine precisely the exact area from where the birds caught in nets come from.

The most abundantly caught species have been analysed in detail, namely: *Fringilla coelebs*, *Parus major*, *P. ater*, *P. cristatus*, *Ficedula hypoleuca*, *Anthus trivialis* and *Erithacus rubecula*.

After H a a r t m a n (1951) it has been assumed that if a bird is caught two or more years after it has been ringed then it occurred on the area investigated in all years in between. This lowers the error caused by catching every year a different number of birds.

First of all the returns of birds after two or more years from the moment of ringing have been analysed, then the returns of birds after one year. It is not known what part of the population has returned after one year as in the nets 11.6–27.5% of birds were caught, but for the next years these values were calculated in relation to the returns of the previous year.

4. RESULTS

4.1. ANALYSIS OF THE STABILITY OF THE COMPOSITION OF BIRD COMMUNITY IN SUCCESSIVE YEARS OF INVESTIGATIONS

Over 7 years (1970–1976) 63 species of birds were observed on the area investigated (Table II); 54 species were caught in nets and 9 only recorded. Birds of 44 species were caught in nets during the breeding period, and up to 50 species in the post-breeding period.

Fringilla coelebs is the most abundant bird in both phenological periods: on the average it constituted one third of the whole community in the breeding period, whereas in the post-breeding period its participation considerably decreased. Considerable prevalence in numbers of the chaffinch over other species is typical of very poor habitats (T o m i a ł o j ć 1974).

According to the mean percentage, *Anthus trivialis*, *Parus major* and *P. cristatus* belong to the group of dominants in the breeding period. In the post-breeding period *Anthus trivialis* no longer remains in the group of most abundant birds, whereas *Parus ater* and *Erithacus rubecula* come into that group. The percentage of all tits in that period increases also due to a greater number of offspring than in the case of other species.

The group of subdominants in the breeding period consists of *Parus ater*, *Phoenicurus phoenicurus*, *Turdus philomelos*, *Erithacus rubecula*, *Ficedula hypoleuca*, *Turdus merula* and *Coccothraustes coccothraustes*.

In the post-breeding period *Ph.phoenicurus*, *T. philomelos* and *F. hypoleuca* remain in this group. Apart from them the subdominant group consists of *Anthus trivialis* (dominant in the breeding period) and *Turdus viscivorus* and *Parus caeruleus* which are "promoted" from the group of influent species.

The participation of particular species of birds in the whole community changes in successive years. For example, *P. major* in the breeding period, despite the fact of being a dominant,

Table V. Return information for particular species

N – absolute number, *P* – percentage in relation to the number of ringed birds, – – lack of return information, · – lack of data

Species	Year of ringing	Number of ringed birds	Return information after											
			1 year		2 years		3 years		4 years		5 years		6 years	
			N	*P*	*N*	*P*	*N*	*P*	*N*	*P*	*N*	*P*	*N*	*P*
Parus cristatus	1970	21	9	42.8	6	28.6	5	23.8	2	9.5	2	9.5	1	4.8
	1971	48	14	29.2	6	12.5	3	6.2	3	6.2	2	4.2	.	.
	1972	31	8	25.8	2	6.4	1	3.2	1	3.2	.	.	.	.
	1973	33	10	30.3	6	18.2	2	6.1	.	.	.	.	.	.
	1974	22	3	13.6	1	4.5	.	.	.	.	.	.	.	.
	1975	18	3	16.7	.	.	.	.	.	.	.	.	.	.
	average			26.4		14.0		9.8		6.3		6.8		4.8
P. ater	1970	7	4	57.1	2	28.6	1	14.3	–	–	–	–	–	–
	1971	31	5	16.1	3	9.7	1	3.2	–	–	–	–	.	.
	1972	77	10	13.0	2	2.6	2	2.6	–	–	.	.	.	.
	1973	78	12	15.4	7	9.0	1	1.3	.	.	.	.	.	.
	1974	47	4	8.5	2	4.2	.	.	.	.	.	.	.	.
	1975	18	–	–	.	.	.	.	.	.	.	.	.	.
	average			18.4		10.8		5.4						
P. major	1970	26	2	7.7	1	3.8	–	–	–	–	–	–	–	–
	1971	76	4	5.3	2	2.6	–	–	–	–	–	–	.	.
	1972	123	6	4.9	1	0.8	–	–	–	–	.	.	.	.
	1973	133	3	2.3	1	0.7	–	–	.	.	.	.	.	.
	1974	33	2	6.1	–	–	.	.	.	.	.	.	.	.
	1975	31	–	–	.	.	.	.	.	.	.	.	.	.
	average			4.4		1.6								

Fringilla coelebs	1970	39	2	5.1	1	2.6	–	–	–	–	–	–	–	–
	1971	133	14	10.5	5	3.8	1	0.7	1	0.7	–	–	.	.
	1972	165	9	5.4	7	4.2	6	3.6	3	1.8	.	.	.	.
	1973	172	9	5.2	9	5.2	5	2.9	.	.	.	.	.	.
	1974	40	3	7.5	2	5.0	.	.	.	.	.	.	.	.
	1975	57	4	7.0	.	.	.	.	.	.	.	.	.	.
	average			6.8		4.2		1.8		0.8				
Ficedula hypoleuca	1970	29	–	–	–	–	–	–	–	–	–	–	–	–
	1971	77	–	–	–	–	–	–	–	–	–	–	.	.
	1972	50	2	4.0	1	2.0	1	2.0	–	–	.	.	.	.
	1973	27	2	7.4	2	7.4	–	–	.	.	.	.	.	.
	1974	11	–	–	–	–	.	.	.	.	.	.	.	.
	1975	11	1	9.1	.	.	.	.	.	.	.	.	.	.
	average			3.4		1.9		0.5						
*Anthus trivialis**	1971	40	3	7.5	–	–	–	–	–	–	–	–	.	.
	1972	28	2	7.1	–	–	–	–	–	–	.	.	.	.
	1973	49	2	4.1	1	2.0	–	–	.	.	.	.	.	.
	1974	15	1	6.7	–	–	.	.	.	.	.	.	.	.
	1975	19	1	5.3	.	.	.	.	.	.	.	.	.	.
	average			6.1		0.5								

*For *A. trivialis* the data for 1970 are omitted because only two birds were then ringed.

became a subdominant for two years. *A. trivialis* and *P. cristatus* were dominants for 5 years and once subdominants. *P. ater*, *Ph. phoenicurus*, *T. philomelos* and *F. hypoleuca* classified as subdominants, according to their mean numbers, were in different years dominants, subdominants and even influents.

In the breeding period *Fringilla coelebs* displayed the smallest coefficient of variability as regards its percentage in the community (12.3%) – over all 6 years it was a distinct dominant (Table III).

P. cristatus had a coefficient of variability (23.5%) higher than *F. coelebs*, but lower than other species. Two other dominant species differed considerably in coefficients of variability although their mean numbers for 6 periods approximated; for *A. trivialis* 30.9% and for *P. major* 50.3%. Thus in the breeding season *F. coelebs* displayed the lowest percentage variability in the community in the group of most abundant species and *P. major* – the highest.

P. ater had a relatively low coefficient of variability (29.5%) – a species in between the dominants and subdominants (dominant in 4 breeding periods, subdominant in 2 breeding periods). Other subdominants had a similar mean percentage in the community (from 2.8 to 3.6%) and the coefficient of variability (from 44.6 to 50.8%), higher on average than for dominants.

Species from the group of influents had the highest coefficients of variability.

Almost all species examined (except *P. major*) had in the post-breeding period higher coefficients of variability than in the breeding period. Even for dominants the values were from 35.8% (*F. coelebs*) to 77.5% (*P. ater*).

4.2. FREQUENCY OF RETURNS TO BREEDING AREAS OF CHOSEN BIRD SPECIES

Detailed return information is given for most numerously caught species (Table V).

No individual of *Erithacus rubecula* was caught again out of the 142 ringed ones. A low number of recaptures was recorded for *Ficedula hypoleuca*, *Parus major*, *Anthus trivialis* and *Fringilla coelebs*. Much more frequently ringed individuals of *Parus ater* were caught and most abundantly *Parus cristatus*.

Return information on adult birds was obtained two or more years after they had been ringed. This allowed me to calculate what percentage of recaptures from successive years was of the birds returning the next year (Table VI). *F. hypoleuca* and *A. trivialis* were omitted in the analysis, because of a small number of recaptures already in the first year after ringing.

Table VI. Returns of adult birds in successive years in relation to the last year

Per cent of ringed birds caught in successive years (previous year = 100%)

Species	Year after ringing		
	second	third	fourth
Fringilla coelebs	61.2	42.9	44.4
Parus major	36.4	0.0	0.0
P. ater	58.7	50.0	0.0
P. cristatus	53.0	70.0	64.3

As regards *F. coelebs* the fraction of individuals recaptured compared with ringed birds caught one year earlier was slightly higher two years after ringing than after 3 and 4 years. In these two last years this value was almost identical. After a longer period the returns were no longer observed.

As regards *P. major* the ringed individuals were caught only up to two years after being ringed. Their fraction was the smallest of all discussed here.

As regards *P. ater* the rate of disappearance of birds banded in two or three years after being ringed was almost identical. In the following years the birds of this species were not caught.

As regards *P. cristatus* the fraction of individuals banded two years after being ringed was slightly lower than after three and four years. Banded individuals were caught for the longest time, even six years after being ringed. The results of the last two study years did not repeat much and these data are not included to Table V as not being sufficiently representative.

Two years after ringing the birds on the breeding area there was 36.4% (*Parus major*) up to 61.2% (*Fringilla coelebs*) of birds in relation to the number of birds with rings recorded a year before. Thus, the annual loss among adult birds was 38.8–63.6%.

Three years after ringing the birds adult *P. major* were not observed, and the returns for other species were from 42.9 (*F. coelebs*) to 70.0% (*P. cristatus*) in relation to returns observed the previous year.

Four years after ringing the birds *F. coelebs* occurred in 44.4% of whole population of the previous year and *P. cristatus* in 64.3%.

After 5 and 6 years from the time of being ringed only banded *P. cristatus* were observed.

One year from the moment the birds were ringed particular species varied in returns to the breeding areas (Table V); no returns of *Erithacus rubecula*, sporadic occurrence of *Fringilla coelebs*, *Parus major*, *Ficedula hypoleuca* and *Anthus trivialis* (between 3.4% and 6.8% of individuals ringed in the previous year), more abundant occurrence of *Parus ater* (18.4%) and most abundant of *P. cristatus* (26.4%).

In the case of *F. coelebs*, *P. ater* and *P. cristatus* these interspecific differences in returns of ringed birds recorded at least once on the area investigated were not so distinte in the later years (Table VI). Therefore, the cause of the differences a year after the birds were ringed had to be studied. For that reason a comparison was made of the returns of adult and young birds (nestlings and flying birds born in the same year when they were ringed). For many birds it was difficult to determine their age when ringing them thus the calculations were made for birds of a known age. This, of course, reduced the size of the sample and the results were less representative.

There is a distinct difference in the returns of young and adult birds (Table VII); the returns of young are less numerous than of adult birds. These differences are much greater if taking the nestlings together with young birds that can fly. If they are divided then among the ringed nestlings there are almost no returns (except for one case of a *Ficedula hypoleuca*). This, among other things, is probably due to much higher mortality of nestlings than of young birds which can already fly.

Among the majority of species examined the young birds that can fly return less frequently than adult ones, only in the case of *Parus ater* the birds of both these groups have returned to similar extent.

As regards the recaptures of young birds that can fly this group is considerably differentiated; no returns for *F. hypoleuca* and *A. trivialis*, very few for *P. major* and *F. coelebs*, quite numerous for *P. ater* and most numerous for *P. cristatus*.

Table VII. Return information for different age groups of birds
A – adult bird (after first year of life), Y – young flying bird (in the first year of life), Ne – nestling, B – number of banded birds, R – recaptures after 1 year (cumulated data)

Species	Age											
	A			Y + Ne			Y			Ne		
	B	R	R : B	B	R	R : B	B	R	R : B	B	R	R : B
Fringilla coelebs	279	28	10.0	56	2	3.6	52	2	3.8	4	0	0.0
Ficedula hypoleuca	64	4	6.2	57	1	1.8	37	0	0.0	20	1	5.0
Anthus trivialis	53	3	5.7	5	0	0.0	5	0	0.0	0	0	0.0
Parus major	59	3	5.1	239	3	1.3	170	3	1.8	69	0	0.0
P. ater	39	4	10.3	94	5	5.3	40	5	12.2	54	0	0.0
P. cristatus	20	8	40.0	18	2	11.1	11	2	18.2	7	0	0.0

As regards adult birds the results are rather homogeneous for the majority of species with one extreme: numerous recaptures of *P. cristatus* (40%).

Assuming, on the basis of catches of hole nesting birds from nest-boxes, that during the season there were 11.6–27.5% of birds from the investigated area in the nets (see Section 3.3) an attempt was made to calculate the limits within which was the real per cent of returns of particular species a year after the birds had been ringed (Table VIII).

Table VIII. Limits containing the real per cent of returns of birds in a year after they had been ringed (mean for 6 years, all age groups together)

Species	Per cent of returns
Fringilla coelebs	12.6–29.8
Ficedula hypoleuca	3.5– 8.4
Anthus trivialis	19.0–45.1
Parus major	10.3–24.5
P. ater	36.6–86.9

For *P. ater* the per cent of returns was very high. Its real value is probably closer to the lower limit of the interval as its upper value exceeds that of the annual survival of population.

The lack of returns in the case of *Erithacus rubecula* has already been mentioned. The lowest number of returns is observed for *Ficedula hypoleuca*. Data for *Parus cristatus* are not given in Table VIII as the results are distinctly overestimated. This is due to the fact that *P. cristatus* is a resident species. In the years when the nets have been distributed in autumn *P. cristatus* was constantly caught, although a number of other species already left the forest examined. Thus, *P. cristatus* was caught more abundantly than other species.

As regards the abundantly caught species a comparison was made in order to find the per cent of birds recaptured in the same places of distribution of nets and in different ones (Table IX). It was found that *Fringilla coelebs*, *Parus major* and *P. ater* occurred in a slightly higher number in places where they had already once been caught, whereas for *P. cristatus*

recaptures in the same places distinctly prevailed over those in new places. Thus the territories of occurrence of *P. cristatus* seemed to be much closer to those from the previous year as compared with territories for other species.

Table IX. Location of captures of ringed birds
Total number of recaptured birds = 100%

Species	Per cent of recaptured birds in the place they had been ringed
Fringilla coelebs	60.0
Parus major	58.8
P. ater	59.1
P. cristatus	77.8

As regards birds ringed at sites 3–4 km from the main area of investigations the results were as follows: among birds ringed in the previous years only one individual of *Turdus viscivorus* was caught (first time caught in 1971 on the main study area). Also three young tits, ringed in nest-boxes, were caught: two *Parus ater* from one brood caught 27 and 31 days after being ringed and one *P. caeruleus* caught 82 days after banding. The birds covered the distance of 4 km.

5. DISCUSSION

Not all species of the 63 occurring on the investigated area were caught in nets and some were only caught in one of the phenological periods. The fact that some species are not caught in the nets (or it happens rarely) can be explained by some objective and methodic reasons:

a. Scarce (as understood by Dobrowolski 1963) occurrence of a species (e.g., *Dendrocopos major* having a relatively large territory).

b. Rare (Dobrowolski 1963) occurrence of a species (e.g., *Lullula arborea* found almost exclusively on the bordering line of forest and open area, or *Alcedo atthis* or *Tringa ochropus* which could fly here from a considerably large swampy area situated not far from the area investigated).

c. Some species keep mainly to the tree crowns and not to the lower forest layer where the nets were distributed (*Streptopelia turtur, Cuculus canorus*).

d. Appearance of some species few years since the investigations began as a result of changes in the habitat (.e.g., *Oenanthe oenanthe* – due to the new clearing, *Passer montanus* – because nest-boxes were distributed on the border of forest and the village).

e. Changing periods of catches into nets (e.g., *Fringilla montifringilla* and *Regulus regulus* were caught mainly in the autumn, and autumn catches were carried out not every year).

For some species several reasons can simultaneously be applied.

An analysis of coefficient of percentage variability of a species in community (W) has displayed a following tendency in successive years: the higher the numbers of the species as regards dominance structure of the community the lower the annual fluctuations in numbers (Table III). Haapanen (1965) has obtained similar results.

A factor of a statistical character may affect this regularity, especially in relation to the least numerous species. The lower are the numbers of a given species the more even a slight deviation from absolute values results in high relative change of percentage. In addition, random factors are of greater significance; the fact that a bird is caught or not is each time highly accidental. Estimations of changes in numbers of influent species as accurate as in the case of dominants would require a greater sample than for dominants to obtain numbers of the same order for analysis. Therefore, the variability coefficient can be only compared for quite numerous species.

The relation between the place of a species in the dominance structure of community and the variability coefficient of its percentage does not concern all species. For example, *Parus major* – a species from the group of dominants – has the *W* coefficient much higher than other species, probably because the pine forest is a marginal habitat for *P. major* which prefers deciduous forests (B a l e n 1973, U l f s t r a n d 1977).

K l u y v e r and T i n b e r g e n (1953) have observed relatively low fluctuations of populations of tits (*Parus major*, *P. caeruleus* and *P. ater*) in habitats attractive for them (densely populated by tits) and high fluctuations in poor not much inhabited biotopes. Therefore, they have reached the conclusion that a habitat suitable for a species is always occupied at a similar degree, whereas the poor habitat is densely populated only in years when a species is abundant. G l a s (1960) has observed the same for *Fringilla coelebs*. According to E n e m a r (1966) this is true of the majority of forest Passeriformes. The following factors act together: suitable habitat for a species, high density of individuals of the species, relatively low fluctuations in numbers. According to studies of P i e l o w s k i and W a s i l e w s k i (1972) in a mixed forest *Parus major* has displayed over 6 years the smallest fluctuations in numbers among the group of dominants. K e n d e i g h (1944) has stated that annual fluctuations in numbers of a species are mainly due to the varying numbers of young birds which matured and returned to the breeding area. This phenomenon may be well observed in a suboptimal biotope of a species. Such habitats are frequently occupied by young birds when better areas are already taken by adult birds.

In the group of subdominants the coefficient of variability in the breeding period for *Ficedula hypoleuca* does not differ much from that for five other species of this group, whereas according to T o m i a ł o j ć (1972) *F. hypoleuca* displays strong fluctuations in numbers.

High values of variability coefficient of percentage of a species in a community, typical of majority of species in the post-breeding period, reflect the lack of stability in the bird community over that period. As in that period the dates of catches vary the results have not been analysed in detail.

When elaborating the return information the material for the breeding and post-breeding period has been treated jointly, because the statistical analysis did not show significant differences in the per cent of returns.

It is worth considering why birds ringed in the breeding and post-breeding period return to the same extent. In each of these periods the relation of birds to the breeding area is different; after the stationary period due to reproduction many species start to wander and then migrate. Still in the breeding period there is a number of non-settled individuals (P i e l o w s k i and W a s i l e w s k i 1972, C z a r n e c k i 1975), whereas in the post-breeding period a part of the population remains on the breeding area. Thus in both periods there are settled and non-settled birds.

An identical per cent of returns may indicate that the proportions between these two groups are the same in both periods; or in the breeding period many non-settled individuals are caught

in nets, or in the post-breeding period a considerable number of ringed birds belongs to the population settled on the area investigated.

This would have to be explained if calculating the returns of particular species in per cents of the number of settled individuals. In this paper, however, the data on returns are relative values comparable only with one another.

Comparison of data on returns of adult *Fringilla coelebs* to the breeding area with the literature data on the mortality of this species (Table X) shows that a majority or all alive adult individuals of *F. coelebs* occur in the region where the breeding took place in the previous year. Considering the rather small area it can be said that the places of repeated occurrence are accurately indicated. Similar results for *F. coelebs* have been obtained by Anven and Enemar (1957).

Table X. Mean annual mortality of adult birds of different species of Passeriformes (acc. to data of different authors)

Species	Country	Mortality	Author
Parus major	Finland	44	Haukioja (1969)
	Switzerland	46	Plattner and Sutter (1947)
	Holland	49	Kluyver (1951)
	Great Britain	50	Lack (1966)
Fringilla coelebs	north-west of the USSR and Finland	47	Paevskij (1974)
	Finland	52	Haukioja (1969)
Ficedula hypoleuca	Federal Republic of Germany	43	Berndt and Sternberg (1963)
	Finland	50	Haartman (1951)
	German Democratic Republic	55	Creutz (1955)
	Finland	63	Haukioja (1969)
Erithacus rubecula	Great Britain	62	Lack (1948)
	north-west of the USSR and Finland	62	Paevskij (1974)
	Finland	76	Haukioja (1969)

Assuming that annual mortality of adult *Parus ater* and *P. cristatus* stays within the limits of mortality observed for some other species of passerine birds (Table X) the conclusions about the attachment of *F. coelebs* to the breeding area can cover also these two species.

It can be assumed that the returns of adult *Ficedula hypoleuca* have a similar character as for the three species discussed. One year after ringing the per cent of returns has been small and this resulted in a small number of return information in the following years. Therefore, *F. hypoleuca* is not included to Table VI. Data in Table V allow me to conclude that the rate of disappearance of adult *F. hypoleuca* from the breeding area approximates the annual mortality given in the literature. According to Haartman's (1951) data adult individuals of *F. hypoleuca* that return once to the own breeding area remain attached to it in the next years.

Out of the species presented in Tabe VI attention should be paid to *Parus major*: two years after ringing the per cent of returns (36.4%) is lower than the survival given in literature (about

50%), and in the next years the ringed birds do not occur. It may be assumed that adult individuals of *P. major* are less attached to the breeding area than the three species already discussed. Possibly not all adult *P. major* return to their breeding regions of the last year, some move to a different area.

It has already been stated that *P. major* displays a high annual variability in numbers during the breeding period. This has been explained by the fact that a poor pine forest is a marginal habitat for this species. This is probably why few adult *P. major* return to the area, where they bred in the previous year.

Anthus trivialis is not much attached to the breeding area and *Erithacus rubecula* does not show any attachment. This fact is difficult to explain.

If we consider the disappearance of adult *Fringilla coelebs*, *Parus ater* and *P. cristatus* as equal to their mortality then it can be stated that the mortality among adult individuals of these species is approximately a constant value, independent of age.

This is confirmed by literature data (e.g., S t e e n b e r g e n 1971). In F a r n e r's (1952b) opinion the annual mortality of adult birds independently of age is even more understandable as the mean life span of birds is a small part of their potential longevity which eliminates death due to old age. D e e v e y (1947) has also observed a constant mortality for adult birds and concludes that life experience is of no significance for avoiding death by birds. However, it seems that there may be a compensation of several factors decreasing and increasing the chances of survival, e.g., on the one hand, lower physical efficiency of older birds and, on the other hand, their experience.

This regularity regarding the constant elimination rate of adult birds of *F. coelebs*, *P. ater* and *P. cristatus* is probably also true for other species discussed. In present studies it has been impossible to trace the long history of these birds because of the small number of birds returning to the breeding area.

On the area investigated the per cent of returns of young birds was lower than of adult ones. One of the causes as regards the returns of different age groups is their different mortality: nestlings have the smallest chance of survival, young birds have a greater one and the adult birds – the greatest one. This is confirmed by the data of C z a r n e c k i (1975) for birds in the riverside willows. H a a r t m a n (1951) has determined the annual mortality of adult *F. hypoleuca* as about 50% and for the young that left nests – 70–73%.

Different attachment of adult and young birds to the area may be another cause of this phenomenon. Among young birds the differentiation of returns is very high – from a lack of returns (*Anthus trivialis*, *Erithacus rubecula*), through some returns (*Fringilla coelebs*, *Ficedula hypoleuca*, *Parus major*), numerous returns (*P. ater*) to the most numerous returns (*P. cristatus*).

Such distribution of returns would indicate some connection with the wintering habits of birds. Species of which the young do not return, or very few return, are migrants or (as *P. major*) partial migrants. *P. ater* which is in the middle as regards the returns is a partly migrating species. The most numerous recaptures observed are those of *P. cristatus* – a stationary species. The fact that the results for *P. major* are similar to those for other species from the group of migrants and not to that of the partial migrants such as *P. ater* can be probably explained by the suboptimal character of the habitat for *P. major*. The phenomenon of less numerous returns of young birds than of old ones has been observed by P i e l o w s k i and W a s i l e w s k i (1972) and P a e v s k i j and V i n o g r a d o v a (1974). They have interpreted this fact also as a strong dispersal effect of young birds. H a a r t m a n (1960) has

observed that adult *Ficedula hypoleuca* returned in 35.6% (males) and 13.9% (females), whereas the young birds ringed before flying from the nests in 2.5% (males) and 1.1% (females).

Adult birds, as a rule, appear more abundantly on the last year's breeding area than young birds, but they also display some interspecific differentiation. Adult individuals of *Parus cristatus* are exceptionally strongly attached to the breeding area. This can be explained by the fact that this is a resident species. The breeding population does not leave the area for winter and breeds there again in spring. Whereas birds that fly away for winter more tend to change the breeding area. These are: *Fringilla coelebs*, *Ficedula hypoleuca*, *Anthus trivialis*, *Erithacus rubecula* and partly *Parus major* and *P. ater*.

This seems to contradict the earlier conclusions that among adult birds of such species as *P. cristatus*, *P. ater* and *F. coelebs* the returns are similar both in successive years and for the species. But this is true only for ringed birds which have returned at least once to the breeding area. They are strongly attached to the breeding area (which confirms H a a r t m a n's (1960) data for females of *Ficedula hypoleuca*). The material discussed shows that this is characteristic of many species regardless of their wintering habits.

But among adult birds caught for the first time there is undoubtedly a fraction of birds which occurred last year on another area and probably some of them will change place also next year. Winter migrations seem to favour such changes.

Real values showing the extent of returns of particular species are probably closer to the lower limit of intervals obtained. It can be assumed that forest Passeriformes, which migrate for winter return to the same extent as birds of this group from other habitats.

C z a r n e c k i (1975) in his studies on banded populations of birds nesting in riverside willows has obtained for a number of species of adult birds a per cent of returns in the next year 23.6–47.0 and for young ones – 2.4–5.3.

The number of recaptured individuals of *P. cristatus* which do not change in successive years its range of occurrence is much higher than for other species.

Birds of the resident species (*P. cristatus*) in successive years have more constant areas of occurrence than those of the migrant species (*Fringilla coelebs*) or those partly migrating (*P. ater* and *P. major*).

Results of catching birds in some distance from the area investigated point to the exchange of birds between this area and surrounding ones. This concerns both young birds which in the post-breeding period disperse from their breeding sites and adult birds which may return to the area close to that on which they occurred in the previous year. This is quite understandable considering the lack of natural border between the investigated area nad the surrounding forest.

Very few data on catches of ringed birds several kilometres from the area where the ringing took place may be due to their greater dispersal in the forest as the distance from the ringing site increases.

6. SUMMARY

The aim of the study has been to investigate the degree of attachment to the breeding area of chosen species of birds. These are: *Parus cristatus* – resident species, *P. major* and *P. ater* – partly migrating species, *Fringilla coelebs*, *Ficedula hypoleuca*, *Anthus trivialis* and *Erithacus rubecula* – migrants.

The relation between the age of birds and their wintering habits and the exchange of individuals in the breeding population has been examined.

Characteristics of the ornitofauna of the area investigated are given, including the changes in composition of the whole bird community during the investigations.

The study was conducted from 1970 to 1976 in a pine forest of the Gostynin Forest District (Fig. 1). The main method was the ringing of birds caught in ornithological nets and nest-boxes over the pariods: breeding, post-breeding and autumn (the last one only in some years) (Fig. 2). Additional quantitative observations were made on transects (Table I). The number of ringed birds was 3474.

On the area investigated 63 species of birds were found (Table II). More abundant species, as a rule, displayed smaller annual fluctuations in numbers in the breeding period than the less numerous species (Table III). An exception here was *Parus major* – an abundant species with high annual fluctuations in numbers. This may be due to the fact that the pine forest is a suboptimal biotope for *P. major*.

There is a relation between the wintering habits of a given species and its attachment to the breeding area. After at least one year since the ringing the highest per cent of banded *Parus cristatus* (a resident species) was observed (Table V), lower per cent of partly migrating *P. ater* and the lowest of migrating very far *Fringilla coelebs, Ficedula hypoleuca, Anthus trivialis*, and of one partly migrating species (*Parus major*).

No individual of *Erithacus rubecula* (of the 142 ringed ones) was caught again in the following years. The composition of this population was new each year. For *Anthus trivialis* and *Parus major* the total exchange of individuals lasted three years, for *Ficedula hypoleuca* and *Parus ater* – four years, for *Fringilla coelebs* – five years and for *Parus cristatus* – seven years.

All or almost all adult individuals of *P. cristatus, P. ater* and *F. coelebs* which survived the winter and had already in the past returned to the given breeding area, were found there again independently of their wintering habits (Table VI). Some returns of adult *P. major* were probably due to the suboptimal for this species character of habitat. The interspecific differences as regards the returns were shown first of all among young and adult birds which appeared for the first time on the breeding area in the year of ringing.

Young birds were the least or not all attached to the last year's area of occurrence (*Anthus trivialis, Erithacus rubecula*) (Table VII).

Individuals of the resident species displayed in successive years more constant breeding territories than the migrant species (Table IX).

7. POLISH SUMMARY

Celem pracy było zbadanie stopnia przywiązania do terenu lęgowego wybranych gatunków ptaków. Były to: *Parus cristatus* – gatunek osiadły, *P. major* i *P. ater* – gatunki częściowo migrujące, oraz *Fringilla coelebs, Ficedula hypoleuca, Anthus trivialis* i *Erithacus rubecula* – gatunki migrujące.

Badano zależność między wiekiem ptaków i sposobem spędzania zimy a wymianą osobników w populacji lęgowej.

Przedstawiono charakterystykę ornitofauny badanego terenu oraz zmiany składu całego zespołu ptaków w okresie badań.

Badania prowadzono w latach 1970–1976 w borze sosnowym w Nadleśnictwie Gostynin (rys. 1). Główną metodą było obrączkowanie ptaków chwytanych w sieci ornitologiczne i w skrzynki lęgowe w okresie lęgowym, polęgowym i jesiennym (w tym ostatnim w niektórych latach) (rys. 2). Dokonano dodatkowo obserwacji ilościowych na transektach (tab. I). Zaobrączkowano 3474 ptaki.

Stwierdzono 63 gatunki ptaków (tab. II). Gatunki liczniejsze wykazywały z reguły mniejsze coroczne wahania liczebności w okresie lęgowym, niż gatunki mniej liczne (tab. III). Wyjątek stanowił *Parus major* – gatunek liczny, o dużych corocznych zmianach liczebności. Być może przyczyną jest to, że bór sosnowy jest dla *P. major* biotopem suboptymalnym.

Stwierdzono istnienie związku między sposobem spędzania zimy przez osobniki danego gatunku, a ich przywiązaniem do terenu lęgowego. Po upływie co najmniej roku od chwili obrączkowania stwierdzono największy procent znakowanych *P. cristatus* (tab. V) – gatunku osiadłaego, mniejszy *P. ater* – częściowo migrującego, a najmniejszy gatunków migrujących na dalekie dystanse (*F. coelebs, F. hypoleuca, A. trivialis*) i jednego gatunku częściowo migrującego (*P. major*).

Ani jeden osobnik *E. rubecula* (spośród 142 zaobrączkowanych) nie został ponownie stwierdzony w latach następnych – całkowite odnowienie składu populacji następowało u tego gatunku co roku. U *A. trivialis* i *P. major* okres całkowitej wymiany osobników obejmował 3 lata, u F. hypoleuca *i P. ater* – 4 lata, u *F. coelebs* – 5 lat, a u *P. cristatus* – 7 lat.

Wszystkie lub prawie wszystkie dorosłe osobniki *P. cristatus, P. ater* i *F. coelebs*, które przeżyły zimę i *które w przeszłości już na dany teren lęgowy wracały, występują na nim ponownie, niezależnie od sposobu*

spędzania zimy (tab. VI). Nieliczne powroty dorosłych *P. major* wynikają być może z suboptymalnego dla tego gatunku charakteru środowiska. Różnice międzygatunkowe w powrotach wykazują przede wszystkim ptaki młode i dorosłe, które na danym terenie lęgowym w roku obrączkowania były po raz pierwszy.

Ptaki młode wykazują najsłabsze przywiązanie do ubiegłorocznego terenu występowania, lub zupełny brak przywiązania (*A. trivialis, E. rubecula*) (tab. VII).

Osobniki gatunku osiadłego mają w kolejnych latach bardziej stałe położenie terytoriów lęgowych, niż osobniki gatunków migrujących (tab. IX).

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